Baseline description of the Benthic Biotopes for two Long-Term Ecological Research (LTER) stations in Algoa Bay, Agulhas ecoregion, South Africa

A thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

at

RHODES UNIVERSITY

by

Shirley Parker-Nance

March 2021

Abstract

Shallow coastal marine ecosystems provide important resources to society but are increasingly under threat from anthropogenic impacts. These systems form an interface between land and sea, providing valuable resources. Global environmental change, overexploitation, habitat transformation, pollution and policies aimed at short-term socio-economic gains are driving the loss of natural resources, productivity and biodiversity. Consequently, a comprehensive and holistic understanding of the current and future states of marine ecosystems is essential. This requires insight into the processes involved in maintaining genetic, species, habitat, community and biotope diversity at an ecosystem level. An understanding of ecosystem processes and the ability to detect changes in biodiversity, biotopes, seascape composition and ecosystem functioning require observation made over time and space. In response to this need, Long-Term Ecological Research (LTER) programmes such as those established by the South African Environmental Observation Network (SAEON) supported by the Department of Science and Innovation's (DSI) Shallow Marine and Coastal Research Infrastructure (SMCRI) collect long–term observational data from different environments and systems.

This study aimed to evaluate data collected as part of the developmental phase of a newly established benthic research platform. The datasets constructed are used to develop a baseline description of the benthic biotopes of two study areas within Algoa Bay. It aimed to gain insight into the feasibility of the methods used and the value of the data and derived essential biological variables (EVB). Assessing the sustainability of the programme over time was done through a practical evaluation of the methodology to be used and the technical feasibility of data collection and analysis. It furthermore aimed to assess the data usefulness in describing biodiversity at various scales and its sensitivity in reporting change.

This pilot study provides valuable insight into data collection methodologies and introduces new sampling platforms. The baseline dataset consisted of data collected during the first 18 months of the SAEON Benthic Ecosystem Long-Term Ecological Research (BELTER) platform in Algoa Bay, Agulhas ecoregion, Western Indian Ocean, South Africa. This comprised of the collection of images for 150 m^2 of the researched benthic seascape and 306 stereo video data streams. The 77 760 point dataset allowed the identification of 12 substrate types, 7 biotopes, 44 sub-biotope units, 377 sessile and sedentary benthic species and 51 ichthyofauna species. The described habitat and benthic communities and the defined benthic biotopes allowed for the assessment of biotope heterogeneity and the construction of a provisional distribution map for the broader biotopes. This work includes a study into the infra- and supra-benthic ichthyofauna associated with the defined biotopes and investigates the role habitat and benthic communities play in the distribution of these fish

assemblages. Lastly, it assesses the value of morphological traits and diversity indices for describing and comparing abiotic and biotic components of observed systems within the shallow coastal marine seascape.

This study shows that species composition differs significantly between biotopes with habitat type playing a key role in the composition of the benthos. Substrate type, consolidated or unconsolidated, depth and the composition of the soft sediment is the most important determining factors. The White Sands Reef station has a higher species diversity than the St Croix Island Complex station with a higher percentage cover associated with the hard substrate. The dissimilarity between biotopes and communities are generally high although similarity within the biotopes or communities was found to be relatively low. This was considered indicative of high heterogeneity within the biotopes and a patch or mosaic-like distribution of communities within the broader biotope. A fine-scale *a posteriori* analysis of the data collected confirmed the high heterogeneous nature of both habitat and communities within the broader biotope. The description of the abiotic and biotic variables resulted in the identification of a diverse suite of biotope subunits. The character of the biotope hinges not only on the composition of the substrate and biota present but the contribution of smaller distinct biotopes subunits, their distribution and representation within broader biotopes and the degree these are shared with other broader biotopes. The distribution of these biotope units at different scales is believed to be important in understanding inherent diversity, niche partitioning and connectivity within a highly heterogeneous seascape.

Ichthyofauna associated with the broader biotopes were indicative of the substrate type. Low profile reef systems with interspaced sandy stretches supported both reef fish and those typically associated with sandy substrates. Benthic biotopes associated characteristically with higher profile reef systems and less sand or soft sediment were mainly utilized by reef-associated fish species. Substrate type, depth and seasonality were found to be important factors in the observed composition and distribution of ichthyofauna over the seascape. Although fish species were found to have a wide distribution and made use of multiple biotopes the average abundance of the species within the observed assemblages differed. Analysis of ichthyofauna species composition indicated that observed fish assemblages were homogeneous within five of the seven biotopes. Broader biotopes that were found to be significantly different between sample locations are characterised by a diverse complement of biotope subunits and are highly heterogeneous.

Traits and diversity indices are important tools for assessing and comparing different systems within the seascape, both spatially and temporally. The classification of the biota into broader phylogenetic groups indicated a significant difference between biotopes. This is especially useful when detailed analysis or species identification is not possible or the skill set is not available. Morphological traits included in this study informed on the physical structure of the communities present and in combination with substrate type provided insight into the three-dimensional structure of the biotope. Species diversity, abundance, density estimates and the Shannon-Weiner diversity index were found to be the most useful diversity indices characterising and comparing biotopes. This was less so for ichthyofauna. Significant differences in the number of species observed were evident only between consolidated and unconsolidated dominated substrates. Although there was no significant difference in the number of individuals observed, both the Shannon-Weiner and Simpson Diversity indices were able to highlight differences in the fish assemblages observed for the different biotopes.

The data collected, although permitting a comprehensive baseline assessment of the benthic environment for two research stations within the SAEON Algoa Bay LTER Sentinel Site, is temporally limited. The ichthyofauna dataset used was small and it is understood that the addition of length-frequency analysis of observed ichthyofauna will benefit our understanding of the biotope use by infra- and supra-benthic fish species over their life history within the larger seascape. Seasonal differences were evident and it is expected that datasets spanning several years, including LTER stations within different marine ecosystems types, will provide valuable insights on system dynamics in the short and long term both spatially and temporally.

This study is the first attempt to evaluate the methodology developed and data collected in the South African Environmental Observation Network's, Elwandle Coastal Node as part of the Shallow Marine and Coastal Research Infrastructure Benthic Ecosystem Long-Term Ecological Research (BELTER) platform. Newly designed and developed sample equipment and a sampling regime allowed for the collection of data on a long-term basis. The study was successful in the description of the biotope and biotope subunits for two research stations in Algoa Bay. It permitted the construction of comprehensive species lists for both benthic sessile and sedentary biota and the associated ichthyofauna. The subset of data used was successful in reporting on both spatial and temporal change. This work demonstrates that in the absence of detailed species identifications, traits may be used to describe habitat and community structure and report on abiotic and biotic biotope characteristics. This study furthermore allowed for the comparison of a comprehensive suite of diversity indices highlighting indices that may be especially useful in routine BELTER reporting.

Acknowledgements

To my family that walked this road with me. My deepest thanks for your endurance.

This work has been made possible by funding received from the National Research Foundation (NRF) Research and Innovation Support and Advancement (RISA) Professional Development Programme (PDP) and grants provided by the South African Environmental Observation Network (SAEON). Infrastructure was provided by the Shallow Marine and Coastal Research Infrastructure (SMCRI) programme funded through the Department of Science and Innovation (DSI) and jointly managed by SAEON and the South African Institute for Aquatic Biodiversity (SAIAB) Marine Remote Imagery Platform (MARIP).

I would like to express my sincere appreciation to my supervisors, Prof Thomas Bornman and Prof Warwick Sauer, you were there when it was needed most. Thank you for working late nights, early mornings and weekends. Thank you to Dr Albrecht Götz, your choices defined my life for the last couple of years. I would like to thank Dr Timothy Langlois for his generosity and guidance in providing advice and blueprints for the development of the sampling equipment and Dr Anthony Bernard and Dr James Seager for advice on all things BRUV. I thank SANParks personnel for their assistance.

Data does not collect itself, it takes the commitment of a team dedicated to the task. I would like to extend a special thanks to: Koos Smith, Travis Smit, Werner Kuntz, Imtiyaaz Malick, Melissa Pollard, Nick Schmidt, Shaun Deyzel, Sean Bailey, Phakama Nodo, Thembani Mkhiza, Peter Riddin, Trevor Coetzee, Carla Edworthy, Nicola James and Margot Brooks with a very special thanks to Jennefa Mohale, you rocked!

Lastly, for camaraderie and friendship, I like to express my deepest thanks to Kyle Smith and Rosie Dorrington.

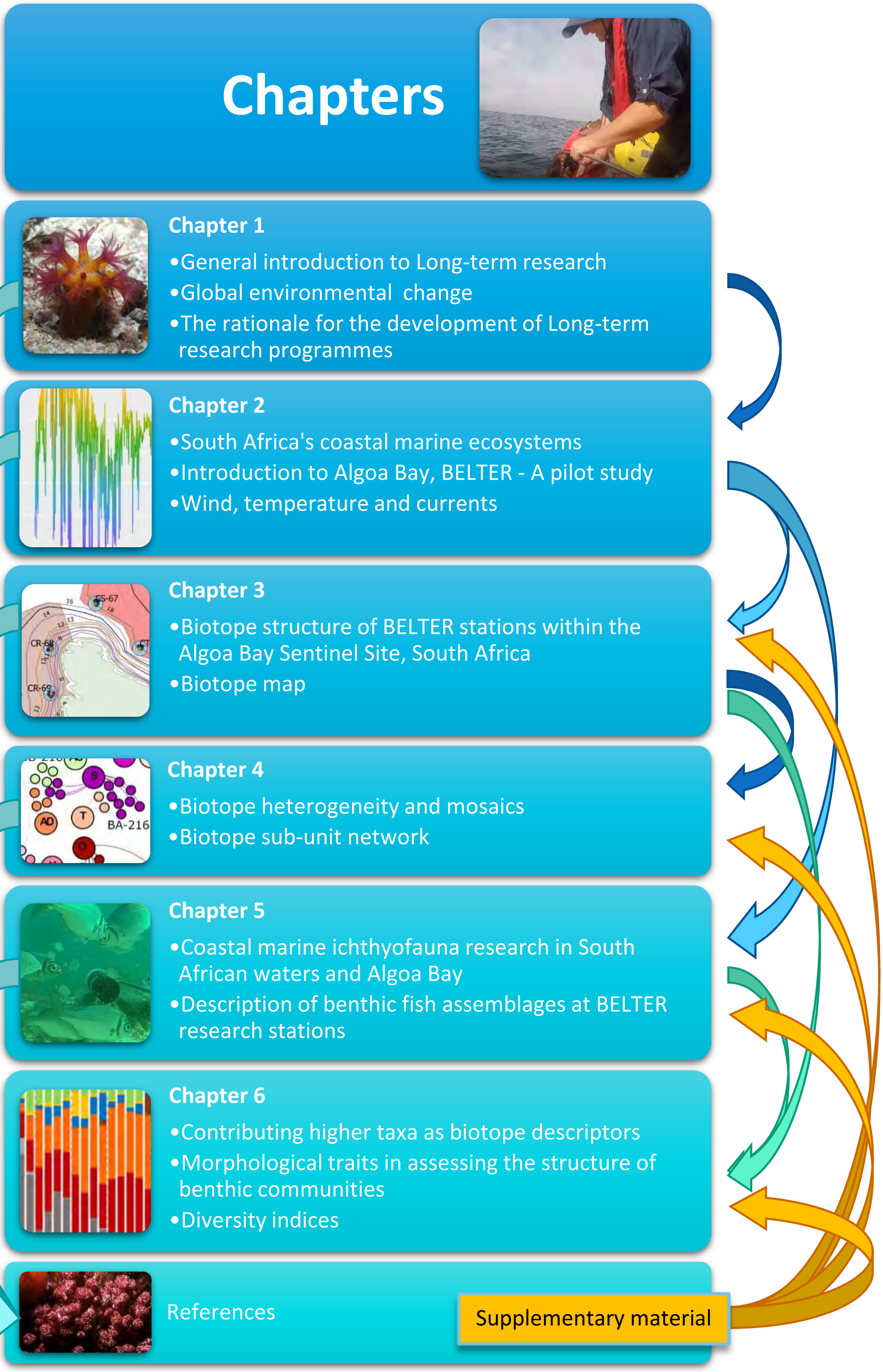
Postscript: I would like to sincerely thank the examinators for their valuable insight and the suggestions provided to improve the overall quality of this work.

Table of Contents

Table of figures

Table of tables

Table of supplementary tables



Chapters

Chapter 1

- General introduction to Long-term research
- Global environmental change
- The rationale for the development of Long-term research programmes

Chapter 2

- South Africa's coastal marine ecosystems
- Introduction to Algoa Bay, BELTER - A pilot study
- Wind, temperature and currents

Chapter 3

- Biotope structure of BELTER stations within the Algoa Bay Sentinel Site, South Africa
- Biotope map

Chapter 4

- Biotope heterogeneity and mosaics
- Biotope sub-unit network

Chapter 5

- Coastal marine ichthyofauna research in South African waters and Algoa Bay
- Description of benthic fish assemblages at BELTER research stations

Chapter 6

- Contributing higher taxa as biotope descriptors
- Morphological traits in assessing the structure of benthic communities
- Diversity indices

References

Supplementary material

Schematic representation of the content of and connectivity between chapters in this thesis.

Chapter 1 General Introduction and rationale for the development of Long-Term Ecological Research (LTER) programmes

1.1 Baseline description of the Benthic Biotopes for two Long-Term Ecological Research (LTER) stations in Algoa Bay, Agulhas ecoregion, South Africa

The research presented here is the first attempt to analyse and evaluate the methodology developed and data collected in the Benthic Ecosystem Long-Term Ecological Research (BELTER) platform being developed by the South African Environmental Observation Network's, Elwandle Coastal Node as part of the Shallow Marine and Coastal Research Infrastructure. It makes use of newly designed and developed sample equipment and a sampling regime that is aimed to allow for the collection of data on a long-term basis. The main goal of the subsequent database is to inform on spatial and temporal change within shallow marine ecosystems of the South African coastal zone.

1.2 Term and definitions

Foremost it is important to clarify some terms that are used through this work. The terms habitat, community or biotopes may be used in different contexts depending on the researcher. The term 'biotope' was originally used to define factors that determine the physical conditions of the existence of the community or 'biocenosis' ('Gewässer und Geländearten') by Dahl (1908) in his work titled 'Principles and basic concepts of biocenotic research'. This concept of the biotope has evolved and has been redefined to now include both abiotic and biotic elements (Connor et al. 2004, Olenin and Ducrotoy 2006, Buhl-Mortensen et al. 2020). In this work, we adopt the modern definition of the biotope which include both the habitat and the community. The habitat is a relatively homogeneous spatial domain with regards to its environmental factors. These consist of the physical (e.g. the water column or substrate) and chemical environmental characteristics. A community is the biotic element of the biotope and is an assemblage of locally occurring species supported by a specific habitat (Olenin and Ducrotoy 2006). Species composition depends on local physical and chemical environmental conditions (e.g. the habitat) and biological requirements, such as successful recruitment of new individuals, food availability (Lasiak 1986) and the trophic relationships between predator and prey. The scale of the biotope depends on the size of the defined habitat that supports the relatively homogeneous biotic unit with regard to the species composition (Olenin and Ducrotoy 2006).

The term data set and dataset is both in use by the scientific community and although the correct use is debated, its definition is largely the same depending on the dictionary consulted, eg. Oxford or

Cambridge respectively. In this work, the term dataset is used as by Wilkinson et al. (2016) in their defining paper on the FAIR data Guiding Principle and maintained in subsequent publication relating to the FAIR data principle (Benson et al. 2018, Canonico et al. 2019, Tanhua et al. 2019).

1.3 Chapter content

Chapter 1 intends to put into perspective the broader research initiative. It starts with a short introduction to Long-Term Ecological Research (LTER), as it is a constant theme throughout this work. This is followed by a very compact synopsis on global environmental change. This is important as the need to detect this change and its impact is the main driver in the development of LTER platforms globally. Following is a short overview of essential variables, technical advances in science and the concept of big data. These overarching themes are then brought into perspective in terms of the South African context by including information on the National Biodiversity Assessment, Marine Spatial Planning and the South African Environmental Observation Network's Shallow Marine and Coastal Research Infrastructure (SMCRI) initiative. The chapter is concluded by revisiting the rationale behind and the development of the Benthic Ecosystem Long-Term Ecological Research (BELTER) platform.

In Chapter 2 the focus is on the study site. To do so a condensed overview is provided of South Africans coastal marine ecosystems. This would be incomplete without mentioning the importance of Algoa Bay as SAEON Elwandle Coastal Node's Sentinel Site and the aspects that play important roles in structuring the environment and the social-economic character of the bay. The general introduction is followed by an overview of the Benthic Ecosystem Long-Term Ecological Research (BELTER), stations selection and the sampling methodology used. The remainder of the chapter is aimed to provide insight into the physical conditions present when biological samples were collected and look specifically at wind and sea temperature in the bay. The wind data used was recorded at the Port Elizabeth Airport and harvested from darksky.net. The UTR data sets used in this chapter is part of the SAEON temperature network dataset. The figures constructed for wind and temperature were created with the assistance of Elwandle's senior developer. The sea bottom water temperature recorded during sBRUV deployments were correlated with UTR data for sample collection trips. The role of nutrients and plankton is reviewed.

Chapters 3 to 6 can be regarded as the data chapters in which subsets of the data collected during the implementation stage of the platform is used. All data collected during the initial implementation phase of BELTER, Jump Camera and BRUV work (for the exception of a single sample event where the candidate was needed for plankton sampling) was lead by the candidate. The collection of the data can not be done single-handedly and is a team effort by scientists, technicians, interns and skippers. All data analysis, the construction of species list and statistics was done by the candidate.

The first two of these chapters use data collected from the benthic environment employing a Jump Camera (JC) system. In Chapter 3 we address the habitat, community structure and define biotopes at the sample location-scale (or broad-scale). The analysis is *a priori* meaning the sample methodology and analysis was developed based on existing information and literature. Multiple samples collected from sample locations were pooled and analysed to define the abiotic and biotic components. Chapter 4 is *a posteriori* investigation and the result of observations made in Chapter 3. This uses a finer scale analysis of the dataset at the quadrat sample point scale. This provides novel information on biotope heterogeneity and the contribution of biotope subunits to the broader biotopes described in the previous chapter.

Chapter 5 makes use of stereo Baited Remote Underwater Video (sBRUV) systems to collect imagery of fish communities. Only a subset of the collected data is used in this work as the main objective was to investigate the ability of the collected data to record change both spatially and temporally. The chapter evaluates the length of data streams needed for analysis and compares this to data collected from different geographical locations. It inspects sample design and integrity by evaluating the possible movement of an indicator species, *Chrysoblephus laticeps*, between sample locations. Within this chapter ichthyofauna, species lists are compiled and compared for the broader biotopes as defined in Chapter 3.

Chapter 6 converts the Chapter 3 dataset to a trait-based dataset to investigate and compare sampled localities, stations and biotopes and evaluate the use of the collected data if genus or species identification is not available. For this, the broader taxa of the biota and the growth form are used in combination with habitat characteristics. The second half of the chapter investigates the ability of a set of diversity indices to detect differences between sampled sites, locations and biotopes for the benthic biota and ichthyofauna.

Chapter 7 consists of general concluding remarks and recommendations for future research. Supplementary data and technical reports follow each chapter and references are provided for all chapters at the end of the document. All collected data, imagery, and compiled sub-datasets are open source.

1.4 General objectives

BELTER aims are to deliver data-rich long term datasets through a sampling platform that is easy to use and maintain. Sample equipment includes a small coastal vessel, Jump Camera (JC) systems and compact stereo Baited Remote Underwater Video (sBRUV) systems (van Rein et al. 2009, Bernard et al. 2014, Langlois et al. 2020). The use of which inherently supports repetitive data collection, quick analysis, that allow for effective data and information dissemination aimed to report on changes within the observed ecosystem.

The two main goals of this work were to perform a baseline study to determine habitat and community composition for two research stations in Algoa Bay and the show that the data collected can record changes within the Algoa Bay seascape over time and space. This makes use of a subset of data collected during the first year and a half of the Benthic Ecosystem Long-term Ecological Research (BELTER) platform.

1.5 Long-Term Ecological Research (LTER)

Global environmental change, overexploitation of natural resources, habitat transformation, pollution of the natural environment and short-sighted socio-economical-environmental trade-offs are evidenced in the loss of natural resources, productivity and biodiversity (Worm et al. 2006, Skelton 2014, O'Garra 2017, Cottrell et al. 2018, Washington 2020). In contrast to the human lifespan, which stretches over only decades, the effects of degradation and environmental change may happen over longer periods (Stevens et al. 2015). Climate change is a gradual process involving small incremental changes in our surroundings. CO_2 emission, temperature shifts, rising sea level (Chen et al. 2017), melting glaciers (Tuckett et al. 2019) and degradation of the ozone layer have taken several generations to attract our interest, be realised, researched, analysed (Anderson et al. 2020) and acted upon. The last is a point of contention, as most actions have been merely theoretical or legislative exercises (Gills and Morgan 2020). Awareness of our surroundings is restricted by our limited perception of space and time. The slow gradual change from one state to another and the infrequency of extreme events, which may occur once or twice in a human lifetime, hamper our capacity to prepare and adapt for the future (Kim 2006). Although none of us can see into the future, we can record the present and analyse the past. This will afford humanity the best chance to prepare for the 'uncharted waters' of tomorrow (Van Jaarsveld and Biggs 2000, Harley et al. 2006) and provide data and information for prognostic modelling and forecasting (Popova et al. 2016, Cao et al. 2017, Chen et al. 2017, Kröner et al. 2017, Datta et al. 2018, Slater et al. 2019, Heymans et al. 2020, Topál et al. 2020).

Long-Term Ecological Research (LTER) programmes mandate observations over many decades (Biggs et al. 1999, Van Jaarsveld and Biggs 2000, Skelton 2014, Vergés et al. 2016). Internationally linked LTER networks encourage globally collaborative multi- and trans-disciplinary research (Vanderbilt and Gaiser 2017, Mirtl et al. 2018) to permit assessment of change on a local, regional, national and global scale. A key factor of sound adaptive ecosystem management is the maintenance of ecosystem sustainability (Kim 2006, Anderson et al. 2017, Katona et al. 2017) and is dependent on biodiversity (Liquete et al. 2016). Investment in science is critically important (Innovation 2018) and a comprehensive understanding of the current and future state of marine ecosystems is essential (Visbeck 2018, Fischer et al. 2019). This, however, requires assessment and an understanding of the status and processes for maintaining genetic, species, habitat, community and biotope diversity at the ecosystem level (Heiskanen et al. 2016, Schmeller et al. 2018).

Different ecosystems respond differently to various stressors, the time of impact and the effect of multiple or combined pressures (Wu et al. 2017, Woodworth-Jefcoats et al. 2019, Gissi et al. 2021). LTER observe ecosystem dynamics and changes within different ecoregions on various spatial and temporal scales (Kim 2006, Jürgens et al. 2012). Differentiating between natural environmental change and anthropogenically induced change is challenging, if not impossible, in the absence of datasets that capture long-term events and trends (Durham and Pauw 2000, Skelton 2014). It requires knowledge of ecosystem structure, function and evolution over many decades to reveal natural oscillations, especially in the case of slow processes, episodic events or processes occurring at infrequent intervals or with major time lags (Davis et al. 2018, Fong et al. 2020), and those with imperceptible trends or compound responses (Kim 2006, Donovan et al. 2020, Griffith and Gobler 2020, Ruhl et al. 2020, Zscheischler et al. 2020).

The commitment of scientists, researchers, technicians, public servants and in many instances ordinary members of the public is invaluable, and today's efforts will be greatly valued in the future.

1.6 Global Environmental Change

Climate change in itself is not a new concept in the earth’s history (Petit et al. 1999, Alley 2000, Wang et al. 2020). However, with the arrival of the Anthropocene, a period in which humans greatly alter their environment, we are in danger of degrading and negatively impacting the environment with direct and indirect consequences for human survival, health and wealth (Harley et al. 2006, Ellis et al. 2016, Waters et al. 2016). Human-driven transformation of the land is undoubtedly evident and long-term indications of ocean warming are increasing (Clark 2006, Vergés et al. 2016, Byrne and O’Gorman 2018, Sallée 2018). This change is driven by the greenhouse effect, an unparalleled change in the concentration of carbon dioxide, methane, nitrous oxide, ozone and halocarbons in the earth's atmosphere, influences temperature, pressure, rainfall, sea level, cloud cover and ultraviolet radiation (Clark 2006, Harley et al. 2006). This results in melting ice sheets, rising sea level, ocean acidification, dead zones, harmful algal blooms, coral bleaching, biodiversity loss and environmental degradation (Hale et al. 2011, Lindstrom et al. 2012a, Rahmstorf 2017, Watanabe et al. 2018, Tang 2020).

Climate change, although a global phenomenon, has significant impacts on the local and regional scale. Atmospheric and ocean warming is exacerbated by unprecedented weather episodes such as flooding, drought and storm surges (Lindstrom et al. 2012a, Stevens et al. 2015, Bai et al. 2018). Uncertainty surrounding global warming calls for improved access to climate-related long-term information and has seen increased investment in data collection platforms (Department of Science and Technology 2016a). But, the collaboration between scientists, policymakers and leadership should focus not only on the 'natural' environment but include research on the transformed environment (Bai et al. 2018). The development of climate change adaptation policies allows for mitigation of, and preparation for, current and future climate change challenges (Baudoin and Ziervogel 2017; Connolly-Boutin and Smit 2016; Swanepoel and Sauka 2019).

Resource revenue from coastal marine systems indicates that these systems are socio-economically significant and global environmental change is predicted to affect many key coastal marine habitats (Clark 2006, Harley et al. 2006). Ecological responses to climate change may include changes in species composition, diversity, community structure, distribution and shifts in species interaction (Harley et al. 2006). Changes in ocean currents or upwelling events will lead to variation in nutrient concentrations, affecting productivity (Harley et al. 2006). Coastal benthic habitats are characterised by prominent latitudinal distribution and vertical zonation and shifts in species distribution (vertical and horizontal), abundance and productivity are predicted to become more apparent as drivers of change. The current measurement of these impacts is often based on measured responses of a single species (indicator species) to abiotic (physical or chemical) environmental change. However, recent research suggests that species interactions are important. Thus, changes in species distribution result in new species interaction which impact structure and function at the community level (Vergés et al. 2016). These multi-species fluxes may impact substantially on resource economics (Bennett et al. 2016b). Socio-economic drivers of change should be included in assessments and allows for an audit of the effect humanity has upon the global environment (Coa et al. 2015). To account for all possible stressors diverse earth environmental observation platforms (such as satellite, ground, air and water-based observatories, scientific field surveys and citizen observations) can contribute to knowledge on global change (Anderson et al. 2017).

Predicting the ecosystem response to climate change is complex and mitigation of negative responses is challenging. The paucity of information, non-linearity of systems response, the unpredictability of effects at multiple scales, our current inability to comprehend all drivers and response variables, human population growth, and increased anthropogenic pressure (Innovation 2018) make future projections and accurate forecasting difficult (Stevens et al. 2015). Complex feedback cycles, which influence both abiotic and biotic components, make forecasting environmental behaviour difficult (Harley et al. 2006). A good example of this complexity to understand variables and scenarios is provided by the multiple predictive models (Al-qaness et al. 2020, Hierro et al. 2020) that have been our response to the SARS-COV-2 virus outbreak. Scientists, politicians and the general public have all participated in recent months, observed and hopefully learnt much about society's reaction, mitigation and adaptation to disease and famine. Although forewarned, world governments and society found themselves ill-prepared for the challenges. Jin (2020) has equated the COVID-19 pandemic with challenges faced as a result of climate change in that we are in it together, we should act before it's too late, science and facts matter, innovation is key, international collaboration is critical and lastly, we need to find solutions that would enable us to live in sustainable social-ecological systems by understanding and respecting planetary boundaries (Rockström et al. 2009) and recognizing earth system tipping points (Biermann and Kim 2020).

Predicting the future depends on sophisticated models and intricate algorithms (Collins et al. 2013, Wong et al. 2014). These are, however, only as good as the data they are based on, and the predicted outcomes are linked to the assumptions made. Consequently, many different possible scenarios are forecasted by the Intergovernmental Panel on Climate Change (IPPC) models, depending on different estimations of global temperature increases (Meehl et al. 2007). Long-term datasets are important model verification tools. As such long-term research platforms are mandated to collect information on environmental and biological variables over large temporal and spatial scales. The main goals are to better understand, conserve, protect and manage ecosystems and their biodiversity. Addressing climate change requires the comparison of ecosystems over time across local, regional and global gradients. The information generated provides services to the scientific community, policymakers, and society in general (Kim 2006, Muller-Karger et al. 2018, Canonico et al. 2019). Models that use observational data provide the most useful avenue for predicting the future (Stevens et al. 2015). In the absence of established LTER programmes, on which we depend for information today, it is important to invest in strategies that aim to deliver sound scientific information and allow predictive understanding of ecological processes in the future (Haase et al. 2018, Lunney et al. 2018, Mirtl et al. 2018).

South Africa's research infrastructure development goals are set out in the South African Research Infrastructure Roadmap (2016). It refers to the close linkage between the Earth and Environment Research infrastructure and existing international facilities and platforms. These include the International Long-Term Ecological Research (ILTER), the Global Biodiversity Information Facility (GBIF), the Global Ocean Observing System (GOOS) and the Group on Earth Observations (GEO) which focus on building the Global Earth Observation System of Systems (GEOSS). These global observation initiatives coordinate and advocate open data sharing and access (Coa et al. 2015, Department of Science and Technology 2016a).

1.7 Essential Variables

The concept of Essential Climate Variables (ECVs), developed in the 1990s, aimed to focus available resources on a selected set of variables that would allow understanding of climate variability. It is now a fundamental information suite used to inform the United Nations Framework Convention on Climate Change (UNFCCC) and the Intergovernmental Panel on Climate Change (IPCC) (Bruford et al. 2013, Muller-Karger et al. 2018). ECVs are individual physical, chemical or biological variables or groups of linked variables that critically contribute to the characterisation of the earth's climate and include those relating to the atmosphere, land and the ocean. Essential Ocean Variables (EOVs) are key indicators of ocean health and change. EOVs can be categorised into three broad disciplines: i) physics e.g. temperature, currents, salinity etc., ii) biogeochemistry e.g. oxygen, nutrients, carbon etc. and iii) biology and ecosystems. Essential Biodiversity Variables (EBVs) include measurement of biomass, diversity, abundance, composition and cover (Bruford et al. 2013, Muller-Karger et al. 2018).

The collaborative initiatives of ECVs, EOVs and EBVs are driven by the Global Climate Observation Systems (GCOS), the Global Ocean Observing System (GOOS) and the Group on Earth Observations Biodiversity Observation Network (GEO BON), respectively (Muller-Karger et al. 2018, Jetz et al. 2019). The Marine Biodiversity Observation Network (MBON), a component of GEO BON, collaborates with GOOS, the Ocean Biogeographic Information System (OBIS), and the Integrated Marine Biosphere Research (IMBeR) to streamline efforts and promote effective advancement of scientific knowledge (Muller-Karger et al. 2018). OBIS, the builder of the most comprehensive global database on diversity, distribution and abundance of life in the ocean, is now extending beyond species occurrence data by incorporating EOVs in support of GOOS and MBON (Klein et al. 2019). Other bodies participating in this international dialogue are the Marine Global Earth Observatory (MarineGEO), the International Network for Scientific Investigations of Deep-Sea Ecosystems (INDEEP) and the Global Acidification Observing Network (GOA-ON). MarineGEO focuses on biodiversity and ecosystem resilience in coastal ecosystems where marine biodiversity and human impact are high (Muller-Karger et al. 2018). The Framework of Ocean Observing (FOO), an expansion of GOOS, works towards the purview of including biogeochemical and biological-ecological variables (Lindstrom et al. 2012a, Tanhua et al. 2019).

Biodiversity Targets and Development Goals (AICHI Biodiversity Targets of the United Nation (UN) Strategic Plan for Biodiversity (2011-2020) and UN Sustainable Development Goals (SDGs)) are two well-known efforts to record and cultivate awareness of the global effort needed to slow anthropogenically driven change (UNEP 2010, United Nations 2016a, 2016b). South Africa's Science, Technology and Innovation sector highlights the importance of SDGs in the pursuit of economic growth and food security while emphasising the value of scientific knowledge (Innovation 2018). However, to achieve the above, several information gaps need to be filled, of which the development of observation research with the mandate to collect long-term environmental data on key variables is foremost (Durham and Pauw 2000, Skelton 2014).

Essential Biodiversity Variables (EBVs) provide information on primary and secondary productivity, allelic and taxonomic diversity, species distribution, population abundance and structure (age and size classes), migratory behaviour, phenology, habitat structure, ecosystem extent, fragmentation, composition and functional type (Kissling et al. 2018a, Muller-Karger et al. 2018). EBVs allow the implementation of biodiversity indicators that inform biodiversity targets such as those set by Aichi Biodiversity Targets, UN Convention on Biological Diversity (CBD), UN 2030 Agenda for Sustainable Development (Sustainable Development Goals) and Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) (Kissling et al. 2018b). Holistically, it is important to assess and reassess the effectiveness of variables and LTER datasets in observing change and identifying trends (Magurran et al. 2010). The observation of change is the primary goal. This insight into changes and the measurement thereof should then be made available to decision-makers and policy writers to allow the development of adaptive management strategies (Geijzendorffer et al. 2016, Miloslavich et al. 2018). This is by no means an easy task with heterogeneity, stochastic processes and nonlinear responses complicating model development and projection (Chase and Myers 2011).

1.8 Technological evolution

The Fourth Industrial Revolution (Innovation 2018) has seen advancements in both science and technology. This includes improved sampling, analysis and reporting incorporate Machine Learning (ML) and quantum computing. These developments will play an ever more important and constructive role in LTER.

The first portable digital camera developed by Steven Sasson in 1975 weighed 3.6 kg. Able to capture and store 30, 0.01-megapixel images on digital cassette, it was a technological breakthrough (Goff 2012). Today, 45 years later, over the counter action cameras routinely used by scientists weigh 120g and can capture 15-megapixel digital images and provide video recording with a horizontal display resolution of 4 000 pixels (4K). It can continuously record underwater video for more than 60 minutes and is powered by a 22-gram battery. This technology has revolutionised how we conduct marine research today.

Technological advances will continue to improve our ability to measure marine biodiversity (Barnes 1952, Goff 2012, Pearlman et al. 2017). EOVs, sampling methodologies, sample techniques, data collection and processing technologies are dynamic and ever-changing and the methods of data collection, processing and analysis evolve constantly (Tanhua et al. 2019). It is thus important to make provision for the possible inclusion of newly developed technologies, methodologies and procedures into existing marine observation programmes, practically and cost-effectively (Muller-Karger et al. 2018). Striving towards interoperability, observations should be verified, calibrated and equated in the face of technological advancement. This requires the inclusion of comprehensive metadata, such as the characterisation of accuracy, the precision of observation and equipment specifications for LTER datasets (Tanhua et al. 2019). Attention to this is essential for the successful comparison of trends over many decades and to detect change across, between or within regions on local, regional and global scales (Muller-Karger et al. 2018). Importantly, this requires the acceptance of and provision for innovations into the long-term research frameworks (Fischer et al. 2019).

1.9 Big data

Big Data is a term that describes the large volumes of information that we are now able to collect, and this presents various challenges (Hampton et al. 2013, Liu et al. 2017). Infrastructure shortfalls, underestimating computing needs and ignoring the time and effort involved in data management are common pitfalls. Many programmes in the past neglected proper data and metadata archiving, but the importance of data curation and the role of 'big' data management has more recently been appreciated (Karasti et al. 2006, Michener and Jones 2012). This highlights essential practices that should be incorporated by all, including preservation of a copy of data free of annotations, raw or as it was collected, and when analysing the dataset, keeping track of one's workflow. Each version of the data worked on should include a detailed workflow and metadata (Nowogrodzki 2020). The bigger the dataset becomes the more time-consuming the extraction of relevant trends can become, thus one should attempt to automate as much as possible. The age of ML has arrived and although automation is still in its infancy valuable information can be extracted from large datasets with automated tools (Peters et al. 2014, Sagi et al. 2020) that make use of large digital infrastructure (Li et al. 2020). In this age of ‘big data’, it is essential that natural scientists value, communicate and collaborate with computer scientists and software developers.

Metadata is not just an add-on, it is an essential requirement of data management and archiving. It should include detail on the data creator(s) and manager(s), data content, format, where the data were collected, the reason for the collection, the equipment, technical specifications, detail on processing equipment as well as information of software used in the analysis and where it is stored (Michener and Jones 2012). Maintenance of ‘big’ datasets is a multi-disciplinary effort, time-consuming and costly, and it is imperative to ensure that adequate funding is set aside for data management, curation and servicing.

Findability, Accessibility, Interoperability and Reusability (FAIR) are data principles, formulated by stakeholders including academia, industry, funding agencies and scholarly publishers with guidelines to achieve ‘good data management’. It advocates the development of standards, promoting interoperability and the ability of data or tools from non-cooperating resources to integrate with minimal effort (Wilkinson et al. 2016, Mons et al. 2017). The FAIR Data Principles have been widely adopted e.g. by the GOOS 2030 Strategy (Benson et al. 2018, Fischer et al. 2019) and FOO, its use assisting interaction between data producer and user (Mons et al. 2017, Benson et al. 2018, Tanhua et al. 2019). The Draft White Paper on Science, Technology and Innovation (DSI 2018) announced the planned reconsideration of the current Intellectual Property Rights from the Publicly Funded Research and Development Act to ensure the support of FAIR guiding principles for scientific data management and storage. South Africa, through the African Open Science Platform and the Open Government Partnership, is committed to developing an open data policy framework, nationally, on the continent and abroad (Innovation 2018).

The need for large long-term observation datasets to understand the function and response of ecosystems (of life on earth) to both natural and anthropogenic induced change, calls for effective data administration and data sharing (Biggs et al. 1999, Tanhua et al. 2019). If the data is not available or only available to a privileged select few, understanding the response to globals change is severely limited and bound by various constraints. The solution lies in open-access data, but the reality falls short, making regional comparisons and global assessments difficult. Data sharing and open access to data is a social responsibility that promotes collaboration, regional and global scientific and policy development and engagement, it highlights ‘missing’ datasets and facilitates the curation of data in so doing minimising the risks of data loss (Muller-Karger et al. 2018, Jetz et al. 2019, Tanhua et al.

2019). Policies in place to promote data accessibility include the Oceanographic Data Exchange Policy (IOC), the Global Earth Observation System of Systems (GEOSS) and the International Oceanographic Data and Information Exchange (IODE) initiatives (Lindenmayer et al. 2018, Muller-Karger et al. 2018, Tanhua et al. 2019).

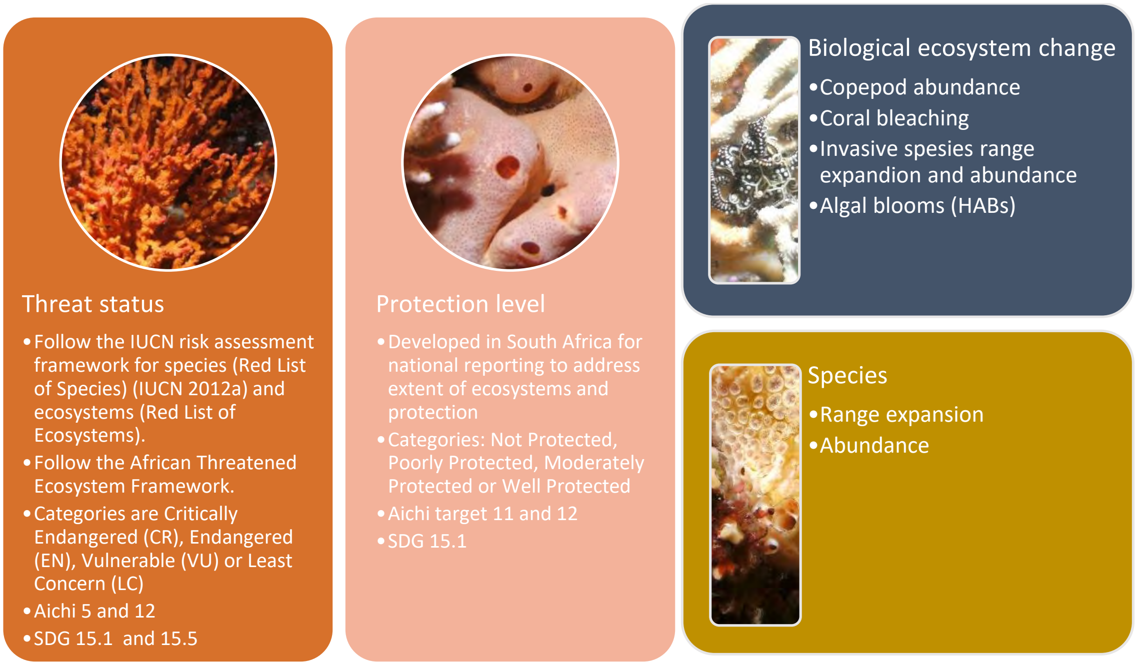
In many instances, the backlog in digitising old datasets is an ongoing challenge. An analysis by Muller-Karger et al. (2018) of data published in OBIS after 2015 showed that the majority of effort is currently allocated to digitising historical records, not uploading more recent observations. A move to the implementation of policies and new technology facilitating automated data uploads will decrease the time between data collection and data availability. Difficulty in data recovery, and the need for specialised technical expertise to do so, is not necessarily the result of technical restraints, but rather the lack of care for valuable digital objects when they are created and preserved (Wilkinson et al. 2016). The evolving 'data ecosystem' necessitates all stakeholders, including increasingly relevant 'computational stakeholders', researchers, special and general-purpose repositories to evolve and to meet the FAIR data challenge (Wilkinson et al. 2016). Workbench applications to facilitate access for data providers to various data portals promotes the deposition of data, even if the data is not immediately freely accessible by others. It should be the goal of the biological research communities to use metadata schemas such as Ecological Metadata Language (EML), ISO 19115/19139, SANS 1878, FGDC, INSPIRE, Darwin and Dublin Core formats and data standards developed through the Biodiversity Information Standards (TDWG), and to deliver datasets to national and international databases. The researcher today needs to take into account the attributes of the digital objects and the requirements of machines to assist in the exploration of data through the application of more generalised interoperability technologies and development of standards at the data/repository level to promote good data stewardship (Wilkinson et al. 2016, Mons et al. 2017). Finally, big data requires detailed attention, specialised expertise and continuous capacity development to ensure data integrity and data services delivery (Miloslavich et al. 2019).

1.10 South African National Biodiversity Assessment

The South African National Biodiversity Assessment (NBA) (Lombard et al. 2004, Sink et al. 2012, 2018, Skowno et al. 2019) is an extensive summary of the collective knowledge of South Africa's science community, the public and many other stakeholders. Its main directive is to build on the Summary Marine Biodiversity Status Report for South Africa (Durham and Pauw 2000) and identify data or information gaps. It informs scientists, consultancies, managers, educators, politicians and policymakers on the status of the country's national resources, social interaction and challenges.

Divided into focus areas, it includes the assessment of the terrestrial, inland aquatic, estuarine, marine, and sub-Antarctic territories across broad scales from genetic to biotope biodiversity. In addition to being a scientific research summary of available knowledge, its success as reference literature and its usefulness to the non-scientific community can be attributed to its people-orientated narrative and the extensive use of indicators that emphasize the value, use and status of natural resources.

The NBA highlights two major indicators, i.e. threat status and protection level (Figure 1.1). These apply to ecosystems and species. It highlights the need for data to compute additional indicators for ecosystem extent and health, habitat loss, biological invasions and genetic diversity. Tracking and evaluating Key Biodiversity Areas (KBAs) and Ecological or Biological Significant Marine Areas (EBSAs) in the future will further strengthen the NBA's links with Aichi targets and SDG associated indicators (Sink et al. 2019).


Threat status

- Follow the IUCN risk assessment framework for species (Red List of Species) (IUCN 2012a) and ecosystems (Red List of Ecosystems).
- Follow the African Threatened Ecosystem Framework.
- Categories are Critically Endangered (CR), Endangered (EN), Vulnerable (VU) or Least Concern (LC)
- Aichi 5 and 12
- SDG 15.1 and 15.5

Protection level

- Developed in South Africa for national reporting to address extent of ecosystems and protection
- Categories: Not Protected, Poorly Protected, Moderately Protected or Well Protected
- Aichi target 11 and 12
- SDG 15.1

Biological ecosystem change

- Copepod abundance
- Coral bleaching
- Invasive spesies range expandion and abundance
- Algal blooms (HABs)

Species

- Range expansion
- Abundance

Figure 1.1: Subset of information for four indicators used in the National Biodiversity Assessment (NBA): Threat status, Protection level, Biological ecosystems and Species. Aichi Target and Sustainable Development Goal (SDG), on which South Africa report, is also indicated for Treat status and Protection level indicators (Sink et al. 2019).

Indicators are important tools to measure and explain the state of species and ecosystems and confer complex messages in a simplified manner (Wicks et al. 2010, McQuatters-Gollop et al. 2019, Sink et al. 2019). The value of data collected on a long-term basis depends on its accessibility and usefulness to end-users. The user-friendliness of the information produced and the ease with which it can be translated into policy documentation will influence its use and role in facilitating adaptive sustainable management. Indicator frameworks aim to simplify and contextualise data and provide up-to-date information to guide management decisions (Smith et al. 2007, Wicks et al. 2010). The development of indicators is not only hypothesis-driven (Wicks et al. 2010), fuelled by pertinent research questions, but, to guarantee effectiveness and uptake by policy-makers, the process should involve the end-users in indicator development (Wicks et al. 2010, McQuatters-Gollop et al. 2019). Indicators that assess the success of management and policy strategies are equally important (Ehler 2003, Smith et al. 2007).

The NBA lists several biodiversity information research priorities, and these include refining the description and extent of ecosystems with the collection of both biological and physical variables. It highlights the need to resolve data deficiency on numerous marine taxonomic groups and species, including the lack of information on life history, distribution and associated trends, and the need to improve methodologies of the assessment change. This will improve our understanding of ecological infrastructure and mapping of resource services, especially those immediately relevant to humanity (Sink et al. 2019). Furthermore, it identifies the need for long-term biodiversity site-specific research and increased demand for observation data linked to scientific information in support of governance and management. This requires increased integrated, coordinated interdisciplinary efforts in observing and understanding the ocean (Lindstrom et al. 2012a, Sink et al. 2019).

1.11 Marine Spatial Planning

South Africa's marine systems, spanning the Atlantic, Indian and Southern Oceans, provide an important opportunity for the study of global climate change (Dorrington et al. 2018). The Marine Spatial Planning Act, 2018 published in May 2019, provides a framework to provide for the development of marine spatial plans, its implementation and governance (Department of Environmental Affairs 2019a). Implementation of an overarching, integrated ocean governance framework for sustainable growth of the ocean economy may maximise socio-economic benefits.

The ability to explore, measure, research and understand the ocean has grown since the 1980s and is now characterised by routine observations from satellites and autonomous devices such as buoys, gliders and *in situ* observatories, real-time data recorders that assess and characterise the state of the ocean (Lindstrom et al. 2012a, Skelton 2014, Muller-Karger et al. 2018). Investment into marine research infrastructure in South Africa (Bornman 2016, Department of Science and Technology 2016a) facilitates and develops the collection of EOVs and EBVs. The strength of a Marine Spatial Plan (MSP) depends on the availability of spatial and temporal data that provide information on social-economic and social-environmental interactions, legislation, physical, geochemical, and biodiversity processes and ecosystem systems interactions and connectivity (Dorrington et al. 2018).

As an important tool in adaptive ecosystem management (Foley et al. 2010, Chalmers 2012), MSP attempts to bring together all ocean resource users and social-economical-environmental interactions in a spatial and temporal context (Ehler and Douvere 2009, Dorrington et al. 2018). Ecosystem-based MSPs focus on the maintenance and delivery of ecosystem services and include the assessment of the vulnerabilities of marine ecosystems to human activities (Foley et al. 2010). The effectiveness and value of a marine spatial plan depend on the information it is built on (Figure 1.2).

Figure 1.2: Highlighted nodes indicate key areas SAEON’s marine long-term research site network established in different ecosystems within South African territorial waters including the Prince Edward Islands may contribute temporal and spatial data to Marine Spatial Planning.

Research on South Africa marine systems has made important contributions (Chalmers 2012, Makwela 2017, Shah 2018, Truter 2019) and suggest a multidisciplinary approach and the use of short and long-term research products are important in developing MSPs (Lombard et al. 2004, Sink et al. 2010, 2012, 2018, Dorrington et al. 2018, Retzlaff and LeBleu 2018).

The development of the South African maritime sector, the unlocking of South Africa's ocean economy, Operation Phakisa, and implementation of the National Development Plan (NDP) 2030 (Matona 2019) focus on South Africa's future economic development and prosperity in the marine sector. Key priorities for the development of the ocean economy include maritime transport and manufacturing, offshore oil and gas, construction, renewable energy, fisheries and aquaculture, desalination, tourism and conservation. The initiative has seen the expansion of South Africa's Marine Protected Network from <0.5% to 5.4% of its continental marine environment in 2019, with the addition of 20 new proclaimed Marine Protected Areas (MPAs) (Department of Environmental Affairs 2019b, 2019c) under various management strategies (Sink et al. 2019). The proclamation of MPAs strengthens South Africa's scientific and environmental management sectors, as it provides a valuable platform for comparative observation and study that permits the disentanglement, identification and study of the effect of natural processes versus those driven by anthropogenic stressors, on a long-term basis.

1.12 Demands of LTER

The scale, effort and cost of running large LTER programmes necessitate a careful evaluation of the variables to be measured (e.g. density, abundance, size structure, species composition, community structure and diversity). It should strive to provide the lowest possible sampling variability while incorporating standardised methodologies to allow for data comparison (Bennett 2007). Economic feasibility, ease and simplicity of equipment deployment, data collection and data analysis requires critical evaluation. The data collected should be independent of resource use data (Bennett 2007) and must be of relevance to science, management and society. The development of comprehensive indicator frameworks with indicators that give a true reflection of sustainability and link to management objectives useful in guiding resource managers and decision-makers is needed (Smith et al. 2007, Smit et al. 2021). To promote data uptake in different fields and by resource managers, the various approaches to the management of our natural resources such as Ecosystem-Based Management (EBM), Large Marine Ecosystem (LME) management, Dynamic management of coast and oceans, Integrated Coastal Management (ICM), Integrated Ocean Managements (IOM) and Cooperative Management should be taken into account (Sherman 1991, Smith 2007, Vousden and Stapley 2013, Long et al. 2015, Winther et al. 2020).

1.13 The South African Environmental Observation Network (SAEON)

An essential function of LTER programmes is to inform and increase insight into natural resource dynamics, including productivity and service provisioning, in response to bio-physico-chemical changes (Van Jaarsveld and Biggs 2000). Long-Term Ecological Research (LTER) in South Africa is in its infancy. Records on marine organism distribution and abundance, except for fisheries catch reports, are sporadic, incomplete or ephemeral owing to their short-term focus. The LTER initiative in South Africa arose from the realisation that short-term projects may not address the need for society to respond to local, regional and global environmental change (Biggs et al. 1999, Durham and Pauw 2000, O'Connor 2010, Skelton 2014). Long-term marine ecological research was conceptualised in the form of the South African Environmental Observation Network (SAEON) in 2002, with the establishment of the Elwandle Coastal Node in 2010.

SAEON, a business unit of the National Research Foundation (NRF), is composed of six distinct but complementary nodes (Arid Lands; Egagasini Offshore; Elwandle Coastal; Fynbos; Grasslands, Forests and Wetlands and Ndlovu Savanna) that serve as observation platforms and hubs of research in various biomes and ecosystems of South Africa. An umbrella data and information platform node (uLwazi) collects and processes all datasets produced by the nodes and facilitates the distribution of verified datasets through selected data pipelines to the scientific community, policymakers, and society in general.

Future goals of the Elwandle Coastal Node include the phased development of a comprehensive long-term observation network in all four major marine bioregions, estuaries and the shallow coastal zone. Research activities are currently focussed on the Algoa Bay Sentinel Site (ABSS) with the Pelagic Ecosystem Long-Term Ecological Research platform (PELTER), the Continuous Monitoring Platform (CMP), the National Estuaries Network (NEN), Marine Protected Area Network (MPAN) and the Coastal Temperature Network (CTN). The node also manages the Shallow Marine and Coastal Research Infrastructure (SMCRI), a component of the South African Research Infrastructure Roadmap (SARIR – DST 2016) funded by the Department of Science and Innovation (DSI) to develop bio-physico-chemical research platforms around the South African coast to collect long-term data (Figure 1.3).

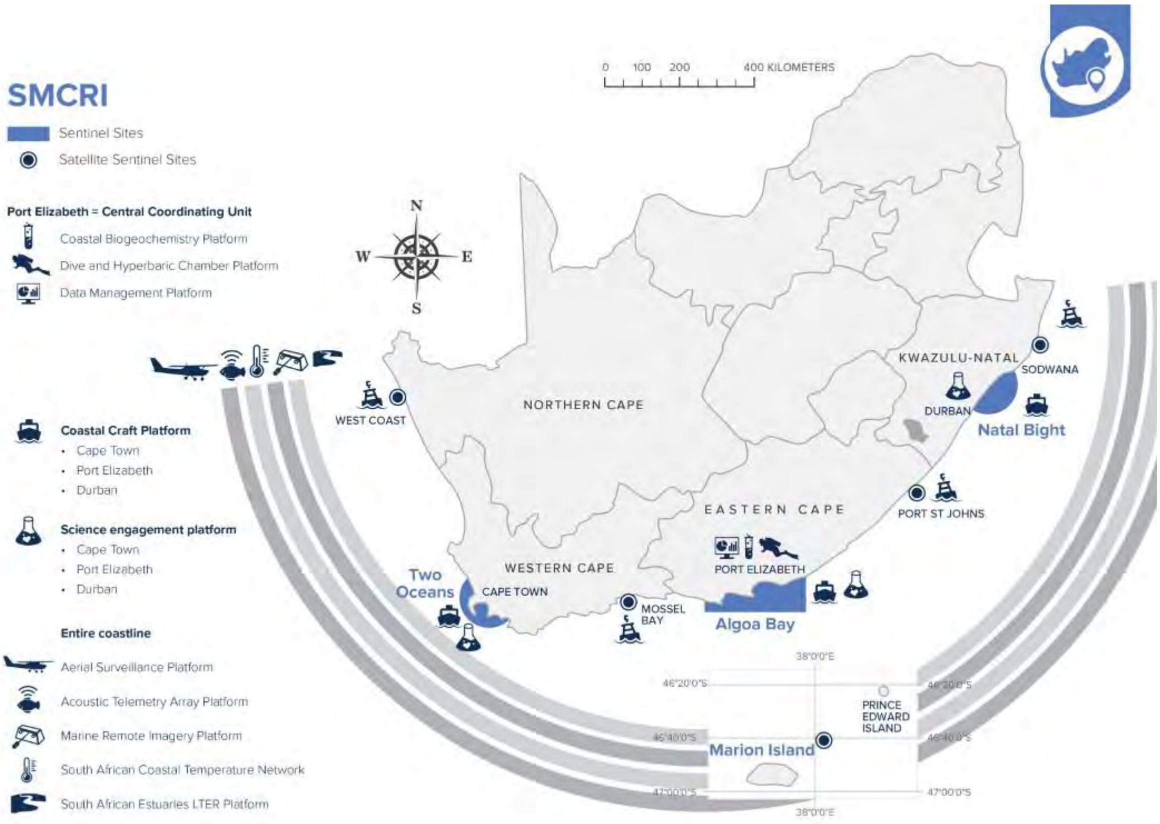


Figure 1.3: Phased expansion of the Shallow Marine and Coastal Research Infrastructure (SMRI) by the South African Environmental Observation Network (SAEON) Elwandle Coastal Node and the South African Institute for Aquatic Biodiversity (SAIAB) within shallow coastal waters of South Africa (available from https://smcri.saeon.ac.za/).

Elwandle's Algoa Bay Sentinel Site (ABSS), within the Agulhas Ecoregion, is well established and SMCRI is now expanding to include additional sentinel and satellite sentinel sites (the Two Oceans Sentinel Site (TOSS), the Natal Bight Sentinel Site (NBSS), the Marion Island Sentinel Site (MISS), several satellite sites and several research hubs located along the coast between Orange River on the West Coast and Kosie Bay along the east coast) and will enable LTER within all the major shallow-water ecoregions along the South African coast (Figure 1.3). The node employs two principle methods for the collection of environmental variables. Data on physical Essential Ocean Variables (EOVs) are collected using a network of strategically placed moorings allowing for continuous monitoring of water currents and temperature. Continuous measurements of this nature provide insight into time phases of specific oceanographic phenomena, systems variability and provide a reliable record of variable parameters (extreme observations such as minimum, maximum, median and mean estimates). The Continuous Monitoring Platforms (CMPs) consist of Acoustic Doppler Current Profilers (ADCPs) for measuring ocean currents and waves, Underwater Temperature Recorder arrays (UTRs) for depth discreet measurement of temperature (up to 80m isobath) and Gully Temperature Probes (GTPs) for measurement of temperature in water <5m deep associated with the shallow subtidal rocky shore. Biogeochemical EOV data in association with biological EOVs are collected as part of the Pelagic Ecosystem Long-Term Ecological Research (PELTER) platform, which incorporates the use of multi-sensor technology, such as SeaBird conductivity, temperature and depth (CTD) sensor casts off coastal vessels, in conjunction with biological sampling (e.g. plankton net tows) enabling phyto- and zooplankton biomass and diversity estimates (Figure 1.4 with variables addressed by the current SAEON Elwandle LTER indicated).

The SAEON Elwandle LTER programme aims to grow and improve its capability to acquire and disseminate data and data products. This includes the availability of real-time environmental observations, such as temperature, current and salinity while *in situ* data collection for plankton and biochemical variables would strengthen the current data infrastructure (Figure 1.4). The existing airborne remote sensing platform, collecting high-resolution imagery of the coastal region, will soon be supported by LiDAR technologies that will allow mapping of not only the terrestrial coastal environment but also the nearshore marine environment. The pelagic environment in shallow coastal marine systems are influenced by the structure and composition of the benthic substrate and supported biotic boundary layer. A holistic approach to understanding system dynamics in the coastal seascape thus require the observation and collection of variables associated with both the pelagic and benthic environment.

1.14 Conclusion

1.14.1 Long-Term Ecological Research (LTER)

Long-term datasets and observations are essential to facilitate adaptive sustainable management of natural resources, but these research programmes face many logistical, technical and conceptual challenges (Haase et al. 2018, Miloslavich et al. 2018, Mirtl et al. 2018). Important considerations include standardisation, data compatibility and continuous or periodic methodological adaptation necessitated by technological advances in data collection and analysis. Long-term research initiatives are dependent on reliable long-term funding sources. Platforms must be developed with the full understanding that the fiscal state may change at any time. Provision should be made for the survival of the programme in times of financial shortfall, taking into account details such as equipment life span, in-house serviceability and calibration, deployment and baseline manpower needs, data relevance and recycling value.

.

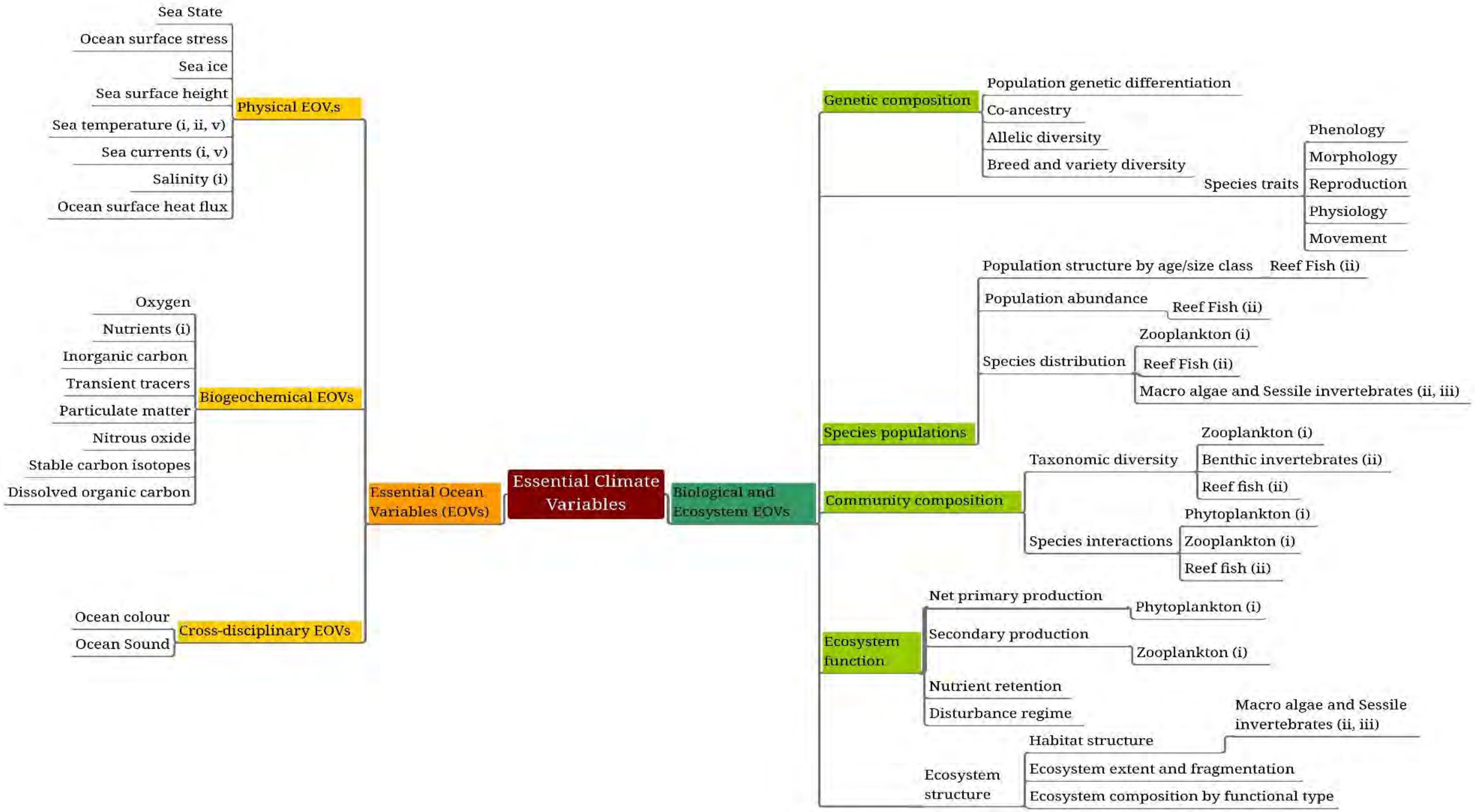


Figure 1.4: A summary of Essential Climate Variables (ECVs) potentially addressed by SAEON, Elwandle Coastal Nodes LTER Platforms (i) pelagic, (ii) benthic, (iii) rocky shores, (iv) sandy beaches (v) Continuous Monitoring Platform (CMP), (vi) aerial and (vii) biogeochemical.

The integrity of the data is extremely important, not only now, but also for future usability. Complementary metadata and calibration records are essential to ensure the data is usable, to its current full potential and in the future. A high reuse value, applicability or usefulness of the data or data products in other research initiatives and experiments, both short and medium-term, is advantageous. Relevance and usability would warrant continuation of the LTER, and help in motivating and securing future support and funding for the platform, ensuring its longevity. Another essential component of the LTER platform is that the data should be easily available and accessible, and to this end, it is essential to keep track of its end-users and their needs. Datasets, in this sense, are the commodity, and proof of use and incorporation into policy enhances their value and that of the LTER platform. Local-scale short-term experiments embedded in long-term research integrates observational data and experimental data. Multi-scale multi-disciplinary collaboration is important. It allows an increased understanding of relevant social-ecological issues and the formulation of pertinent research questions which aid in the development of new hypotheses contributing to the ability to predict ecosystem responses and shift due to future global change (Collins et al. 2011, Miloslavich et al. 2018, Picone et al. 2020).

1.14.2 Benthic Ecosystem Long-Term Ecological Research (BELTER)

The Benthic Ecosystem Long-Term Ecological Research (BELTER) platform falls under the SAEON/SAIAB jointly managed Marine Remote Imagery Platform (MARIP). It provides information related to the benthic environment and will complement the existing research PELTER platforms. The research includes the collection of video and still imagery of the benthic substrate using Jump Camera Systems (JC) of sessile organisms that form a transitional layer between the substrate and the overlying pelagic system. It will furthermore include the collection of stereo data streams using stereo Baited Remote Underwater Video (sBRUV) systems that focused on ichthyofauna associated with the benthic seascape, for both consolidated and unconsolidated sediments (Figure 1.5). This will enrich SAEON Elwandle Coastal Node’s current data suite and provide multi-layered information on community structure, species diversity, distribution and abundance of benthic and pelagic systems.

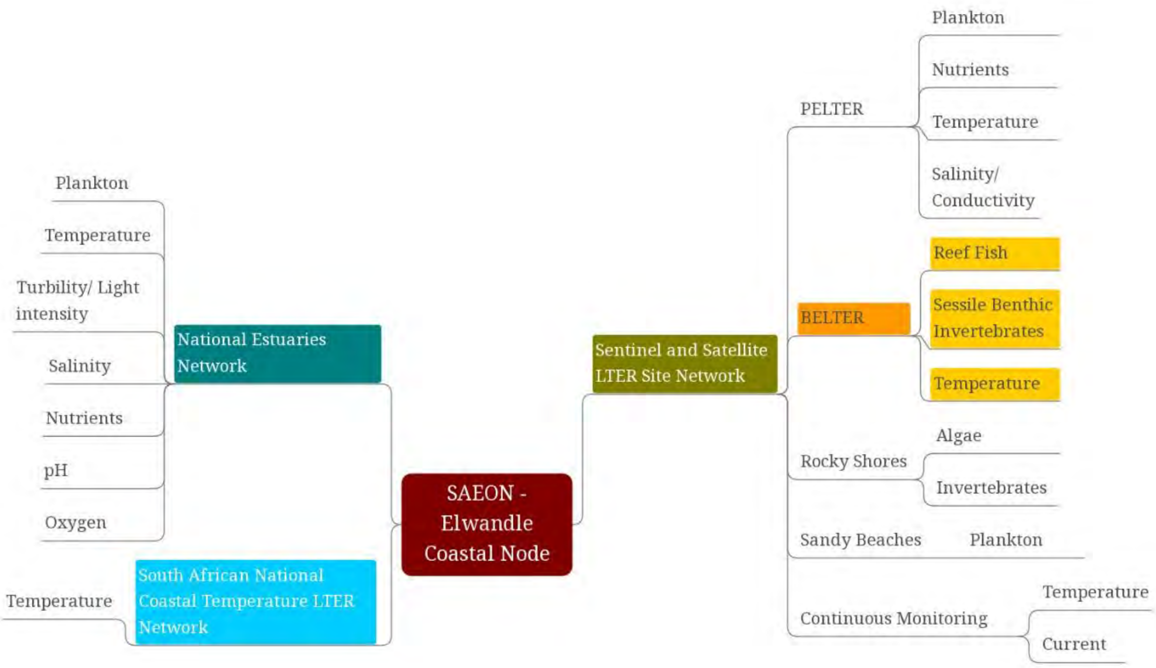


Figure 1.5: The organogram shows SAEON Elwandle Coastal Node's three current research focus areas (adapted from Bornman 2016) those related to the Benthic Ecosystem Long-Term Ecological Research (BELTER) indicated in orange and yellow.

Chapter 2 Study site

2.1 Objectives

This chapter provides a condensed overview of the South African coastal marine ecosystems with a focus on the study site, Algoa Bay. It looks at the importance of Algoa Bay as SAEON Elwandle Coastal Node's Sentinel Site. It provides a general introduction of the Benthic Ecosystem Long-Term Ecological Research (BELTER), stations selection and the sampling methodology used. It provides insight into the condition of the physical environment during the initial year and a half of the programme with a focus on environmental conditions during data collection events.

2.1.1 Specific goals

- Discuss the selection of sample stations within the Algoa Bay Sentinel Site (ABSS),
- discuss sample design and methodology,
- discuss and correlate wind and sea temperature in the bay during the implementation phase of the BELTER programme and
- give a short overview of the importance of nutrients and plankton in Algoa Bay.

2.2 South Africa's coastal marine ecosystems

Weather, climate and marine ecosystems along the south and east coast of South Africa are influenced by the prominent Agulhas Current system. The source water originates from the Mozambique Channel as well as from the East Madagascar Current and contributes substantially to the Indian Ocean Gyre through the Agulhas Return Current (Lutjeharms 1976, Beal et al. 2006, Dencausse et al. 2010, Lutjeharms and Bornman 2010). On its way south it is pushed offshore along an ever-widening continental shelf, influencing shelf water through shear-edge eddies, plumes and large episodic meanders or 'Natal Pulses' (Lutjeharms and Roberts 1988, Lutjeharms 2007, Goschen et al. 2015). The southern part of this boundary current flows westward, curling around the Agulhas Bank, and leaks warm saline Indo-Pacific water into the southern Atlantic Ocean (Beal et al. 2011). The shredded Agulhas rings mix into the surrounding Benguela region on their way to the South Atlantic (De Ruijter et al. 1999). The south-westward flowing Western Boundary Current forms an important component of global ocean circulation (Olson and Evans 1986, De Ruijter et al. 1999, Penven et al. 2001, Lutjeharms 2007, Beal et al. 2011, Caley et al. 2011) and the northward-flowing Benguela Current drives large upwelling events and productivity along the West Coast of southern Africa (Kirkman 2016).

The coastal zone of South Africa is divided into five ecoregions. The cold, temperate Southern Benguela, which contains the Namaqua and Cape subregions and extends from Namibia to Cape Point. The coastal area with the highest recorded endemism (Awad et al. 2002a) is the warm temperate Agulhas ecoregion from Cape Point to the Mbashe River. The subtropical Natal ecoregion extends from the Mbashe River to Cape Vidal and includes the Southern KwaZulu-Natal, Wild Coast and KwaZulu-Natal Bight subregions. The Delagoa ecoregion that extends from Cape Vidal to Bazaruto Island in Mozambique is a transitional zone between the subtropical and tropical coastal waters. (Sink et al. 2018). Set separately from the mainland is the Prince Edward Islands ecoregion that forms part of the Subantarctic Island Province in the Southern Ocean (Spalding et al. 2007) characterised by cold ocean conditions (Figure 2.1).

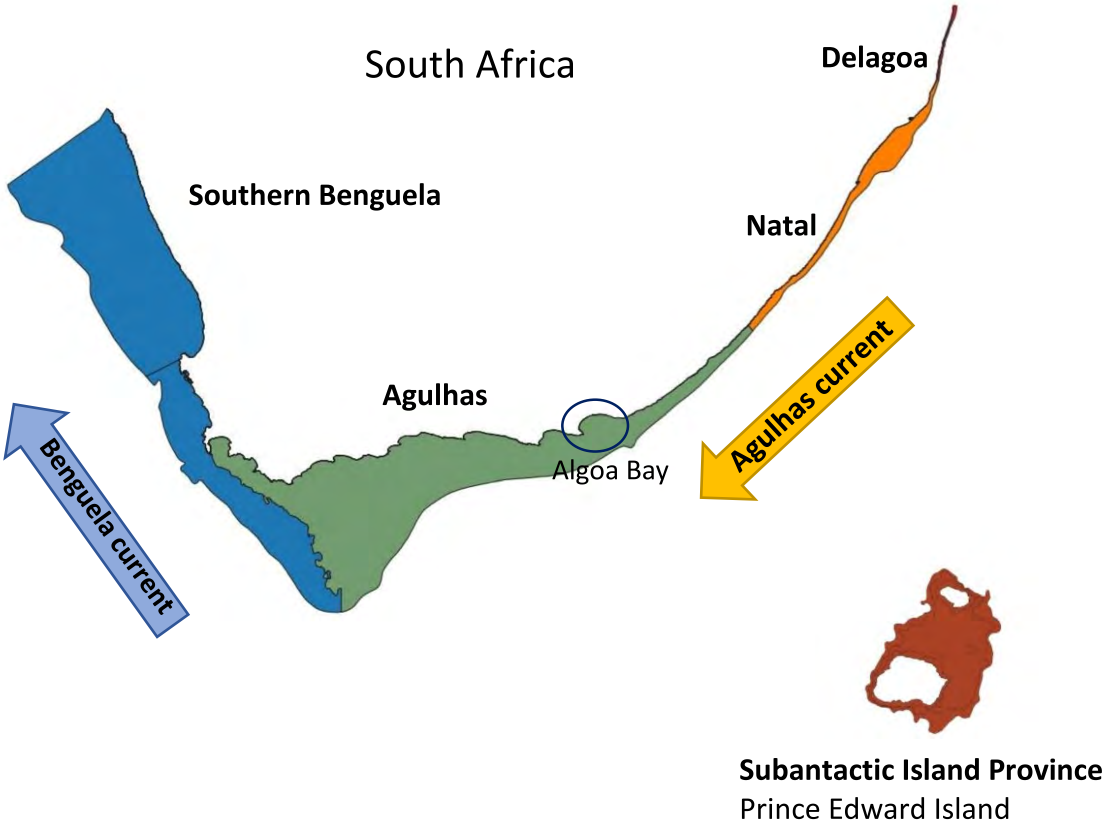


Figure 2.1: Simplified map of South Africa to illustrate the position of the five coastal ecoregions. The Prince Edward Island group is not to scale or in the correct geographical position to the mainland (modified from Sink et al. 2018).

Previous studies within the South African subtidal benthic environment focussed largely on unconsolidated bottom types (Field 1971, Masikane 2011, Harmer 2014, Lange and Griffiths 2014) with most of the hard substrate research restricted to coral reef systems along the subtropical east coast (Riegl et al. 1995, Schleyer and Celliers 2005, Schleyer et al. 2006, Celliers and Schleyer 2008, Porter and Schleyer 2017). Mapping of temperate reefs and reef-associated substrates and communities is, however, less well represented. The majority of the work has been done in Marine Protected Areas (MPAs) including Betty's Bay MPA (Joshua et al. 2018), Tsitsikamma MPA (Heyns 2015, Heyns et al. 2016, Heyns-Veale et al. 2016, 2019b, 2019a), Pondoland MPA (Celliers et al. 2007), canyons off KwaZulu-Natal coast (Sink et al. 2006) and Prince Edward Islands (von der Meden et al. 2017). Benthic invertebrate distributions and endemicity has also been used as a tool in the identification of priority marine conservation areas (Awad et al. 2002a).

Ichthyofauna associated with reefs and reef-associated environments is economically important in both the recreational and commercial line fish industries (Branch and Clark 2006, Chalmers 2012). As an important commodity and resource, many of these species are good indicators of system use (Smith 2007, Bernard 2012) and it is not surprising that most research has focused on reef-associated fish species (Götz et al. 2008). This includes studies that have investigated the effectiveness of MPAs in the management of these important resources (Buxton and Smale 1989, Attwood and Bennett 1995, Cowley et al. 2002, Götz 2005, Mann et al. 2018, Heyns-Veale et al. 2019a). This includes research on species composition (Mann et al. 2006), distribution (Burger 1990), movement (Brouwer and Griffiths 2005, Kerwath et al. 2007, Bennett et al. 2017), growth (Buxton and Allen 1989, Brouwer and Griffiths 2004), feeding and diet (Smale 1986, Mann and Buxton 1992), reproduction (Buxton and Clarke 1986, Buxton and Garratt 1990, Brouwer and Griffiths 2005) and the effect of environmental conditions on fish populations (Hanekom et al. 1989). The link between the benthic environment, sessile benthic communities and infra- and supra-ichthyofauna distribution has received less attention (Buxton and Smale 1984, Götz et al. 2009a, Heyns 2015, Heyns et al. 2016, Heyns-Veale et al. 2016, Wahab et al. 2018).

2.3 Algoa Bay Sentinel Site

Algoa Bay and St Francis Bay are two log-spiral shaped embayments on the south eastern Cape coast of South Africa (Bremner 1991a, 1991b, Goschen and Schumann 2011). Classified as Eastern Agulhas Bay marine ecosystems within the Agulhas ecoregion (NBA 2018), these systems extend from the back of the surf zone to the edge of the embayment demarcated by the prominent capes. Of this, the Algoa Bay ecosystem spans a total area of 1631.23 km^2 and includes the Agulhas Island ecosystems, which include the St Croix and Bird Island groups (Sink et al. 2018), both made up of quartzitic Table Mountain Sandstone (Beckley and McLachlan 1979).

The city of Port Elizabeth is located in the southwestern sector of the bay, with a population in excess of 1.2 million (SA Census 2016, Maluleke 2016). This large ever-expanding metropole and industrial development have led to the degradation and pollution of rivers, estuaries and the marine nearshore environment. Modification of the geomorphology of the basin and shoreline of the bay started with the construction of the Port Elizabeth Harbour wall in 1922 (McCleland 2020). The prevailing longshore current and the mainly sandy character of the Algoa Bay basin has resulted in the accumulation of sand on the south side of the harbour wall and the formation of Kings Beach. This coincided with the gradual erosion along large sections of the sandy shoreline north of the harbour mouth. The need to safeguard the inland infrastructure led to the reinforcement of some 8.5 km of sandy shoreline with massive concrete dolosse to combat erosion (Goschen and Schumann 2011). The newly formed beach reached sand capacity in 1990, which led to sand accumulation along the breakwater and finally, around the sea wall into the mouth of the harbour. In the absence of a sand bypass system, this necessitated dredging to ensure access to the port (Goschen and Schumann 2011). The development of a new deepwater port, Port of Ngqura, has led to an increase in shipping and since 2016 the waters adjacent to the port, which can accommodate up to 50 ships at anchor simultaneously, has been used for bunkering, trading 2 million tonnes of fuel in the first years of operation (Mdlalose 2019). Increasing shipping operations and bunkering bring the possible introduction of alien species from hull fouling and ballast water exchange (Wu et al. 2019) and the possible occurrence of catastrophic pollution events due to oil spills leading to the mortality of marine organisms and the threat to ecosystem functioning within Algoa Bay (Crawford et al. 2000, Munilla et al. 2011, Yaghmour 2019). The increase and effects of noise pollution associated with these activities are not yet fully understood and may affect seasonal use and migration patterns of marine animals (Weilgart 2018, Erbe et al. 2019, Ivanova et al. 2020).

The coastline between Cape Recife and Cape Padrone extends approximately 108 km, and today consist of 70.3% sandy beaches, 16.5% rocky outcrops or rocky shores, 4.5% harbour walls, 7.8% sandy shores stabilised with dolosse and less than 1% estuary mouths. The 77.6 km mouth of the bay, considered the dividing line between Algoa Bay and the rest of the continental shelf, is characterised by the discontinuous Cape Recife Bird Island Ridge (Goschen and Schumann 2011).

Freshwater enters the bay from several tributaries, which include ephemeral systems, temporarily open/closed and permanently open estuaries. The small Shark River flows through Happy Valley (Urquhart 2007) and is today an ephemeral creek and its role in supplying subsurface water into the nearshore is unclear. The Baakens River, which flows into the Port Elizabeth harbour basin, and the Papenkuils River situated to the north of the Port Elizabeth harbour wall, are both highly modified systems, canalised and in poor ecological condition. The Swartkops Estuary, a permanently open system, flows through extensive industrial, formal and informal residential developments (Niekerk et al. 2015), resulting in a high pollution load (Binning and Baird 2001, Nel et al. 2015). The Coega River is a temporarily open/closed system that has been extensively modified by the development of salt works and the new Ngqura Harbour. The Sundays Estuary, situated on the southern border of the Alexandria dune system, is a permanently open estuary. The river system is supplemented with water from the Orange River Valley, via an extensive aqueduct system, into the Great Fish River, then the Fish River-Sundays River Canal Scheme and into the Sundays River system (Lustenberger 2010). The Algoa Bay aquifer system, with an estimated surface area of 2490 km^2 is located along the northern boundary of the bay (Campbell et al. 1992) and supplies groundwater directly into the surf and subtidal zone. This is believed to fuel important marine processes (Campbell and Bate 1998).

The substrate of Algoa Bay consists largely of unconsolidated sediments with scattered reef systems (Bremner 1991a, 1991b). Research on unconsolidated substrates and their biota (McLachlan et al. 1977, Malan and McLachlan 1985, Masikane 2011, Truter 2019) has in some cases indicated the presence of isolated reef complexes, many of which are not documented. Notwithstanding the paucity of information on some areas, a wealth of information exists on the sandy beaches (Mclachlan 1977, McLachlan et al. 1981), rocky shores (Garner 2013), algae (Beckley and McLachlan 1980), plankton dynamics (Cockcroft and McLachlan 1986, Webb and Wooldridge 1990, Pitcher et al. 2014), ichthyofauna (Coetzee and Baird 1981, Buxton and Clarke 1986, Coetzee 1986, Chalmers 2012, Ensair 2019), sharks (Smale 1991), marine mammals (Karczmarski et al. 2000, Melly 2011, Dicken et al. 2013, Koper and Plön 2016, Bouveroux et al. 2018, Melly et al. 2018) and sea birds (Randall et al. 1971, Klages et al. 1992, Potter 2013) of Algoa Bay. Use of the Algoa Bay seascape by fish larvae (Lasiak 1981, 1984, 1986, Beckley 1984, 1985, Beckley and Buxton 1989, Pattrick and Strydom 2008, Pattrick 2013, Whitfield and Pattrick 2015, Costalago et al. 2018), nutrient dynamics and input into the bay (Lemley et al. 2019), research on benthic species that produce marine natural products (McPhail et al. 2001, Sikorska et al. 2012, Bromley et al. 2013, Matobole et al. 2017, Kalinski et al. 2019) and the effects of pollution (Adeniji et al. 2019) have also received attention. The characterisation of the reef biota at Bird Island has been the first attempt to provide insight into community structure and species diversity (SANParks Report: Chalmers, Parker-Nance et al. In press) with valuable work in assessing unconsolidated habitat and identifying mixed and low profile reef substrate in Algoa Bay done by Truter (2019).

St Croix, Brenton and Jahleel Islands are situated in the mid-western sector of the bay (Figure 2.2) and historically supported the largest breeding colony of African penguins (*Spheniscus demersus*) (Crawford et al. 2011), but resource competition has resulted in a steep decline in the number of breeding pairs as an ever-growing demand for protein has caused the depletion of many fish stocks and endangered the survival of predatory species (Lescroël and Bost 2006, Bearzi et al. 2008, Pichegru et al. 2009). In 1981 the island group was the first to be proclaimed a marine reserve, with a marine protected zone of 300 m around the outcrops. This was increased to 500 m in 1991. The island group is now included in the Addo Elephant National Park MPA restricted use zone which prohibits any fishing activities (Department of Environmental Affairs 2019b, 2019c). The second group of islands, including Bird, Stag, Seal Islands and Black Rocks, is situated about 8.5 km offshore from Woody Cape in the north-eastern sector of the bay (Figure 2.2). Bird Island is the largest known rookery for Cape Gannets (*Morus capensis*) but also serves as home to penguins, terns and cormorants. Black Rocks is home to the easternmost breeding colony of Cape fur seals (*Arctocephalus pusillus*). Proclaimed a terrestrial Provincial Nature Reserve in 1987 and a MPA in 2004, it was included into the Addo Elephant National Park MPA in 2005 (South Africa Department of Environmental Affairs 2004, Chalmers 2012). The shallow coastal marine environment, Alexandria Coastal Dune Field and the islands now fall within an extensive 1200 km^2 multi-use marine national park (Department of Environmental Affairs 2019c), which covers 39% of the 3100 km^2 of Algoa Bay (Figure 2.2) (Melly et al. 2018) and managed by South African National Parks (SANParks).

2.4 Benthic Ecosystem Long-Term Ecological Research (BELTER)

2.4.1 Introduction

Benthic Ecosystem Long-Term Ecological Research (BELTER) aims to facilitate sustainable long-term observation of the shallow coastal marine benthic environment that will provide information on change within the environment. It should inform on natural and anthropogenic driven stressors, provide insight and be useful for management and in policy development and execution, thereby assisting Marine Spatial Planning (MSP) and adaptive Ecological-Based Management (EBM).

The classification of habitats and communities within the seascape can be done on different scales using satellite imagery, LiDAR, multibeam sonar and a diverse complement of autonomous or remote image platforms and towed video equipment (Brock et al. 2004, Wedding et al. 2008, Costa et al. 2009, Smale et al. 2012, Turner et al. 2016). The plethora of methodologies, many project-specific, used at different scales (van Rein et al. 2009, Roelfsema et al. 2013) and depths however all make use of analyses based on digital imagery (Mallet and Pelletier 2014). The use of imagery in the description of biotopes and mapping of the seafloor is advantageous as it can be used over many substrates not conducive to conventional sampling methods (Buhl-Mortensen et al. 2020).

The data generated by the BELTER platform will in the near future benefit not only from variables collected by its pelagic counterpart (Pelagic Ecosystem Long-Term Ecological Research (PELTER)) platform but will be able to incorporate imagery collected from LiDAR and Multibeam Sonar. This will allow for the construction of high-resolution maps including information on the distribution and extent of substrate types, bottom hardness, elevation, substrate architecture and community structure of the benthos.

Aside from collecting high-quality reusable imagery, the curation and preservation of the data and associated metadata is critical. Currently, the analysis of the data is tedious and time-consuming, requiring people trained in species identification. As technology progresses Machine Learning (ML) will change the way data processing and analysis is done (Mohamed et al. 2018, Li et al. 2020) effectiveness of the processing of historical data, however, depends on the information provided by the accompanying metadata. Well, curated image-based data streams (with accompanying metadata info-sets) are the best way to capture observations that allow re-analysis in the future. It permits the reformulation of research questions, modification of analytical methodologies and subsequent re-analysis addressing novel research questions. This allows for historical collected datasets to provide ongoing new and current information.

2.4.2 Research stations and sample locations

A hierarchical naming convention is used by SAEON (Elwandle) for referring to the place where samples are collected. The general geographical area within a targeted ecoregion is called a Sentinel Site. These may be associated with a number of satellite sentinel sites that are spatially separate from the main area of research but still fall within the same ecoregion such as areas of particular research interest or MPAs. *In situ* instrumentation and repeated sample or data collection occur at predefined stations within the sentinel site. A station could contain a collection of predefined collection localities around which random sampling and data collection may take place and are referend to at sampling points.

The first and oldest South African coastal marine Sentinel Site for LTER is the Algoa Bay Sentinel Site (ABSS). This was established in 2010 and encompassing an area offshore from Port Alfred to Thyspunt. Port Alfred is situated on the linear coastline north of Algoa Bay and Thyspunt is a rocky cape west of Cape St Francis. In the implementation of BELTER, two stations were selected within the Algoa Bay Sentinel Site (ABSS): White Sands Reef (WSR), and St Croix Island Complex (SCC) including St Croix and Benton Island. Each station consists of between 18 and 24 referenced sample collection localities. The BELTER stations within the ABSS were selected as representative of two geographically distinct areas within the bay in close proximity to existing *in situ* observatories. Both stations are represented by consolidated and unconsolidated substrates. The first, WSR, is situated in the south-western sector of the bay, 2 km north of Cape Recife point (Figure 2.2). The sample collection location closest inshore is 500 m from land, while the furthest sample collection locality is 2300 m offshore (Figure 2.3 insert). The second station encompasses the nearshore of St Croix Island and Brenton Island. It is referred to in this work as the St Croix Island Complex (SCC) and is situated 20 km from the Port of Port Elizabeth and 7 km from the Port of Ngqura Harbour at Coega, in the central-western sector of Algoa Bay (Figure 2.2).

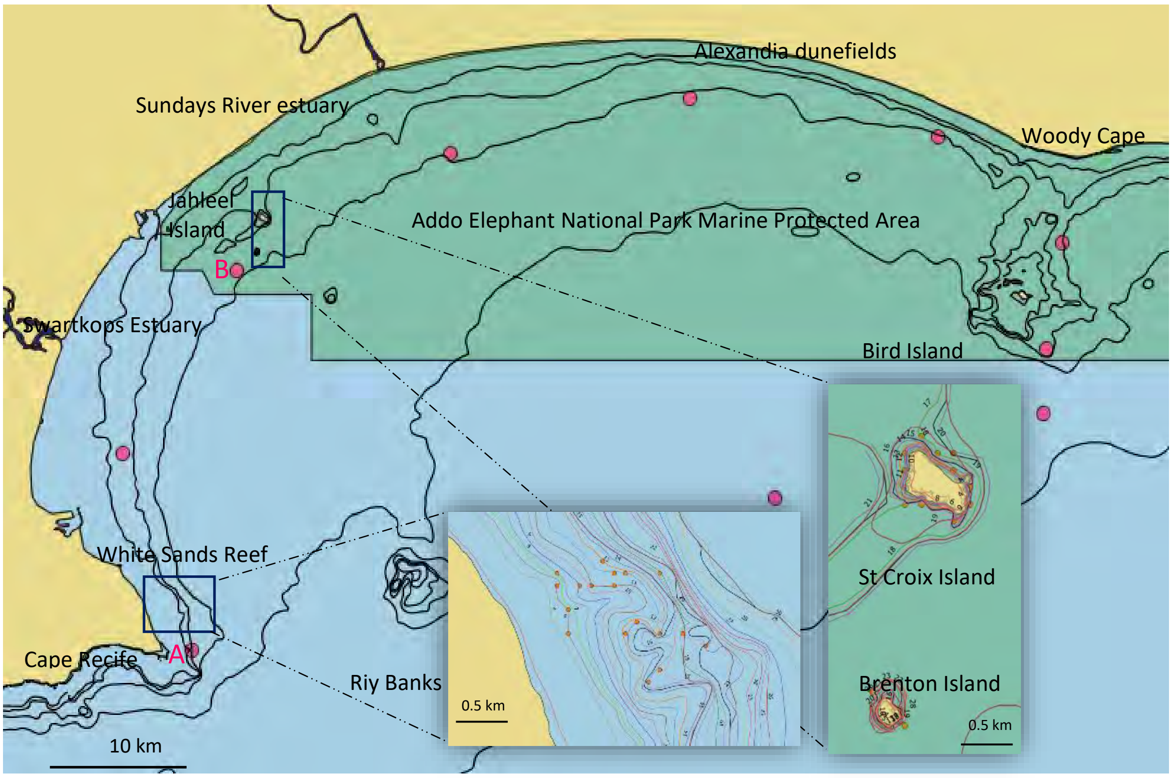


Figure 2.2: Algoa Bay with insets of the two sampling stations, White Sands Reef (WSR) on the left and the St Croix Island Complex (SCC) on the right. Temperature data was obtained from SAEON's Continuous Monitoring Platform (CMP) indicated by A and B.

2.4.3 Materials and methods

Sample locations at each of the research stations were identified by superimposing a 150 m square grid over the entire bay. Sample locations within the stations were randomly selected, and where data collection repeatedly proved unsuccessful (e.g. because of equipment toppling due to the bottom topography, fouling, repeated low visibility conditions, or obstructed view) the particular location was excluded and a new location selected from the initial randomised list. This process was repeated until the desired number of reference locations (n = 24) were identified within each station. All subsequent data collection events used these data reference locations and all samples collected around these locations are referred to as sampling points for the specific location. This selection process imposes several assumptions and biases on the BELTER datasets. These include absence in data from environments with steep pinnacle-like high profile reef structure, areas with almost vertical uneven surfaces, narrow and deep crevices or gullies. These areas may cause the equipment to get trapped or roll or move excessively during deployment. Collection of data from persistently low visibility areas such as in deeper areas may be mitigated in the future by the use of lights attached to the BRUV frames although the presence of persistent thick algae blooms, as is the case for around Jalheel Island, is not conducive to the collection of usable video footage.

Imagery-based data to assess ichthyofauna assessment was collected using stereo Baited Remote Underwater Video (sBRUV) systems. Data collection started in March 2018 for WSR and in May 2018 for SCC. Sample collection at Jahleel Island, a small island situated next to the harbour wall, however, started only in February 2019 with limited data collection success owing to poor visibility. This data was subsequently not used in this study.

The sampling protocol grouped closely located sample sites within a station together, allowing for the consecutive deployment of six sBRUVs within 15 minutes. All deployments were done in the same order during each sampling event. Overall the programme aimed to collect data at the two stations (WSR and SCC) each month dependent on platform availability and weather windows or available sea-going days. In the first 18 months of the programme, sampling was possible twelve times for WSR and only four times for SCC. The initial aim of 24 sBRUV deployments a day was regularly feasible for the closely situated WSR but travelling time and weather windows allowed for only 18 deployments at SCC, St Croix Island and Brenton Island, but not Jahleel Island. In general, three cycles of six deployments per morning allowed for 18 samples to be collected in the morning weather window. By amending the daily sample load from 24 to 18 allows for the use of more good morning weather windows. Subsequently, this study only includes 18 samples from each station to validate sample methodology and analysis for BELTER.

In addition to imagery data collection for the assessment of ichthyofauna, a Jump Camera (JC) system was deployed off a small research vessel, equipped with a davit arm and winch. An onboard global positioning system (Garmin GPS) was used to locate the position of the reference location. The objective was to collect 10 video streams, randomly within a 25 m radius of the reference location. Date, depth, surface and bottom temperature and GPS position were recorded for each sampling point (Figure 2.3). JC data collection could easily be completed for 18 research locations per morning weather window (n = 180 samples). Ocean surface conditions affect the deployment of JC systems more than the sBRUV systems. The sBRUV systems can be quickly deployed and the buoy line released breaking the connection with the moving vessel. This however is not the case for the JC as it is lowered to the seafloor, kept in place for at least 30 seconds and retrieved. Increased surface chop and wind makes keeping the research vessel in place more challenging and sampling in calmer conditions preferable.

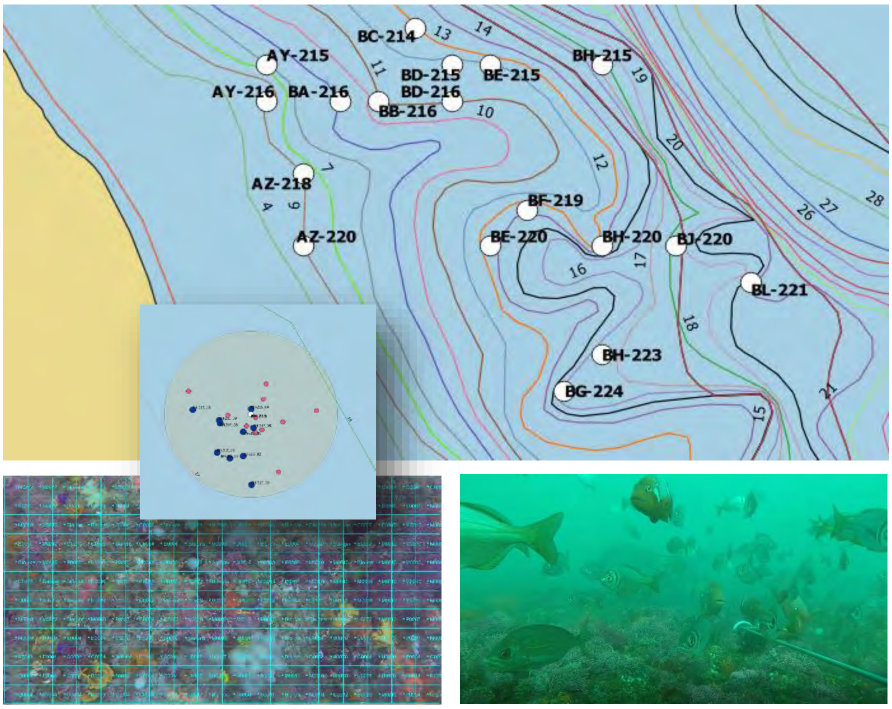


Figure 2.3: Example of a map of a research station (White Sands Reef) with bathymetry indicated by coloured lines. Reference locations are indicated by white circles and enlarged by an inset. This indicates the target sample area around the predetermined central research location in grey with (in this case) the position of random JC deployments (in blue) and sBRUV deployments (in pink). The bottom left image illustrates the structure of the superimposed grid over images collected with the JC systems and the bottom right is a typical image captured in a sBRUV deployment.

A subset of sBRUV and JC image data from only 18 locations per station is used in this pilot study. All 360 JC data streams were of sufficient quality to allow an analysis of the benthic environment. All four data collection events for SCC (n = 62) are included and corresponding data collected for WSR (n = 72) was selected. The shortfall of samples for SCC was due to bad deployment (toppled instrument) or low visibility making analysis of the collected data not feasible. The four sBRUV sampling events incorporated in this study were done in November 2018 (spring), February 2019 (summer), May/ June 2018/2019 (autumn) and the end of August/early September 2018 (end of winter).

2.5 Wind at the study site

The wind is an important driving force in Algoa Bay (Schumann et al. 1982, Roberts 2010). Surface currents in the bay generally flow in the direction of the wind, with longshore surface currents predominating (Goschen and Schumann 2011). Nearshore surface water responds directly to wind with very little or no lag period and the underlying water column current profile is not homogeneous (Pattrick et al. 2013). Wind also drives upwelling, a process in which deep cold nutrient-rich bottom water is brought to shallower coastal waters (Schumann et al. 1982), influencing nutrient dynamics in the bay. The nutrient-rich water drives plankton productivity and trophic dynamics (Brown 1992, Goschen et al. 2015).

For this study, the wind data, recorded at the Port Elizabeth International Airport, were reduced to average wind speed per day (Figure 2.4) and represented in wind roses for percentage frequency of counts by wind direction for each month over the 18-month sampling period (Figure 2.5). It is acknowledged that this is not representative of the whole bay, as patterns can vary in position and active periods over its extent (Schumann et al. 1988, 1991, Roberts 2010, Goschen and Schumann 2011).

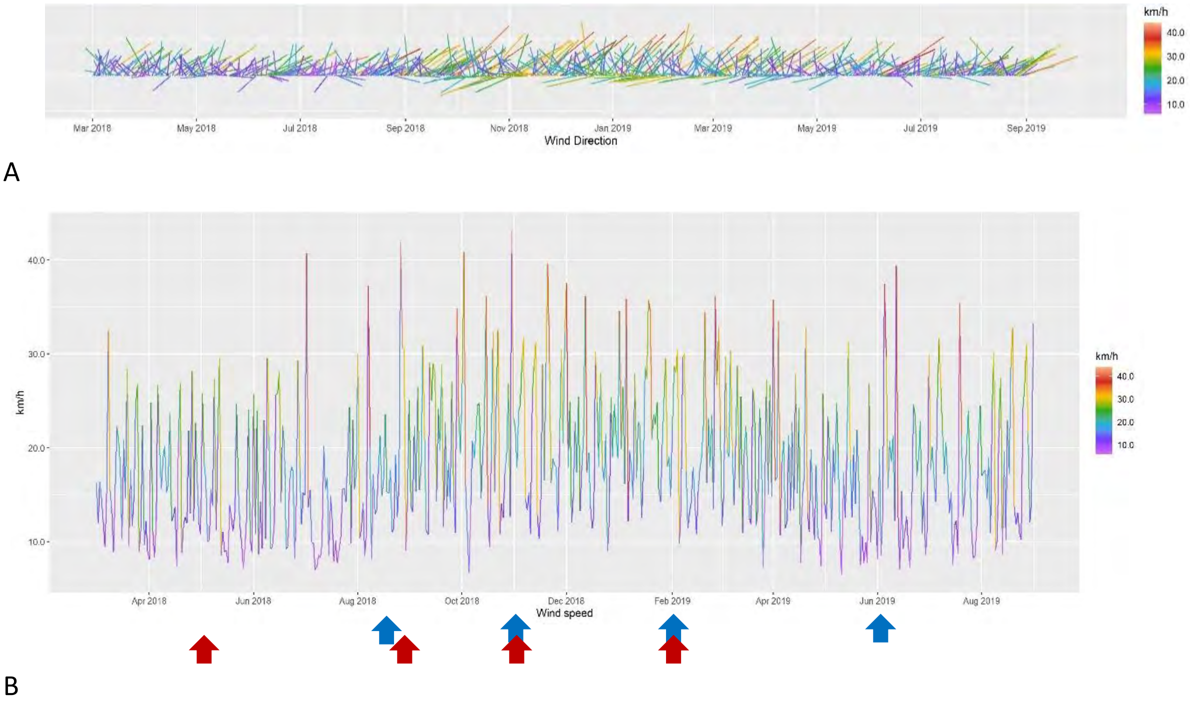


Figure 2.4: Average daily wind speed over the 18-month study period recorded at the Port Elizabeth Airport: A) daily average wind direction and speed and B) corresponding daily average wind speed. Arrows, blue for WSR and red for SCC indicate sample events. The sample collected in May 2018 for WSR was in extremely low visibility and therefore the June 2019 samples were used in data analysis.

During this study, minimum wind speeds were evident for the period May to July, most prominently in 2018 and less so in 2019. Maximum wind speeds occurred from September to November (Figure 2.4). This is a well-described phenomenon (Schumann et al. 1991, Goschen and Schumann 2011) with winds over Algoa Bay known to have an increased easterly component during summer, as evident over the study period. A marked difference in wind velocity is evident when comparing May 2018 and June 2019 (Figure 2.4B) but the composition of the winds during these months is similar although the increase in westerlies is also evident (Figure 2.5).

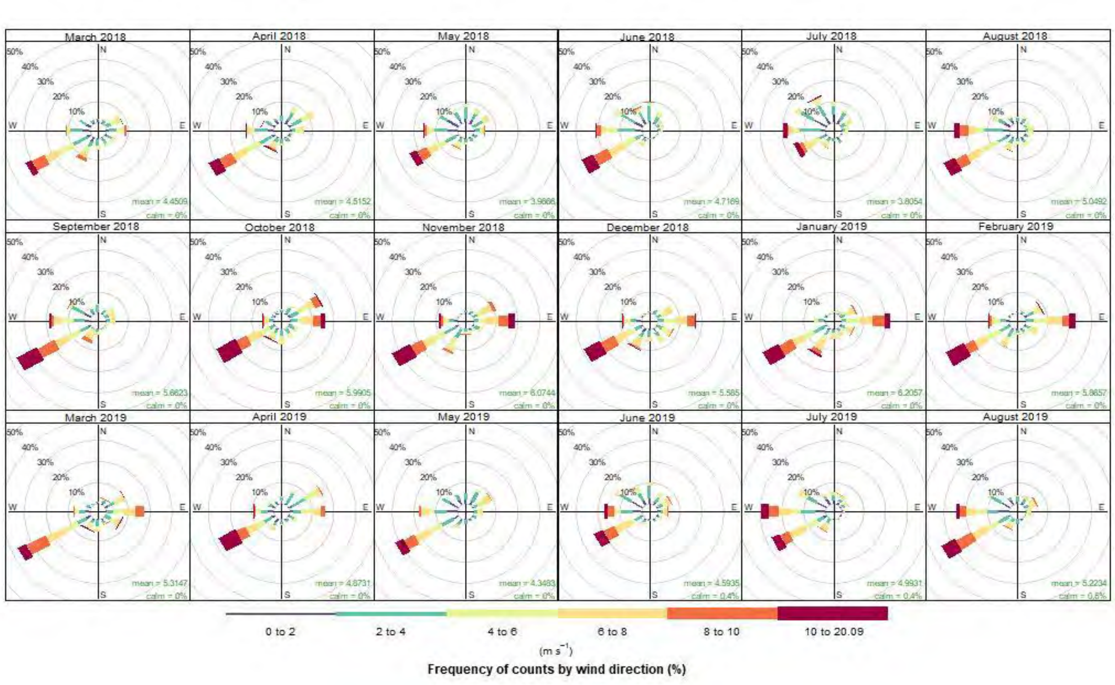


Figure 2.5: Wind roses for each month over the 18-month study period recorded at the Port Elizabeth Airport.

2.6 Sea temperature at the study site

The South African Environmental Observation Network's (SAEON) Elwandle Coastal Node maintains and services *in situ* observatories within the Algoa Bay Sentinel Long-Term Research Site. Temperature data obtained from two stations, Cape Recife (close to White Sands Reef) and St Croix, were used to compile temperature profiles for depths at 10, 15, 20 and 30 m recorded with Underwater Temperature Recorders (UTRs) on thermistor strings as part of the SAEON Continuous Monitoring Platform (CMP) (indicated by A and B in Figure 2.2).

Temperature profiles differ for the two stations in both the profile and the occurrence of warm and cold water events. The WSR station experienced well-stratified water temperature conditions from March to May 2018 and 2019 with temperatures of around 10 °C recorded at 30 m depth (Figure 2.6).

Mixed, more homogeneous warm water throughout the column temperatures is evident from May to October. Warm water, 20 to 22 °C, reaches down to a depth of 30 m during the peak summer period of December and January. During November and for short periods during middle April 2018 and March 2019, following an increase in the frequency of easterly winds, upwelling of cold bottom water occurred and lead to a decrease in surface water temperatures. These cold-water events, due to upwelling, are well documented in Algoa Bay (Schumann et al. 1988). The sampling during May 2018 and November 2018 took place during similar bottom temperature profiles. The collection during September 2018 was done during warmer conditions while the February 2019 sampling was characterised by cold bottom water conditions (Figure 2.6).

The temperature profile for SCC did not exhibit the same degree of cooling of surface waters as that experienced during the corresponding period at WSR. Although the general temperature profile of the bottom water was similar for WSR and SCC, the latter seems more variable with frequent fluctuation in bottom water temperature. Although the cold water did not reach the surface, a decrease in the surface and mid-water column water temperature did occur. The warm water did not frequently penetrate to a depth of 30 m in December and January, as was the case for WSR, but frequently fluctuated during this period. Sampling in May 2018, November 2018 and February 2019 was conducted during cold bottom water temperature conditions, while warmer conditions were prevalent in September 2018 (Figure 2.6 and Figure 2.8).

A comparison of temperature recorded on the day during the sampling event between the UTR stations at Cape Recife (White Sands Reef) and St Croix Island and that recorded by the Hobo temperature loggers attached to the BRUV system deployed at WSR and SCC highlight two phenomena (Figure 2.6, Figure 2.7 and Figure 2.8). Firstly, the temperature may vary with depth. Secondly, the bottom temperature in the shallow BELTER station close to the deeper water UTR station corresponds to the temperature at the same depth.

2.7 Nutrients and plankton

Natural processes and dynamics within the pelagic ecosystem, especially in the shallow coastal marine environment and embayments, such as Algoa Bay, have largely been compromised by anthropogenic driven changes such as an increase in nutrient input into the system. Land-based nutrient loading into Algoa Bay occurs from several sources, e.g. waste water works, rivers and stormwater drainage.

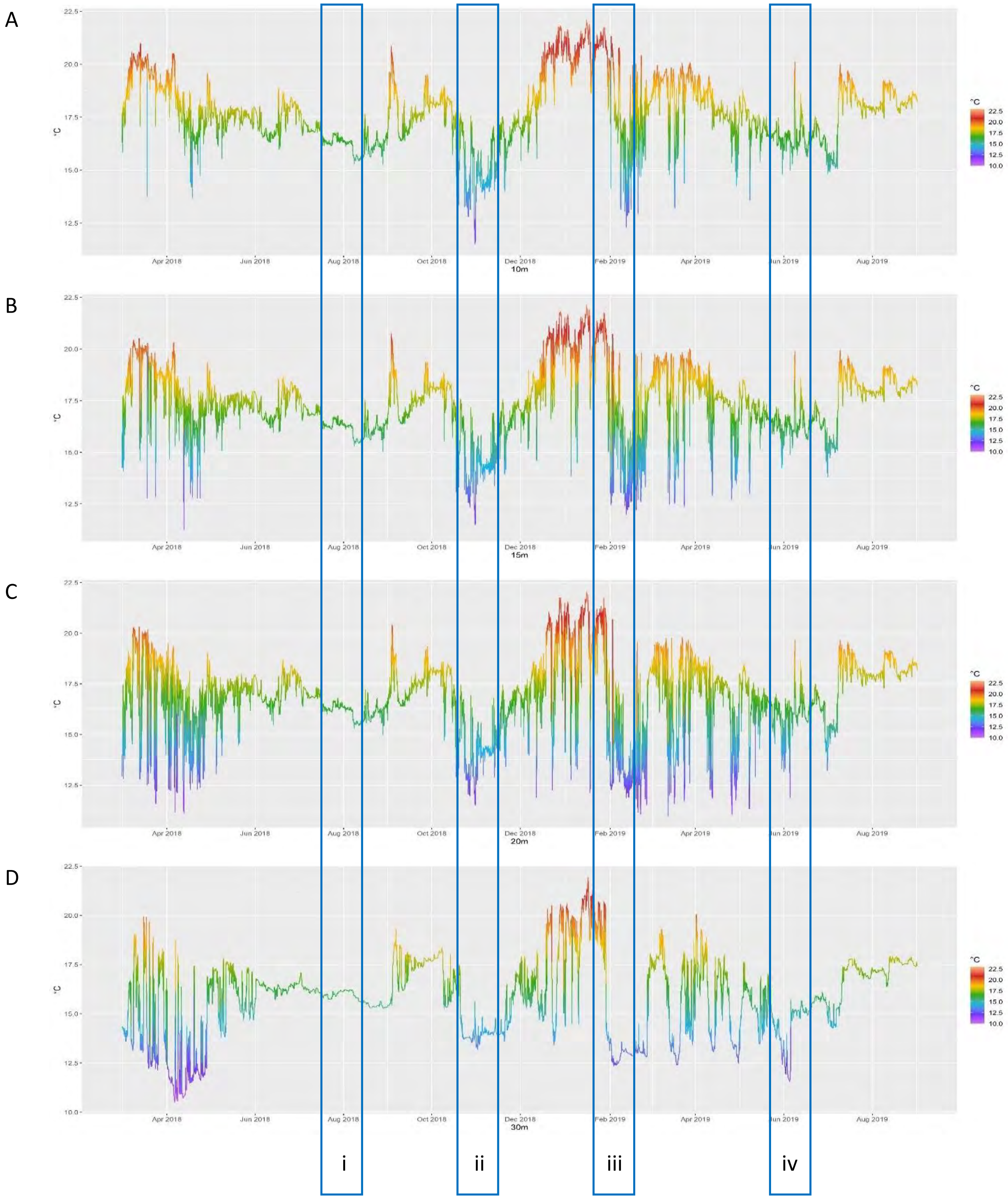


Figure 2.6: Water temperature profiles at A) 10, B) 15, C) 20 and D) 30 m depths for White Sands Reef (WSR). Sampling events included in this study are indicated by blue boxes. Also, see Figure 2.7 (i to iv) for a comparison between the UTR and BRUV Hobo temperature data.

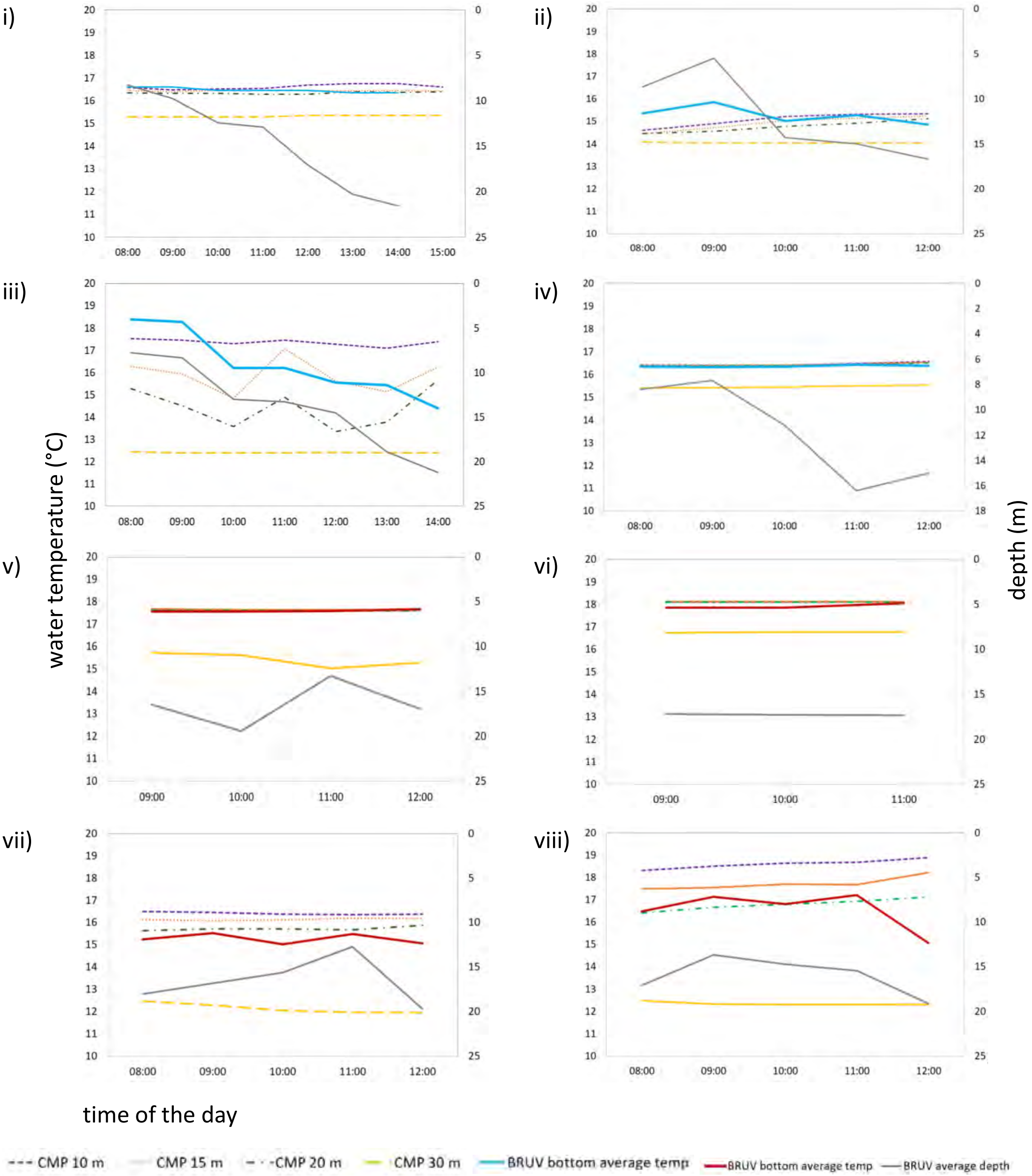


Figure 2.7: Water temperature recording on the day of sampling as obtained from UTR and Hobo attached to BRUVs temperature loggers. Depth of the recording is indicated on the y-axis and time on the x-axis for WSR in blue on i) 30 August 2018, ii) 14 November 2018, iii) 5 February 2019, iv) 20 June 2019 and SCC in red on v) 17 May 2018, vi) 13 September 2018, vii) 15 November 2018, viii) 6 February 2019.

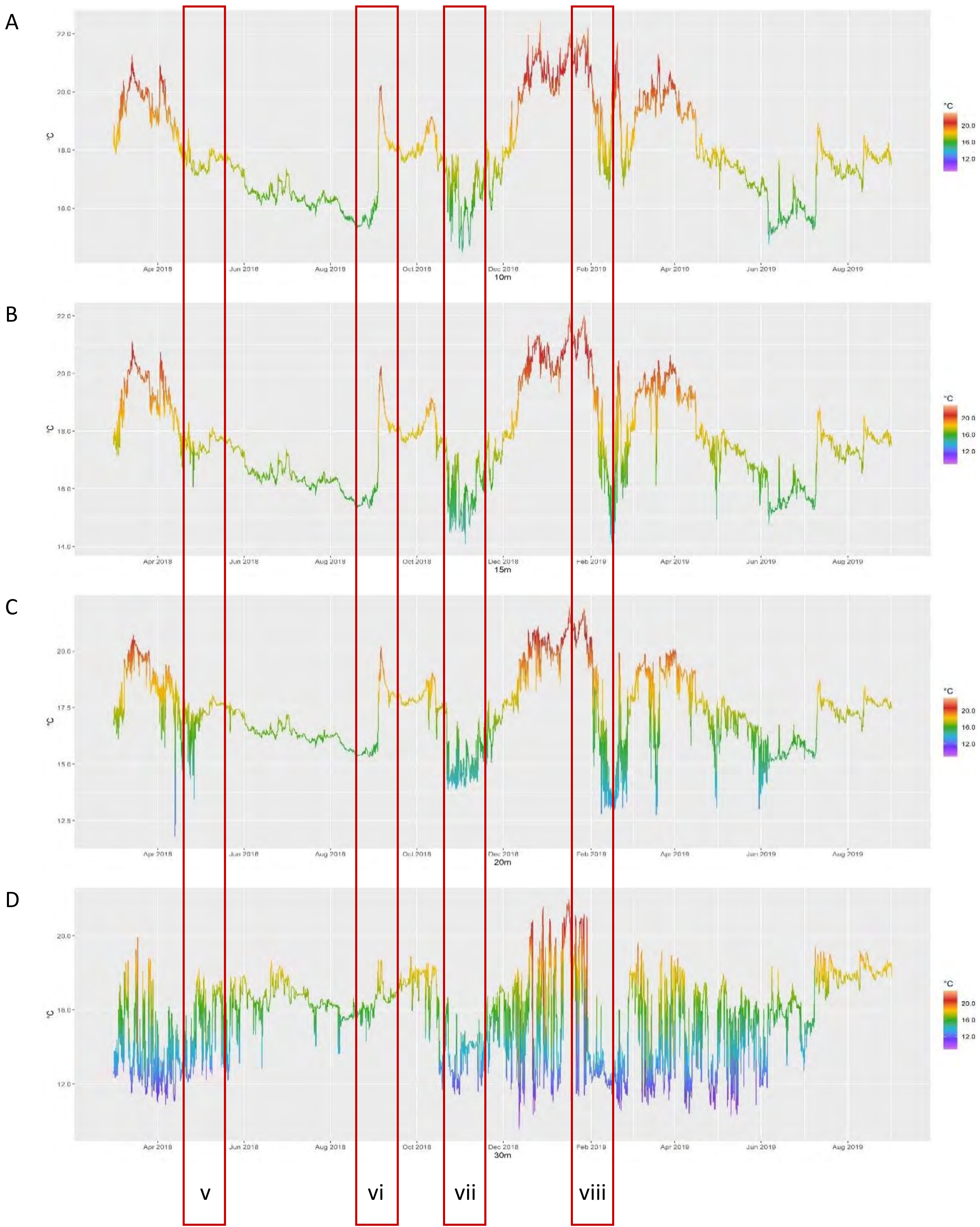


Figure 2.8: Water temperature profiles at A) 10, B) 15, C) 20 and D) 30 m depths for St Croix Island Complex (SCC). Sampling events included in this study are indicated by red boxes. Also, see Figure 2.7 (v to viii) for a comparison between UTR and BRUV Hobo temperature data.

Change in nutrient dynamics in the nearshore would result in changes in plankton distribution, abundance and the increasing occurrence of harmful algal blooms (HABs) (Mbambo 2006, Griffith and Gobler 2020). Large episodic events may lead to widespread mortality or biota, habitat degradation, reduction in diversity, changes in trophic dynamics and may impact aquaculture and fisheries (Pitcher et al. 2017). The response to nutrient loading into the system is complex and dependent on the source and oceanographic conditions with sites closely associated with the point of nutrient input characterised by higher phytoplankton biomass (Lemley et al. 2019).

The health of the pelagic environment is important given that pelagic primary producers (phytoplankton) and primary consumers (zooplankton) form the base of large complex food webs that support many economically important marine species (Hays et al. 2005). Increased carbon dioxide in the atmosphere has resulted in a decrease in carbonate ion concentrations in the ocean and studies suggest that ocean acidification may affect the capacity of marine invertebrates to form calcium carbonate (Fox et al. 2020). This will negatively impact the survival of these species, as many are part of the primary food chain, and may alter the marine carbon pump affecting the carbon sequestration capacity of the ocean (Hofmann and Schellnhuber 2009, Tréguer et al. 2018).

The physical and biotic properties of the water column also play an important role in the dispersal of genetic material and/or larvae of sessile marine invertebrates (Navarrete et al. 2005), algae and ichthyofauna (Pattrick and Strydom 2008, Pattrick et al. 2013, Porri et al. 2014, Emilie Villar et al. 2015). The dynamics between the pelagic biota and their benthic predators, the sessile marine filter and suspension feeders, and the effect of HABs on benthic systems are poorly understood. It is believed that benthic-pelagic coupling is sensitive to climate change although the extent and implications thereof is largely unknown (Griffiths et al. 2017).

2.8 Conclusion

In this chapter, we provided a short overview of the South African coastal marine ecosystems and introduced Algoa Bay as SAEON Elwandle Coastal Node’s Sentinel Site. The research stations were selected based on their accessibility and the lack of information available on benthic biotope and associated ichthyofauna. Deployment of the newly developed equipment and the subsequent assessment of the collected data from these environmentally different stations would inform on equipment usability and robustness. It would test the feasibility and executability of the sampling protocol while providing a dataset that could be analysed to determine if the data collected would be able to observe change spatially and temporally. The bay is well researched but knowledge on the benthic sessile and sedentary biota and the associated ichthyofauna is poor. This study will inform on the shallow benthic seascape by conducting a baseline assessment of the benthic environment at the two stations which will provide insight into habitat structure, composition and distribution as well species distribution, abundance and community structure of both the benthic sessile and sedentary biota boundary biota and the associated ichthyofauna.

Chapter 3 Biotope structure of Benthic Ecosystem Long-Term Ecological Research localities within the Algoa Bay Sentinel Site, South Africa

3.1 Objective

One of the main goals of the pilot study using data collected during the implementation phase of the Benthic Ecosystem Long-Term Ecological Research (BELTER) platform was to test the newly developed equipment within the existing infrastructure of the South African Environmental Observation Network's (SAEON) Elwandle Coastal Node. This process allowed for the identification of potential problems in data collection, equipment use and platform implementation. It allowed for changes to be made to the workflows, before the large scale implementation of the BELTER platform along the South African coast. In this chapter, the data collected using the Jump Camera (JC) system was used to do a detailed description of the habitat and the sessile and sedentary benthic biota for the predefined LTER locations within the BELTER stations. This investigates the capacity of the data to identify characteristic biotopes, determine community composition and constructs extensive species lists.

3.1.1 Specific goals

- Compile an image-based substrate type reference guide,
- construct a trait-based searchable image reference database of benthic organisms,
- describe community composition and biotope types,
- compile extensive species lists for each of the biotopes described and

  use the acquired information to construct biotope maps for the two research stations in Algoa Bay.

3.2 Introduction

3.2.1 The benthic boundary layer

Shallow marine coastal ecosystems are increasingly affected by anthropogenically driven climate change and these systems are important indicators of this change (Wahab et al. 2018). The South African shallow coastal marine seascape is a complex and multifaceted transitional system, stretching from the cool productive west coast to the species-rich warm tropical east coast (Awad et al. 2002b, Griffiths et al. 2010). Benthic biotope description and mapping are the first steps in understanding dynamics within the seascape and the connectivity between its components. Marine communities are part of larger systems (Porter et al. 2017a, Wahab et al. 2018) and dependent on meteorological and hydrographical processes (Bremner 1991b), governed by upwelling (Schumann et al. 1982, 1988, Goschen et al. 2015, Lourenço et al. 2020) and advection (Pattrick et al. 2013, Porri et al. 2014). The importance of substrate mineralogical composition (Guidetti et al. 2004), geomorphology (Etnoyer et al. 2010, Harris et al. 2014) or architecture (Trebilco et al. 2015), sedimentation (Bremner 1991b, 1991a, Celliers and Schleyer 2008), depth (Heyns et al. 2016), temperature, currents (Sink et al. 2019) and geochemical composition of the water column (Lutjeharms et al. 1996) in determining community structure is well recognized (Eidens et al. 2015, Porter et al. 2017a).

Benthic communities are highly structured biotic boundary layers containing a diverse range of trophic strategies (e.g. photosynthesis, suspension-feeding, and active filtration) and are directly influenced by and impact the overlaying pelagic ecosystem (Gili and Coma 1998). Bentho-pelagic or pelago-benthic coupling has recently received renewed interest, particularly in more holistic research approaches (Götz et al. 2009a, Heyns-Veale et al. 2016, Dames 2021). The modular structure, ever-increasing complexity, stochastic processes, and the functional influence of multiple variables challenge our ability to interpret the processes and the drivers of change and anthropogenic impacts within the seascape (Magurran et al. 2010, Dodds et al. 2012). Data on habitat characteristics, species composition and community structure over different temporal and spatial scales is needed to understand local and regional scale variation in diversity (Shears and Babcock 2007, Carlos-Júnior et al. 2019), seascape connectivity (Reis-Filho et al. 2019) and bentho-pelagic coupling (Bell 2008, Griffiths et al. 2017). This long-term ecosystem-based research (SAEON BELTER) investigating the biological linkage between benthic sessile biota (invertebrate and macroalgae), the focus of this chapter, and associated pelagic ichthyofaunal communities, the focus of Chapter 5, is the first for Algoa Bay.

3.2.2 Taxonomy

Benthic community studies depend heavily on taxonomic works (Kissling et al. 2018b) and the lack of skill capacity in this field has been acknowledged (Skelton 2014, Sink et al. 2019). Historically, the earliest known description of South African marine biota is from 1685. Since then several pivotal events have marked taxonomic research in South Africa, notably the establishment of the South African Museum in Cape Town in 1825 (today the Annals of the South African Museum form the cornerstone of descriptive reference works for the majority of South African marine species) and the appointment of Dr John D.F Gilchrist by the Department of Agriculture of the Cape of Good Hope in

1895 as a marine biologist and later as the curator of the South African Museum (Brown 1999, Griffiths et al. 2010). In Algoa Bay, an increased focus on specimen collection coincided with the arrival of the British 1820 settlers (Brown 1999). Today the persisting shortage of taxonomists is exacerbated by the current ever-increasing focus on benthic systems and the need to record large numbers of still undiscovered, undocumented, uncatalogued, and undescribed species (Brown 1999, Gibbons 1999). The shift, in 1999, of the singularly focused JLB Smith Institute of Ichthyology, established in 1968/9 to the now internationally acclaimed South African Institute for Aquatic Biodiversity (SAIAB) is evidence of the renewed realisation of marine invertebrate taxonomy as a major contributor to a more holistic and multidisciplinary ecosystem research strategy.

The disconnect between detailed description, drawing and full-colour images is undeniable. Image-based identification differs from that of the physical identification of biological specimens which consists of the examination, dissection and microscopic study of collected species. Images of collected or preserved material are often of little use in the identification of living *in situ* specimens. The Tunicate and Marine Invertebrate Research Assistant (TAMIRA) database used here is based on several decades of species collection and identification from mainly the Eastern Cape coast and allows for the linkage between collected taxonomically described specimens and an extensive library of *in situ*, collected and preserved images. This data is shared with the SAIAB catalogue Specify when specimens are housed in SAIAB. This chain of evidence is an important tool in connecting specimens in collection facilities with those recorded in underwater images. It is however pertinent that the user of image-based identification data understands the limitations and caveats associated with image-based species identification. An identification can rarely ever be confirmed without physical examination of the specimen. It is thus suggested that in accordance with the recommendation for the use of open taxonomic nomenclature, all image-based identification in this chapter (and Chapter 4) be regarded as 'incerta' and that species identification when cited be followed by 'sp. inc.' (Horton et al. 2021).

The large number of taxa still unknown, undescribed, awaiting description or in the case of South Africa, awaiting discovery and collection, is not a problem unique to South Africa. Many international researchers have to deal with the challenge of describing communities when the species in these assemblages are unknown. Moreover, species identification of benthic biota using image-based data may be problematic due to phenotypic plasticity or the presence of cryptic species. To mitigate these challenges many studies use broad classes or depend on traits-based classification (Althaus et al. 2014, 2015, Costello et al. 2015, Davies et al. 2017, James et al. 2017, Langlois et al. 2018, 2020, Dames 2021, Pillay et al. 2021b).

3.2.3 Sampling strategies and focus areas

Globally the development of inventive sampling strategies has led to an abundance of publications reporting on the merits and performance of analytical techniques for the collection of species data using image quadrats (Dethier et al. 1993, Brown et al. 2004, van Rein et al. 2009) along random transects (Carleton and Done 1995) or from permanent plots (Vallès et al. 2019). Past research within the shallow coastal belt (< 30 m depth) depended heavily on SCUBA divers equipped with underwater camera systems to collect image quadrats of benthic biota (Brash 2006, Celliers et al. 2007, Celliers and Schleyer 2008, Olbers et al. 2009, Bennett et al. 2016a, Berov et al. 2016, Heyns et al. 2016) (Table 3.1). Remote Operated Vehicles (ROVs) (Heyns 2015, Heyns et al. 2016, Makwela et al. 2016, Adams et al. 2020), towed underwater camera systems or Ski Monkeys (von der Meden et al. 2017, Carroll et al. 2018, Buhl-Mortensen et al. 2020) and Autonomous Underwater Vehicles (AUVs) (James et al. 2017) allow work in depths beyond the reach of SCUBA divers. Technological advances have seen the development of over-the-counter action cameras (Struthers et al. 2015) with the ability to collect high-quality still and video images (Funke, N., Claasen, M., Maissner, R., Nortje 2014, Truter 2019). The use of Jump Camera (JC) systems allows for the collection of image data from small coastal vessels and eliminates the need for dive teams and requires less crew on deck. The use of small action cameras in a JC system deployed in the shallow marine environment has proven to provided good quality imagery even without external lightning.

Research focused on defining shallow water habitat types and determining the associated community structure along the South African coast is in its infancy compared to global efforts (Skelton 2014). Subtidal systems that have received attention in the past include kelp forests and rock lobster habitats (Blamey et al. 2010, Coppin 2017), both important natural resources (Blamey and Bolton 2018), as well as unconsolidated sediments (Field 1971, McLachlan et al. 1977, Gumede 2001, Kruger et al. 2005), mixed unconsolidated sediments (Atkinson et al. 2011, Lange and Griffiths 2014, Truter 2019) and subtropical reef, including coral reef, along the KwaZulu-Natal coast (Celliers et al. 2007, Celliers and Schleyer 2008, Olbers et al. 2009). Research programmes focused on temperate reef systems (those without kelp) along the south and south-eastern coast has been limited and focusses mainly on the effectiveness of marine protected areas (Joshua et al. 2018), especially with regard to the efficacy of different management strategies in protecting important reef angling fish species (Götz 2005, Götz et al. 2009a, Heyns 2015, Heyns et al. 2016).

Table 3.1: Synopsis of studies based on data collected using digital image quadrats for subtidal benthic community composition assessment and description for South African shallow coastal marine habitats.

Area and depth sampled	**Method used**	**Data collection per sample collection point**	**Analyses methodology**	**Sample point resolution (m2/point)**	**Reference**
Algoa Bay 5-30 m	JC	0.43 m^2 random	regular point grid (n = 216)	0.002	current work
St Lucia / Kosi Bay 6-28 m	SCUBA	0.32 m^2 along transect	% cover	-	(Schleyer and Celliers 2005)
Aliwal Shoal 8-22 m	SCUBA	Point on transect	1 point/metre along 10 metres	-	(Schleyer et al. 2006)
Aliwal Shoal 10-25 m	SCUBA	0.26 m^2 and 0.29 m^2 along transect (n = 35)	12 regular linear point intercept	0.021 – 0.024	(Brash 2006, Olbers et al. 2009)
Pondoland < 31m	SCUBA	0.17 m^2 quadrat (~n = 50) along transect	10 regular linear point intercept	0.017	(Celliers et al. 2007)
Sodwana Bay 9-27 m	SCUBA	0.35 m^2 quadrats along a transect	10 regular linear point intercept	0.035	(Celliers and Schleyer 2008)
Tsitsikamma MPA 11-75 m	SCUBA , ROV	0.2 m^2 transect (n = 30)	54 points	0.004	(Heyns et al. 2016)
Sodwana Bay 13-17 m	SCUBA	0.25 m^2 permanent mark sites	area calculation	-	(Porter and Schleyer 2017)
Prince Edward Islands 140-500 m	SkiMonkey	1 m^2 along transect and 0.66-0.79 m^2	>80 point/ m^2	<0.013	(von der Meden et al. 2017)
Betty's Bay 10-29 m	SCUBA	0.33 m^2 along a 50 m transect (n = variable)	10 X10 point grid	0.003	(Joshua et al. 2018)

3.3 Materials and methods

The BELTER stations within the Algoa Bay Sentinel Site (ABSS) that were used in this study consist of two geographically distinct areas within Algoa Bay; White Sands Reef (WSR) station and St Croix Island Complex (SCC) station including St Croix and Brenton Island (see Chapter 2). Data were collected from 18 reference sample collection locations within the two research stations (WSR and SCC). The study aimed to collect image quadrats for the description and characterization of the benthic biotope at each of the research locations, including physical habitat characteristics, depth, temperature and the species composition of the benthic sessile or sedentary biotic organisms associated with the substrate. A Jump Camera (JC) system was deployed off a small research vessel equipped with a davit arm and winch. An onboard global positioning system (Garmin GPS) was used to locate the position of the reference location. The objective was to collect 10 video streams, randomly within a 25 m radius at each reference location. Date, depth, surface temperature and GPS position were recorded for each sampling point.

Video imagery of the substrate was collected with a GoPro Hero5 Black action camera mounted in a custom waterproof housing attached to a stainless steel frame that permitted the camera to be lowered to the seafloor (see Appendix 3.1 for the Technical Report of the JC design and specifications and Appendix 3.2 for the Standard Operating Procedure (SOP) for the sample collection, downloading, file naming, data storage and access protocol). The camera system was left on the bottom for at least 30 seconds to mitigate any disturbance as a result of the JC landing on the bottom, e.g. sediment mobilization, thus facilitating the capture of a clear image. The system was then raised above the substrate, the boat manoeuvred into the next random sample point position and the camera resettled. The JC was retrieved after ten drops. Video imagery collected constitutes a visual representation of 900 X 490 mm or 0.43 m^2 of the substrate. The collective sample of the ten images provides a substrate area representation of 4.3 m^2 for each reference sample location within the stations and is used to describe the biotope at the research locality.

An image reference database was constructed and populated with more than 1600 images of some 1100 benthic organisms known to occur within the shallow coastal benthic zone of the Agulhas Ecoregion. The database also includes reference images for various 'bin' assignments. Bins refer to groups of entities that cannot be identified individually, mainly due to the size and optical limitations. Bins were constructed for unidentifiable assemblages of hydroids, mixed short coralline algae and small mixed soft algae. Species reference images were assigned file names, as per the naming convention defined specifically for use in SeaGIS^{TM} TransectMeasure's image viewer function. This enables retrieval of and searches for images by group, traits and TAMIRA reference code. All images referred to in SeaGIS^{TM} TransectMeasure are listed in a custom-built species database TAMIRA which supports the construction of species lists, taxonomic hierarchy, distribution, etc. The database contains records of all morphological samples collected from Algoa Bay under curation at SAIAB. However, a large component of the benthic biota of South Africa, including that of Algoa Bay, still awaits description. Many of the species concerned were assigned preliminary species identifications based on morphological characteristics visible in the images. Each species within the species reference database was assigned a TAMIRA code, which is unique and does not change. This allowed for the regeneration of the species list as more information becomes available and new species are described.

Two images captured with the JC system were used in the analysis, the first for point count data generation and the second for area measurement. The frames were captured when the JC was stationary and sequential frames were assumed the same. The first captured frame was used to compile the species dataset and the following frame a habitat database. The datasets used were prepared from 360 video frames over which an 18 x 12 point grid (point coverage of 0.002 m^2, x separation = 50mm and y separation = 40 mm) was superimposed over the selected frame. The selection of sample resolution was based on point cover analysis approaches used in the relevant literature (Table 3.1). Organisms were identified to the lowest taxa possible. The habitat dataset was, in part, constructed from data points in the absence of biotic point counts, and data points in the grid assigned to biota were transformed to consolidated/hard substrate or unconsolidated/soft substrate data points, depending on the type and species of biota identified. Substrate topography and type were determined per scaled image quadrat in SeaGIS^{TM} TransectMeasure's area measurement function. The area measurement of habitat features was made on the second image in SeaGIS^{TM} TransectMeasure and included substrate types were: consolidated (pebbles, cobbles, boulders and rock) or unconsolidated (mud, sand, gravel and shell), as well as substrate heterogeneity and complexity (outcrops and crevices). Depth was recorded with the onboard depth sounder.

Three datasets were constructed, i.e.: (1) The environmental dataset consisted of i) depth; ii) substrate type measured as the area of the image quadrat represented by soft/unconsolidated (mud, sand, gravel and shell) and hard/consolidated (pebbles, cobbles, boulders and rock) substrate; and iii) topography or rugosity, measured as the area in the image quadrat represented by a smooth surface (consolidated or unconsolidated) and the presence of crevices and overhangs or outcrops (formed by abiotic or biotic outcrops); (2) The biotope composition dataset consisted of all point data collected, including the identification of the substrate type e.g. sand, gravel etc. In instances where biota were absent, substrate data was later transformed to indicate only consolidated or unconsolidated substrate; (3) A community composition dataset consisting of only species data, where substrate data has been removed and the dataset standardised.

An exploratory investigation into data structure and relation was done using PRIMER analytical tools (Clarke and Warwick 2001) and Paleontological Statistics Version 4.05 (PAST) (Hammer 2001). The environmental variables were assessed by Draftsman plots and Pearson's correlation matrices (PRIMER) that were constructed to compare and identify strongly correlated variables. Environmental data were normalised preceding Principle Component Analysis (PRIMER). Species accumulation curves were plotted for a subsample of the quadrats (the five individual quadrats with the highest number of species recorded were selected from each station). All quadrats were pooled for the station species accumulation curves. Data transformation of biological data was determined by the 2STAGE analytical tool in PRIMER with Spearman's correlation. The relation between environmental and biological datasets was investigated with BEST analysis (using Spearman's correlation) for normalised environmental resemblance matrix, constructed using Euclidean distance and square root transformed Bray Curtis resemblance matrix of the biological data sets within PRIMER. A binary split of the substrate data was done in LINKTREE analysis to investigate the relationship of the recorded substrate types between the research localities (Clarke et al. 2008). Biotope and community composition species count remembrance matrix was used to describe similarity in the sessile benthic assemblage structure within and between localities using PRIMER’s SIMPER and CLUSTER with SIMPROF (at 95% confidence limits) analysis tools.

Biotope distribution maps of each station were constructed. Information for this was obtained from Naval chart ZA30126A, VAF002R-South Africa v201635 Garmin navigational charts and GPS depth sounding information and Google Earth imagery digitised into shapefile layers in QGIS 3.6. All reference location points (Supplementary Table 3.1) and drop camera deployment positions were plotted. Biotopes were colour coded using depth and location.

3.4 Results

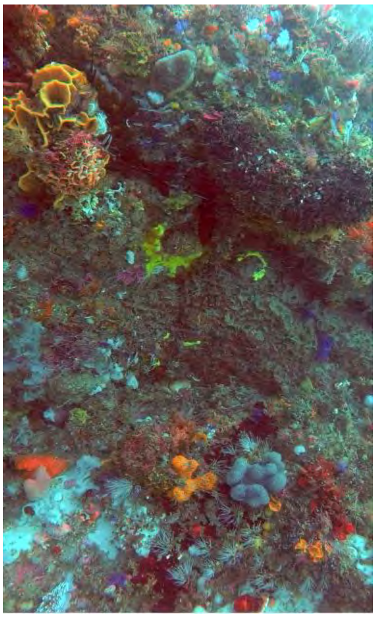
An overview of deployment positions for the collection of images with the JC were all clustered within a 50 m diameter area. In instances where the JC samples were not collected within 25 m of the reference locality (n = 4), the suitability of the area as a research locality should be reassessed and may need to be revised, to allow for sample collection in more variable weather conditions.

The overall dataset consisted of 77 760 biotic and abiotic data points. A substrate type reference image guide for the classification of the substrate was constructed (Table 3.2). Species accumulation curves with the number of species plotted on the y axis and the number of points or number of quadrats on the x-axis were constructed for a selected subset of quadrats (Figure 3.1A). The data from White Sands Reef (WSR in blue) and St Croix Complex (SCC in red) were plotted separately (Figure 3.1B). A logarithmic function was fitted to the averaged values for all quadrats for the two stations. In both cases, the exponential phase of the increase in the number of species is well contained within the adopted sampling effort. It is also evident that more species were recorded at WSR than at SCC.

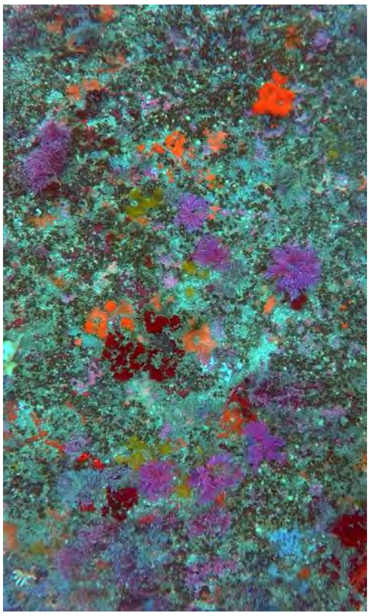
Table 3.2: Substrate type reference image guide for classification of the substrate.

Consolidated (hard)

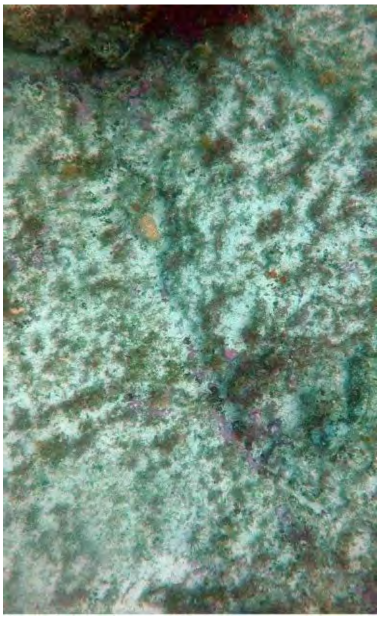
Rock with a veneer of sand and biota



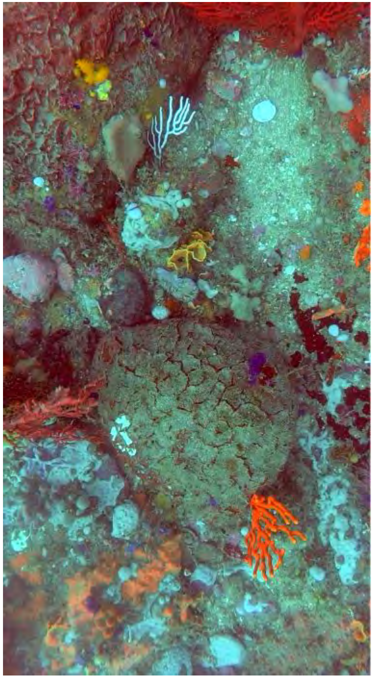
Rock (flat reef) with biota



Rock with a veneer of sand and biota



Boulders
(> 255 mm)



Cobbles
(65 – 255 mm)

Pebbles
(10 - 64 mm)

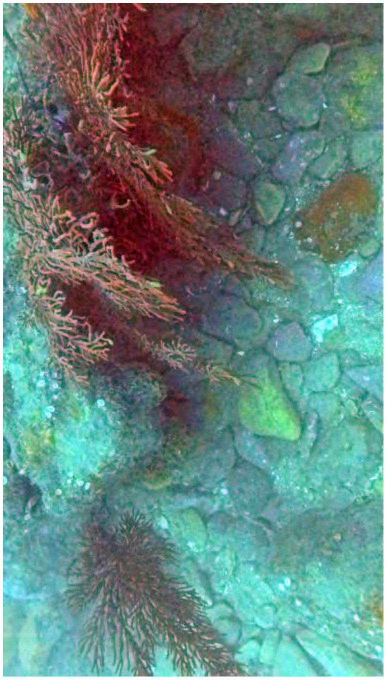
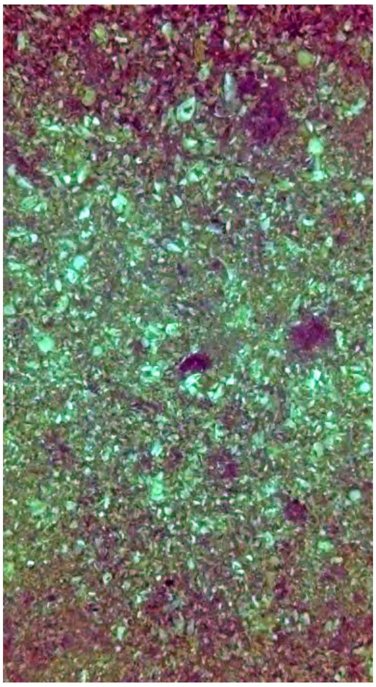


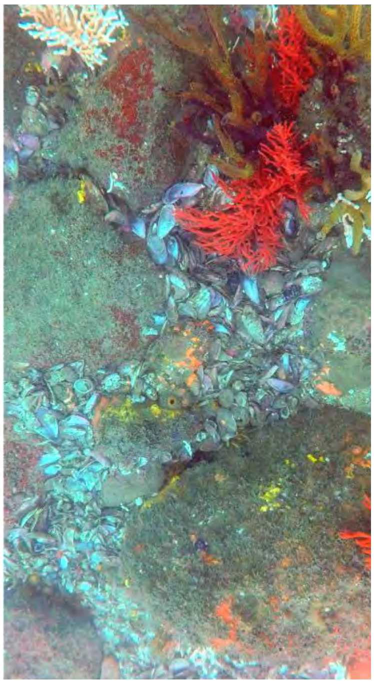
Table 3.3 continued: Substrate type reference image guide for classification of the substrate.

Unconsolidated (soft)

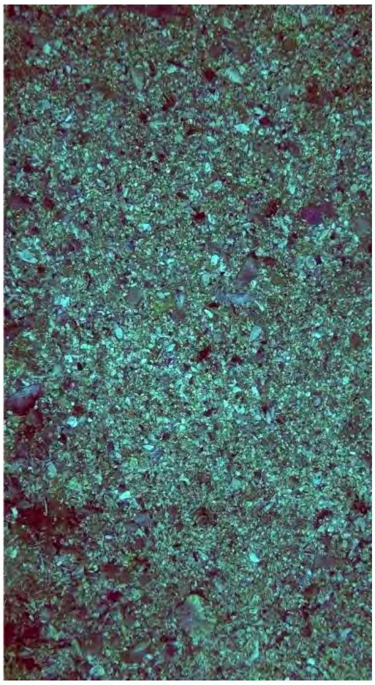
Small loose shell fragments



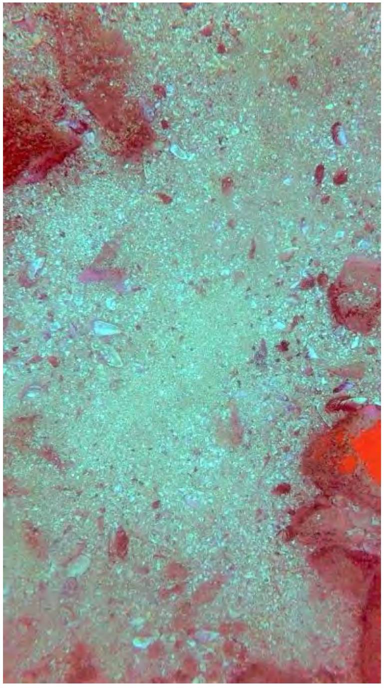
Mostly large intact shells



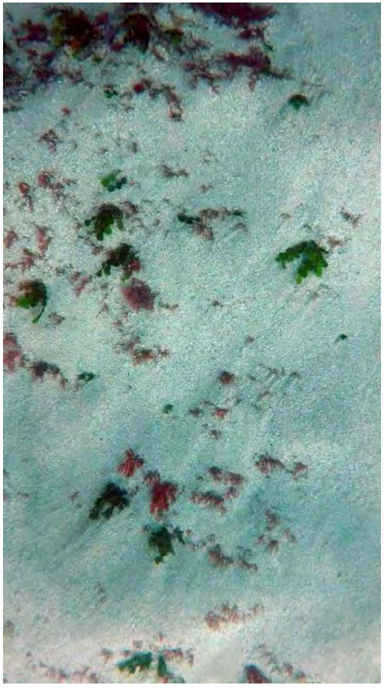
Gravel (2 - 10 mm)



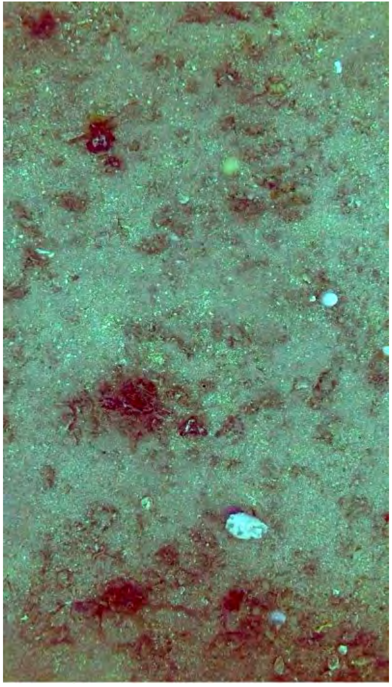
Fine sand with shell fragments
(< 2mm)



Fine sand no shell fragments
(< 2 mm)



Mud/Silt
(<64 um)



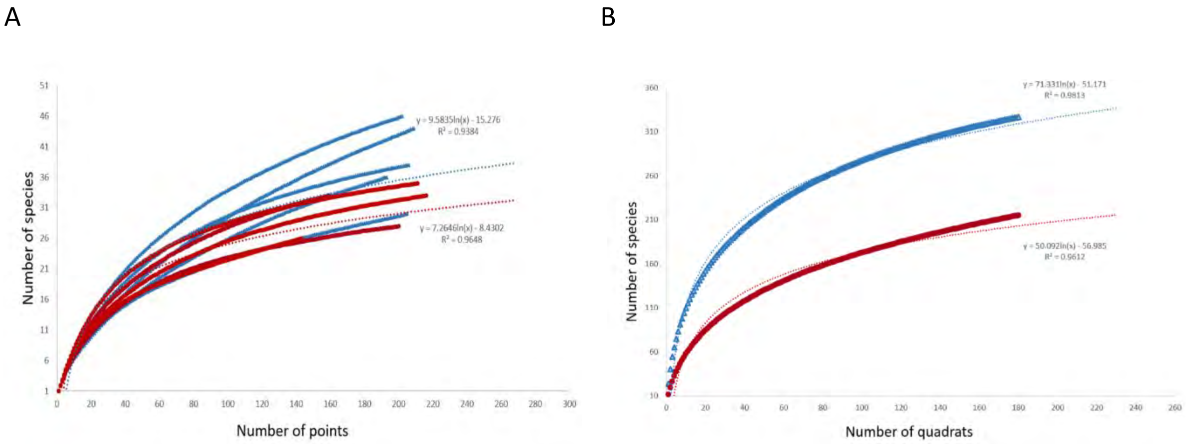


Figure 3.1: Species accumulation curves for the image quadrat samples A) Number of species increase with increasing points analysed per quadrat and B) number of species increase with additional quadrats analysed (each quadrat with 216 superimposed grid arranged points) for the two stations. Samples collected from White Sands Reef are indicated in blue triangles and St Croix Island complex in red dots. Logarithmic trend lines were fitted A) the average of the subsample of quadrat for each station and B) for all quadrats sampled for each station.

The effect of data transformation and construction of resemblance matrices and non-metric multi-dimensional scaling (MDS) plots of resemblance matrices, supported the decision to select square root transformation as an intermediate level of transformation to find a balance between the abundance of dominant taxa, but not overemphasise the importance of rarer taxa that might occur randomly (Olsgard et al. 1997). The best fit of the environmental data to biological species data was calculated by Pearson's correlation coefficient and a PRIMER BEST analysis between normalised environmental variables and square root transformed biotope data and community and resemblance matrices. This highlighted the importance of the influence of hard substrate and depth ($r = 0.81$) for the biotope database (Figure 3.2 Ai), while three variables, i.e. depth, percentage hard substrate and substrate of fine sand with shell fragments was the best fit ($r = 0.78$) for the community dataset (Figure 3.2 Aii).

The plot was repeated for the individual quadrat dataset (Figure 3.2 Bi and Bii). Bubble plots were superimposed over the location dataset (as in Figure 3.2 Ai and Aii) for the number of species recorded (Figure 3.2 Ci) and percentage biotic cover (Figure 3.2 Cii). A two-way PARMANOVA (in PAST) indicates that station and depth have a significant effect on the community structure ($p < 0.01$), but that there is no significant interaction between location and depth.

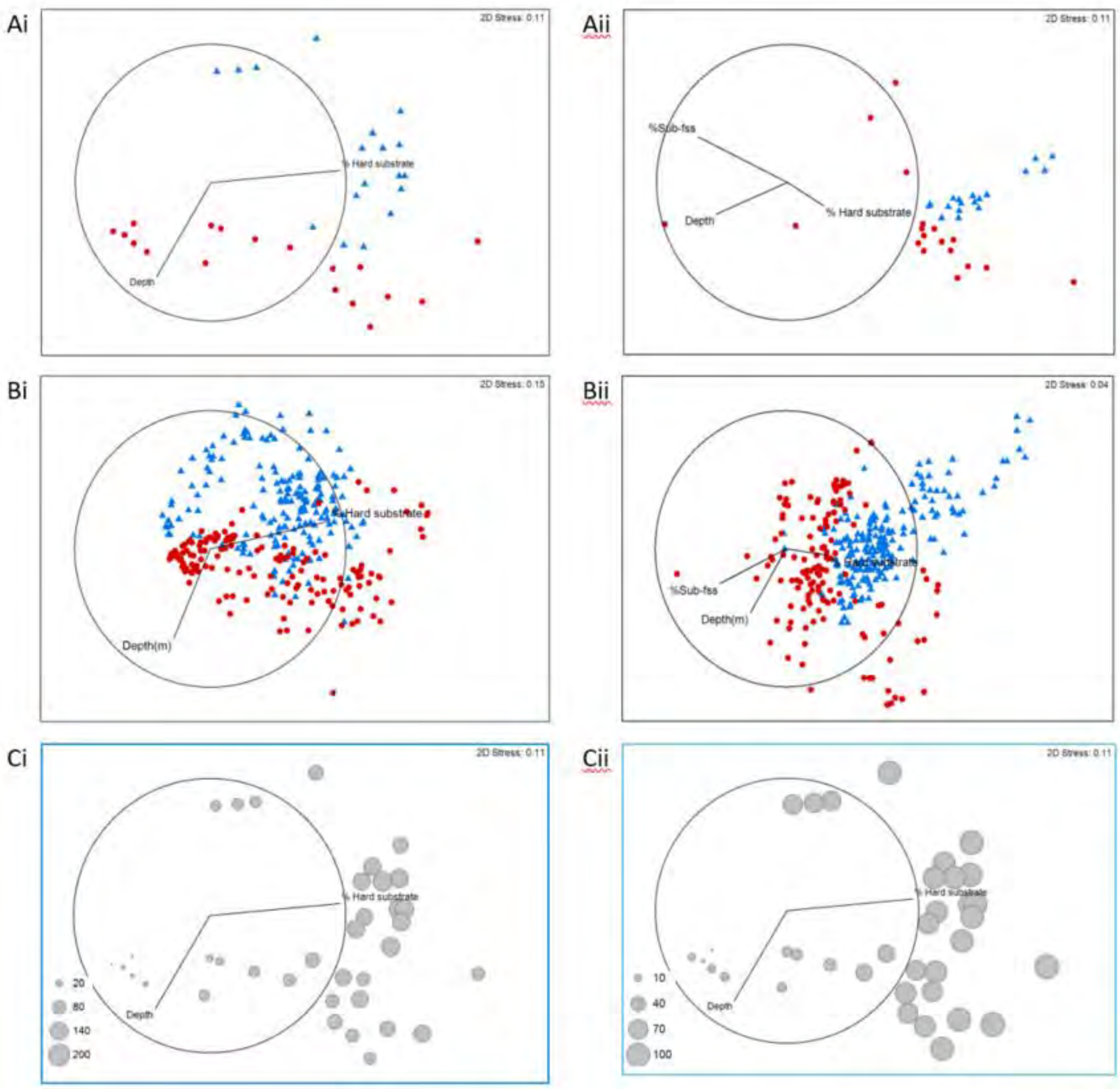


Figure 3.2: Principal Component Analysis (PCA) of highly correlated (BEST analysis) normalised environmental variable data superimposed over Non-metric Multi-Dimensional Scaling (MDS) plot of square-root transformed, Bray Curtis similarity for (all point count data including biotic and abiotic data, abiotic data is classed in two categories of substrate types in the absence of biota) n_{points} = 77 760, $n_{locations}$ = 36, $n_{quadrats}$ = 10. A) Location data for i) biotope dataset with datapoint orientation relative to hard substrate and depth (metres) and ii) standardised community dataset with a hard substrate, depth (metres) and fine sand with shell fragments (Sub-ffs). B) Quadrat data for i) biotope dataset and ii) the community dataset. C) Bubble plots are provided for the locations biotope dataset for i) the number of species recorded and ii) percentage biotic cover indicative of high species diversity and overall abundance.

A Linkage tree (LINKTREE analysis SIMPROF at 95% confidence limits) (Clarke et al. 2008) of Euclidean distance resemblance measures produces three values (Pi, ANOSIM R and B%) and was constructed to investigate the sedimentary relationship of the different sampling localities (Figure 3.3). Dissimilarity in the habitat structure, the contribution of unconsolidated sediment types and consolidated reef, between the two stations WSR and SCC is evident in the high B (%) value split which signifies an absolute measure of dissimilarity between clusters of locations characterised by one of these substrate types (Figure 3.3).

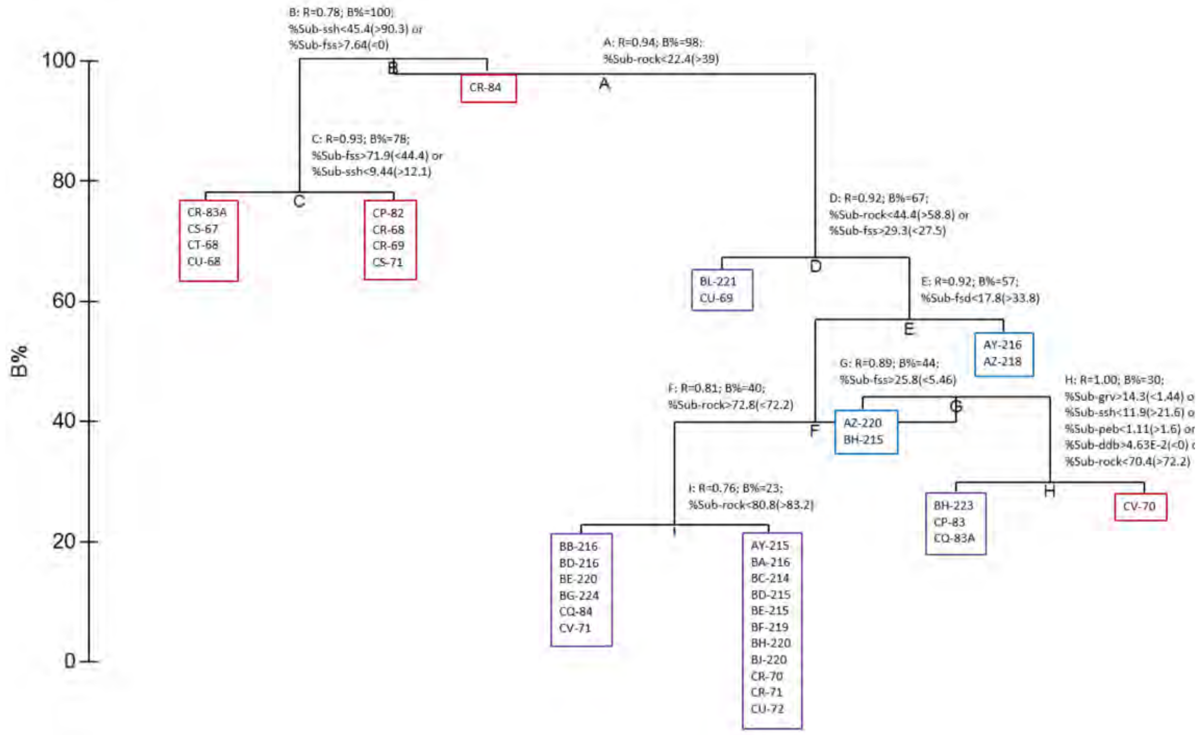


Figure 3.3: LINKTREE analysis for substrate type at sample localities. Localities are colour coded (WSR in blue blocks and SCC in red blocks – grouping shared between the two stations are given in purple blocks). Substate codes are as follows: Sub (substrate), rock (rocky reef), bol (boulders), cob (cobbles), pep (pebbles), ddb (debris), lsh (mostly large intact shells), ssh (mostly small shell fragments), grv (gravel), fss (fine sand with shell fragments) and fsd (fine sand no shell fragments).

CLUSTER analysis with SIMPROF (at 95% confidence limits) of Bray Curtis resemblance measures was generated from the square root transformed biotope dataset (this includes all points identified in the point count analysis for both biotic and abiotic variables) and the community dataset (representative of only standardised biotic species data). Groups average hierarchical CLUSTER analysis was done for both datasets (Figure 3.4A and Figure 3.4B). SIMPER and CLUSTER analysis of image point count data for image quadrats (pooled for each station n = 180) indicated an average similarity within the stations as 47.6% and 52.68% for WSR and SCC, respectively. Analysis of the pooled point count data for each locality indicates a dissimilarity of 75.8% between the two stations and an average similarity of 38.82% and 30.69% for localities within the White Sands Reef and St Croix Complex stations, respectively. This analysis delivered a similar grouping of the different localities for both the biotope and community analysis (Figure 3.1A and B). Seven broad groupings are suggested (based on a 50% similarity and 95% SIMPROF confidentiality guidance). The groups, as identified in the CLUSTER analysis of point count data, for both biotope and community datasets, were used to produce an amended dataset and the similarity and dissimilarity for the identified groups determined with SIMPER in PRIMER (Table 3.4). Similarity within the defined groups was generally lower when the abiotic variables were removed from the dataset. However, the dissimilarity between the defined groups was generally high, except for groups VI and VII, where unconsolidated sediments dominate the benthic habitat.

A species list was compiled for each of the sampled locations (Supplementary Table 3.2). A synopsis of species contributing more than 5% to the similarity within the assemblage is supplied in Table 3.5. A substrate type abundance dataset was constructed in the same manner as the biotic abundance data for the defined groups. TAMIRA species codes and average depth (SD)[min – max] given in brackets, for all biotopes as defined in CLUSTER (Figure 3.4) and SIMPER analysis (PRIMER) are

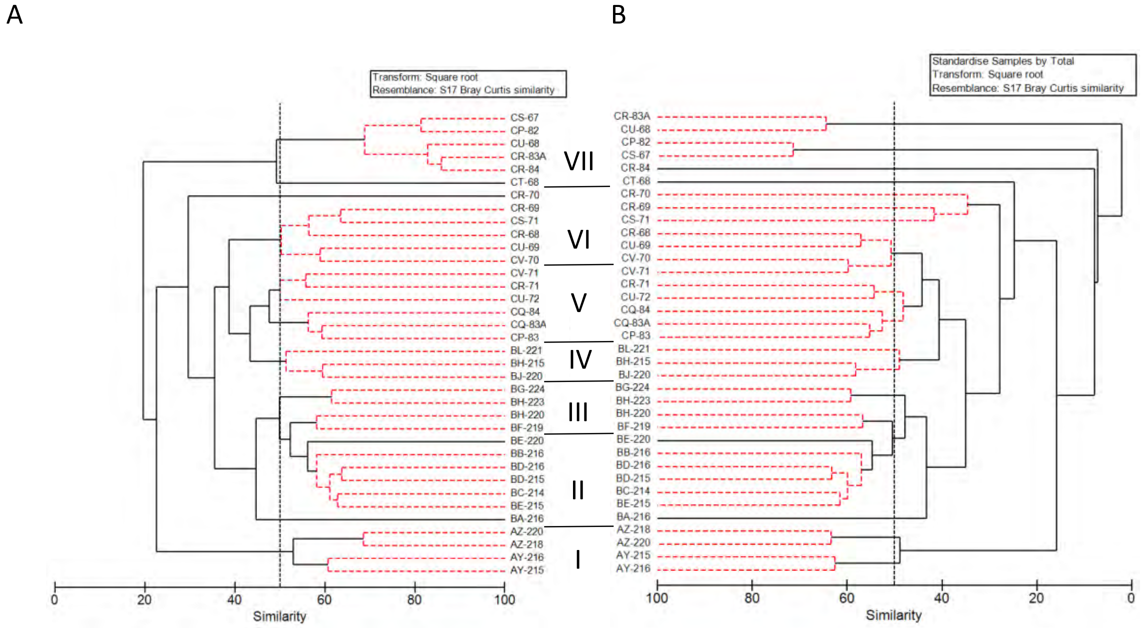


Figure 3.4: Exploratory cluster analysis of combined quadrat data for each location. A) Community analysis for all biota recorded at each location (points without biota were removed from the dataset). Data was standardised and square root transformed B) Biotope analysis, for all data point analysis at sample locations, including all biota and substrate identification. Substrates not covered by biota were classified as either consolidated (Cobble and boulder) or unconsolidated (mud, sand, gravel and pebbles). Group average hierarchical CLUSTER analysis with SIMPROF (at 95% confidence limits) of Bray Curtis resemblance measures generated from square root transformed species and substrate abundance data obtained from pooled (n = 10) samples collected at each of the locations (n = 36) White Sand Reef Station (AY-BL)) and St Croix Complex (CP-CR/CS)).

provided (Table 3.4 and Supplementary Table 3.2). The habitat component is based on a resemblance matrix that was constructed from standardised untransformed substrate point count data, and the biotic component on a Bray Curtis similarity resemblance matrix constructed from a standardised square root transformed community dataset. Average similarity (with standard deviation (SD) given in brackets), the contribution to groups similarity (standardised square root transformed dataset) and calculated average percentage relative abundance of the species in the community assemblage (calculated from the untransformed dataset) (with standard deviation (SD) given in brackets) was calculated (Table 3.4).

Table 3.4: Summary of % average similarity (SIMPER) of groups defined in Figure 3.4 for biotopes (abiotic and biotic variables) and standardised (not transformed) communities (biotic component only) with a Bray Curtis resemblance matrix of average dissimilarities between groups. The upper triangle of values gives are for the biotope and the lower triangle that for communities.

Group		I	II	III	IV	V	VI	VII
Biotope average similarity %		53.1	52.8	50.9	54.9	45.1	48.1	88.2
Community average similarity %		45.7	51.7	46.8	53.8	44.1	42.6	14.1
Dissimilarity between groups								
Biotopes (upper triangle)	I		74.1	76.0	72.7	84.0	72.3	71.2
Communities (lower triangle)	II	79.6		54.2	65.2	71.4	73.4	88.0
	III	88.4	57.8		51.4	59.8	67.2	81.8
	IV	93.8	67.8	54.8		58.41	58.40	63.93
	V	96.8	75.2	63.9	62.3		68.61	82.72
	VI	91.5	72.1	68.1	69.9	69.8		47.38
	VII	98.0	94.1	93.2	88.3	94.4	94.7	

This study separated the studied area into seven biotopes and associated communities, four for the White Sands Reef station (Figure 3.6) and three in the shallow coastal water of St Croix Island and Brenton Island (Figure 3.7).

Biotope I is situated in the inshore areas within the WSR station with a depth range of 4.6 to 7.6 m, is a shallow habitat characterised by low, flat, sand veneered reef (69.6%) with fine sand (21.1%). This habitat predominantly supports Hypnea tenuis (29.8%) contributing 12.1% to the similarity of the sampled quadrats within this area.

Biotope II, located in the western section of the mid-shore at a depth range of 5.8 to 13.6 m, consists of numerous stabilised pebbles and cobbles on or between the largely rocky substrate (83.6%), with only small patches of sand. The biotic community is dominated by articulated coralline algae *Amphiroa ephedraea* (17.5%) and hydroid tufts (10.7%) and encrusting coralline algae *Leptophytum acervatum* (8.6%) covering the pebbles and small cobbles.

Biotope III is located in the eastern section of the mid-shore between a depth of 12.3 to 17.2 m with a habitat characterised by large stable cobbles and boulders (78.1%) interspersed with gravel (10.1%), supporting biota consisting of the sponge *Placospongia* sp. 001 encrusting large boulders, various sea fans, predominately *Leptogorgia palma*, with the main algal component consisting of articulated coralline algae *Amphiroa ephedraea* and the thin encrusting coralline *Leptophytum acervatum*.

Biotope IV is the most off-shore of the biotopes, identified within the WSR station at a depth range of 17.5 to 20.5 m. The area is mostly reef substrate (64.8%), but fine sediment with shell fragments is a prominent component (26.1%) of the habitat. The hard substrate consists of low to medium profile reef characterised by small overgrown outcrops typically encrusted with *Placospongia* sp. 001 sponge (18.8%), *Leptogorgorgia palma* sea fans (10.2%) and the crinoid *Tropiometra carinata* (10.0%) in crevices. The increased elevation provided by the rocky outcrops changes the distribution of loose sediment, resulting in an accumulation of sand in the shallow gullies or depressions, with decreased sand inundation over the rocky surface itself.

Biotope V occurs at both St Croix Island (south and south-east shore) and Brenton Island (west, south and east shore) over a depth range of 12.9 to 26.4 m. It consists predominantly of reef substrate (80.7%) with tall sea fans, *Leptogorgia palma* (12.6%) and *Homophyton verrucosum* (7.6%) are the species with the highest relative abundance.

Biotope VI was only present along the west and northeast shore of St Croix Island at the depth range 4.1 to 18.1 m, characterised by mixed substrate consisting of rocky reef (43.8%), unconsolidated sediment composed of small loose shell fragments (18.8%) and fine sand with shell fragments (16.3%.). The biotic component was predominately classified as mixed tufts of small hydroids (27.1%) and the sea fan *Leptogorgia palma* (14.1%).

The last group consisted of several identifiable subunits. The substrate, although different in the groups, is classified as unconsolidated. Biotope VIIa, recorded at a depth of 17.5 to 23.3 m on the north side of the islands, consists primarily of fine sand with shell fragments (68.3%), with little rock (12.3%). Biota, although highly variable (SD = 43.9%), consists of *Triopiometra carinea* (63.1%) associated with the rocky patches. Biotope VIIb is represented by a single sample locality found in deeper water (28.2-28.9 m) off the southeastern shore of Brenton Island and is characterised by a substrate of mostly small loose shell fragments. *Leptophytum acervatum* was the only recorded biota.

Table 3.5: List of species and substrate types contributing an average of more than 5% to the similarity of community assemblages listed. Group identifications, reference locality identification codes and average depth (SD) [min – max] in metres is listed. Abiotic (substrate) percentage data SIMPER results (Bray Curtis similarity resemblance matrix constructed from standardised untransformed data) are given in the description of the habitat. Average similarity (with standard deviation (SD) given in brackets) and contribution to groups similarity as calculated by SIMPER analysis (Bray Curtis similarity resemblance matrix constructed from standardised square root transformed data). Average percentage relative abundance of the species in the community assemblage (untransformed data) with standard deviation (SD) is given in brackets.

	Average similarity (similarity SD) %	**Contribution to similarity %**	**Average relative Abundance %**
Biotope I			
Average depth 6.1 (1.0) [4.6-7.6] m	**AY-216, AY-215, AZ-220, AZ-218 (n = 4)**		
Habitat assemblage Group I: Average similarity = 74.8			
Rocky reef	47.1 (29.2)	82.6	69.6 (14.1)
Fine sand without shell fragments	12.2 (1.2)	16.3	21.1 (15.2)
Community assemblage I: Average similarity = 53.6			
Hypnea tenuis (M0151)	6.5 (0.9)	12.1	29.8 (25.5)
Mixed tufts of soft macroalgae (Bio-mal)	5.7 (1.8)	10.6	17.6 (14.8)
Leptophytum acervatum (M0272)	4.8 (4.6)	8.9	6.9 (3.9)
Plocamium corallorhiza (M0194)	4.1 (5.02)	7.6	4.0 (1.4)
Amphiroa ephedraea (M0010)	3.5 (1.25)	6.4	11.0 (11.7)
Portieria hornemannii (M0203)	3.2 (4.6)	6.0	2.7(1.2)
Polyclinum isipingense (U0027)	3.0 (10.6)	5.7	2.7 (1.9)
Halimeda cuneate (M0264)	3.0 (3.1)	5.5	2.9 (1.7)
Biotope II			
Average depth 11.3 (1.6) [5.8-13.6] m	**BA-216, BE-215, BC-214, BD-215, BD-216, BB-216, BE-220 (n = 7)**		
Habitat assemblage II: Average similarity = 86.3			
Rocky reef	78.2 (11.1)	90.6	83.6 (9.0)
Community assemblage II: Average similarity = 54.8			
Amphiroa ephedraea (M0010)	4.9 (3.1)	8.9	17.5 (9.5)
Mixed tufts of small hydroids (Bio-cns)	4.0 (7.6)	7.37	10.7 (4.3)
Leptophytum acervatum (M0272)	3.47 (6.1)	6.3	8.6 (4.8)
Biotope III			
Average depth 14.7 (1.5) [12.3-17.2] m	**BF-219, BH-220, BH-223, BG-224, (n = 4)**		
Habitat assemblage III: Average similarity = 80.56			
Rocky reef	69.4 (5.8)	86.2	78.1 (14.0)
Gravel	5.6 (2.8)	6.93	10.1 (7.6)
Community assemblage III: Average similarity = 52.5			
Mixed tufts of small hydroids (Bio-cns)	4.0 (4.0)	7.6	11.2 (5.9)
Placospongia sp. 001 RSA (P0032)	3.6 (2.5)	6.9	13.1 (9.5)
Leptogorgia palma (C0023)	3.5 (7.3)	6.7	10.6 (8.4)
Amphiroa ephedraea (M0010)	2.8 (3.2)	5.3	6.4 (4.0)
Leptophytum acervatum (M0272)	2.7 (3.7)	5.1	8.2 (8.0)
Biotope IV			
Average depth 18.9 (0.8) [17.5-20.5] m	**BJ-220, BH-215, BL-221 (n = 3)**		
Habitat assemblage IV: Average similarity = 69.1			
Rocky reef	51.9 (4.0)	75.1	64.8 (19.4)
Fine sand with shell fragments	13.6 (1.1)	19.7	26.1 (18.8)
Community assemblage IV: Average similarity = 52.1			
Placospongia sp. 001 RSA (P0032)	7.2 (20.9)	13.7	18.8 (1.9)
Leptogorgia palma (C0023)	4.6 (5.9)	8.8	10.2 (4.5)
Mixed tufts of small hydroids (Bio-cns)	4.0 (4.2)	7.8	8.0 (3.5)
Tropiometra carinata (E0007)	3.6 (1.4)	6.9	10.0 (7.3)
Leptophytum acervatum (M0272)	2.9 (25.7)	5.6	6.1 (5.5)

Table 3.6: continued

Biotope V			
Average depth 18.0 (3.4) [12.9-26.4] m	**CP-83^{BI}, CQ-83Ai^{BI}, CQ-84i^{BI}, CU-72^{SC}, CR-71^{SC}, CV-71^{SC} (n = 6)**		
Habitat assemblage V: Average similarity = 77.2			
Rocky reef	72.6 (8.9)	94.1	80.7 (13.2)
Community assemblage V: Average similarity = 49.51			
Leptogorgia palma (C0023)	4.3 (3.2)	8.6	12.6 (10.5)
Homophyton verrucosum (C0016)	4.1 (5.0)	8.2	7.6 (2.8)
Mixed tufts of small hydroids (Bio-cns)	3.7 (1.8)	7.5	9.4 (6.0)
Chondrilla sp. 004 (P0240)	3.2 (2.7)	6.6	6.4 (3.4)
Placospongia sp. 001 RSA (P0032)	3.1 (2.8)	6.2	7.3 (5.4)
Sertularella arbuscula (C0032)	3.0 (5.6)	6.0	5.2 (3.3)
Biotope VI			
Average depth 13.0 (3.4) [4.1-18.1] m	**CV-70^{SC}, CU-69^{SC}, CR-68^{SC}, CS-71^{SC}, CR-69^{SC}, CR-70^{SC} (n = 6)**		
Habitat assemblage VI: Average similarity = 46.48			
Rocky reef	23.9 (1.5)	51.48	43.8 (33.7)
Mostly small loose shell fragments	9.3 (1.1)	20.0	18.8 (15.8)
Fine sand with shell fragments	7.7 (0.69)	16.5	16.3 (14.7)
Community assemblage VI: Average similarity = 41.8			
Mixed tufts of small hydroids (Bio-cns)	10.8 (2.9)	25.8	27.1 (11.6)
Leptophytum acervatum (M0272)	6.6 (2.8)	15.7	14.1 (10.8)
Placospongia sp. 001 RSA (P0032)	3.5 (1.5)	8.3	7.3 (7.5)
Aplidiopsis sp. 004 RSA (U0167)	2.4 (0.8)	5.7	5.6 (4.7)
Tedania stylonychaeta (P0055)	2.4 (2.2)	5.7	4.4 (6.5)
Biotope VII			
Community assemblage VII: Average similarity = 14.0			
Habitat assemblage VII: Average similarity = 50.6			
Biotope VIIa			
Average depth 19.5 (2.2) [17.5-23.3] m	**CP-82^{BI}, CS-67^{SC}, CT-68^{SC} (n = 3)**		
Habitat assemblage component VIIa: Average similarity = 69.3			
Fine sand with shell fragments	53.6 (3.4)	77.3	68.3 (22.4)
Rocky reef	11.6 (19.7)	16.7	12.3 (1.0)
Community assemblage component VIIa: Average similarity = 38.8			
Tropiometra carinata (E0007)	26.8 (1.0)	69.1	63.1 (43.9)
Pseudopotamilla sp. 001 RSA (W0003)	8.2 (1.9)	21.0	6.7 (5.1)
Biotope VIIb			
Average depth 28.4 (0.2) [28.2-28.7] m	**CR-84^{BI} (n = 1)**		
Habitat assemblage component VIIb			
Mostly small loose shell fragments			90.3 (12.3)
Community assemblage component VIIIb			
Leptophytum acervatum (M0272)			60.0 (51.6)
Biotope VIIc			
Average depth 24.1 (3.2) [20.1-27.5] m	**CR-83Ai^{BI}, CU-68^{SC} (n = 2)**		
Habitat assemblage component VIIc: Average similarity = 77.1			
Fine sand with shell fragments	73.9	95.8	83.2 (13.1)
Community assemblage component VIIc: Average similarity = 64.4			
Tethya sp. 004 RSA SPN (P0220)	64.4	100	90.0 (14.1)
Eunephthya celata (C0009)	0	0	3.3 (4.7)
Sertularella arbuscula (C0032)	0	0	1.7 (2.4)
Wrightella sp. 001 RSA (C0036)	0	0	1.7 (2.4)

Biotope VIIc, recorded from a depth between 20.1 to 27.5 m, was found only off the north-eastern shore off St Croix Island. The bottom is characterised by a predominantly sandy substrate (83.2%) with what was preliminarily and tentatively identified as a burrowing or endopsammic sponge species cf. *Tethya* sp. 004 (Table 3.5).

3.5 Biotope maps

The preliminary biotope distribution maps constructed is based on the possible occurrence of the biotope along bathymetric lines (Figure 3.6 and Figure 3.7).

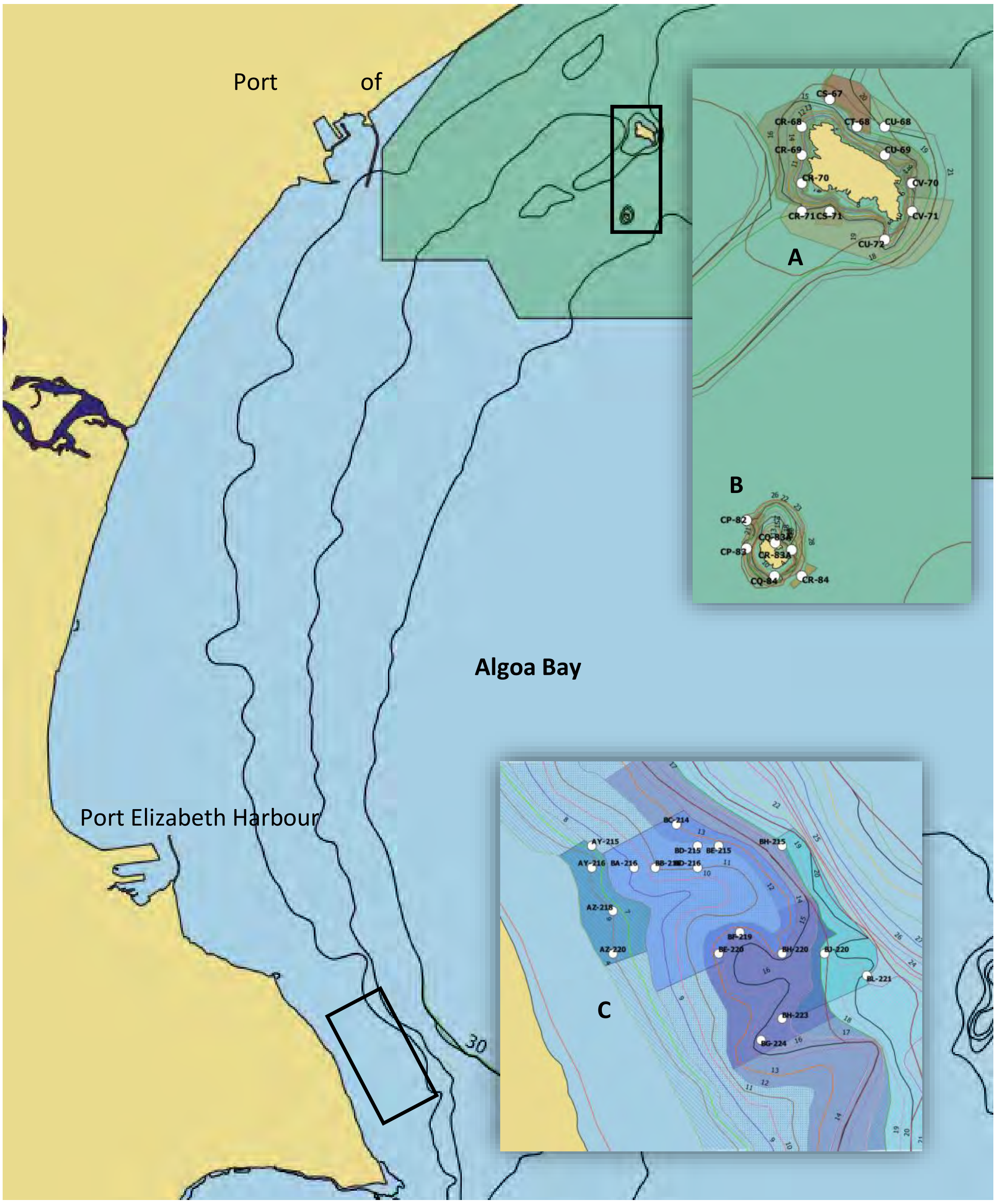


Figure 3.5: Algoa Bay and position of A) St Croix Island, B) Brenton Island and C) White Sands Reef. See Figure 3.6 and Figure 3.7 for an enlarged map with a colour-coded key.

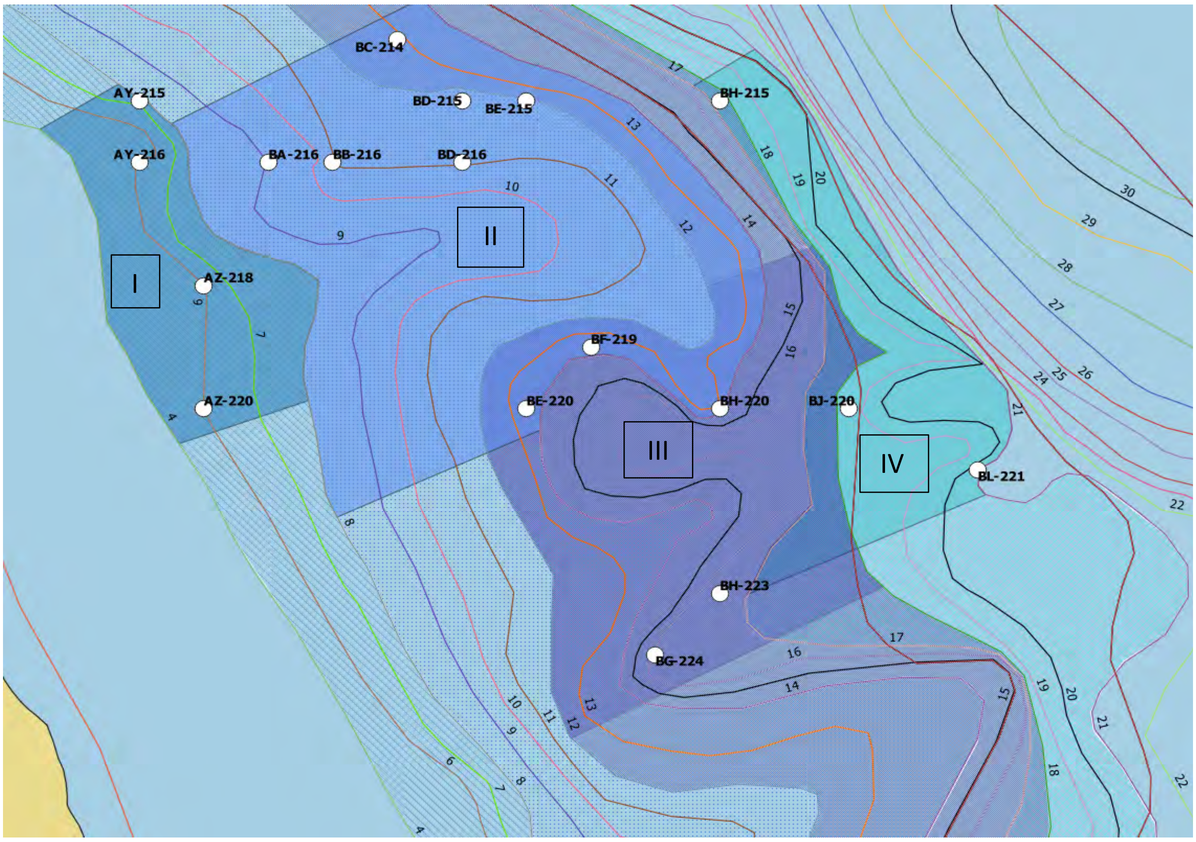


Figure 3.6: Biotopes distribution for White Sands Reef (WSR). Biotope numbers correspond to Table 3.5. Key for biotope cover: I, II, III and IV.

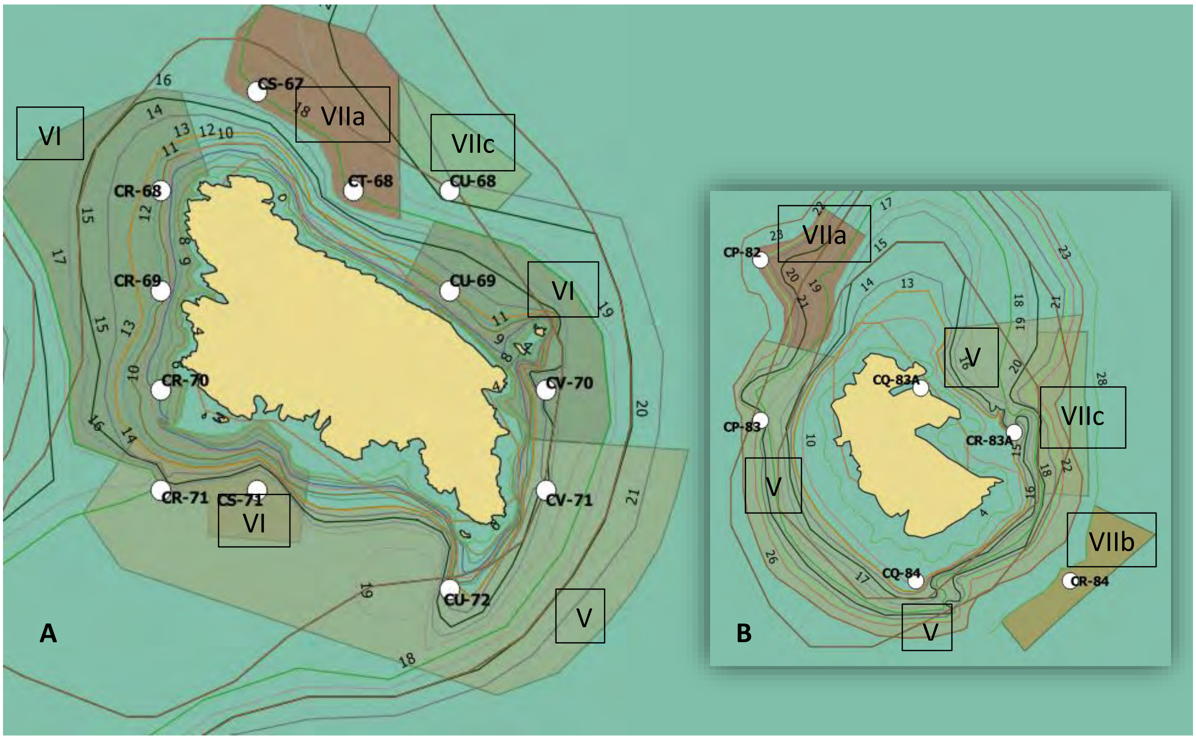


Figure 3.7: Biotopes distribution for A) St Croix Island and B) Brenton Island (SCC) not to scale. Biotope numbers correspond to Table 3.5. Key for biotope cover: V, VI, VIIa, VIIb and VIIc.

3.6 Discussion

Data collecting and analytic methodologies used should allow for upscaling without compromising data quality. It should not overload resources and should work within the limits of supporting infrastructure capacity. It should allow for routine data collection that over time and space can be used to observe changes in species distribution, abundance, diversity and community structure of components within the seascape. This could then be related to the observed change in environmental conditions of climate-related change.

The sampling approach implemented here made use of the collection of environmental and biological variables that are used to describe the habitat and community structure of a focus area, in this chapter the sample location within a station. These abiotic and biotic variables observed were then used to define and map these biotopes (Figure 3.8). This study shows that closely located sample locations may share a biotope by the shared habitat type and the communities it supports or may differ considerably primarily governed by the habitat type, unconsolidated versus consolidated.

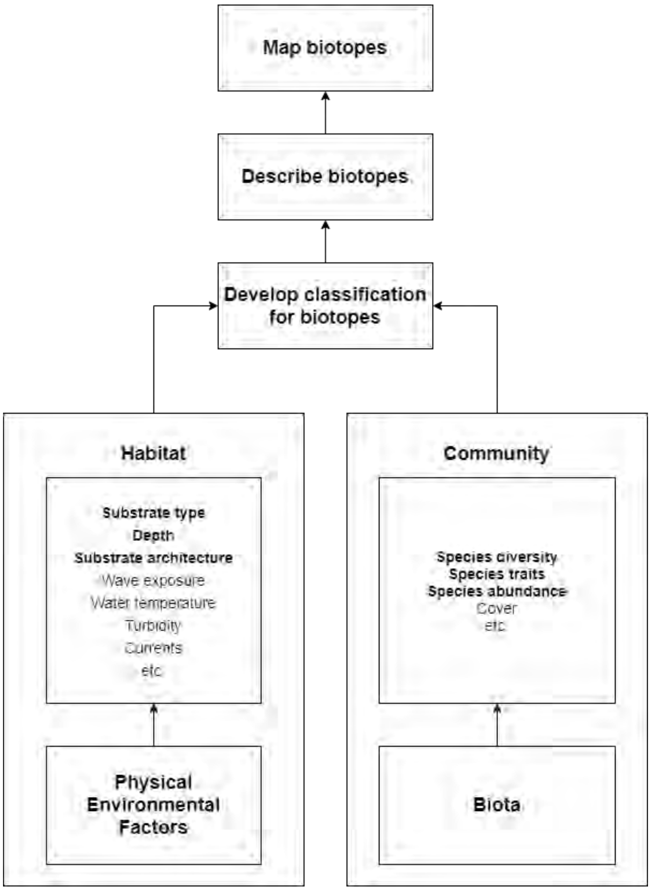


Figure 3.8: Scheme illustrating the procedure and steps followed to map the different biotopes.

The sampling system developed to collect data for this chapter, unlike that in many previous studies, eliminates the need for SCUBA divers. This means less labour is required, the activity is safer, less legislatively burdened and consequently reduces the cost of data collection significantly. The Jump Camera (JC) system is compact, easily assembled, economical yet robust, is relatively cheap, readily replaceable and easy to use. This new method allows for SCUBA diver-independent data collection and, if the JC were to be equipped with a light source, could be deployed beyond the photic zone or in low visibility environments. The system has proved to have low handling requirements while it allows fast and reliable data collection. The permanent point-random sampling method worked well and samples could be reliably deployed within a 25 m radius of the GPS reference locations. It is noteworthy that all deployments, a total of 360 drops, delivered footage that could be analysed and is included in this work. The exercise also showed that it is possible to collect all JC data per station in a typical morning weather window (180 drops in 4.5 hours).

Data collection and the analytical software was easy to use. The trait-based searchable reference library allows for image-to-image species identification that would assist and reduce ramp-up time for new platform users. The constructed species accumulation curves indicate that the sampling effort delivered a comprehensive account of species present within the sampled area. The data collected permitted the definition and comparison of biotopes, the habitats and community structures for two stations in Algoa Bay (Figure 3.5). The lack of detailed substrate data across a wider spatial area meant that the constructed biotope distribution maps are mostly speculative and incomplete. Taking into account physical environmental factors and the biota, allowed for the description of habitat and community structure. Only a subset of environmental variables were included in this study (substrate type, depth, substrate architecture, species diversity and abundance) and the inclusion of additional variables (such as turbidity, currents, nutrients, plankton biomass and distribution), which may influence the community structure of the biotopes benthic sessile biota, should be considered (Figure 3.8).

The study sites include both unconsolidated and consolidated substrates, this contrasts to previous studies where the focus was either on consolidated (Götz 2005, Joshua et al. 2018, Pillay et al. 2021b) or unconsolidated (Truter 2019) substrates. Algoa Bay consists of large areas of unconsolidated substrates (Bremner 1991a) and the effect of soft sediment and its movement on the nearby consolidated substrate and its biota should be taken into account (Porter et al. 2017a). This study highlights that unconsolidated substrates associated with reefs are important and suggest it plays a role in community structure of reef communities.

The biotope composition was station-specific and biotopes were not shared between to two stations. The difference found between the two stations within Algoa may be due to several factors. These may include geographic location and the difference in upwelling event intensity and duration. This is evident from the different temperature profiles for the two stations (see Figure 2.6 and Figure 2.8). This may be a result of the location of the stations in the bay itself, the proximity of the cape, islands and the difference in wind regimes (see Chapter 2). Other factors that may play a role is reef profile, unconsolidated and consolidate habitat patch size, proximity, sediment mobility and bottom currents.

White Sands Reef (WSR) is situated just inside the bay of a protruding cape (Figure 3.5), exposed to southerly swell entering the bay from the open ocean as well as south-easterly winds driving local currents. Situated between the shipping approach lanes to the Port Elizabeth harbour and the flat reef shoreline, it is frequently used for recreational fishing, both shore and boat-based, diving and spearfishing. The area is afforded no special protection but its macroalgal beds may provide important coastal nursery areas for several economically valuable fish species (Beckley and Buxton 1989, Evans et al. 2014). Overall, WSR supports a higher diversity of species than its SCC counterpart does. This was somewhat surprising, as the initial perception was that the SCC includes more distinct habitat (sand, shell, reef, both low and high profile habitats), with increased nutrient input due to guano runoff from the roosting birds on the islands (Bosman et al. 1986, Wootton 1991, Gagnon et al. 2013) compared to the generally sand-inundated, low profile patch reef of WSR. It may however support the hypothesis that disturbances, such as sediment flux driven by turbulence and currents, could be possible drivers of diversity (Porter et al. 2017a). The St Croix and Brenton Island group, although regularly fished in the past, is now a restricted (no fishing zone) zone within the newly established MPA (Department of Environmental Affairs 2019c). The dataset used here was collected before the management of the area changed and it will be interesting to observe any changes in habitat and community structures due to the new protection it is afforded over time. The islands are situated close to the deepwater Port of Ngqura, which brings ever-increasing shipping traffic, anchoring and ballast water exchange which may indirectly impact the island environment and its biota.

This study indicates that depth and substrate type are important drivers determining benthic community structure of and within biotopes (Figure 3.2). The habitat descriptions (Table 3.5; Figure 3.3, Figure 3.6 and Figure 3.7) and species lists (Table 3.5 and Supplementary Table 3.2) indicate that the biotopes described here are diverse (traits and diversity indices for the biotopes defined here are discussed and compared in Chapter 6), and although they share habitat variables (Figure 3.3), they differ considerably from each other, as is evident from the high dissimilarities calculated (Table 3.4). However, low similarity within the biotope and community groups is an indicator of heterogeneity and the possible contribution of fine-scale biotope mosaics or patches each presenting a characteristic habitat (abiotic) and community (biotic) composition. Habitat heterogeneity supports an increase in available niches and promotes beta diversity and may be driven by several ecological processes such as productivity, disturbance and connectivity (McClain and Barry 2010), not only over the mesoscale but also over finer spatial scales (Pickett and Cadenasso 1995).

Productivity in the bay is fuelled by local upwelling events (Brown 1992) that may be driven by south-westward currents during Natal Pulses and large meanders in the Agulhas Current (Goschen et al. 2015). Wind energy moves water, generating currents that facilitate the mixing of the stratified water column, distributing nutrients and fuelling productivity (Margalef 1997). Wind-generated water movement readily reaches the benthic biota occurring within or close to the photic zone, which is constantly replenished with a fresh supply of plankton, particulate matter and a wide range of microorganisms (Arntz et al. 1999). The presence of plankton is an important biological variable, especially for communities consisting of filter and suspension feeders. These organisms can effectively use the moving water column and even alter local turbulence, thereby increasing their ability to collect food as well as disperse and retain reproductive material (Margalef 1997). Wave action and depth of water movement are important variables governing community composition on a small and large scale (Porter et al. 2017a). The mobility of soft substrates and the ability of this material to infiltrate reef environments (by periodic initiation, veneering or smothering), water movement and productivity may all be part of a suite of biological and physical forces driving biodiversity under natural disturbance regimes (Harris 2014, Porter et al. 2017b).

Heterogeneity, often intentionally overlooked in ecological studies, is recognised as the primary driver in ecological processes (Pickett and Cadenasso 1995, Yeager et al. 2011). Increased habitat heterogeneity drives biodiversity and community heterogeneity (Thrush et al. 2010). Benthic community complexity is, however, also a function of the trophic complexity, in this case, the availability of suitable prey in the overlying water column. The low cost of and the success in capturing prey, especially in dense aggregations, is believed to play a significant role in the energy flow from the pelagic to the benthic environment (Gili and Coma 1998). The water column functions as a conduit in the dispersal of genetic material and reproductive products. The sessile benthic invertebrates and algae support important supra-benthic predatory fish species by providing food (Coetzee and Baird 1981, Buxton 1984, Buxton and Smale 1984, Buxton and Clarke 1986, Coetzee 1986, Smale 1986, Mann and Buxton 1992), refuge or functioning as larval and post-settlement juvenile nurseries for infra- and supra-benthic ichthyofauna species (Beckley 1985, Tilney et al. 1996).

There is no doubt that unconsolidated sediment harbours epifauna. However, in highly dynamic systems, especially in shallow water systems where the effect of wind-driven currents and turbulence is great and the stability provided by consolidated attachment areas is absent, recorded epifaunal diversity is expected to be lower than that of consolidated substrates (Post et al. 2017). In these habitats research on the infauna community may be more valuable in characterising community structures. The focus on epifauna alone could account for the poor performance of the community database to define soft-sediment dominated biotopes. Statistical comparison of both datasets (excluding group IV) shows no significant difference ($p = 0.05$) for estimated similarity within the groups (groups I to VI dominated by hard substrate) as defined in the CLUSTER analysis (Figure 3.4). These findings support and motivate the inclusion of macrobiotic epi- and infauna datasets in the analysis and description of complex consolidated and unconsolidated mosaic habitats within the seascape.

3.7 Conclusion

The implementation phase of the Benthic Ecosystem Long-Term Ecological Research (BELTER) platform successfully tested and implemented newly designed and constructed sample equipment. The use of this equipment was easily done within the existing infrastructure of the South African Environmental Observation Network's (SAEON) Elwandle Coastal Node. Although a few problems were experienced in the deployment of the equipment, it was easy to use and robust. It has allowed for insight into challenges such as sample location accessibility, workable sea conditions and manpower requirements. This will play a role in the selection of new sample stations along the South African coast.

This pilot study attempts to define and describe the benthic biotopes for the two research stations in Algoa Bay. The stations although geographically separated are contained within a single deep embayment. The wind is an important driving force in Algoa Bay and past research has shown that conditions may vary over the extent of the bay (Schumann et al. 1988, 1991, Roberts 2010, Goschen and Schumann 2011). This is reflected in the water temperature profiles especially during wind-driven upwelling events for the two stations (as per Chapter 2 Figure 2.6 and Figure 2.8). Both research stations experienced upwelling events although duration and frequency differ.

The dataset examined in this chapter took ca. 8 hours to collect (two mornings at sea) and produced 360 video streams, 720 frames for the analysis of 154.8 m^2 of the benthic environment and generated over 77 000 data points, identifying 326 and 214 species for the WSR and SCC stations, respectively. With images collected and those obtained from an existing image database on benthic species (TAMIRA) an image-based substrate type reference guide, a trait-based searchable image reference database was constructed. The data was successfully used to describe the habitat and species composition for each of the 36 research locations. This allowed the identification and description of seven broad biotopes. Although habitat types were shared between the research stations, biotopes were not. Although a basic map of the possible biotope distribution was compiled, the project identified the need for a comprehensive multi-beam sonar data layer that would allow for the modelling of the biotopes distribution for the study areas as successfully done for other mapping projects (Pillay et al. 2020, 2021b). The research suggested a high heterogeneity of the samples collected from the sample points at each location and warrants further investigation. The development of a biotope identification database, as implemented for the habitat types within the study area, demand a closer, finer-scale assessment of the habitat and community components that make up a broader biotope.

A multi-temporal and spatial scale approach and a fundamental understanding of the abiotic and biotic components within a system are essential. The interaction between these components constitutes the first steps in interpreting natural interactions and dynamics in an attempt to identify anthropogenically induced responses of an ecosystem and its components over the long term. Heterogeneous systems supporting high biodiversity necessitate assessment at various scales. This dataset forms the baseline for future research, facilitating the assessment of biological diversity and temporal and spatial change. The programme plans to repeat this collection every two to three years or after catastrophic events such as major oil spills or large plankton blooms e.g. Harmful Algal Blooms (HABs).

3.8 Supplementary Material

Supplementary Table 3.1: Reference location geographical positions.

Locality	Station	Latitude	Longitude	Locality	Station	Latitude (S)	Longitude (E)
AY-215	WSR	-33.9968	25.69385	CP-82	SCCBI	-33.8162	25.76351
AY-216	WSR	-33.9981	25.69385	CP-83	SCCBI	-33.8175	25.76351
AY-218	WSR	-34.0009	25.69547	CQ83A	SCCBI	-33.8173	25.76519
AZ-220	WSR	-34.0036	25.69547	CQ-84	SCCBI	-33.8189	25.76513
BA-216	WSR	-33.9981	25.69709	CR-68	SCCSC	-33.7972	25.76675
BB-216	WSR	-33.9981	25.69871	CR-69	SCCSC	-33.7985	25.76675
BC-214	WSR	-33.9954	25.70033	CR-70	SCCSC	-33.7999	25.76675
BD-215	WSR	-33.9968	25.70195	CR-71	SCCSC	-33.8012	25.76675
BD-216	WSR	-33.9981	25.70195	CR-83A	SCCBI	-33.8176	25.76616
BE-215	WSR	-33.9968	25.70357	CR-84	SCCBI	-33.8189	25.76675
BE-220	WSR	-34.0036	25.70357	CS-67	SCCCS	-33.7958	25.76837
BF-219	WSR	-34.0022	25.70519	CS-71	SCCSC	-33.8012	25.76837
BG-224	WSR	-34.009	25.70681	CT-68	SCCSC	-33.7972	25.76999
BH-215	WSR	-33.9968	25.70843	CU-68	SCCSC	-33.7972	25.77161
BH-220	WSR	-34.0036	25.70843	CU-69	SCCSC	-33.7985	25.77161
BH-223	WSR	-34.0077	25.70843	CU-72	SCCSC	-33.8026	25.77161
BJ-220	WSR	-34.0036	25.71167	CV-70	SCCSC	-33.7999	25.77323
BL-221	WSR	-34.0049	25.71491	CV-71	SCCSC	-33.8012	25.77323

WSR: White Sands Reef, SCC: St Croix Complex, SC: St Croix Island, BI: Brenton Island

Supplementary Table 3.2: List of species that contribute more than 1% of the average abundance for the groups with the Standard Deviations. n = total number of species identified in the community groups. TAMIRA codes are listed for future reference.*

Biotope I	(n = 90)	Average% contribution to community assemblage	SD
M0151	*Hypnea tenuis*	29.82647	25.49851
Bio-mal	Soft short mixed macro-algae bin	17.59818	14.79967
M0010	*Amphiroa ephedraea*	11.07131	11.67042
M0272	*Leptophytum acervatum*	6.904734	3.849822
M0194	*Plocamium corallorhiza*	4.034641	1.352937
M0264	*Halimeda cuneata*	2.873116	1.685616
U0027	*Polyclinum isipingense*	2.765569	1.896161
M0203	*Portieria hornemannii*	2.744663	1.233286
M0277	*Gelidium capensis*	1.988037	3.976073
Bio-crs	Red coralline algae mix bin	1.670275	1.069187

M0276	*Codium incognitum*	1.425081	1.979555
M0197	*Plocamium suhrii*	1.354718	1.513878
M0013	*Amphiroa anceps*	1.283495	0.7835
P0030	*Penares* sp. 001 cf *alata*	1.237111	1.365683
M0257	Calliblepharis fimbriata	1.166558	1.208507
U0150	*Aplidium* sp. 004 RSA	1.001473	0.899087
Biotope II	(n = 237)		
M0010	*Amphiroa ephedraea*	17.44666	9.500332
Bio-cns	Cnidaria short mix bin	10.79994	4.269423
M0272	*Leptophytum acervatum*	8.633535	4.810528
P0032	*Placospongia* sp. 001 RSA	7.468222	6.782292
M0168	*Lobophora variegata*	6.890628	9.723071
C0032	*Sertularella arbuscula*	2.856447	2.657081
C0064	*Macrorhynchia* sp. 003 RSA	2.589982	1.701232
P0207	*Clathria* sp. 001 RSA	2.212408	1.698944
U0086	*Gynandrocarpa placenta*	2.063971	1.714989
Bio-crs	Red coralline algae mix bin	1.9593	1.979434
P0240	*Chondrilla* sp. 004 RSA	1.692469	1.924877
E0007	*Tropiometra carinata*	1.446416	1.905683
M0017	*Arthrocardia carinata*	1.414591	0.654603
E0004	*Comanthus wahlbergii*	1.380816	0.800962
M0187	*Peyssonnelia capensis*	1.355632	1.006286
C0002	*Alcyonium fauri*	1.218492	1.021993
M0013	*Amphiroa anceps*	1.193838	1.272058
P0237	*Tedania* sp. 003 RSA	1.110994	0.927551
C0023	*Leptogorgia palma*	1.016122	0.699686
Biotope III	(n = 180)		
P0032	*Placospongia* sp. 001 RSA	13.07264	9.481283
Bio-cns	Cnidaria short mix bin	11.21175	5.904407
C0023	*Leptogorgia palma*	10.56302	8.436138
M0272	*Leptophytum acervatum*	8.156414	7.964648
M0010	*Amphiroa ephedraea*	6.354738	3.963166
P0240	*Chondrilla* sp. 004 RSA	4.903863	5.019481
C0032	*Sertularella arbuscula*	3.608984	1.935994
P0207	*Clathria* sp. 001 RSA	3.511314	2.709689
C0015	Eunicella tricoronata	2.406132	3.125199
P0029	*Mycale* sp. 005 RSA	2.198996	2.880018
C0002	*Alcyonium fauri*	1.624573	0.346074
C0035	*Thuiaria articulata*	1.242951	1.162197
B0004	*Adeonella purpurea*	1.127118	0.7758
B0011	*Gigantopora polymorpha*	1.103527	2.133673
M0187	*Peyssonnelia capensis*	1.100625	1.05533
E0007	*Tropiometra carinata*	1.045304	0.446585
Botope IV	(n =116)		
P0032	*Placospongia* sp. 001 RSA	18.79001	1.893299

C0023	*Leptogorgia palma*	10.2262	4.50474
E0007	*Tropiometra carinata*	10.03711	7.336738
Bio-cns	Cnidaria short mix bin	8.017976	3.514582
M0272	*Leptophytum acervatum*	6.109001	5.475096
C0032	*Sertularella arbuscula*	4.982326	4.376256
C0025	*Macrorhynchia filamentosa*	3.684326	2.911756
B0017	*Menipea trispriata*	3.006111	4.974201
C0002	*Alcyonium fauri*	2.537603	1.451934
C0064	*Macrorhynchia* sp. 003 RSA	2.249934	2.229534
C0035	*Thuiaria articulata*	2.062213	1.859167
C0016	*Homophyton verrucosum*	1.625695	2.405273
P0240	*Chondrilla* sp. 004 RSA	1.533824	0.970503
C0047	*Ideogorgia capensis*	1.258441	2.179683
C0015	*Eunicella tricoronata*	1.235202	0.465455
P0060	*Tsitsikamma favus*	1.230504	0.847909
P0024	*Isodictya* sp. 005 RSA	1.221105	1.566048
Biotope V	(n = 179)		
C0023	*Leptogorgia palma*	12.56126	10.45916
Bio-cns	Cnidaria short mix bin	9.39169	6.040357
C0016	*Homophyton verrucosum*	7.603475	2.800107
P0032	*Placospongia* sp. 001 RSA	7.324041	5.373368
P0240	*Chondrilla* sp. 004 RSA	6.408638	3.388058
C0032	*Sertularella arbuscula*	5.172851	3.264063
P0173	*Psammocinia* sp. 008 RSA	4.34303	4.04598
P0091	*Mycale* sp. 004 RSA	2.875941	3.647172
P0036	Unknown sp. 002 RSA	2.616036	3.632021
W0003	*Pseudopotamilla* sp. 001 RSA	2.527447	4.334097
C0012	*Eunicella papillosa*	2.406285	2.359572
C0064	*Macrorhynchia* sp. 003 RSA SPN	2.399814	5.878319
C0035	*Thuiaria articulata*	2.147031	3.580881
B0001	*Adeonella* sp. 001 RSA	2.127073	4.636943
M0272	*Leptophytum acervatum*	1.838798	2.333479
C0047	*Ideogorgia capensis*	1.697572	2.552699
P0055	*Tedania stylonychaeta*	1.428176	0.864052
P0013	*Cyclacanthia bellae*	1.391354	2.079785
P0022	*Halichondria* sp. 001 RSA	1.177663	1.144696
C0027	*Acabaria rubra*	1.049251	1.068711
P0029	*Mycale* sp. 005 RSA SPN	1.047167	1.424166
Biotope VI	(n = 109)		
Bio-cns	Cnidaria short mix bin	27.11475	11.55079
M0272	*Leptophytum acervatum*	14.09679	10.83315
P0032	*Placospongia* sp. 001 RSA	7.326331	7.452605
U0167	*Aplidiopsis* sp. 004 RSA	5.591838	4.701689
P0055	*Tedania stylonychaeta*	4.405635	6.451272
C0023	*Leptogorgia palma*	4.374772	5.460233
U0088	*Pyura stolonifera*	4.00626	9.813292

P0013	*Cyclacanthia bellae*	3.651222	4.840461
P0091	*Mycale* sp. 004 RSA	2.964468	3.089338
C0016	*Homophyton verrucosum*	2.071148	2.559039
P0036	Unknown sp. 002 RSA SPN Encrusting red sponge	1.773896	2.503475
M0197	*Plocamium suhrii*	1.298246	3.180039
C0017	*Macrorhynchia* sp. 001 RSA SPN	1.29108	3.162487
P0029	*Mycale* sp. 005 RSA SPN	1.278798	1.844748
P0182	*Spheciospongia* sp. 002 RSA SPN	1.205891	1.916462
P0173	*Psammocinia* sp. 008 RSA SPN	1.160612	1.122318
C0012	*Eunicella papillosa*	1.041092	1.391175
P0237	*Tedania* sp. 003 RSA SPN	1.031346	1.685135

Biotope VII	(n = 40)		
E0007	*Tropiometra carinata*	31.52404	44.30314
P0220	*Tethya* sp. 004 RSA SPN	30	46.90416
M0272	*Leptophytum acervatum*	17.27187	40.54549
W0003	*Pseudopotamilla* sp. 001 RSA	3.323898	4.842413
P0032	*Placospongia* sp. 001 RSA	2.279635	5.583943
C0032	*Sertularella arbuscula*	2.062861	2.677639
P0084	*Hymeraphia* sp. 001 RSA	1.671733	4.094892
C0003	*Amphisbetia orperculata*	1.215805	2.978103
C0019	*Eudendrium deciduum*	1.212428	2.683062
C0006	*Anthostella stephensoni*	1.111111	2.721655
U0151	Sycozoa sp. 002 RSA SPN	1.06383	2.60584

Sub-group VIIa	(n = 37)		
E0007	*Tropiometra carinata*	63.04809	43.88193
W0003	*Pseudopotamilla* sp. 001 RSA	6.647796	5.047525
P0032	*Placospongia* sp. 001 RSA	4.559271	7.896888
P0084	*Hymeraphia* sp. 001 RSA	3.343465	5.791051
C0032	*Sertularella arbuscula*	3.014611	3.391636
C0003	*Amphisbetia orperculata*	2.431611	4.211674
U0151	*Sycozoa* sp. 002 RSA SPN	2.12766	3.685214
P0124	*Inflatella* sp. 001 RSA	1.823708	3.158755
P0182	*Spheciospongia* sp. 002 RSA	1.41844	2.45681
M0272	*Leptophytum acervatum*	1.21041	1.611443
C0025	*Macrorhynchia filamentosa*	1.114488	1.93035
B0015	*Chaperiopsis multifida*	1.089585	1.188461
U0078	*Didemnum* sp. 003 RSA	1.013171	1.754864
U0152	*Synoicum* sp. 010 RSA	1.013171	1.754864

Sub-group VIIb	(n = 1)	Average	SD
M0272	*Leptophytum acervatum*	60	51.63978

Sub-group VIIc	(n = 5)	Average	SD

P0220	*Tethya* sp. 004 RSA	90	14.14214
C0019	*Eudendrium deciduum*	3.333333	4.714045
C0006	*Anthostella stephensoni*	3.333333	4.714045
C0032	*Sertularella arbuscula*	1.666667	2.357023
C0036	*Wrightella* sp. 001 RSA	1.666667	2.357023

*NOTE: All species identification is based on visual identification only.

Supplementary Table 3.3: Taxonomic tree for all species listed in Supplementary Table 3.2.*

Species	**Genus**	**Family**	**Order**	**Class**	**Phylum**
Acabaria rubra	*Acabaria*	Melithaeidae	Alcyonacea	Anthozoa	Cnidaria
Adeonella purpurea	*Adeonella*	Adeonoidae	Cheilostomatida	Gymnolaemata	Bryozoa
Adeonella sp. 001 RSA	*Adeonella*	Adeonoidae	Cheilostomatida	Gymnolaemata	Bryozoa
Alcyonium fauri	*Alcyonium*	Alcyoniidae	Alcyonacea	Anthozoa	Cnidaria
Amphiroa anceps	*Amphiroa*	Corallinaceae	Corallinales	Florideophyceae	Rhodophyta
Amphiroa ephedraea	*Amphiroa*	Corallinaceae	Corallinales	Florideophyceae	Rhodophyta
Amphisbetia orperculata	*Amphisbetia*	Sertulariidae	Leptothecata	Hydrozoa	Cnidaria
Anthostella stephensoni	*Anthostella*	Actiniidae	Actiniaria	Anthozoa	Cnidaria
Aplidiopsis sp. 004 RSA	*Aplidiopsis*	Polyclinidae	Aplousobranchia	Ascidiacea	Chordata
Aplidium sp. 004 RSA	*Aplidium*	Polyclinidae	Aplousobranchia	Ascidiacea	Chordata
Arthrocardia carinata	*Arthrocardia*	Corallinaceae	Corallinales	Florideophyceae	Rhodophyta
Calliblepharis fimbriata	*Calliblepharis*	Cystocloniaceae	Gigartinales	Florideophyceae	Rhodophyta
Chaperiopsis multifida	*Chaperiopsis*	Chaperiidae	Cheilostomatida	Gymnolaemata	Bryozoa
Chondrilla sp. 004 RSA	*Chondrilla*	Chondrillidae	Chondrosiida	Demospongiae	Porifera
Clathria sp. 001 RSA SPN	*Clathria*	Microcionidae	Poecilosclerida	Demospongiae	Porifera
Codium incognitum	*Codium*	Codiaceae	Bryopsidales	Bryopsidophyceae	Chlorophyta
Comanthus wahlbergii	*Comanthus*	Comasteridae	Comatulida	Crinoidea	Echinodermata
Cyclacanthia bellae	*Cyclacanthia*	Latrunculiidae	Poecilosclerida	Demospongiae	Porifera
Didemnum sp. 003 RSA	*Didemnum*	Didemnidae	Aplousobranchia	Ascidiacea	Chordata
Eudendrium deciduum	*Eudendrium*	Eudendriidae	Anthoathecata	Hydrozoa	Cnidaria
Eunicella papillosa	*Eunicella*	Gorgoniidae	Alcyonacea	Anthozoa	Cnidaria
Eunicella tricoronata	*Eunicella*	Gorgoniidae	Alcyonacea	Anthozoa	Cnidaria
Gelidium capensis	*Gelidium*	Gelidiellaceae	Gelidiales	Florideophyceae	Rhodophyta
Gigantopora polymorpha	*Gigantopora*	Gigantoporidae	Cheilostomatida	Gymnolaemata	Bryozoa
Gynandrocarpa placenta	*Gynandrocarpa*	Styelidae	Stolidobranchia	Ascidiacea	Chordata
Halichondria sp. 001 RSA	*Halichondria*	Halichondriidae	Suberitida	Demospongiae	Porifera
Halimeda cuneata	*Halimeda*	Halimedaceae	Bryopsidales	Bryopsidophyceae	Chlorophyta
Homophyton verrucosum	*Homophyton*	Spongiodermidae	Alcyonacea	Anthozoa	Cnidaria
Hymeraphia sp. 001 RSA	*Hymeraphia*	Raspailiidae	Axinellida	Demospongiae	Porifera
Hypnea tenuis	*Hypnea*	Cystocloniaceae	Gigartinales	Florideophyceae	Rhodophyta
Ideogorgia capensis	*Ideogorgia*	Keroeididae	Alcyonacea	Anthozoa	Cnidaria
Inflatella sp. 001 RSA	*Inflatella*	Coelosphaeridae	Poecilosclerida	Demospongiae	Porifera
Isodictya sp. 005 RSA	*Isodictya*	Isodictyidae	Poecilosclerida	Demospongiae	Porifera
Leptogorgia palma	*Leptogorgia*	Gorgoniidae	Alcyonacea	Anthozoa	Cnidaria
Leptophytum acervatum	*Leptophytum*	Hapalidiaceae	Corallinales	Florideophyceae	Rhodophyta
Lobophora variegata	*Lobophora*	Dictyotaceae	Dictyotales	Phaeophyceae	Ochrophyta
Macrorhynchia filamentosa	*Macrorhynchia*	Aglaopheniidae	Leptothecata	Hydrozoa	Cnidaria
Macrorhynchia sp. 001	*Macrorhynchia*	Aglaopheniidae	Leptothecata	Hydrozoa	Cnidaria

Macrorhynchia sp. 003	*Macrorhynchia*	Aglaopheniidae	Leptothecata	Hydrozoa	Cnidaria
Menipea trispriata	*Menipea*	Candidae	Cheilostomatida	Gymnolaemata	Bryozoa
Mycale sp. 004 RSA SPN	*Mycale*	Mycalidae	Poecilosclerida	Demospongiae	Porifera
Mycale sp. 005 RSA SPN	*Mycale*	Mycalidae	Poecilosclerida	Demospongiae	Porifera
Penares sp. 001 cf *alata*	*Penares*	Ancorinidae	Tetractinellida	Demospongiae	Porifera
Peyssonnelia capensis	*Peyssonnelia*	Peyssonneliaceae	Peyssonneliales	Florideophyceae	Rhodophyta
Placospongia sp. 001	*Placospongia*	Placospongiidae	Clionaida	Demospongiae	Porifera
Plocamium corallorhiza	*Plocamium*	Plocamiaceae	Plocamiales	Florideophyceae	Rhodophyta
Plocamium suhrii	*Plocamium*	Plocamiaceae	Plocamiales	Florideophyceae	Rhodophyta
Polyclinum isipingense	*Polyclinum*	Polyclinidae	Aplousobranchia	Ascidiacea	Chordata
Portieria hornemannii	*Portieria*	Rhizophyllidaceae	Gigartinales	Florideophyceae	Rhodophyta
Psammocinia sp. 008	*NG Polymastiidae*	Polymastiidae	Polymastiida	Demospongiae	Porifera
Pseudopotamilla sp. 001	*Pseudopotamilla*	Sabellidae	Sabellida	Polychaeta	Annelida
Pyura stolonifera	*Pyura*	Pyuridae	Stolidobranchia	Ascidiacea	Chordata
Sertularella arbuscula	*Sertularella*	Sertulariidae	Leptothecata	Hydrozoa	Cnidaria
Spheciospongia sp. 002	*Spheciospongia*	Clionaidae	Clionaida	Demospongiae	Porifera
Sycozoa sp. 002 RSA	*Sycozoa*	Holozoidae	Aplousobranchia	Ascidiacea	Chordata
Synoicum sp. 010 RSA	*Synoicum*	Polyclinidae	Aplousobranchia	Ascidiacea	Chordata
Tedania sp. 003 RSA	*Tedania*	Tedaniidae	Poecilosclerida	Demospongiae	Porifera
Tedania stylonychaeta	*Tedania*	Tedaniidae	Poecilosclerida	Demospongiae	Porifera
Tethya sp. 004 RSA	*Tethya*	Tethyidae	Tethyida	Demospongiae	Porifera
Thuiaria articulata	*Thuiaria*	Sertulariidae	Leptothecata	Hydrozoa	Cnidaria
Tropiometra carinata	*Tropiometra*	Tropiometridae	Comatulida	Crinoidea	Echinodermata
Tsitsikamma favus	*Tsitsikamma*	Latrunculiidae	Poecilosclerida	Demospongiae	Porifera
Unknown sp. 002 RSA	*UnknownGenus1*	UnkownFamily1	UnknownClass1	Demospongiae	Porifera
Wrightella sp. 001 RSA	*Wrightella*	Melithaeidae	Alcyonacea	Anthozoa	Cnidaria

*NOTE: All species identification is based on visual identification only.

Chapter 4 Heterogeneity and biotope mosaics: *a posteriori* analysis

4.1 Objective

4.1.1 *A posterior* analysis

In Chapter 3 it is suggested that the defined biotope are constructed of heterogeneous components. Image driven identification databases require the identification of homogenous units to facilitate effective and confident identification and description of a component. The development of a biotope identification database, as implemented for the habitat types within the study area, demand a closer, finer-scale assessment of the subunits that make up a broader biotope. The species accumulation curve constructed in Chapter 3 indicates that the exponential phase of the increase in the number of species is well contained within the adopted sampling effort for the quadrat. To investigate the heterogeneity of the broader biotope the habitat and community component of the quadrat is used to construct the database used in this chapter.

4.1.2 Specific goals

- Investigate the possible usefulness of the quadrat as a sample unit in the investigation and description of the habitat and community composition,
- define and describe the biotope subunits that constitute the broader biotopes units identified in Chapter 3,
- construct a biotope subunit image library that could facilitate the subjective assessment of collected samples images and
- construct a biotope subunits network as a means to visualise broader biotope heterogeneity and graphically assess biotope subunit contribution to broader biotopes.

4.2 Introduction

The Agulhas bioregion extends from the cooler waters of the southern Cape to the warm temperate waters of the Eastern Cape coast (Lombard et al. 2004, Sink et al. 2012, 2019) and is heavily influenced by the extent of the continental shelf and the dynamics of the Agulhas Current (Lutjeharms et al. 1996, Goschen et al. 2015, Smit et al. 2017). The shallow coastal seascape is characterised by a mosaic of consolidated and unconsolidated substrate, shallow embayments and protruding rocky capes. The area is well known for its high diversity of seaweed (Beckley and McLachlan 1980, Bolton and Stegenga 2002, Anderson et al. 2009, Smit et al. 2017), fish (Turpie et al. 2000, Chalmers 2012) and marine invertebrates (Awad et al. 2002b, Scott 2018). However, reviews and assessments of the knowledge status of South African marine biodiversity highlight several gaps and data deficiencies (Griffiths et al. 2010, Sink et al. 2018). The paucity of information on benthic species distribution and community composition precludes a temporal assessment of the effects of climate change.

The South African Environmental Observation Network's (SAEON) Long-term Ecological Research (LTER) programme collects physical, biogeochemical essential ocean variables (EOVs) and essential biodiversity variables (EBVs) (O'Connor 2010, Bornman 2016). The Pelagic Ecosystem LTER established in Algoa Bay in 2010 focuses on the collection of variables from the water column. The Benthic Ecosystem LTER developed in 2018 as part of the Department of Science and Innovation's Shallow Marine and Coastal Research Infrastructure (SMCRI) programme (Bornman 2016, Department of Science and Technology 2016b) focuses on the boundary layer between the substrate and the overlying pelagic system. The establishment of PELTER and BELTER stations in the Algoa Bay Sentinel Site (ABSS) will be followed by a phased expansion of this research into other SAEON SMCRI shallow marine research sites along the South African coast.

The main goal of BELTER is to provide a scientific platform for other researchers and to observe the benthic ecosystem response to anthropogenic stressors and global climate change. This will inform management and policymakers and enable adaptive governance of South Africa's natural coastal marine resources. The biotic boundary layer between the abiotic substrate and the water column forms the interface between the ocean floor and the water column above. The importance of this boundary layer has been repeatedly highlighted in research focused on and aimed at informing and improving the management of South Africa's economically important reef-associated ichthyofauna (Götz 2005, Clark 2006, Heyns et al. 2016, Heyns-Veale et al. 2016). Phytoplankton primary production is the driving force in coastal systems and is dependent on nutrients governed by ocean dynamics such as upwelling and currents (Brown 1992, Lutjeharms et al. 1996, Goschen et al. 2015). Benthic invertebrates are dependent on plankton within the water column for food (Gili and Coma 1998). Coastal systems are, however, increasingly influenced by anthropogenic factors driving change that may result in local, national and global shifts in ocean current patterns, temperature flux and upwelling regimes. These are predicted to then drive changes in nutrient dynamics, impacting benthic processes and resource productivity (Harley et al. 2006).

The understanding and mitigation of shifts due to climate change depend on knowledge attained by long-term observation and the collection of EOVs and EBVs in accordance with Aichi targets and UN Sustainable Development Goals (Kissling et al. 2015, Anderson et al. 2017, Schmeller et al. 2018). The SAEON LTER concept aligns well with the International Long-term Ecological Research Network (ILTER) in its mandate to collect, document and provide long-term data on ecosystems, ecosystem processes and interactions at different spatial scales (Kim 2006, Mirtl et al. 2018) and forms part of the multi-disciplinary Group on Earth Observations Biodiversity Observation Network (GEO BON) (Walters 2012, Haase et al. 2018).

Habitat heterogeneity of the seascape drives processes within an ecosystem (Pickett and Cadenasso 1995, McClain and Barry 2010) and heterogeneous environments are believed to provide more niches, while an increase in the incidence of fragmentation supports more complex and diverse biota (Tews et al. 2004, Schlacher et al. 2007). Many environmental factors drive species and community distribution, diversity and heterogeneity (Porter et al. 2014, 2017a, 2017b, Post et al. 2017), however, these are poorly understood. The long-term ecological research data collected from different systems will allow for a progressively improved understanding of the composition, distribution, interaction and function of these systems and their components. This, in turn, will enable refinement in the choice of appropriate indicators to observe change (Harvey et al. 2020, Smit et al. 2021). Species distribution, population abundance, community composition, ecosystem heterogeneity, extent, fragmentation and composition are considered valuable EBVs. Indicators of change, such as the number of individuals and species in a given population, species distribution in space and time and ecosystem heterogeneity are priority EBVs to be addressed by long-term research (Schmeller et al. 2018).

The biotope concept is applicable at many scales (van Rein et al. 2009, Cresswell et al. 2017), and also applies to habitat and community classification and mapping of the South African coast (Sink et al. 2019). Sample collection of soft-sediment macrofauna amongst unconsolidated substrates generally makes use of trawl nets and suction, cone or grab samplers (Field 1971, Harmer 2014, Karenyi 2014, Lange and Griffiths 2014, Maduna 2017, Shah 2018). Research associated with consolidated substrates has generally been dependent on SCUBA diver *in situ* assessment (Porter et al. 2017b), or the collection of imagery for analysis (Anderson et al. 2005, Brash 2006, Sink et al. 2006, Celliers et al. 2007, Celliers and Schleyer 2008, Olbers et al. 2009, Porter et al. 2013, Heyns 2015, Heyns et al. 2016, Joshua et al. 2018). Jump Camera (JC) systems, Remotely Operated Vehicles (ROVs) and underwater video systems (e.g. sBRUVs) allow for the collection of high-resolution imagery of the benthic environment (Heyns 2015, Makwela et al. 2016, Makwela 2017, Truter 2019, Dames 2021). Several studies within Algoa Bay have focussed on macroalgal assemblages and distribution (Beckley and McLachlan 1980, Anderson and Stegenga 1989), but very little information is available on subtidal reef benthic community composition and distribution (Truter 2019).

Data analysis in the previous chapter followed *a priori* methodologies, but exploratory data analysis strongly suggested a more complex system highly patch-like in nature. It was found that samples collected in close proximity to each other were highly heterogeneous in their abiotic and biotic components. This was not addressed in the previous chapter and is further investigated in this chapter. Accordingly, the main goal of this chapter is to define and describe the components that constitute the broader biotopes units identified in the previous chapter. It is acknowledged that a still finer scale investigation into the distribution of assembled species within the unit area sampled here (the quadrat) may reveal specific sub assemblage structures. However, for this investigation, each 0.43 m^2 quadrat dataset, containing 216 abiotic and biotic data points, is regarded as a single sample unit and is analysed independently of other such units. This assumes that the habitat and community structure within a particular unit is a homogeneous entity that represents a typical biotope subunit, identifiable by specific characteristics, and which may form the substructure or a component of broader biotopes, each defined by its specific subcomponents. This fine-scale investigation follows from the suggested heterogeneous character of the biotopes as described in Chapter 3. It was not originally included in the scope of this study, and is, therefore, views as *a posteriori* analysis. It is furthermore believed that the dataset does sample the majority of visually presceivable species within a single quadrat based on the construction of species accumulation curves in Chapter 3 (Figure 3.1) and would permit investigation into species associations, relationships and occurrence patterns.

The description of biotope components in this work is dependent on species identifications from images. This cannot be without caveats (Horton et al. 2021) as the identification is reliant on the quality of the image and the expertise and experience of the person analysing the data. Libraries of *in situ* images of species are helpful aids in accomplishing this task (Kohler and Gill 2006, Seager 2008). The absence of complete species records or comprehensive species image libraries poses challenges in describing the benthic environment and, in response, analyses based on functional groups or traits have become increasingly popular (Althaus et al. 2014, 2015, Post et al. 2017, Pillay et al. 2021b). The need to characterise habitat and community structure has encouraged the development of various hierarchical classification approaches (Lombard et al. 2004, Spalding et al. 2007, Douglass et al. 2014) and fuel the popularity of biotope classification schemes (Shears 2007, Davies et al. 2017, Buhl-Mortensen et al. 2020). The biotope presents a convenient unit for the measurement of ecosystem seascape heterogeneity. It is noteworthy that extensive species, habitat, community and biotope image libraries are fundamentally important in machine learning (ML) algorithm training (Shihavuddin et al. 2013, Gómez-Ríos et al. 2019, González-Rivero et al. 2020), in addition to their intrinsic value.

The goal here is to quantify and describe biotope subunits, investigate the contribution of these subunits to the broader biotope (as defined in Chapter 3) and the spatial distribution of biotope subunits over the sampled area (Algoa Bay). The *a priori* and *a posteriori* grouping of samples are compared and variables that play important roles in the structuring and relation of these subunits are identified.

4.3 Material and methods

The data were collected from the two sample stations, White Sands Reef (WSR) and St Croix Complex (SCC), within Algoa Bay. A 77 760-point dataset was constructed from 360 images collected from 36 research sample localities. An 18 x 12-point grid (point coverage of 0.002 m^2, x separation = 50 mm and y separation = 40 mm) was superimposed over the selected frame (216 point counts per quadrat image) in SeaGIS^{TM} TransectMeasure. This dataset was analysed in Chapter 3 to determine the biotope structure for the research sample locality situated centrally in the predefined 150 m grid superimposed over the sampling stations. Each locality consisted of ten quadrats sampled randomly around a reference point and grouped into a single sample representative of the selected location identified for long-term data collection, as determined *a priori*. The underlying properties of the dataset analysed in the previous chapter, however, suggested the presence of 'building blocks', 'mosaics', 'patches' or 'subunits' contributing to the organization of the broader biotope. To address this, the scale of our investigation was reduced from 150 m^2 to 0.43 m^2, i.e. the area sampled by the quadrat. Samples (quadrats) collected were independently analysed to investigate underlying relationships, *a posteriori*.

Resemblance matrices investigating the similarity/dissimilarity of the samples were constructed with Cluster analysis (PRIMER). A Non-metric Multi-Dimensional scaling (MDS) ordination was constructed, to visually assess the grouping of all quadrats. Similarity within the *a priori* grouping (as per locality, reported in Chapter 3) and the *a posteriori* grouping, investigated in this chapter, were compared with SIMPER analysis. Gephi 0.9.2 (Bastian et al. 2009) graph visualisation and manipulation tool was used the construct a network indicative of the relationship between the subunits clustered into broader biotopes defined per sample location. The network built include all 44 biotope subunits identified, including 12 independent samples. Principle Component Analysis (PCA) of the standardised dataset was constructed and variables that play a dominant role in the structure of the sample dataset were identified with BEST BVSTEP analysis using Spearman's correlation (in PRIMER).

A quadrat image library was constructed for the biotope subunits identified. The images were complemented by similarity and abundance statistics and a list of the dominant species that contribute to the community structure within each biotope subunit.

4.4 Results

Taxonomic richness was calculated by constructing a Gamma+ resemblance matrix weighting based on taxonomic richness (Supplementary Table 4.1). Non-metric Multi-Dimensional scaling (MDS) performed on the square root transformed dataset and the Gamma+ resemblance matrix, inclusive of all biotic point counts and two categories of substrate type (consolidated and unconsolidated) recorded in the absence of biota, was plotted (Figure 4.1). The MDS plots for using A) Bray Curtis and B) Gamma+ resemblance matrix weighting based on taxonomic richness compare the clustering of the quadrats (Figure 4.1) and a Spearman's rank correlation indicates a moderate to good correlation (r = 0.625) between the two resemblance matrices (PRIMER).

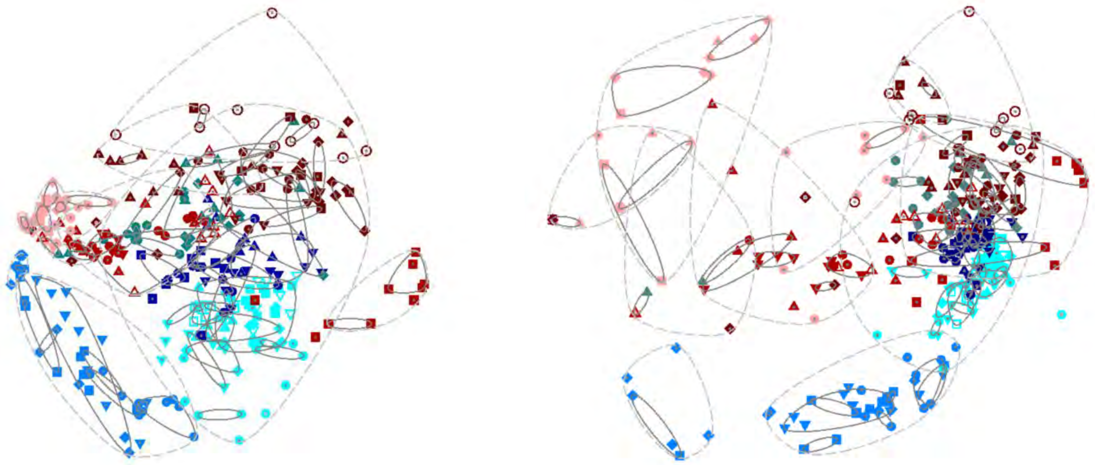


Figure 4.1: Non-metric Multi-Dimensional Scaling (MDS) constructed from A) Square root transformed Bray Curtis similarity and B) Gamma+ dissimilarity resemblances. Kruskal stress formula (2D stress: 0.015 and 0.12, respectively). Quadrats collected from WSR are coloured in blue and those for SCC in red. The symbol shape is indicative of the locality where the quadrat was collected. Contour lines are representative of 80% (solid line) and 60% (dashed line) similarity.

The close similarity of samples (SIMPER 95% confidence) based on the taxonomic richness estimate is shown in Figure 4.4 with symbols on the dendrogram above the sample identification code. The Dendrogram is constructed from the square root transformed Bray Curtis similarity hierarchical CLUSTER analysis (PRIMER) for all biotic and abiotic variables in the dataset (Figure 4.4).

The grouping of samples into suggested biotope subgroups considered three resemblance matrices. The first employed Bray Curtis resemblances of untransformed data for each of the samples and investigated the relationship within the *a priori* quadrat groupings within each research location. The second constructed a hierarchical dendrogram using the Gamma+ taxonomic dissimilarity measure (Clarke and Warwick 1999, Clarke et al. 2006) with weight determined from taxon richness using the Linnaean taxonomy tree (Supplementary Table 4.1). This is a natural extension of Bray-Curtis dissimilarity on presence/absence data and a complement of Sørensen presence/absence similarity and is formally defined, as in PRIMER Manuals (Clarke and Warwick 2001, Clarke and Gorley 2015). Substrate variables were not removed from the dataset and both the abiotic variables were given the same hierarchical structure and, as the Gamma+ analysis reduces the abundance data to 'presence' data, the influence of the two variables in a 380 variable dataset was justified. The resulting grouping of the samples, as per the Gamma+ Cluster analysis and indicative of close taxonomic similarity, is incorporated into the third Cluster analysis and indicated by symbols above the sample location labels. The third, a Bray Curtis resemblance matrix, was constructed from square root transformed data. This moderates the effect of dominant taxa but does not overemphasise the importance of rarer taxa that might occur randomly (Olsgard et al. 1997). The hierarchical grouping of samples as per the CLUSTER analysis of this matrix was used to identify biotope subunits. Groups were selected on the lowest branch as per SIMPROF (95% confidence limit), while species composition and contribution of the similarity of the groups were calculated using SIMPER PRIMER (Figure 4.4).

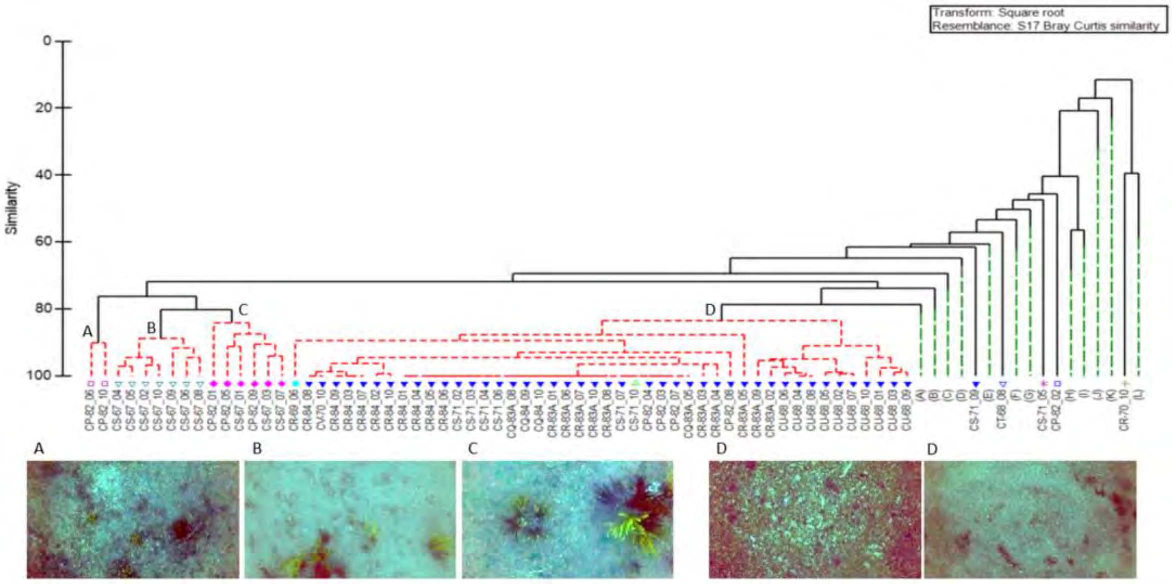


Figure 4.2: see the caption on p 100.

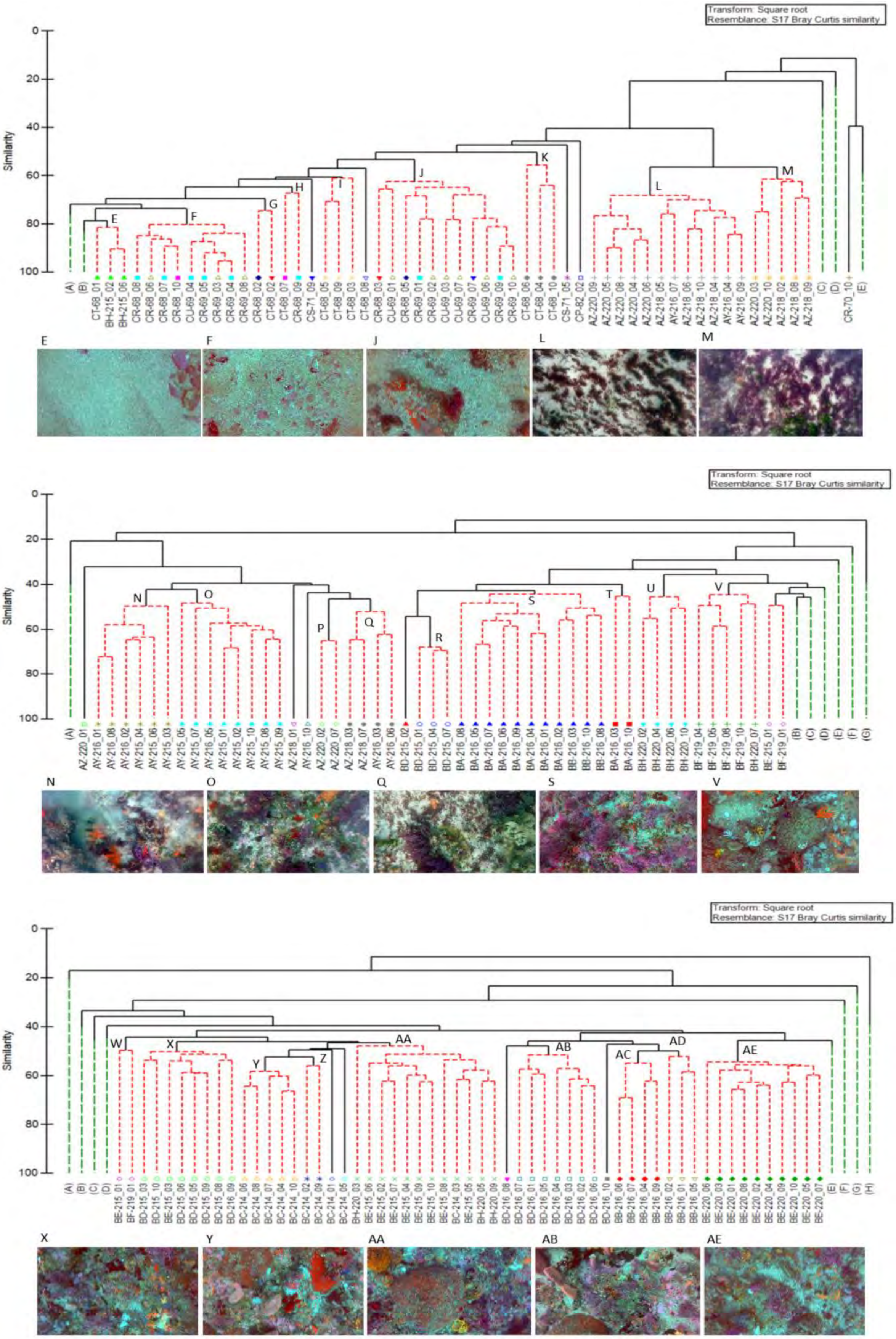


Figure 4.3: see the caption on p 100.

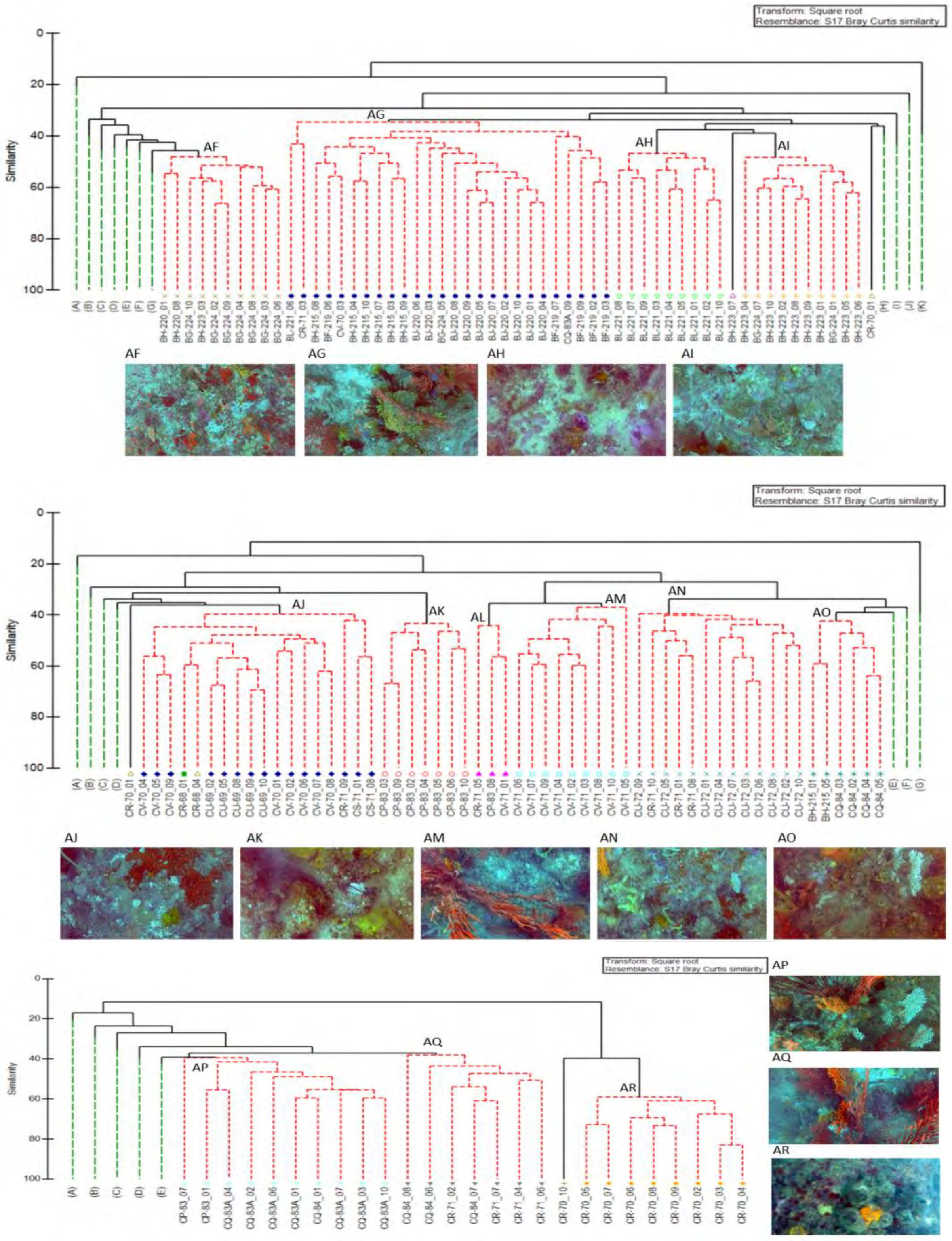
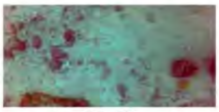
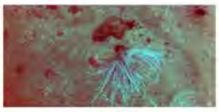
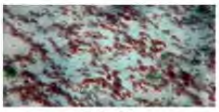
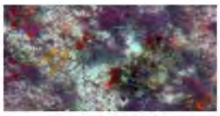
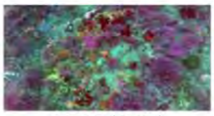
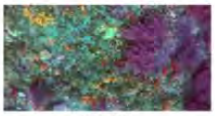
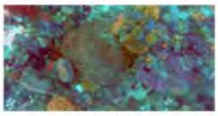
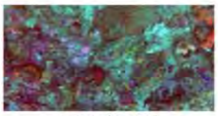


Figure 4.4: Hierarchical dendrograms of CLUSTER analysis with SIMPROF (at 95% confidence limits) of Bray Curtis resemblance matrix from the square root transformed biotope dataset with taxonomic similarity (Gamma+ similarity indicated by symbols). Biotope subunit characteristic image and alphabetic code correspond to the biotope subunit identification and are also used in Figure 4.5.

An image reference library containing multiple images per biotope subunit was constructed (a subset of this given in Table 4.1).

Table 4.1: Examples of images in the constructed library for biotopes. Biotope subunit identification code, average similarity within the group as a whole, as well as an average similarity for the top three contributing variables with Standard Deviation (SD) and percentage contribution of each to the similarity, are given for the square root transformed dataset. The average percentage abundance listed for each variable is calculated from a standardised dataset. The number of quadrats that are included in the biotope is given by n. Species names are listed with TAMIRA codes in brackets.

	Average % abundance	**Average similarity (SD)**	**% Contribution to the similarity**
Biotopes subunit C Average similarity: 87.45 (n = 6)			
Unconsolidated sediment	81.40	57.93 (12.86)	66.24
Tropiometra carinata (E0007)	15.74	20.59 (4.32)	23.54
Pseudopotamilla sp 001 RSA (W0001)	1.70	7.31 (5.36)	8.36
Biotope subunit F Average similarity: 72.92 (n = 9)			
Unconsolidated sediment	84.77	55.40 (8.34)	75.97
Bio-cns	4.42	9.51 (5.61)	13.05
Leptophytum acervatum (M0272)	3.86	6.70 (1.48)	9.19
Biotope subunit L Average similarity: 71.88 (n = 6)			
Unconsolidated sediment	57.48	37.56 (5.07)	52.25
Hypnea tenuis (M0151)	33.68	26.10 (3.49)	36.31
Halimeda cuneata (M0264)	3.13	2.87 (0.98)	3.99
Biotope subunit O Average similarity: 54.92 (n = 8)			
Amphiroa ephedraea (M0010)	29.80	12.68 (5.58)	2.308
Soft short mixed macro-algae bin	13.66	7.08 (2.70)	12.90
Leptophytum acervatum (M0272)	9.26	6.54 (5.81)	11.91
Biotope subunit S Average similarity: 49.00 (n = 11)			
Amphiroa ephedraea (M0010)	30.39	12.12 (2.69)	24.74
Lobophora variegata (M0168)	24.41	11.04 (3.16)	22.53
Red coralline algae mix bin	5.98	4.69 (1.91)	9.57
Biotope subunit AA Average similarity: 52.98 (n = 12)			
Placospongia sp 001 RSA (P0032)	26.39	9.02 (3.62)	17.03
Amphiroa ephedraea (M0010)	7.99	5.12 (5.35)	9.66
Unconsolidated sediment	7.87	4.62 (4.31)	8.71

The similarity of the samples within an assigned location, the *a priori* grouping, and the grouping suggested in the above cluster analysis for samples independently analysed, were compared. Eight of the localities contained samples assigned to the same biotope subunits, while in 72.2% the calculated similarity index improved (Figure 4.5 and Supplementary Table 4.2). In total, 44 biotope subunits were identified, 12 samples were not closely associated with groups but were assigned unique codes and included in the network mapping (Figure 4.6).

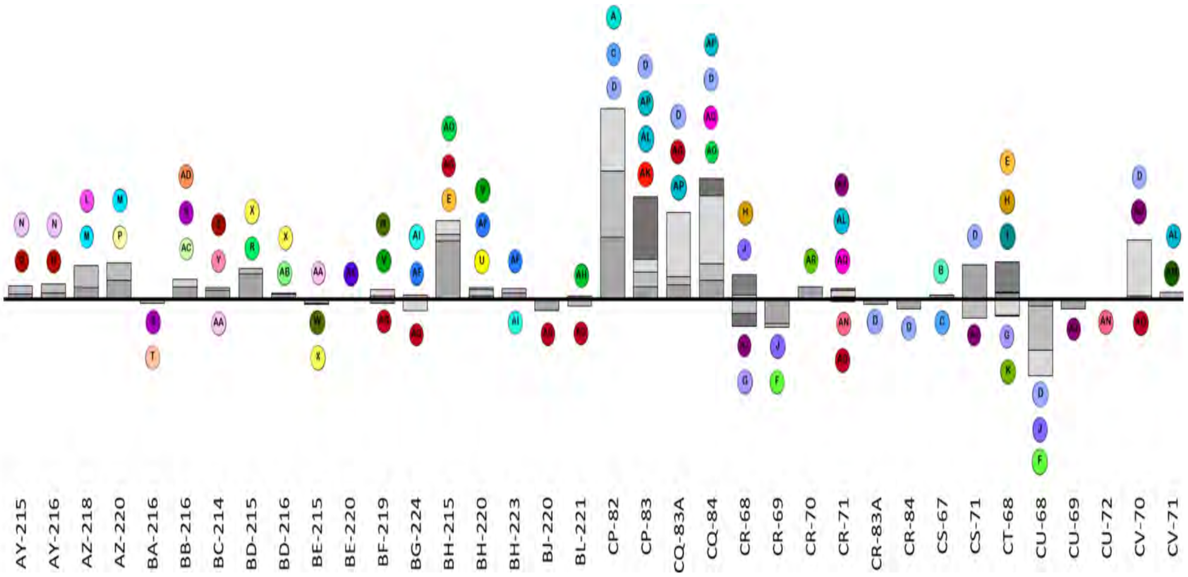


Figure 4.5: Difference in average similarity as calculated by SIMPER analysis in PRIMER for the complement (n = 10 samples) quadrats at each locality and the groups as per CLUSTER analysis of the quadrat point count data, irrespective of location affinity. Values above the line indicate an improvement in the similarity of the defined biotope subunits in comparison to the *a priori* grouping of quadrat defined by sample location; values below the line are indicative of a poorer association within the biotope subunit. (An enlargement of this figure is included with the supplementary material).

The network constructed in Gephi 0.9.2 (Bastian et al. 2009) is built on the spatial distribution of members of a biotope subunit in relation to the locality where they were sampled (Figure 4.6). Singletons or independent samples (quadrats) were included. Habitat and community heterogeneity are evident from the presence of different biotope substructures within the *a priori* 50 m diameter predefined sample area at each research location (n = 10). Several biotope subunits are shared between research localities. Connectivity between localities within the biotopes described in the previous chapter is apparent. Some research locations present a high degree of similarity of the quadrats sampled and six of the research localities (BCU-72, CU-68, CR-83A, CR-84; BJ-220 and BE-220) are more homogeneous (represented by biotope AN, D, AG and AE). (Figure 4.6).

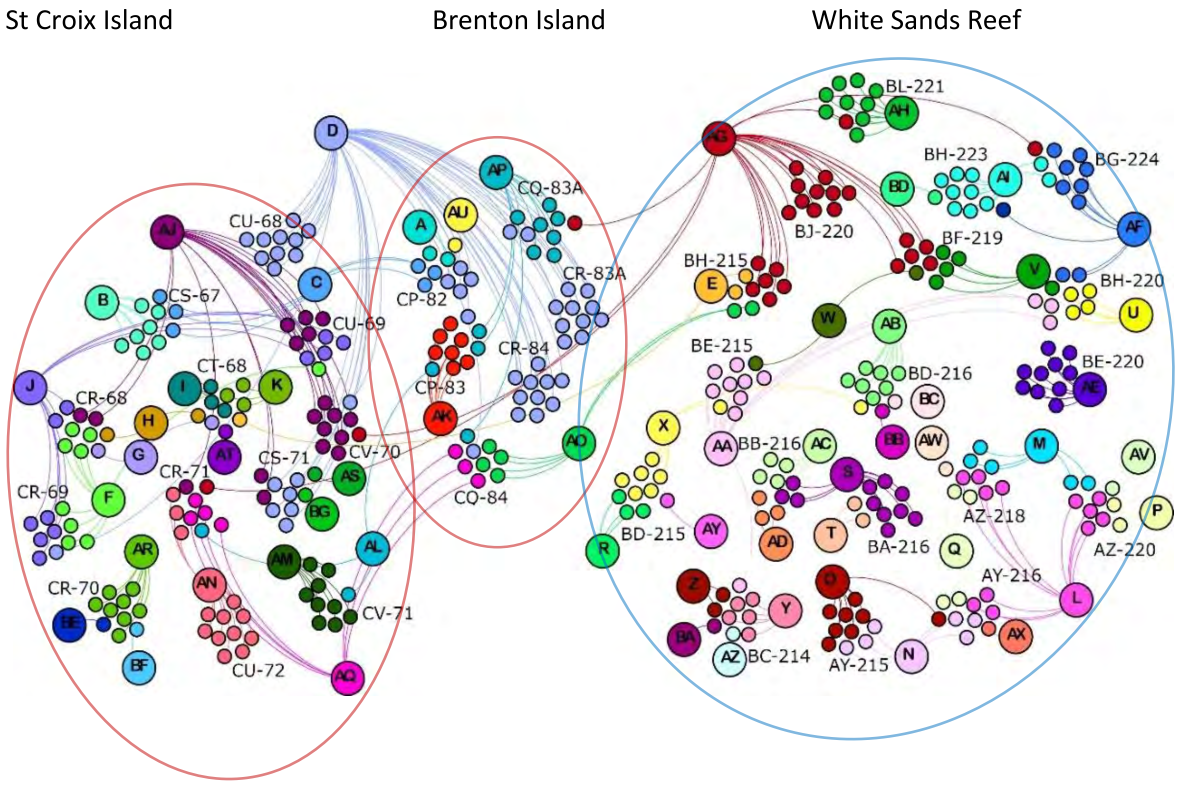


Figure 4.6: Visual network indicating the spatial relationship of biotope subunit components across the sampled localities. The large nodes are labels for the different biotope subunits defined and the label names correspond with that as indicated in the cluster analysis (Figure 4.4). The small nodes represent each quadrat collected from a sample site, n = 10 at each sample location. The name of the sample location is indicated next to the node cluster. The biotope subunit composition for each of the locations and the occurrence of these biotope subunits at other locations are colour coded and connected to the biotope subunit labels in the large nodes. Small node clusters of sample sites bound by a red border are from St Croix and Brenton Island (SCC) respectively and those in blue from White Sands Reef (WSR).

Thirty-seven species contributed an average abundance of more than 5% and 20 species contributed a maximum average abundance of more than 10% to the character of the biotope subunits. BEST BVSTEP analysis using Spearman's correlation (r = 0.955) identified 10 of the 380 variables within the Bray Curtis square root transformed dataset that best explain the relationship presented between the samples. These include *Leptogorgia palma* (C0023), *Homophyton verrucosum* (C0016), mixed tufts of small hydroids (Bio-cns), *Sertularella arbuscula* (C0032), soft short mixed macroalgae bin (Bio-mal), *Chondrilla* sp. 004 (P0240), Placospongia sp. 001 RSA (P0032), *Amphiroa ephedraea* (M0010), *Leptophytum acervatum* (M0272) and unconsolidated sediment (Unconsol). The biotope subunits distributions on the PCA plot underline their similarity. The impact of unconsolidated or soft sediment and the characterisation of biotope subunits by coralline algae (*Amphiroa ephedraea* and *Leptophytum acervatum*) and sea fans (*Leptogorgia palma* and *Homophyton verrucosum*) is furthermore clearly evident (Figure 4.7).

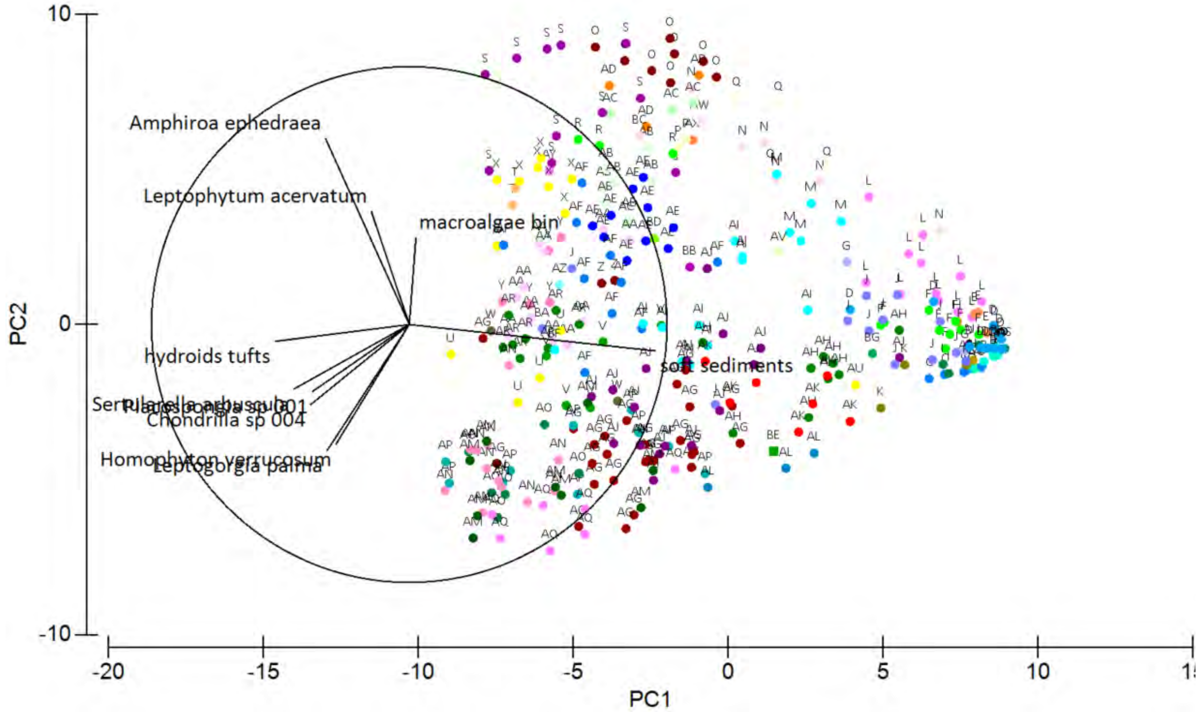


Figure 4.7: PCA of samples coded in biotope subunit groups with BEST BVSTEP analysis using Spearman's correlation (rho >0.95, delta rho < 0.001, r = 0.955) identified 10 variables within the Bray Curtis square root transformed dataset that best explain the relationship between the samples.

4.5 Discussion

The *a priori* quadrats collected within a 50 m diameter circle of each other (within a (πr^2) 1963.5m^2 area) were summed (data from 10 quadrats to represent a 4.3 m^2 sampled area) to describe the broader biotope, habitat and community structure for each of the research locations (Chapter 3). Exploratory analysis of these groups showed a low similarity within the locality grouping, as well as in the resulting defined biotopes. A comparison of the individual quadrat dataset indicated that some samples collected near each other differ greatly from each other (Supplementary Table 4.2). The species accumulation data for each quadrat (covering an area of 0.43 m^2) collected indicates that the exponential phase for the accumulation of species within a single sample was well contained within the 216 points identified (Figure 3.1).

The functionality of the quadrat as a sample unit in investigating habitat and community heterogeneity is investigated in this study. Analysis of the square root transformed dataset of all 360 quadrats (77 760-point count dataset) identified a potential 44 biotope subunits (with a confidence limit of 95% SIMPROF) (Supplementary Table 4.3). Only in six instances did all the quadrats from a particular sample location belong to the same biotope subunit (Figure 4.6). This homogeneity is evidenced by individual samples from the sample location belonging to the same biotope subunit. It is furthermore evident that biotope subunits were frequently spatially closely associated but some had a wider distribution and were present at both sample stations. The heterogeneity of both the habitat and community composition is reflected in the different biotope subunits represented. A strong relationship between St Croix Island and the neighbouring Brenton Island, and the relationship between the western and eastern localities of White Sands Reef, are highlighted. The character of the habitat and community found at each location and within each station is a product of the contribution of these identifiable biotope subunits.

The results support the initial observations that habitat and community structure within the small target sample locality may be highly heterogeneous. In this analysis, we made use of standard PRIMER cluster analysis with a 95% SIMPROF confidence limit, of primarily a square root transformed dataset which included biotic and abiotic variables. The abiotic variables were included when there was a visible absence of biota and classed into two categories to simplify the dataset and to give more weight to the diversity in the biotic community composition. The fundamental role that substrate type and sediment play in determining the community structure, and thus the composition of the biotope, is well established (Porter et al. 2017a, 2017b). This work reiterates the key role that unconsolidated sediment plays in Algoa Bay with regard to biotope character and community presence (Figure 4.7).

The visual plane of the collected quadrat sample is of importance. Unconsolidated and consolidated unpopulated substrates play an important role in the visual perception of the biotope and this is the main motivation for the inclusion of abiotic substrate count data in the analysis. The image database provides quick access to collected and categorised images, with information on the substrate and characteristics of the biota recorded, allowing clear and easy visual comparison (biotope representative images are provided in Figure 4.4 and a brief comparison of selected contrasting biotopes and images are provided in Table 4.1). This quick preliminary evaluation of collected image data directly after each sampling event enables expedient preliminary or ‘snap shot’ assessment of newly collected data images and biotope spatial distribution and extent. It will supply valuable metadata or metadata tags to archived images and provide the end-user with more insightful metadata information when harvesting images for future study, research and assessment. Complete analysis of the image data collected is time-consuming and, until such time that ML becomes a routine analysis tool, we propose a quick classification of the collected images, using well-defined biotope units, each represented by multiple quadrat images.

The functionality of the biotope subunit (as defined in this chapter) as an identification tool is underpinned by the homogeneity and integrity of the defined biotope subunit. It is substantiated by images that collectively demonstrate a high degree of similarity or resemblance within the group and a high dissimilarity from other such groups (both visually and analytically). These images will form the basis of the BELTER biotope library and can hierarchically include units of different scales. As with the species image library, this assemblage of biotope images will be of considerable value as a fundamental resource in ML image recognition software training.

4.6 Conclusion

In this chapter, the broader biotope components are described. Data collected from the sample points around the research locations were independently analysed and using cluster analysis the heterogeneity was confirmed. The homogenous subunits were described and a biotope subunit image library that could facilitate the subjective identification and assessment of collected samples images were compiled. The biotope subunits were described and their contribution to the broader biotopes was assessed. It was shown that although the broader biotope units were characteristic of the sample stations, several biotope subunits were shared between stations.

The identification and description of biotope subunits and their contribution to broader biotopes is an important step in understanding the heterogeneity of the ecological seascape. It is clear that some biotope units have a wider distribution than others and contribute differently to the overall seascape. Unconsolidated sediment is an important variable and, although 378 species were identified within the study area, only nine species play a dominant role in defining biotope subunit structure. This study is the first assessment of biotope characterisation in South African waters at this scale and the results suggest a highly diverse and heterogeneous patch-like character of the habitat and community assemblages at a relatively fine-scale. Biotope heterogeneity and patchiness define the seascape and, as drivers of diversity, are important factors to consider in understanding the dynamics at play between sessile benthic biotopes and other species, such as infra- and supra-benthic ichthyofauna. It is further envisioned that using a hierarchical scale based classification approach to mapping biotopes within the South African marine domain will provide valuable insights into the composition, distribution and change within the marine environment.

The BELTER biotope library is expected to augment and improve as more samples are collected, thereby enhancing and expediting the classification of the benthic environment and mapping of biotopes within the coastal marine environment of South Africa. These biotope subunits can be used to do a ‘snap shot’ analysis of the data collected whereby a newly collected image is assigned to a biotope subunit before detailed analysis is possible. Changes in the biotope types collected from research localities and stations, changes in the contribution of different biotope subunits or ratio of contribution of different biotope subunits to broader biotopes, research localities or stations may be indicative of a change in the seascape. As such functioning as an early coarse-level warning indicator highlighting the need for in-depth assessment and full analysis of the dataset.

The BELTER platform aims to collect long-term data at several proposed sites along the South African coast and will include data collection for short term projects and research in other areas. The accumulative dataset will allow for a better understanding, not only of the spatial heterogeneity of the ecosystem seascape but changes that may occur over time. Increasing the scope of data collection to areas surrounding the LTER stations, especially at the proposed 150 m^2 grid cell spatial scale, will enable the use of biotope modelling (Buhl-Mortensen et al. 2020, Sterne et al. 2020) and contribute to marine spatial planning (Dorrington et al. 2018, Livingstone et al. 2018).

4.7 Supplementary material

Supplementary Table 4.1: Weight values in the calculation of Phylogenetic diversity indices and Gamma+ resemblance using taxon richness.

Taxon	Richness	Weight
Species	380	14.815
Genus	195	26.207
Family	122	43.169
Order	54	63.457
Class	18	71.91
Phylum	13	100

Supplementary Table 4.2: Comparison of the average similarity calculated for the *a priori* grouped quadrat samples collected at each research sample locality and the *a postriori* defined biotope subunits. This is graphically presented in Figure 4.5.

Location ID	**Average similarity**	**Biotope subunit ID and Average similarity**									
AY-215	50.73	**O**	54.92	**N**	57.63						
AY-216	50.09	**O**	54.92	**N**	57.63						
AZ-218	54.25	**M**	63.86	**L**	71.88						
AZ-220	49.79	**P**	65.45	**M**	63.86						
BA-216	48.56	**S**	49	**T**	45.4						
BB-216	48.53	**AC**	58.52	**S**	49	**AD**	54.33				
BC-214	53.34	**Y**	60.19	**Z**	55.97	**AA**	52.98				
BD-215	47.95	**R**	68.69	**X**	52.18						
BD-216	51.21	**AB**	54.89	**X**	52.18						
BE-215	52.9	**AA**	52.98	**W**	49.71	**X**	52.18				
BE-220	56.98	**AE**	56.98								
BF-219	44.78	**AG**	41.41	**V**	47.59	**W**	49.71				
BG-224	50.75	**AF**	51.92	**AI**	53.16	**AG**	41.41				
BH-215	36.14	**E**	84.38	**AG**	41.41	**AO**	47.38				
BH-220	46.01	**U**	48.18	**AF**	51.92	**V**	47.59				
BH-223	48.23	**AI**	53.16	**AF**	51.92						
BJ-220	51.07	**AG**	41.41								
BL-221	47.2	**AH**	49.49	**AG**	41.41						
CP-82	36.26	**C**	87.45	**A**	90.17	**D**	88.14				
CP-83	36.26	**AK**	46.56	**AL**	48.5	**AP**	46.14	**D**	88.14		
CQ-83A	34.75	**AP**	46.14	**AG**	41.41	**D**	88.14				
CQ-84	31.8	**AO**	47.38	**AQ**	45.17	**D**	88.14	**AP**	46.14		
CR-68	56.58	**J**	56.81	**AJ**	44.75	**H**	59.74	**G**	46.04	**F**	72.92
CR-69	76.59	**J**	56.81	**F**	72.92						
CR-70	53.01	**AR**	62.82								
CR-71	43.3	**AQ**	45.17	**AN**	42.99	**AL**	48.5	**AJ**	44.75	**AG**	41.41
CR-83A	92.05	**D**	88.14								
CR-84	96.24	**D**	88.14								
CS-67	88.31	**B**	91.25	**C**	87.45						
CS-71	60.2	**D**	88.14	**AJ**	44.75						
CT-68	59.38	**I**	64.36	**H**	59.74	**G**	46.04	**K**	58.45	**E**	84.38
CU-68	93.67	**D**	88.14	**J**	56.81	**F**	72.92				
CU-69	52.76	**AJ**	44.75								
CU-72	43.88	**AN**	42.99								
CV-70	42.01	**AJ**	44.75	**AG**	41.41	**D**	88.14				
CV-71	44.31	**AM**	45.31	**AL**	48.5						

Supplementary Table 4.3: Synopsis of variables, average abundance and contribution to similarity to the structure of the defined biotope subunits.

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Group A	Average similarity: 94.91				
Unconsolidated sediment	90.74	88.89		93.66	93.66
Pseudopotamilla sp. 001 RSA (W0003)	3.01	2.78		2.93	96.59
Tropiometra carinata (E0007)	3.01	1.85		1.95	98.54
Group B	Average similarity: 92.70				
Unconsolidated sediment	91.14	87.92	17.95	94.84	94.84
Bio-bur	4.56	2.8	2.78	3.02	97.86
Tropiometra carinata (E0007)	4.23	1.98	1.16	2.14	100
Group C	Average similarity: 87.53				
Unconsolidated sediment	81.4	75.71	10.31	86.5	86.5
Tropiometra carinata (E0007)	15.74	10.28	1.9	11.74	98.24
Group D	Average similarity: 93.22				
Unconsolidated sediment	95.99	92.81	9.84	99.56	99.56
Tethya sp. 004 RSA SPN (P0220)	2.38	0.37	0.23	0.39	99.95
Group E	Average similarity: 95.22				
Unconsolidated sediment	92.13	91.2	113.74	95.79	95.79
Leptophytum acervatum (M0272)	5.25	3.4	1.27	3.57	99.35
Group F	Average similarity: 84.65				
Unconsolidated sediment	84.77	80.13	13.64	94.67	94.67
Mixed tufts of small hydroids (Bio-cns)	4.42	2.57	1.86	3.04	97.71
Leptophytum acervatum (M0272)	3.86	1.71	0.9	2.02	99.73
Group G	Average similarity: 60.65				
Unconsolidated sediment	74.54	58.33		96.18	96.18
Leptophytum acervatum (M0272)	8.33	1.39		2.29	98.47
Group H	Average similarity: 91.20				
Unconsolidated sediment	91.2	91.2		100	100
Group I	Average similarity: 83.80				
Unconsolidated sediment	84.26	79.94	14.95	95.4	95.4
Sycozoa sp. 002 RSA SPN (U0151)	1.08	0.93		1.1	96.5
Placospongia sp. 001 RSA (P0032)	2.31	0.93	0.58	1.1	97.61
Group J	Average similarity: 62.42				
Unconsolidated sediment	65.24	51.12	2.02	81.9	81.9
Mixed tufts of small hydroids (Bio-cns)	8.67	5.03	2.25	8.06	89.97
Leptophytum acervatum (M0272)	8.84	4.39	0.84	7.04	97.01
Group K	Average similarity: 75.15				
Unconsolidated sediment	73.61	67.13	41.86	89.32	89.32
Tropiometra carinata (E0007)	5.56	4.48	3.35	5.95	95.28
Pseudopotamilla sp. 001 RSA (W0003)	1.54	1.08	4.04	1.44	96.71
Group L	Average similarity: 74.94				
Unconsolidated sediment	57.48	47.99	3.9	64.04	64.04
Hypnea tenuis (M0151)	33.68	24.59	2.31	32.81	96.85
Group M	Average similarity: 73.06				
Hypnea tenuis (M0151)	56.48	49.31	6.09	67.49	67.49
Unconsolidated sediment	18.24	14.63	5.43	20.03	87.52
Group N	Average similarity: 55.83				
Soft short mixed macro-algae bin (Bio-mal)	45.68	32.84	1.85	58.82	58.82
Unconsolidated sediment	27.62	14.44	2.16	25.87	84.69
Amphiroa ephedraea (M0010)	5.48	3.33	1.63	5.97	90.66
Group O	Average similarity: 56.35				
Amphiroa ephedraea (M0010)	29.8	22.8	3.41	40.46	40.46
Soft short mixed macro-algae bin (Bio-mal)	13.66	7.97	1.31	14.14	54.61
Leptophytum acervatum (M0272)	9.26	6.22	2.62	11.03	65.64
Unconsolidated sediment	8.28	5.75	1.78	10.21	75.85
Codium incognitum (M0276)	4.63	3.36	2.47	5.96	81.81
Plocamium corallorhiza (M0194)	4.46	2.7	1.18	4.78	86.59
Calliblepharis fimbriata (M0257)	3.18	1.98	1.01	3.52	90.11

Group P	Average similarity: 48.61				
Hypnea spicifera (M0150)	10.88	10.19		20.95	20.95
Gelidium capensis (M0277)	9.26	8.8		18.1	39.05
Plocamium corallorhiza (M0194)	15.97	6.02		12.38	51.43
Hypnea tenuis (M0151)	8.1	5.09		10.48	61.9
Amphiroa anceps (M0013)	3.01	2.78		5.71	67.62
Unconsolidated sediment	3.47	2.78		5.71	73.33
Portieria hornemannii (M0203)	13.19	2.31		4.76	78.1
Halimeda cuneate (M0264)	4.17	1.85		3.81	81.9
Soft short mixed macro-algae bin (Bio-mal)	2.55	1.85		3.81	85.71
Leptophytum acervatum (M0272)	5.56	1.85		3.81	89.52
Group Q	Average similarity: 48.69				
Unconsolidated sediment	20.72	15.74	3.37	32.33	32.33
Hypnea tenuis (M0151)	17.01	11.96	2.47	24.56	56.89
Soft short mixed macro-algae bin (Bio-mal)	16.78	7.72	1.53	15.85	72.74
Amphiroa ephedraea (M0010)	12.85	5.32	1.26	10.94	83.68
Portieria hornemannii (M0203)	3.59	1.85	3.65	3.8	87.48
Polyclinum isipingense (U0027)	4.05	1.47	0.84	3.01	90.49
Group R	Average similarity: 70.68				
Lobophora variegata (M0168)	37.19	33.33	5.2	47.16	47.16
Mixed tufts of small hydroids (Bio-cns)	10.8	7.1	1.4	10.04	57.21
Amphiroa ephedraea (M0010)	6.94	6.33	11.84	8.95	66.16
Unconsolidated sediment	9.26	5.56	2.31	7.86	74.02
Macrorhynchia sp. 003 RSA (C0064)	4.63	4.32	16.17	6.11	80.13
Tedania sp. 003 RSA (P0237)	5.09	4.32	16.17	6.11	86.24
Leptophytum acervatum (M0272)	6.94	2.62	4.91	3.71	89.96
Group S	Average similarity: 50.38				
Amphiroa ephedraea (M0010)	30.39	20.09	1.86	39.88	39.88
Lobophora variegata (M0168)	24.41	16.46	1.91	32.68	72.56
Red coralline algae mix bin (Bio-crs)	5.98	3.34	1.2	6.63	79.2
Leptophytum acervatum (M0272)	3.28	1.98	1.39	3.93	83.12
Mixed tufts of small hydroids (Bio-cns)	5.13	1.88	0.58	3.73	86.85
Unconsolidated sediment	3.7	1.48	0.74	2.94	89.79
Group T	Average similarity: 32.41				
Lobophora variegata (M0168)	13.66	11.11		34.29	34.29
Mixed tufts of small hydroids (Bio-cns)	10.88	4.17		12.86	47.14
Amphiroa ephedraea (M0010)	19.44	2.78		8.57	55.71
Tennysonia stellate (B0022)	3.47	1.85		5.71	61.43
Cystodytes dellachiajei (U0048)	2.31	1.85		5.71	67.14
Comanthus wahlbergii (E0004)	2.08	1.39		4.29	71.43
Tropiometra carinata (E0007)	2.31	1.39		4.29	75.71
Haliclona sp. 004 RSA (P0093)	2.55	1.39		4.29	80
Mycale sp. 004 RSA (P0091)	1.62	1.39		4.29	84.29
Peyssonnelia capensis (M0187)	3.01	1.39		4.29	88.57
Group U	Average similarity: 41.13				
Placospongia sp. 001 RSA (P0032)	19.91	12.19	2.25	29.64	29.64
Reteporella lata (B0020)	5.56	3.94	4.3	9.57	39.21
Mixed tufts of small hydroids (Bio-cns)	4.86	3.4	2.33	8.26	47.47
Chondrilla sp. 004 (P0240)	4.63	2.55	0.9	6.19	53.66
Acabaria rubra (C0027)	3.59	2.39	1.37	5.82	59.47
Amphiroa ephedraea (M0010)	3.47	2.39	2.66	5.82	65.29
Alcyonium fauri (C0002)	2.2	1.7	1.97	4.13	69.42
Gigantopora polymorpha (B0011)	8.45	1.62	0.41	3.94	73.36
Macrorhynchia sp. 003 RSA (C0064)	2.43	1.47	1.32	3.56	76.92
Tennysonia stellate (B0022)	2.08	1	0.9	2.44	79.36
Tropiometra carinata (E0007)	1.74	0.93	1.83	2.25	81.61
Unconsolidated sediment	2.89	0.93	0.82	2.25	83.86
Sertularella arbuscula (C0032)	3.82	0.85	0.52	2.06	85.93
Adeonella purpurea (B0004)	3.01	0.77	0.53	1.88	87.8
Pseudodistoma sp. 003 SPN (U0083)	1.62	0.62	0.82	1.5	89.31
Comanthus wahlbergii (E0004)	1.5	0.62	0.57	1.5	90.81
Group V	Average similarity: 46.62				
Placospongia sp. 001 RSA (P0032)	24.07	14.35	1.08	30.78	30.78

Unconsolidated sediment	12.87	9.03	2.82	19.36	50.15
Chondrilla sp. 004 (P0240)	12.87	7.73	1.19	16.58	66.73
Mixed tufts of small hydroids (Bio-cns)	6.3	4.07	2.34	8.74	75.47
Sertularella arbuscula (C0032)	3.8	2.22	2.13	4.77	80.24
Amphiroa ephedraea (M0010)	3.52	1.53	0.99	3.28	83.52
Leptophytum acervatum (M0272)	1.48	1.11	3.43	2.38	85.9
Alcyonium fauri (C0002)	1.39	1.02	3.48	2.18	88.08
Tedania stylonychaeta (P0055)	1.2	0.97	6.64	2.09	90.17
Group W	Average similarity: 39.81				
Mixed tufts of small hydroids (Bio-cns)	8.1	6.48		16.28	16.28
Placospongia sp. 001 RSA (P0032)	8.1	6.02		15.12	31.4
Leptogorgia palma (C0023)	6.94	5.09		12.79	44.19
Amphiroa ephedraea (M0010)	4.86	3.7		9.3	53.49
Alcyonium fauri (C0002)	3.24	2.78		6.98	60.47
Sertularella arbuscula (C0032)	3.47	2.78		6.98	67.44
Pseudodistoma sp. 001 RSA (U0081)	3.01	1.85		4.65	72.09
Pseudodistoma sp. 002 RSA (U0080)	2.78	1.85		4.65	76.74
Macrorhynchia filamentosa (C0025)	2.55	1.39		3.49	80.23
Tropiometra carinata (E0007)	2.55	1.39		3.49	83.72
Unconsolidated sediment	10.19	1.39		3.49	87.21
Comanthus wahlbergii (E0004)	0.93	0.93		2.33	89.53
Group X	Average similarity: 53.62				
Amphiroa ephedraea (M0010)	20.83	17.39	5.31	32.44	32.44
Mixed tufts of small hydroids (Bio-cns)	9.61	8.04	3.33	14.99	47.43
Clathria sp. 001 RSA (P0207)	7.41	4.96	1.91	9.25	56.68
Leptophytum acervatum (M0272)	6.13	4.38	2.15	8.17	64.85
Unconsolidated sediment	4.98	3.29	1.8	6.14	70.98
Placospongia sp. 001 RSA (P0032)	5.38	1.7	0.66	3.18	74.16
Macrorhynchia sp. 003 RSA (C0064)	2.84	1.52	1.1	2.84	77
Sertularella arbuscula (C0032)	2.37	1.36	1.77	2.53	79.53
Alcyonium fauri (C0002)	1.56	1.04	1.52	1.94	81.47
Comanthus wahlbergii (E0004)	1.5	0.71	0.96	1.33	82.79
Amphiroa anceps (M0013)	1.74	0.68	0.61	1.26	84.06
Chondrilla sp. 004 (P0240)	3.07	0.66	0.78	1.23	85.29
Bio-crs	1.45	0.6	1.01	1.11	86.4
Didemnum sp. 029 RSA (U0173)	1.5	0.6	0.8	1.11	87.51
Pycnoclavella filamentosa (U0066)	1.04	0.48	0.77	0.89	88.41
Tedania sp. 003 RSA (P0237)	1.04	0.45	0.76	0.83	89.24
Arthrocardia carinata (M0017)	0.69	0.41	1.3	0.77	90.01
Group Y	Average similarity: 56.44				
Mixed tufts of small hydroids (Bio-cns)	13.33	10.88	3.19	19.28	19.28
Unconsolidated sediment	6.57	5.28	2.38	9.35	28.63
Leptophytum acervatum (M0272)	6.57	4.86	3.35	8.61	37.24
Amphiroa ephedraea (M0010)	5.09	3.98	3.87	7.05	44.3
Chondrilla sp. 004 (P0240)	5.74	3.94	1.94	6.97	51.27
Placospongia sp. 001 RSA (P0032)	9.81	3.84	0.77	6.81	58.08
Macrorhynchia sp. 003 RSA (C0064)	4.54	3.7	3.1	6.56	64.64
Gynandrocarpa placenta (U0086)	3.43	1.85	1.26	3.28	67.92
Clathria sp. 001 RSA (P0207)	2.59	1.85	2.19	3.28	71.21
Tropiometra carinata (E0007)	3.89	1.81	0.77	3.2	74.41
Macrorhynchia filamentosa (C0025)	3.7	1.76	1.97	3.12	77.52
Alcyonium fauri (C0002)	2.59	1.62	1.35	2.87	80.39
Comanthus wahlbergii (E0004)	2.5	1.34	2.42	2.38	82.77
Peyssonnelia capensis (M0187)	1.2	1.06	4.76	1.89	84.66
Arthrocardia carinata (M0017)	1.39	0.83	1.29	1.48	86.14
Pseudodistoma africanum (U0063)	1.02	0.65	2	1.15	87.28
Leptogorgia palma (C0023)	0.93	0.6	1.12	1.07	88.35
Sertularella arbuscula (C0032)	1.76	0.6	0.71	1.07	89.42
Reteporella sp. 001 RSA (B0019)	0.83	0.56	1.16	0.98	90.4
Group Z	Average similarity: 55.09				
Unconsolidated sediment	14.58	14.35		26.05	26.05
Mixed tufts of small hydroids (Bio-cns)	15.97	13.89		25.21	51.26
Peyssonnelia capensis (M0187)	5.09	3.7		6.72	57.98

Amphiroa ephedraea (M0010)	3.7	2.78		5.04	63.03
Tedania sp. 003 RSA (P0237)	2.78	2.31		4.2	67.23
Leptophytum acervatum (M0272)	9.72	2.31		4.2	71.43
Macrorhynchia filamentosa (C0025)	4.17	1.85		3.36	74.79
Clathria sp. 001 RSA (P0207)	2.55	1.85		3.36	78.15
Pseudodistoma africanum (U0063)	1.39	1.39		2.52	80.67
Leptogorgia palma (C0023)	3.47	1.39		2.52	83.19
Placospongia sp. 001 RSA (P0032)	1.85	1.39		2.52	85.71
Didemnum sp. 003 RSA (U0078)	0.93	0.93		1.68	87.39
Pseudodistoma sp. 017 RSA (U0002)	0.93	0.93		1.68	89.08
Chondrilla sp. 004 (P0240)	3.24	0.93		1.68	90.76
Group AA	Average similarity: 53.65				
Placospongia sp. 001 RSA (P0032)	26.39	19.56	2.23	36.47	36.47
Amphiroa ephedraea (M0010)	7.99	6.36	2.73	11.86	48.33
Unconsolidated sediment	7.87	5.13	2.21	9.57	57.9
Mixed tufts of small hydroids (Bio-cns)	6.17	4.22	1.73	7.86	65.76
Leptophytum acervatum (M0272)	4.67	2.48	0.94	4.63	70.38
Macrorhynchia sp. 003 RSA (C0064)	3.32	2.08	1.83	3.87	74.25
Sertularella arbuscula (C0032)	2.66	1.84	1.8	3.43	77.68
Alcyonium fauri (C0002)	2.16	1.39	1.83	2.59	80.27
Comanthus wahlbergii (E0004)	2.12	1.37	1.38	2.56	82.83
Chondrilla sp. 004 (P0240)	2.24	0.98	0.86	1.83	84.66
Reteporella lata (B0020)	2.39	0.94	0.71	1.75	86.41
Gynandrocarpa placenta (U0086)	2.78	0.86	0.53	1.6	88.01
Clathria sp. 001 RSA (P0207)	1.43	0.8	1.26	1.49	89.5
Gigantopora polymorpha (B0011)	1.77	0.72	0.6	1.35	90.85
Group AB	Average similarity: 55.73				
Unconsolidated sediment	14.95	13.27	6.12	23.81	23.81
Leptophytum acervatum (M0272)	14.35	9.46	1.59	16.97	40.78
Amphiroa ephedraea (M0010)	11.84	9.06	2.62	16.26	57.04
Mixed tufts of small hydroids (Bio-cns)	10.71	6.64	1.59	11.91	68.95
Gynandrocarpa placenta (U0086)	4.17	2.31	1.02	4.15	73.1
Placospongia sp. 001 RSA (P0032)	4.43	2.14	1.03	3.84	76.94
Clathria sp. 001 RSA (P0207)	2.45	1.59	1.21	2.85	79.79
Eudistoma sp. 010 RSA (U0007)	2.45	1.41	1.38	2.53	82.32
Cheilosporum sagittatum (M0063)	2.98	1.21	0.73	2.18	84.49
Sertularella arbuscula (C0032)	2.05	1.17	1.3	2.1	86.59
Macrorhynchia sp. 003 RSA (C0064)	1.92	0.86	0.79	1.54	88.13
Red coralline algae mix bin (Bio-crs)	1.32	0.64	0.78	1.15	89.28
Ralfsia expansa (M0214)	1.32	0.55	1.06	0.99	90.27
Group AC	Average similarity: 58.64				
Leptophytum acervatum (M0272)	19.91	14.97	10.29	25.53	25.53
Unconsolidated sediment	17.13	14.66	4.72	25	50.53
Amphiroa ephedraea (M0010)	20.6	13.97	6.93	23.82	74.34
Mixed tufts of small hydroids (Bio-cns)	8.56	4.71	1	8.03	82.37
Lobophora variegate (M0168)	5.67	3.01	1.01	5.13	87.5
Haliclona sp. 019 RSA (P0211)	3.82	1.47	0.54	2.5	90
Group AD	Average similarity: 66.05				
Amphiroa ephedraea (M0010)	29.94	27.78	11.55	42.06	42.06
Unconsolidated sediment	16.2	12.65	3.64	19.16	61.21
Leptophytum acervatum (M0272)	14.51	12.5	5.2	18.93	80.14
Lobophora variegate (M0168)	3.86	3.09	5.77	4.67	84.81
Mixed tufts of small hydroids (Bio-cns)	3.7	2.47	1.32	3.74	88.55
Group AE	Average similarity: 60.57				
Unconsolidated sediment	19.49	16.84	4.89	27.81	27.81
Mixed tufts of small hydroids (Bio-cns)	13.7	11.07	3.98	18.28	46.08
Amphiroa ephedraea (M0010)	11.94	9.96	3.01	16.44	62.53
Sertularella arbuscula (C0032)	6.9	4.55	1.51	7.51	70.04
Placospongia sp. 001 RSA (P0032)	5.56	3.1	1.02	5.11	75.15
Leptophytum acervatum (M0272)	5	3.08	1.65	5.08	80.23
Gynandrocarpa placenta (U0086)	2.64	1.57	1.52	2.6	82.83
Comanthus wahlbergii (E0004)	1.94	1.11	1.59	1.83	84.66
Arthrocardia carinata (M0017)	2.31	1.05	0.75	1.73	86.39

Dictyota dichotoma (M0104)	1.48	0.81	1.09	1.34	87.74
Tedania sp. 001 RSA (P0195)	1.53	0.74	0.91	1.22	88.96
Tedania sp. 003 RSA (P0237)	1.34	0.6	0.71	0.99	89.94
Laurencia complanata (M0162)	1.25	0.59	0.83	0.97	90.91
Group AF	Average similarity: 50.24				
Mixed tufts of small hydroids (Bio-cns)	14.4	11.3	3.03	22.49	22.49
Unconsolidated sediment	16.11	10.85	2.07	21.61	44.09
Amphiroa ephedraea (M0010)	11.39	7.19	1.66	14.31	58.41
Placospongia sp. 001 RSA (P0032)	8.38	5.08	1.59	10.12	68.52
Leptophytum acervatum (M0272)	6.16	4.44	2.56	8.85	77.37
Sertularella arbuscula (C0032)	4.72	2.97	1.81	5.92	83.29
Alcyonium fauri (C0002)	1.39	0.92	1.96	1.82	85.11
Leptogorgia palma (C0023)	3.84	0.68	0.34	1.35	86.46
Clathria sp. 001 RSA (P0207)	1.9	0.65	0.66	1.29	87.75
Adeonella purpurea (B0004)	1.3	0.63	0.82	1.25	89
Hildenbrandia rubra (M0145)	1.34	0.56	0.89	1.11	90.11
Group AG	Average similarity: 39.77				
Unconsolidated sediment	16.51	11.13	1.59	27.97	27.97
Placospongia sp. 001 RSA (P0032)	15.67	9.65	1.3	24.26	52.24
Leptogorgia palma (C0023)	15.44	6.1	0.67	15.34	67.58
Mixed tufts of small hydroids (Bio-cns)	5.7	3.17	1.26	7.96	75.53
Tropiometra carinata (E0007)	7.14	2.6	0.6	6.55	82.08
Sertularella arbuscula (C0032)	3.47	1.3	0.75	3.28	85.36
Chondrilla sp. 004 (P0240)	2.8	1.14	0.88	2.86	88.22
Leptophytum acervatum (M0272)	2.12	0.98	0.78	2.46	90.68
Group AH	Average similarity: 59.26				
Unconsolidated sediment	51.85	44.16	3.67	74.52	74.52
Placospongia sp. 001 RSA (P0032)	9.05	3.77	0.68	6.36	80.88
Leptophytum acervatum (M0272)	6.94	3.5	1.38	5.9	86.78
Mixed tufts of small hydroids (Bio-cns)	4.12	1.61	0.97	2.71	89.5
Group AI	Average similarity: 54.96				
Unconsolidated sediment	29.21	23.76	4.39	43.22	43.22
Leptophytum acervatum (M0272)	14.77	9.14	1.63	16.62	59.85
Mixed tufts of small hydroids (Bio-cns)	11.76	7.59	1.55	13.82	73.66
Mycale sp. 005 RSA (P0029)	5.37	3.64	2	6.63	80.29
Clathria sp. 001 RSA (P0207)	5.97	3.42	1.31	6.21	86.5
Leptogorgia palma (C0023)	5.79	2.06	0.75	3.74	90.25
Group AJ	Average similarity: 43.99				
Unconsolidated sediment	29.27	18.49	1.99	42.04	42.04
Mixed tufts of small hydroids (Bio-cns)	16.54	11.2	1.6	25.45	67.5
Placospongia sp. 001 RSA (P0032)	8.74	3.12	0.68	7.09	74.58
Leptophytum acervatum (M0272)	5.43	2.59	1.69	5.9	80.48
Aplidiopsis sp. 004 RSA (U0167)	6.07	1.96	0.5	4.45	84.93
Mycale sp. 004 RSA (P0091)	4.06	1.79	0.7	4.07	89
Group AK	Average similarity: 46.85				
Unconsolidated sediment	35.12	27.98	3.12	59.72	59.72
Placospongia sp. 001 RSA (P0032)	9.85	5.31	1.32	11.34	71.06
Adeonella sp. 001 RSA (B0001)	11.11	3.75	0.85	8	79.06
Homophyton verrucosum (C0016)	5.36	2.8	1.11	5.98	85.04
Thuiaria articulata (C0035)	5.16	1.81	0.65	3.86	88.89
Group AL	Average similarity: 56.94				
Unconsolidated sediment	31.64	27.16	12.7	47.7	47.7
Leptogorgia palma (C0023)	23.46	20.22	15.13	35.5	83.2
Group AM	Average similarity: 42.37				
Leptogorgia palma (C0023)	28.03	19.11	2.12	45.1	45.1
Mixed tufts of small hydroids (Bio-cns)	16.56	7.64	0.85	18.03	63.13
Mycale sp. 004 RSA (P0091)	9.36	5.95	1.61	14.05	77.18
Pseudopotamilla sp. 001 RSA (W0003)	7.72	3.24	0.75	7.65	84.83
Homophyton verrucosum (C0016)	5.25	2.51	1.25	5.92	90.74
Group AN	Average similarity: 38.19				
Psammocinia sp. 008 RSA SPN (P0173)	12.29	7.78	1.71	20.38	20.38
Mixed tufts of small hydroids (Bio-cns)	9.26	5.97	1.42	15.64	36.01
Leptogorgia palma (C0023)	8.01	4.31	0.96	11.28	47.3

Macrorhynchia sp. 003 RSA SPN (C0064)	11	3.83	0.62	10.04	57.34
Homophyton verrucosum (C0016)	3.88	2.62	1.45	6.87	64.21
Chondrilla sp. 004 (P0240)	6.09	2.55	0.72	6.68	70.89
Sertularella arbuscula (C0032)	4.1	2.16	1.18	5.66	76.55
Mycale sp. 004 RSA (P0091)	4.13	2.02	1.08	5.3	81.85
Placospongia sp. 001 RSA (P0032)	5.7	1.34	0.45	3.5	85.34
Tedania stylonychaeta (P0055)	1.99	0.89	0.87	2.33	87.67
Didemnum sp. 007 (U0114)	1.21	0.5	0.93	1.32	89
Wrightella sp. 001 RSA (C0036)	1.1	0.43	0.58	1.13	90.13
Group AO	Average similarity: 45.40				
Sertularella arbuscula (C0032)	18.44	14.51	2.99	31.95	31.95
Mixed tufts of small hydroids (Bio-cns)	16.82	10.56	1.13	23.25	55.2
Homophyton verrucosum (C0016)	10.57	6.2	1.11	13.66	68.86
Leptogorgia palma (C0023)	8.1	3.55	1.09	7.82	76.68
Eunicella papillosa (C0012)	4.55	3.06	1.6	6.73	83.41
Tropiometra carinata (E0007)	8.33	1.51	0.27	3.33	86.74
Alcyonium fauri (C0002)	2.55	1.39	0.96	3.06	89.8
Group AP	Average similarity: 41.08				
Homophyton verrucosum (C0016)	11.25	7.81	2.59	19.01	19.01
Placospongia sp. 001 RSA (P0032)	13.06	6.12	0.85	14.9	33.91
Chondrilla sp. 004 (P0240)	9.07	5.82	1.42	14.17	48.08
Sertularella arbuscula (C0032)	5.51	3.36	1.18	8.19	56.27
Eunicella papillosa (C0012)	5.14	3.25	1.64	7.91	64.19
Mixed tufts of small hydroids (Bio-cns)	8.15	3.19	0.7	7.76	71.95
Unconsolidated sediment	8.29	3.01	0.65	7.34	79.29
Ideogorgia capensis (C0047)	6.02	2.88	0.92	7.01	86.3
Alcyonium fauri (C0002)	2.08	1.4	2.49	3.41	89.71
Group AQ	Average similarity: 42.24				
Leptogorgia palma (C0023)	26.98	16.18	1.63	38.31	38.31
Chondrilla sp. 004 (P0240)P0240	14.02	9.48	1.4	22.44	60.75
Homophyton verrucosum (C0016)	5.56	4.81	6.15	11.38	72.13
Sertularella arbuscula (C0032)	5.16	2.54	1.48	6	78.13
Unconsolidated sediment	4.76	2.07	0.67	4.91	83.04
Placospongia sp. 001 RSA (P0032)	5.89	1.79	0.71	4.23	87.27
Eunicella papillosa (C0012)	2.25	1.17	0.76	2.77	90.03
Group AR	Average similarity: 65.15				
Mixed tufts of small hydroids (Bio-cns)	44.27	37.4	6.23	57.41	57.41
Pyura stolonifera (U0088)	21.01	13.53	1.57	20.76	78.17
Macrorhynchia sp. 001 RSA SPN (C0017)	9.38	5.31	1.04	8.15	86.32

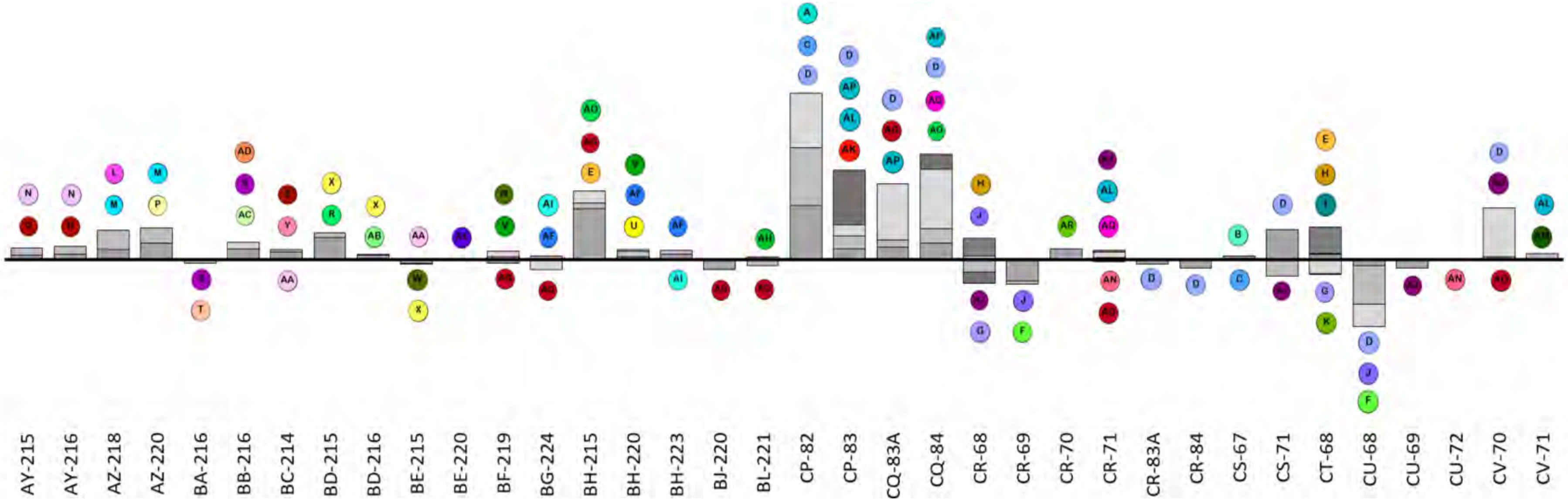


Figure 4.8: Difference in average similarity as calculated by SIMPER analysis in PRIMER for the complement (n = 10 samples) quadrats at each locality and the groups as per CLUSTER analysis of the quadrat point count data, irrespective of location affinity (values above the line indicate an improvement in the similarity of the defined biotope subunits in comparison to the *a priori* grouping of quadrat defined by sample location; values below the line are indicative of a poorer association within the biotope subunit).

Chapter 5 Ichthyofauna as indicators of change in Long-Term Ecological Research (LTER)

5.1 Objective

This chapter aims to describe the ichthyofauna populations associated with the broader biotopes. A subset of the data collected during the first 18 months of BELTER was used to investigate the ability of the analysed dataset to recorded spatial and temporal differences in ichthyofauna distribution and composition. This is a preliminary study using a time-curtailed dataset and seasonal changes were used as a proxy to investigate the ability of the dataset to record change over time. The argument was that if the selected sub-dataset used is able to observe seasonal change over the short term (18 months) for seasonal driven changes then it would be sensitive to climate-driven change over many years.

Sixty-minute Stereos Baited Remote Video (sBRUV) steams are collected as part of the BELTER platform however, in this chapter, a 15-minute analysis is done of the single video stream and although BELTER includes length analysis in its reporting framework it falls outside the scope of this chapter.

5.1.1 Specific goals

- Assess the length of video needed to obtain a representative estimation of species composition and relative abundance,
- assess sample locality proximity and the possibility that an individual fish may visit more than one BRUV system during a sample event and
- assess the ichthyofauna assemblage for each described broader biotope type over space and time.

5.2 Introduction

5.2.1 Ichthyofauna distribution and habitat use

South Africa’s east and south coast regions are known for high fish species endemism with richness generally increasing from the cool temperate west to the warm temperate east (Turpie et al. 2000, Awad et al. 2002b). Nearshore fish species are heavily impacted due to increasing fishing pressure (Götz et al. 2009a, Chalmers 2012), habitat transformation and loss (Ortega-Cisneros et al. 2018). Spatial and temporal distribution of fish species in the seascape differ, some through the course of a species' life history due to ontogenetic diet shifts, feeding, migration, aggregation and spawning (Beckley 1985, Smale 1986, Compton et al. 2012, Fobert et al. 2020), while others have a high residency or site fidelity (Kerwath et al. 2007). The use of different environments, or biotopes, within the seascape by ichthyofauna, has important management implications (Kerwath et al. 2007, Bennett et al. 2017) and should be taken into account in Marine Spatial Planning (MSP) and Ecosystem-based management approaches (Reis-Filho et al. 2019) especially in developing fisheries management strategies for the subsistence, recreational and commercial fishing industries.

5.2.2 Benthic biotopes and ichtyofauana

The link between reef fish distribution, benthic habitat type and associated biotic, the biotope, is increasingly recognised (Beckley 1985, Heyns 2015, Heyns et al. 2016, Heyns-Veale et al. 2016). Reef associated fish depend on a wide variety of benthic reef invertebrates for food (Buxton and Clarke 1986, Coetzee 1986, Mann and Buxton 1992) and changes in the associated reef fish populations due to fishing pressures have been shown to drive changes in benthic community composition (Götz et al. 2009a). The inability of sessile benthic species to escape short-term variations in the environment suggest the importance of these communities in evaluating long-term changes in ecosystem structure and in understanding the response of fish communities to long-term change, both natural and anthropogenic (Chalmers 2012, Parker 2015). Investigation of fish community shifts within Marine Protected Areas (MPA), where anthropogenic impacts, such as fishing are absent or managed, provides insight into the natural drivers of environmental change (Cowley et al. 2002, Chalmers 2012, Heyns-Veale et al. 2019a) and interaction between sessile and sedentary benthic biota and ichthyofauna (Heyns 2015).

5.2.3 Indicator species

It has been suggested that indicator species could be useful to assess changes, especially in instances where a direct link exists between the stressor and the species response, e.g. to assess fishing pressure on red roman, *Chrysoblephus laticeps* (Bennett 2007, Götz et al. 2008, Harasti et al. 2018). Red roman are members of the well-represented family Sparidae, endemic and a favourite reef line angling fish. They inhabit shallow coastal reef systems and are known for their high residential fidelity with small home ranges (Kerwath et al. 2007). They feed on benthic organisms, mainly crinoids, but their diet also includes algae, sponges, cnidarians and bryozoans (Buxton 1984, Götz 2005, Götz et al. 2009a). The species impacts on the abundance of prey organisms and influences interspecific competition in subtidal reef fish communities (Götz et al. 2009a). As with many sparids, this species is a protogynous hermaphrodite. It is vulnerable to over-exploitation and has been identified as a species possibly sensitive to climate change (Ortega-Cisneros et al. 2018), with life-history traits having been found to differ between protected and exploited areas (Götz 2005). In addition to the presence of indicator species, research has suggested that the co-occurrence patterns of some chondrichthyan species may form umbrella species-complexes that indirectly inform on other taxa, such as teleosts (Osgood et al. 2020).

5.2.4 Variables

The character of the benthic habitat and the sessile and sedentary benthic biota it supports is an important variable governing the ichthyofauna species diversity, distribution and abundance within the seascape (Götz et al. 2014, Heyns 2015). Physical environmental variables such as depth (Heyns et al. 2016, Heyns-Veale et al. 2016, Wahab et al. 2018), temperature (Bernard 2012, Sbragaglia et al. 2019) and tidal currents (Compton et al. 2012) have also been shown to play an important role in species distribution and assemblage composition of both the biota of the biotic boundary layer and the ichthyofauna that use the resource. Resource availability, provided by the benthic sessile biotic boundary layer, and resources used, by predators of this biotic layer, play important role in the community structure of both (Götz et al. 2009a,2009b).

5.2.5 Baited Remote Underwater Video (BRUV)

The use of underwater video systems and Baited Remote Underwater Video (BRUV) equipment in the study of ichthyofauna is well established (Pelletier et al. 2012, Mallet 2014, Mallet and Pelletier 2014, Langlois et al. 2018, 2020). This non-destructive sampling method (Bernard et al. 2014), has been widely applied in many different environments including estuaries (Gladstone et al. 2012, Wakefield et al. 2013), intertidal, demersal and pelagic waters (Heagney et al. 2007, Folpp et al. 2013, Whitmarsh et al. 2017, Langlois et al. 2018, Clarke et al. 2019). Short-term studies using BRUV platforms include validation of management strategies, especially those for protected versus unprotected systems (Sanguinetti 2013, Heyns-Veale et al. 2019a, Dames 2021), assessment of spatial and temporal variation in fish (Williams et al. 2019) and their habitat (Colton and Swearer 2012, Fitzpatrick et al. 2012, Bach et al. 2019, Heyns-Veale et al. 2019a), the effect of noise on fish movement (Roberts et al. 2016), the development of monitoring frameworks (Bernard 2012, Chalmers 2012) and the identification of indicators (Hill et al. 2018) to assess fish diversity, abundance and size composition (De Vos 2012, Sanguinetti 2013, Heyns 2015, Heyns-Veale et al. 2016, Cundy et al. 2017, Dames et al. 2020, Dando 2020, Dames 2021) (Table 5.1).

BRUVs have been shown to be valuable tools in the construction of long-term datasets that allow for the observation of changes in temperature and species interactions, changes in the benthic community and fish community structure and abundance (Vergés et al. 2016, Smith et al. 2020). Long-term Ecological Research (LTER) on subtidal ichthyofauna in South Africa, primarily for the observation of subtidal reef fishes, using BRUV systems was established in 2007 in the Tsitsikamma Marine Protected Area (TMPA) of the Garden Route National Park (Parker 2015). A short-term dataset also exists for the Goukamma MPA (GMPA) for the period 2013 to 2017 (Dando 2020) and several similar programmes have been established internationally (Table 5.2).

Table 5.1: Publications of short-term research with datasets of no more than three years using BRUVs within South African waters.

Study area	Data collection times/duration	Number of deployments	Reference
False Bay	September to December 2012	64	(Sanguinetti 2013)
Still Bay	11 October to 30 November 2011	29	(De Vos 2012, De Vos et al. 2014)
Pondoland	January 2014 and May 2015	50	(Heyns-Veale et al. 2019a)
Amathole	May 2015 and March 2016	73	(Heyns-Veale et al. 2019a)
Algoa Bay, Bird Island	March and April 2014	47	(Heyns-Veale et al. 2019a)
De Hoop	March to April 2015	65	(Heyns-Veale et al. 2019a)
Tsitsikamma	February 2013 and 2014	101	(Heyns-Veale et al. 2019a)
	Jun 2008-February 2010	28	
iSamangaliso	November 2016 to June 2017	105	(Dames 2021)
	November 2016	32	(Dames et al. 2020)
Betty's Bay	ca. 2014 (12 days)	58	(Roberson et al. 2015)

The use of BRUV systems (see Supplementary Table 5.6) and the assumptions and comparisons made when using them are associated with many caveats. Strengths and limitations have been broadly identified (Bernard and Götz 2012, Harvey et al. 2013). Variation includes differences in data collection methodologies (Cundy et al. 2017), camera configuration, bait amounts used (Hardinge et al. 2013, Pearson and Stevens 2015), bait type (Dorman et al. 2012), bait container type and plume size (Heagney et al. 2007, Taylor et al. 2013), deployment time (Bernard 2012, Bernard and Götz 2012, Harasti et al. 2015), the effect of currents, temperature and visibility (Harvey et al. 2013). Research has furthermore addressed and assessed sampling and statistical methods used for long-term monitoring of subtidal reef fishes (Parker 2015).

Table 5.2: Long-term Ecological Research (LTER) publications of studies of fish populations and interactions using Baited Remote Underwater Video (BRUV) systems.

Study site	**Year**	**Methodology**	**Interest and ref.**
Solitary Island region, New South Wales, Australia	2002-2011	12 sites, 25 km of coast, 3 replicates at each site, depth 15-21m, BRUV separation approximately 200 m, bait *Sardinops neopilchardus* (amount not provided), deployment time 30 min, sampled annually, MaxN	Changes in temperature and species interaction (Vergés et al. 2016)
	2002-2018 not 2012, 2016, 2017	3 replicates, 5 different reef systems, at each site, 200 m apart, deployed within 5-10 min of each other, 30 min deployment time, annually, 800 g of bait, 1.5 m bait arm, counts within 3 m, *Sardinops neopilchardus*, MaxN, trophic guilds, total MaxN.	Kelp loss and shift in trophic composition (Smith et al. 2020)
Houtmans Abrolhos Island, Australia	2005-2010 and 2013	4 sites, 220 deployments, 8-26 m, 60 min, 800 g bait *Sardinops* spp., mesh bag, 1.2 m bait arm, counts within 7 metres, 250 m separation, MaxN	Response to long-term protection (Bornt et al. 2015)
Port Stephens-Great Lakes Marine Park, NSW, Australia	2006 to 2017 various intervals	13 locations, 20-50 m deep, 30 min deployment, 4 at a time, about 200 m separation, about 1000g bait, *Sardinops neopilchardus*, 1.5 m bait arm, MaxN	Increase in relative abundance and size of snapper (Harasti et al. 2018)
Tsitsikamma, Rheeders Reef	2006-2013, BRUV data only 2013	maximum depth 30m, About 1000g pilchard, 1.2 m in front of cameras, 60 min, MaxN	Sample and statistical method evaluation (Parker 2015)
Goukamma	2013-2017	328 deployments, 5 – 41.5 m depth, MaxN, annual and biannually, *Sardinops sagax*	Ichthyofauna community structure (Dando 2020)

Although deployment time varies greatly among studies from as little as 15 minutes (Misa et al. 2016) to more than 90 minutes (Brooks et al. 2011) recent guidelines (Langlois et al. 2020) and publications use a deployment time of 60 minutes (Heyns 2015, Whitmarsh et al. 2017, Heyns-Veale et al. 2019a). A study conducted within the TMPA suggests that only 29 minutes is required to observe 95% of the ichthyofaunal species, and 48 minutes to detect 95% of their maximum abundance (Bernard 2012, Bernard and Götz 2012).

In an attempt to standardise methodologies, most research in subtidal systems make use of large sBRUV (stereo BRUV) systems with a 700 mm separation between cameras, turned 7 degrees inward, a 1.5 m bait arm with PVC bait canister, 800 to 1000 g of *Sardinops sagas* bait, deployed a minimum of 300 m apart, for 60 minutes (Heyns 2015, Parker 2015, Langlois et al. 2018, 2020, Heyns-Veale et al. 2019a, Dames et al. 2020).

5.2.6 Standardisation

Standardisation of sample equipment design, bait, and deployment methodologies allows for the temporal and spatial comparison of datasets (Dorman et al. 2012, Harvey et al. 2013). Such standardisation may not, however, be attainable as new approaches and applications are driven by increased technological advancement in available equipment. In mitigation, it is suggested that datasets should rather include extensive metadata records on the technical specifications of the equipment used, data analysis methods and software, as this would allow for comparison between different BRUV setups and data analysis used in data collection or the study thereof (Whitmarsh et al. 2017). Biases due to the effect of multiple variables that cannot be controlled should be strongly taken into account, as they may reduce the sensitivity of the methods used to detect long-term change (Bernard and Götz 2012).

5.2.7 Ichthyofauna research in Algoa Bay

Recently research on ichthyofauna in Algoa Bay using BRUV systems assessed the effect of environmental protection on fish communities within and outside the Bird Island Marine Protected Area (MPA) (Heyns-Veale et al. 2019a). The investigation compared data collected from reefs surrounding the Bird Island group to those collected from Riy Banks, a submerged rocky outcrop located on the discontinuous Cape Recife Bird Island Ridge, recognised as the boundary between Algoa Bay and the continental shelf waters (Goschen and Schumann 2011). It was found that species targeted by commercial and recreational fisheries were more abundant inside the MPA than outside (Heyns-Veale et al. 2019a).

Non-BRUV research conducted on ichthyofauna in Algoa Bay includes that on larvae and juvenile fish (Lasiak 1981, 1986, Beckley 1984, 1985, 1986, Pattrick and Strydom 2008, Pattrick 2013, Pattrick et al. 2013, Costalago et al. 2018), age, abundance, growth and feeding of reef fish (Coetzee and Baird 1981, Lasiak 1984, Buxton and Clarke 1986, Coetzee 1986, Bennett et al. 2017, Ensair 2019), pelagic fish

(Potter 2013), elasmobranchs (Smale 1991, Dicken and Booth 2013, Dicken et al. 2013) and commercial and recreational fishing activities (Chalmers 2012).

5.2.8 SAEON Benthic Ecosystem Long-Term Ecological Research (BELTER) platform

A major limitation of ichthyofaunal research initiatives, including short and long-term efforts, is that these programmes were established independently, use different methodologies and are not standardised, thereby making direct comparisons problematic (Bernard 2012, Bernard et al. 2014, Parker 2015). The SAEON Benthic Ecosystem Long-Term Ecological Research (BELTER) programme will develop, through this study, a standard methodology for spatial and temporal data collection in LTER sites established along the South African coast in all ecoregions, within and outside MPAs.

This study aims to describe the fish populations associated with the broader biotopes identified in the previous chapters. The investigation will assess species occurrence and relative abundance. BELTER makes use of sBRUV systems of which the design has been modified (see Supplementary Table 5.6 for the Technical report) to allow for deployment in shallow coastal waters, deployable from a small coastal vessel, and if needed can be deployed and retrieved routinely by hand. The compact form, smaller frames, and smaller bait canister size set it aside from other BRUV systems.

5.3 Material and methods

The Baited Remote Underwater Video system (BRUVs) used in this study were equipped with two Hero 5 Black GoPro action cameras, separated by 500 mm and turned inward by five degrees toward a one-metre long bait arm with a small bait canister able to hold 250 to 350 g of bait (*Sardinops sagax*) (description given in Supplementary Table 5.1). BRUV systems were deployed for 60 minutes at predetermined sample locations set a minimum of 150 metres apart. This grid size was selected based on research on reef fish movement (Bennett 2007, Bernard 2012) and subsequently also used for sampling benthos (Chapters 3 and 4).

BRUV data was collected from one station in the Tsitsikamma Marine Protected Area (TMPA), Garden Route National Park a SAEON BELTER satellite sentinel site and two stations, White Sands Reef (WSR) and St Croix Complex (SCC) within the Algoa Bay Sentinel Site (ABSS). Biotope subunit description in Chapter 4 showed connectivity between WSR and SCC stations for both habitat type and community structure (shared biotope subunits). Data from TMPA was subsequently included in this study to ensure greater geographical separation between stations from which the test datasets were constructed to investigate the length of video segment needed in the analysis.

Sample localities were selected as described in Chapter 2. The sample reference locality was determined using the onboard global positioning system (GPS) and the BRUVs were deployed as close to the reference locality as possible. Sampling was done from a small coastal research vessel equipped with a davit arm. A Hobo temperature logger was attached to the frame to allow recording of bottom water temperature during the deployment (set to record data every 5 min). BRUVs were deployed in batches of six, within 15 minutes and repeated until all localities were sampled.

The work is divided into distinct sections. The first assesses the length of a video stream that needs to be analysed. The second investigates the possible movement of *Chrysoblephus laticeps* between sample locations and the probability that the same fish is recorded in two different samples. The third describes the ichthyofauna assemblages observed within each of the broader biotopes (as defined in chapter 3) and tests if these are significantly different from each other.

5.3.1 Assessment of length of video stream needed for analysis

At the time of this study, the Addo Elephant National Park MPA only consisted of two satellite partially protected areas around the St Croix Island and Bird Island Group and the area was impacted by fishing. Previous assessment of optimum soak or deployment time for the observation of fish assemblage (Bernard 2012, Bernard and Götz 2012) was done within the TMPA. Utilising an MPA no-take zone as a control site is considered important as its biota is in a more 'natural condition' where anthropogenic stressors are reduced and managed. In assessing the length of the video stream that needed to be analysed and adopted in this BELTER it was deemed essential to include data collected from a station where the fish population were not harvested in comparison to WSR. Furthermore, analysis in Chapter 4 indicated that WSR and SCC share biotope subunits and it was considered more prudent for this assessment to used stations geographical further apart. Bi-annual BELTER, using the same platform, had been conducted for TMPA allowing for a direct comparison between WSR and TMPA.

Subsets of ten video data streams collected from WSR (ABSS) and Rheeders Reef (RR) in the TMPA were included in these investigations. Species diversity and the maximum number of species recorded in a frame (MaxN) is compared for two different lengths of video. MaxN was recorded for all ichthyofaunal species in a single frame every 15 seconds during a 60-minute video. The data collected for the first 15 minutes of the video and that for the entire 60-minute video data stream were compared using a nonparametric Mann-Whitney paired U test, and resemblance estimates were calculated. Four samples from WSR and six samples from TMPA were collected in good visibility conditions.

5.3.2 Assessment of movement of red roman *Chrysoblephus laticeps*

The main concern with the deployed sBRUV systems in close proximity to one another is the effect bait might have on the movement and attraction of fish. This es especially in consecutive deployment nearby where hypothetically an individual fish may visit and be recorded in one deployment and subsequent move, due to the attraction of the neighbouring bait plume, to a closely located BRUV and being counted again. This is especially concerning when large predatory species are included in the analysis. Many of these have the ability to move considerable distances in a very short time span. The use of large quantities of bait, variable currents or water column movement that facilitates the dispersion of the bait plume, bait plume extent and bait attraction are but a few concerns highlighted in the literature that may affect sample integrity (Parker 2015). In BELTER the research aims to observe the fish present in a small radius from the sampled point. The target species are those that are generally resident in the area and make use of the benthic environment. However, it is unknown if fish would move during deployment from one sample point to the next. This was investigated by visually identifying individual red roman, *Chrysoblephus laticeps*, for closely associated sample events. This was done by taking an image of the right side of each *C. laticeps* and comparing it visually with all others. Differences in colouration and colour patterns were the main characteristics used to identify individual fish (see Supplementary Table 5.1 for all fish compared).

5.3.3 Assessment of ichthyofauna assemblage for broader biotopes

In the initial 18 months of the BELTER a total of twelve sample events were completed at WSR and four as SCC in ABSS. This totals 306 deployments of which 134 were used in this study. This section includes data from 12 to 18 deployments per sample station (WSR and SCC). Adverse weather conditions and low visibility were the main reasons if less than 18 samples were included in the analysis per sample event. This represents four collection events during the study period. Ichthyofaunal species, teleosts and elasmobranchs were identified and counted using the better of the left or right camera footage. Species were identified and the maximum number of individuals of a particular species per frame counted (MaxN) using SeaGIS^{TM} EventMeasure software. MaxN is considered a conservative estimate of abundance as it only considers individuals of the same species in a single frame during the period for which the video footage is analysed.

Fish diversity and abundance are described for the broader biotope (the habitat, benthic algal, invertebrate and tunicate community) as defined in Chapter 3. Data collected during sampling events conducted during the same time of the year were assigned as representative of the season and this was used to assess any seasonal effects. A multivariate two-way (PERMANOVA) in PAST was used to test whether relative abundance (MaxN) for species differed among seasons (Table 5.3) and biotopes (Table 5.4). All data collected over the study period were subsequently pooled and the similarity percentage was calculated (SIMPER analysis in PRIMER) to determine species contribution to fish assemblage for the different biotopes.

Table 5.3: Time and number of samples collected during the study period (n = 134).

Station	**Date**		**Number of samples (n)**
WSR	20180830 August	Winter	18
	20181114 November	Spring	18
	20190205 February	Summer	18
	20190620 June	Late Autumn/Early Winter	18
SCC	20180517 May	Autumn	16
	20180913 September	Later Winter/early Spring	12
	20181115 November	Spring	16
	20190206 February	Summer	18

The relationship between environmental data, benthic data and ichthyofaunal data was investigated by constructing three datasets. These were compared using the BVSTEP (with 999 permutations) BEST analysis in PRIMER based on Spearman’s Rank. Multi-Dimensional Scaling (MDS) plots of highly correlated, environmental variables and biological benthic variables were constructed. Principal Component Analysis (PCA) ordination for collected ichthyofaunal multivariate data in relation to depth and the bottom water temperature was plotted. Environmental variables, depth, hard substrate, even or non-rugose substrate and bottom temperature were used to assess the relationship between ichthyofaunal taxa (elasmobranchs and teleosts), environmental variables and biotopes and were plotted using Canonical Correspondence Analysis CCA using PAST. Univariate and multivariate one- and two-way permutational analysis of variance (PERMANOVANA in PAST) was used to establish significant differences ($p < 0.05$) between biotope, season and bottom temperature.

Table 5.4: Synopsis of the sample location, biotopes, habitat and community assemblages as discussed in Chapter 3.

Biotope	**Locations**	**Habitat and depth**	**Community assemblage**
I	AY-215 AY-216 AZ-218 AZ-220	Rocky reef with fine sand without shell fragments (4.6 to 7.6 m)	Soft red algae *Hypnea tenuis* with mixed tufts of soft macroalgae, crustose *Leptophytum acervatum*, red *Plocamium corallorhiza*, green *Halimeda cuneate* algae with the colonial ascidian *Polyclinum isipingense*.
II	BA-216 BE-215 BC-214 BD-215 BD-216 BB-216 BE-220	Rocky reef (5.8 to 13.3 m)	Articulated red coralline algae *Amphiroa ephedraea*, encrusting *Leptophytum acervatum* with mixed tufts of small hydroids.
III	BF-219 BH-220 BH-223 BG-224	Rocky reef with gravel (12.3 to 17.2 m)	Mixed tufts of small hydroids, red encrusting sponge *Placospongia* sp. 001, red *Leptogorgia palma* seafans with articulated coralline algae *Amphiroa ephedraea* and thin crustose *Leptophytum acervatum*
IV	BJ-220 BH-215 BL-221	Rocky reef Fine sand, with shell fragments 17.5 to 20.5 m)	Red encrusting *Placospongia* sp. 001, red *Leptogorgia palma* seafans, mixed tufts of small hydroids, with feather crinoids *Tropiometra carinata* and thin encrusting *Leptophytum acervatum*
V	CP-83 CQ-83A CQ-84 CU-72 CR-71 CV-71	Rocky reef (12.9 to 26.4 m)	Red *Leptogorgia palma*, spongy finger *Homophyton verrucosum* seafans with mixed tufts of small hydroids, smooth grey encrusting liver *Chondrilla* sp. 004 and red *Placospongia* sp. 001 sponges with upright *Sertularella arbuscula* hydroids.
VI	CV-70 CU-69 CR-68 CS-71 CR-69 CR-70	Rocky reef with mostly small loose shell fragments and fine sand (4.1 to 18.1 m)	Mixed tufts of small hydroids, thin crustose *Leptophytum acervatum* algae, red encrusting *Placospongia* sp. 001 sponge, red mats of *Aplidiopsis* sp. 004 ascidians with encrusting orange cushion *Tedania stylonychaeta*.
VII*	CT-68 CP-82 CS-67	Fine sand with shells and some reef	*Tropiometra carinata* with sandy annelid tube worms
	CR-84	Mostly small loose shell fragments	Thin crustose *Leptophytum acervatum* on shells and small stones
	CR_83A CU-68	Fine sand with shell fragments	Craterlike marking in sediment possibly formed by endopsammic sponge *Tethya* sp. 004*,* soft coral *Eunephthya celata*, upright *Sertularella arbuscula* hydroid and multicoloured seafans *Wrightella* sp. 001

Note: *Unconsolidated habitats (subgroupings VIIa-c) assigned to Biotope VII are grouped together as unconsolidated substrate with very little biota present and, owing to small sample size, are treated as a unit.

5.4 Results

5.4.1 Assessment of length of video stream needed for analysis

Accumulation curves for all species observed during a 60-minute video for a subset of data obtained from WSR and RR were constructed (Figure 5.1). Figure 5.1 indicates that the majority of taxa were observed within the first 15 minutes of video footage collected. It is also evident that species numbers were generally higher for the samples from TMPA, but fluctuated greatly between the samples from WSR.

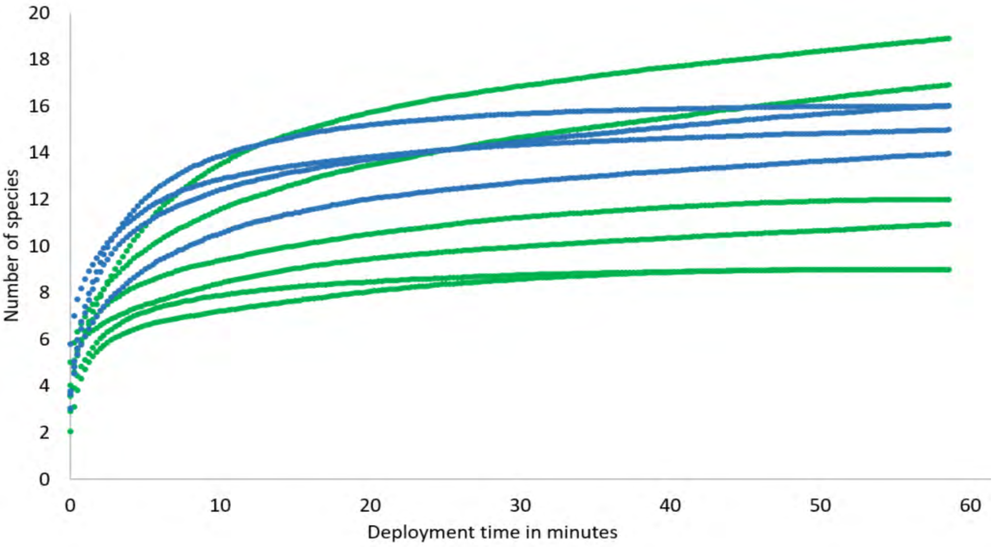


Figure 5.1: Species accumulation curves, the Tsitsikamma Marine Protected Area, Garden Route National Park (TMPA) data indicated in green and the Algoa Bay Sentinel Site (ABSS), White Sands Reef (WSR) observations in blue.

Compared with other studies (Table 5.1 and Table 5.2 which deploy BRUV systems at least 300 m apart), this study aimed to observe and describe ichthyofauna, within a smaller target area (150 x 150 m) around a central sample location. Limiting the size of the bait plume or restricting the time for the fish to be attracted to the bait will affect the number of species and the number of individuals per species (MaxN) that will be observed. MaxN was calculated for all ichthyofaunal species within the first 15 minutes of the video and the entire 60-minute deployment. This was done by counting and identifying all species every 15 seconds during ten 60-minute video streams (a total of 50 095 fish were identified and counted in the subset of ten videos). The mean distribution for observed relative abundance (MaxN) for the data pairs was compared using a nonparametric Mann-Whitney U test and indicated no significant difference between the means. Bray Curtis similarities were calculated for the data pairs and are provided in Table 5.5. A two-way PERMANOVA test to determine differences for the two different analysis periods and between sample stations (15 and 60 minutes and TMPA and WSR) indicate no significant difference between the length of the video analysis, but a highly significant difference between WSR and TMPA (bottom of Table 5.5).

The 15-second, 60-minute analysis provided an insight into the behaviour of fish species around the bait during BRUV deployment. Interestingly, the decrease in catch frequency and increase in the size of red roman caught during controlled fishing sampling methods (Götz 2005) is mirrored in observation of the arrival of these fish at the bait. Small to medium size fish arrive first followed by a large, seemingly dominant individual. They frequently chase other fish away with aggressive displays, powerfully attacking the bait. The MaxN for red roman is generally reached early in the deployment and stays stable throughout (Figure 5.2).

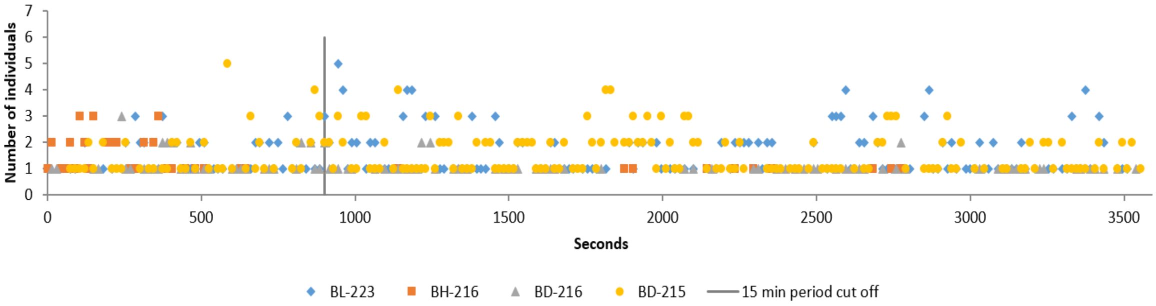


Figure 5.2: Number of individuals of *Chrysoblephus laticeps* counted every 15 seconds of a 60-minute video of samples collected from White Sands Reef, Algoa Bay. The vertical grey line indicates 900 seconds or 15-minute period analysed.

The research aims to describe the ichthyofaunal assemblage in the direct vicinity of the research location to assess the association between the benthic environment, the habitat and the benthic biotope, and relate biotope composition to that of the associated fish assemblage. The effect of bait is well established (Hardinge et al. 2013) and, even in this case where a relatively small amount of bait was used generally results in the attraction of more species and individuals over time (Figure 5.3). The result and comparison between data collected for the 15-minute and 60-minute video streams support this and is not unexpected. However, analysis of the 15-minute section only resulted in an average loss of 18.34% in similarity to that observed for species abundance and richness over the full 60-minute deployment. The concerns related to the effect of the bait plume on neighbouring deployments and in the expectation of curtailing attraction of ichthyofauna from the area outside the focus area support the use of shorter deployment times when sample sites are in close proximity of each other. These results also support the use of snapshot analysis (use of only the first 15 minutes of video collected) as it will decrease the time spent analysing the collected data and counteract bottlenecks in information dissemination.

Table 5.5: Nonparametric Mann-Whitney U test for significant difference between means of MaxN during 15-minute and the full 60-minute data stream, Bray Curtis similarity estimate, number of species, individuals and a two-way PERMANONA to test for differences for factors analysis period and stations.

Nonparametric Mann-Whitney U test				**Bray Curtis**		
Sample	**U**	**z**	**p**	**similarity estimate %**	**number of species 15 min (60 min)**	**number of individuals 15 min (60 min)**
TMPA 01	43	-0.5081	0.6114	90	9 (10)	81 (99)
TMPA 02	20	-1.255	0.2096	71.43	4 (8)	10 (18)
TMPA 03	25.5	-0.6755	0.4987	92.86	8 (8)	39 (45)
TMPA 04	48	-0.8086	0.4188	61.54	9 (11)	48 (108)
TMPA 05	110.5	-1.191	0.2338	93.18	12 (17)	164 (188)
TMPA 06	101.5	-2.069	0.0355	79.41	10 (18)	54 (82)
ABSS WSR 01	90	-1.471	0.1412	82.35	12 (16)	28 (40)
ABSS WSR 02	87	-1.56	0.1187	76.50	12 (16)	83 (134)
ABSS WSR 03	89	-0.9674	0.3333	81.38	11 (15)	177 (258)
ABSS WSR 04	80.5	0.8168	0.4141	87.93	11 (14)	51 (65)

U = test statistic, z = continuity correction

Two way PERMANOVA in PAST			*p < 0.05, **p < 0.01
Factors	df	F	p
Period time: 15 min X 60 min	1	0.30674	0.9859
Station: WSR X TMPA	1	2.4071	0.0002 **

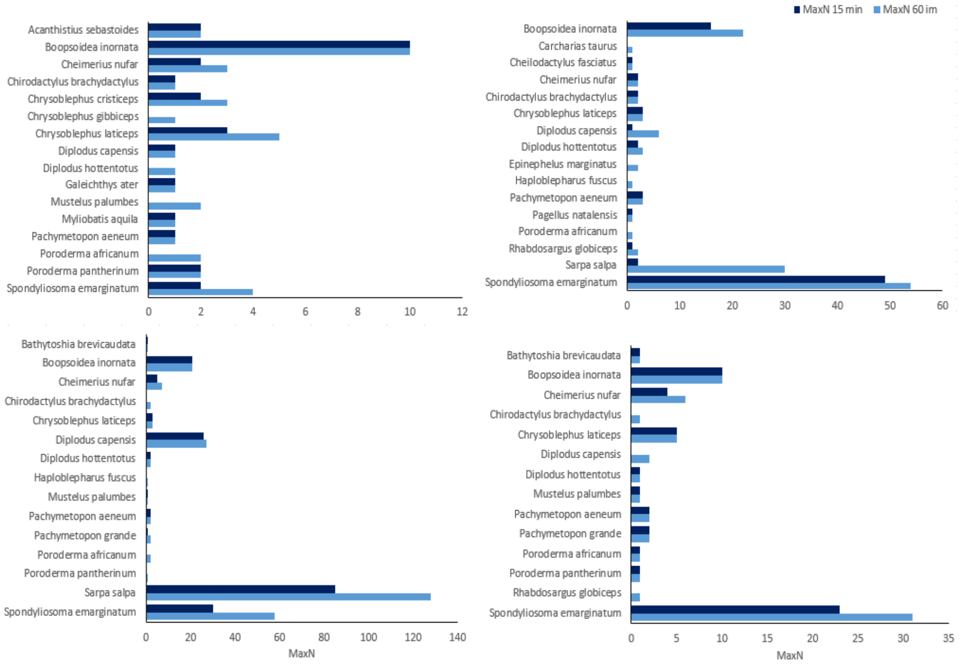


Figure 5.3: Visual comparison between MaxN observations of fish species for the four WSR sub-dataset. Dark blue indicates species and MaxN counts for analysis of the first 15 minutes and light blue for the whole 60 minutes of the video data stream collected.

5.4.2 Assessment of movement of the red roman *Chrysoblephus laticeps*

This study used the central point in a 150 x 150 m grid for the selection of sample location, both for benthic biotope assessment and associated fish species. sBRUVs were deployed in closely located sample locations in groups of six. These locations were randomly selected but once established, samples were collected from a specific location with sample deployment in a set order during each sampling event. The sBRUVs were deployed a minimum of 150 m apart and, wherever possible, within 15 minutes, so that for the majority of the deployment they were in the water at the same time. Pairs of samples that a) belonged to the same deployment groups (video collected from sBRUVs that were in the water at the same time) and situated 150 m apart, and b) belonged to different deployment groups (video from sBRUVs that were deployed after a neighbouring sBRUV had been retrieved) but in which case the sample locations were situated 150 m apart, were identified. In all situations, the video footage for the pair of samples was examined and all red roman individuals identified a minute before and after the MaxN reading within the 15-minute period. No red roman individual (n = 43) was found at more than a single locality (Supplementary Table 5.1). It can therefore be assumed that deployment type, whether of (a) or (b), does not influence the observed species for research localities 150 m apart for the observations made within the first 15 minutes of the collected video footage with the bait amount used in this study. This is only a preliminary assumption and further investigation of the effect on other species and observed MaxN should be considered.

5.4.3 Assessment of ichthyofauna assemblage for broader biotopes

Video footage for four seasonal sampling events during the study period for both sampling stations WSR and SCC were analysed to assess ichthyofauna during the first 15 minutes of deployment. A two-way PERMANOVA analysis was done to detect if there was any difference in the means for the relative abundance of fish species between biotope and seasons for both Bray Curtis and Gower distance measures (Clarke et al. 2006). Both indicated a significant difference in the observed data ($p < 0.05$), although no interaction between the tested factors, season and biotope, is evident (Table 5.6). A further one-way PERMANOVA analysis of all seasonal data for ABSS (WSR and SCC stations) was calculated using Bray Curtis, Gower and Manhattan distance to detect differences between location in and between biotopes (Supplementary Table 5.2). A significant difference was found between spring, autumn and winter as well as between summer, winter and spring, no significant difference was found between winter and autumn (Table 5.6).

Table 5.6: Two-way multivariate PERMANOVA analysis to detect differences between MaxN abundance measures for defined biotopes and data collection for the seasons during the study period and a one–way PERMANOVA for the difference in bottom temperature for the different seasons (values in bold indicate significant difference $p < 0.05$).

		Bray Curtis distance measure		Gower distance measure	
Factors	df	F	p	F	p
Biotope	6	1.9144	**0.0001**	7.5489	**0.0001**
Season	3	0.17164	**0.0025**	1.8598	**0.0001**
Interaction	18	-0.24412	0.9935	-0.96262	0.5914

Result of analysis for differences in MaxN between localities provided in Supplementary Table 5.1

One-way PERMANOVA in bottom temperature for the different seasons using Euclidean distance.

F	32.05		autumn	winter	spring	summer
P	**0.0001**	autumn				
		winter	0.4498			
permutations	9999	spring	**0.0001**	**0.0001**		
		summer	0.0919	**0.0425**	**0.0001**	

A SIMPER analysis (PRIMER) of standardised abundance Bray Curtis resemblance matrix was used to calculate pairwise average dissimilarity estimates for samples collected in different seasons (Table 5.7). The data were pooled for the four seasons and a species list for each biotope (I to VII) constructed in SIMPER (PRIMER) giving ichthyofaunal species contribution to the average abundance and similarity for each biotope over the study period (Table 5.8).

Table 5.7: SIMPER average dissimilarity percentage estimates between seasons

Groups	Average dissimilarity
Spring & Summer	53.37
Spring & Autumn	52.73
Summer & Autumn	60.07
Spring & Winter	50.65
Summer & Winter	54.35
Autumn & Winter	51.85

Table 5.8: SIMPER species abundance per biotope, showing only those that contribute more than 5 % of the fish community.

Species	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**	**Cum.%**
Biotope I				**Average similarity: 39.41**	
Cheimerius nufar	11.09	7.6	1.83	19.28	19.28
Diplodus capensis	14.58	7.54	0.84	19.13	38.42
Pagellus natalensis	11.19	5.25	1.57	13.33	51.74
Rhabdosargus holubi	8.71	4.6	0.8	11.66	63.4
Sarpa salpa	15.7	4.22	0.39	10.7	74.11
Spondyliosoma emarginatum	12.22	4.12	0.41	10.45	84.55
Boopsoidea inornata	8.43	2.04	0.62	5.17	89.72

Table 5.9: continued

Biotope II				**Average similarity: 48.58**	
Boopsoidea inornata	35.92	23.97	1.64	49.34	49.34
Chrysoblephus laticeps	10.86	6.88	1.52	14.16	63.5
Spondyliosoma emarginatum	12.4	6.09	0.87	12.54	76.04
Cheimerius nufar	6.68	3.5	1.26	7.2	83.24
Diplodus capensis	6.32	3.12	0.91	6.42	89.66
Sarpa salpa	7.85	1.06	0.17	2.19	91.85
Biotope III				**Average similarity: 59.93**	
Boopsoidea inornata	52.19	43.3	2.21	72.25	72.25
Spondyliosoma emarginatum	7.55	3.46	0.65	5.78	78.03
Chrysoblephus laticeps	5.42	2.85	1.07	4.75	82.78
Pachymetopon aeneum	5.5	2.1	0.8	3.5	86.28
Chrysoblephus cristiceps	6.37	1.95	0.69	3.26	89.54
Biotope IV				**Average similarity: 62.87**	
Boopsoidea inornata	38.66	33.92	2.74	53.96	53.96
Spondyliosoma emarginatum	19.36	10.32	0.88	16.42	70.38
Chrysoblephus laticeps	10.3	7.75	2.9	12.33	82.71
Pachymetopon aeneum	5.48	2.41	0.89	3.83	86.54
Biotope V				**Average similarity: 44.10**	
Boopsoidea inornata	22.76	15.1	1.47	34.23	34.23
Spondyliosoma emarginatum	23.3	12.21	0.77	27.69	61.92
Chrysoblephus laticeps	10.31	6.83	1.45	15.49	77.42
Cheimerius nufar	6.12	4.17	1.26	9.46	86.87
Biotope VI				**Average similarity: 42.46**	
Spondyliosoma emarginatum	22.21	14.31	0.85	33.7	33.7
Pagellus natalensis	22.14	8.93	0.57	21.02	54.72
Cheimerius nufar	10.63	6.44	1.33	15.16	69.88
Boopsoidea inornata	14.77	5.39	0.63	12.7	82.58
Rhabdosargus holubi	6.83	2.4	0.75	5.66	88.24
Chrysoblephus laticeps	5.6	2.12	0.61	4.99	93.23
Biotope VII				**Average similarity: 42.18**	
Pagellus natalensis	51.21	31.21	1.17	74	74
Spondyliosoma emarginatum	11.27	3.7	0.8	8.78	82.78
Galeichthys ater	8.94	3.26	0.76	7.73	90.5

All species with average abundance per biotope provided in Supplementary Table 5.4

Three datasets, a normalised environmental dataset, a square root transformed benthic dataset and an untransformed ichthyofaunal dataset, were compared using the BVSTEP (with 999 permutations) BEST analysis in PRIMER based on Spearman's rank. The BEST fit of the environmental data from different sampled localities as collected with Jump Camera (JC) systems to the ichthyofaunal data collected with sBRUV systems highlights the importance of four environmental variables in fish distribution and relative abundance. These include depth, rocky substrate (%Sub-rock), mostly small shell fragments (%Sub-ssh) and fine sand with shell fragments (%Sub-fss) (r = 0.641) (Figure 5.4A). This analysis was repeated using the benthic species dataset for the different sampled localities, taking into account only those biotic variables that contribute at least 10% to the average abundance of the benthic algae and invertebrate community. This includes *Amphiroa ephedraea* (M0010), Hypnea tenuis (M0151), *Leptogorgia palma* (C0023), *Leptophytum acervatum* (M0272), mixed tufts of small hydroids (Bio-cns), mixed tufts of soft macroalgae (Bio-mal), *Placospongia* sp. 001 RSA (P0032), Tethya sp. 004 RSA SPN (P0220) and *Tropiometra carinata* (E0007). The correlation was relatively low for four of the variables (r = 0.572); mixed tufts of small hydroids (Bio-cns), mixed tufts of soft macroalgae (Bio-mal), *Leptogorgia palma* (C0023) and *Amphiroa ephedraea* (M0010).

Correlation analyses between fish species distribution and relative abundance and the complete set of biotic variables (n = 378) identified 23 variables (list given in Supplementary Table 5.5) that show a strong correlation with the observed ichthyofauna (r = 0.711) (Figure 5.4 B). These species, although in some cases large and well represented, have limited distributions. Principal Component Analysis (PCA) ordination indicates the importance of depth (Figure 5.4 C) and percentage of hard substrate or consolidated (Figure 5.4 D) in the distribution of selected ichthyofauna.

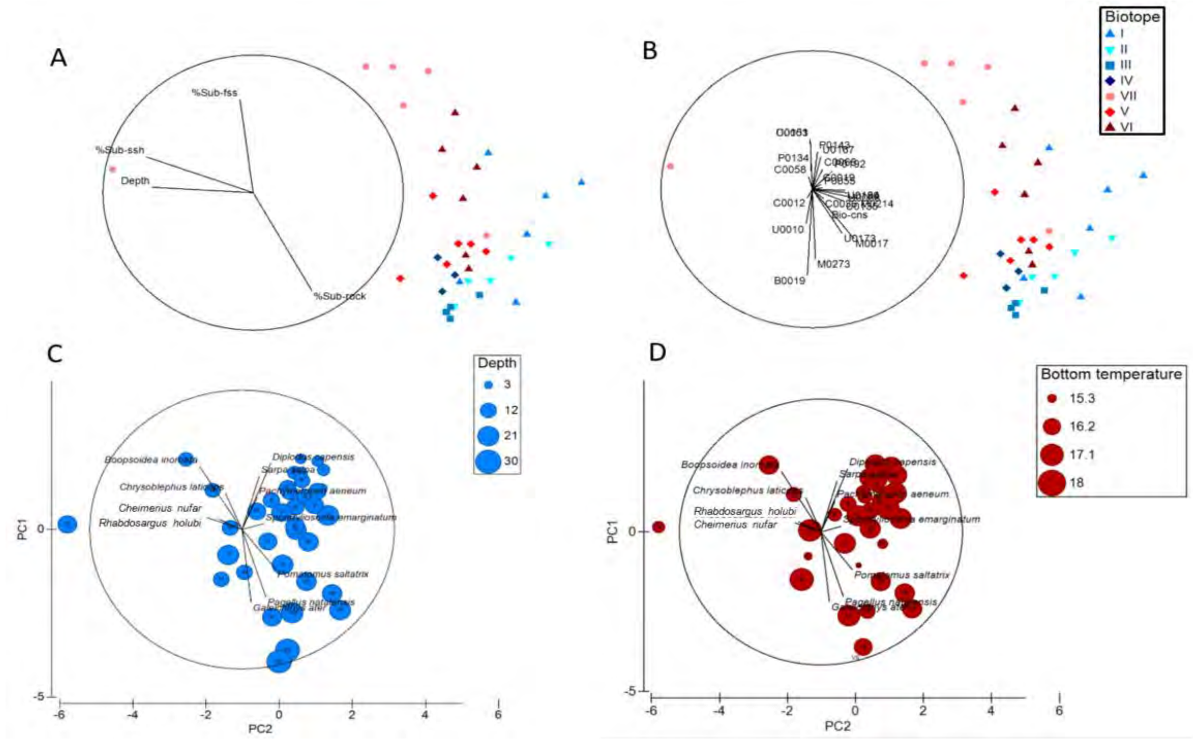


Figure 5.4: MDS plot for relative fish abundance (MaxN) per sample location colour coded into biotopes with, A) environmental variables and, B) biological benthic variables (list given in Supplementary Table 5.5). Blue symbols for WSR and red symbols for samples at location SCC. PCA ordination for ichthyofaunal multivariate data contributing at least 5% to the relative abundance for research locations, bubble plots representing, C) depth and D) bottom water temperature recorded during sBRUV deployment at the sample localities.

Canonical Correspondence Analysis (CCA; PAST) plotted the environmental variables, depth, hard substrate, substrate rugosity (even or non-rugose) and bottom temperature to investigate the primary relationship between the selected suite of environmental variables and selected teleosts species (Figure 5.5 A). A secondary plot looks at the relationship between the subset of teleost species and the previously defined biotopes (Figure 5.5 B). The graph (Figure 5.6 B) is split for the biotopes and environmental variables to fish (to relieve clutter). The same is shown for the elasmobranch taxa (Figure 5.6). This clearly shows the relation of rays and hammerhead sharks to unconsolidated, flat substrates and *Mustelus* spp. preference for shallower reef habitats. The preference of typical reef teleost species e.g. *Chrysoblephud laticeps*, *C. cristiceps* and *Pachymetopon aeneum* is contrasted with species associated more with soft bottoms e.g. *Pagellus natalensis* and *Galeichthys ater*.

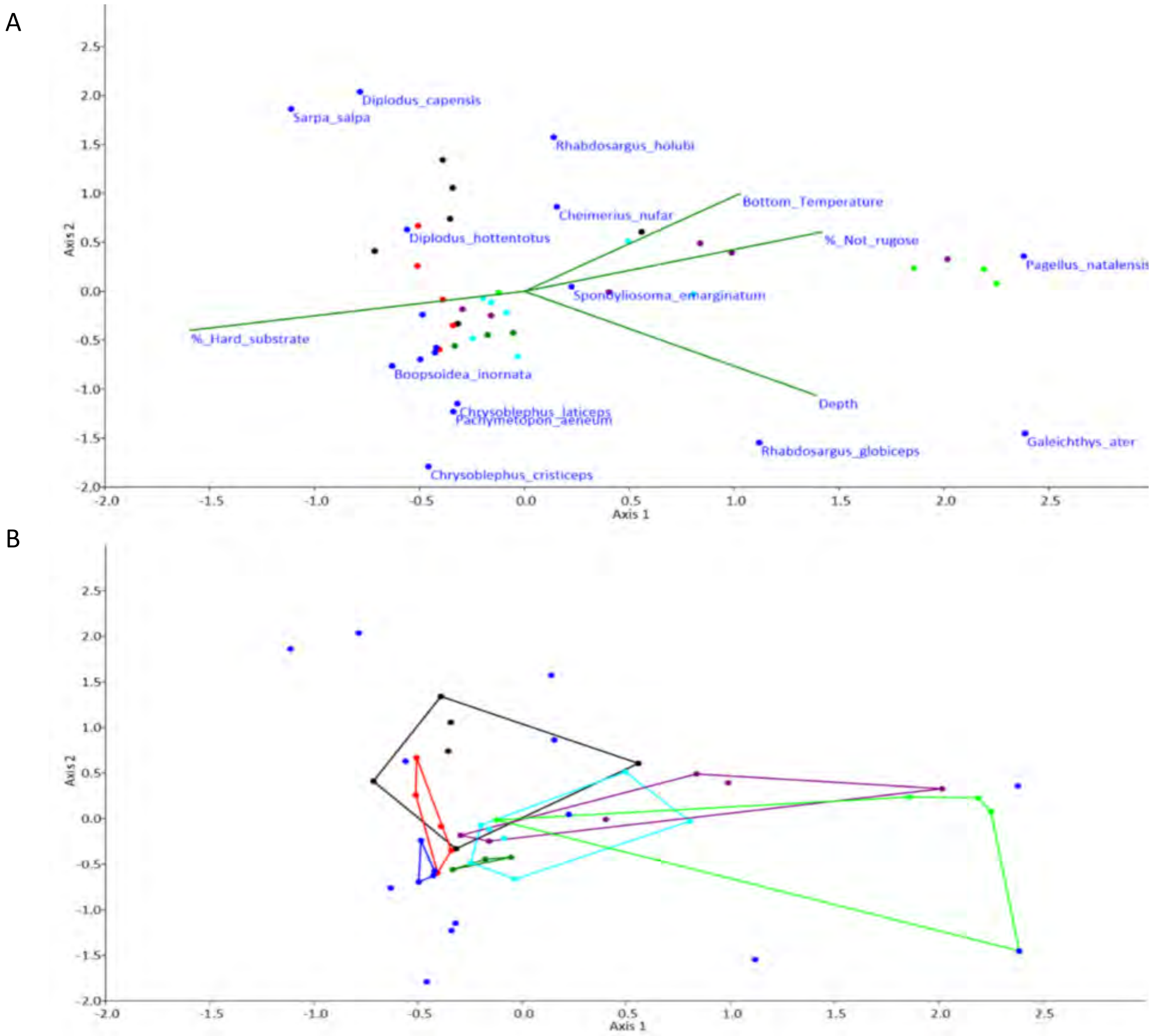


Figure 5.5: Canonical Correspondence Analysis CCA (PAST) plotting environmental variables, depth, hard substrate, even or non-rugose substrate and bottom temperature with the focus on the relationship between selected teleosts, graph environmental variable to fish (A) and split into the biotopes (B) labels are sample localities allocated to defined biotope (per colour). Blue dot in B corresponds to species in A.

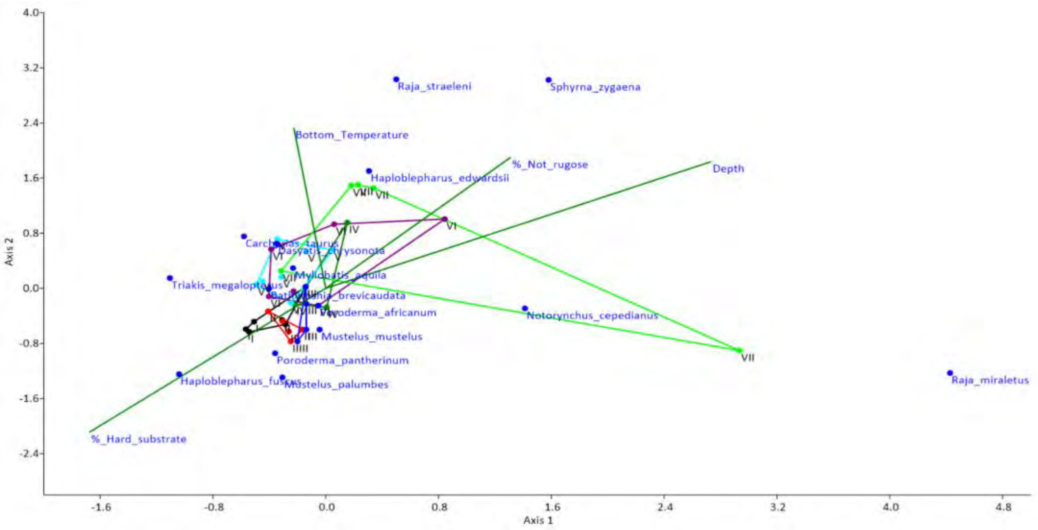


Figure 5.6: Canonical Correspondence Analysis CCA (PAST) plotting environmental variables, depth, hard substrate, even or non-rugose substrate and bottom temperature with the focus on the relationship between elasmobranch taxa and the environmental variables, secondarily in relation to the biotopes and relationship of the biotope.

5.5 Discussion

The functionality of the biotope as a classification unit is well recognised for the benthic seascape (Costello 2009, Buhl-Mortensen et al. 2020) This study differs from most previous studies in that the focus is on observing and describing ichthyofauna associated with specific benthic biotopes. Although the coupling between the benthic sessile benthic biota and ichthyofauna has been investigated (Buxton and Smale 1984, Götz et al. 2009a, Heyns 2015, Heyns et al. 2016, Heyns-Veale et al. 2016, Wahab et al. 2018).

Reduction in the analysis time of the video footage from 60 to 15 minutes would allow for faster processing and data assessment times, thereby facilitating the collection of a greater number of long-term datasets across a wider spatial and temporal scale. The shorter period provided an estimated average similarity of 81.66% (SD = 10.05%) to that observed in a 60-minute video. The trade-off between the reduced number of species and relative abundance estimation (MaxN) and reducing data production time is deemed acceptable (Campbell et al. 2015). This snapshot analysis will not only allow more prompt data processing and assessment of the collected information but will lessen the bottlenecking of data processing by reducing processing time by three quarters.

It is noteworthy that the data collected (the full 60-minute video material), will be archived and will thus be available for future analysis in a Machine Learning environment. This will in the very near future eliminate the need to constrain analytical effort. It is envisioned that data analysis will be automated and that archived material will be reassessed as needed. It is believed that the snapshot analysis used here will assist LTER programmes to at least start data collection and analyses without the risk of large data processing backlogs and delays in access to information.

The adoption of a finer scale analysis of the ichthyofauna corresponding to that of the benthic scale, using a smaller BRUV system and less bait, produced meaningful results and managed to collect long-term observations for ichthyofaunal assemblages and associated benthic biotopes at the same spatial scale. This study found that the fish assemblage was significantly different between the different biotopes. The fish assemblages within biotopes generally share a similar species list, however, the contribution of each of these species and their average abundance define these differences found.

Substrate plays an important role in determining the occurrence of ichthyofauna and this is evident in the complement of fish observed for consolidated substrates versus unconsolidated substrates. The timing of sampling events, seasonal difference and bottom water temperature fluctuation were found to differ significantly over the span of the sampling period (Figure 2.6, Figure 2.7 and Figure 2.8). The seasonal difference in species composition for the data collected in this study suggests that the effects of seasonal variation and difference in bottom temperature regimes should be carefully considered before seasonal data is pooled. It however supports LTER sampling to be conducted bi-annually to include winter and summer as fish abundance was shown to differ significantly between these seasons. A comprehensive seasonally multi-year seasonal dataset would allow a better understanding of ichthyofauna distribution and movement across the seascape during and in the absence of upwelling events.

5.6 Conclusion

This chapter described the ichthyofauna populations associated with the broader biotopes. The feasibility of using a shorter video data stream was illustrated and its future used motivated. The 15-minute snapshot analysis used in this study allows for the characterisation of fish assemblages in different biotopes. It reduced time spent on the analysis of video data streams. It will not only allow quicker data processing and assessment of the collected information but will counteract the bottlenecking of data processing by significantly reducing processing time. The collection and storage of the full hour of the stereo video stream will, however, allow additional analysis and length-frequency analysis of the fish. The compliment of horizontal images of the benthos and vertical images collected with sBRUV systems of the seafloor provide insight into the three-dimensional nature of the seascape. This investigation furthermore showed that that individual fish displayed high fidelity to the bait with no movement of fish between deployments.

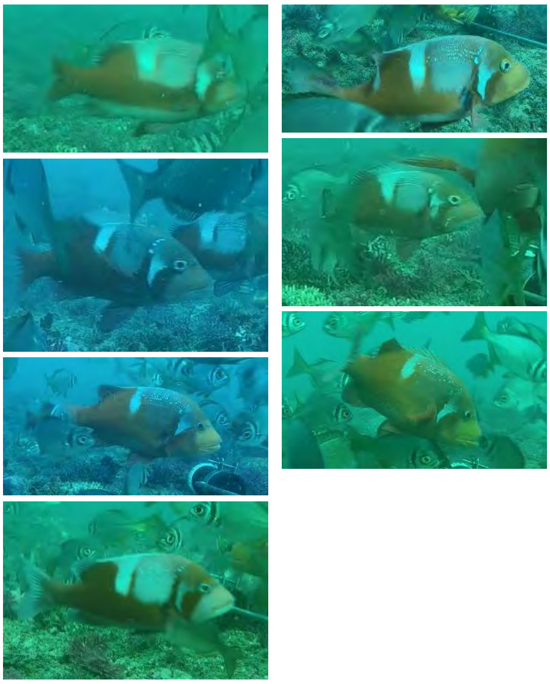
Ichtyhyfauan assemblages were identified and described for the broader benthic biotopes. Many reef species are important economically as part of the commercial or recreational fishing industry. And it is believed that species are useful tools in observing change. This time-curtailed dataset showed a significant difference in the abundance of fish observed during summer and winter. The ability of the analysis to detect changes in assemblage in different seasons suggest that it will be able to detect a change in fish assemblage resulting from global change, anthropogenic stressors e.g. pollution, natural short term changes such as induced by heavy freshwater input into the nearshore, increases in productivity due to episodic events such as Harmful Algal Blooms (HABs) and large upwelling episodes. The significant difference in the species assemblages observed for TMPA and WSR indicates that the data analysed using this methodology can also detect not only temporal change but also spatial differences between geographically separated ecosystems.

It is important to note that the baseline data used in this analysis for SCC was before the proclamation of the new Addo Elephant Marine Protected area in 2019. It is expected that changes in the fish assemblages for the SCC station will occur as the area now falls within the restricted zone where fishing is prohibited (Department of Environmental Affairs 2019b, 2019c). Subsequent sampling of fish, especially with the inclusion of length-frequency data, will be an important indicator of change over time for the SCC station. Research has shown that protection of fisheries targeted species affect the interaction of non-target fish due to interspecific competition and their impact on the benthos due to a change to trophic pressures on the benthic algae and invertebrates (Götz et al. 2009a, 2009b). The restriction on fishing is expected to have a cascading effect and changes in the species composition of the benthic sessile and sedentary biota are also expected.

Annual surveying of the benthic communities complemented and multi-year seasonal collected datasets would allow for the identification of short-term oscillations and long-term changes. The establishment of BELTER sites along the entire South African coast within different ecosystems, using standardised equipment, sample collection and analytical methodologies and the shortened analysis time for video data proposed here, will produce information faster over a broader spatial and in time, longer temporal scale. These comprehensive datasets including information for seasonal ichthyofauna abundance and biotope association in combination with annual benthic biotope assessment (BELTER), correlated with the observed biological and physical variables of the accompanying pelagic system, as part of the SAEON’s Pelagic Ecosystem Long-Term Ecological Research (PELTER) platform will be an important tool in assessing and understanding long-term change in the South African shallow marine coastal seascape as a whole.

5.7 Supplementary material

Supplementary Table 5.1: Photo comparison of red roman, *Chrysoblephus laticeps*, collected at WSR during one season (winter).

Neighbouring sample location 150 m apart, same deployment stacks (in the water at the same time)	
ABSS_WSR_20190620_BA-216 (MaxN = 5)	ABSS_WSR_20190620_BB-216 (MaxN = 5)
	
ABSS_WSR_ 20190620_BD-215 (MaxN = 4)	ABSS_WSR_ 20190620_BE-215 (MaxN = 7)
	

ABSS_WSR_20190620_AY-215 (MaxN = 1)

ABSS_WSR_20190620_AY-216 (MaxN = 1)

Neighbouring sample location 150m apart, subsequent deployment stacks (not in the water at the same time)

ABSS_WSR_ 20190620_BH-215 (MaxN = 5)

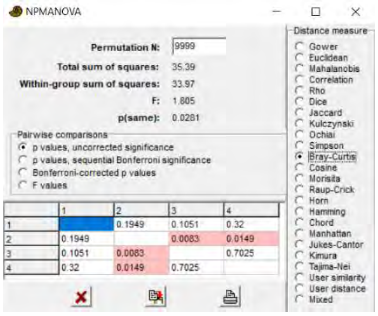
ABSS_WSR_ 20190620_BH-216 (MaxN = 4)

ABSS_WSR_ 20190620_BF-219 (MaxN = 4)

ABSS_WSR_ 20190620_BE-220 (MaxN = 2)

Supplementary Table 5.2: PERMANOVA biotope and seasonal difference in observed MaxN multivariate comparison. A significant difference between seasons 1 to 4 indicated by $p < 0.05$.

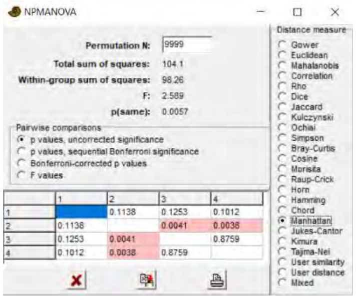
One way PERMANOVA to detect differences between season for the study ABSS as a whole, Bray Curtis, Gower and Manhattan distance measures



Permutation N: 9999
Total sum of squares: 35.39
Within-group sum of squares: 33.97
F: 1.805
p(same): 0.0281

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Bray-Curtis

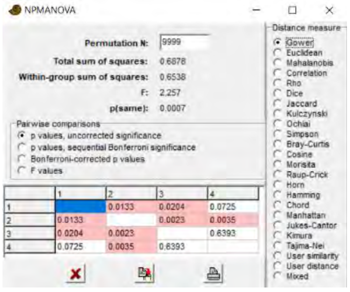
	1	2	3	4
1		0.1949	0.1051	0.32
2	0.1949		0.0083	0.0149
3	0.1051	0.0083		0.7025
4	0.32	0.0149	0.7025	



Permutation N: 9999
Total sum of squares: 104.1
Within-group sum of squares: 98.26
F: 2.589
p(same): 0.0057

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Manhattan

	1	2	3	4
1		0.1138	0.1253	0.1012
2	0.1138		0.0041	0.0038
3	0.1253	0.0041		0.8759
4	0.1012	0.0038	0.8759	

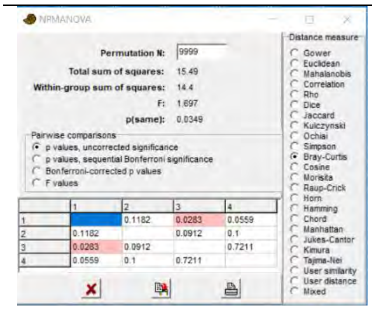


Permutation N: 9999
Total sum of squares: 0.6878
Within-group sum of squares: 0.6538
F: 2.257
p(same): 0.0007

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Gower

	1	2	3	4
1		0.0133	0.0204	0.0725
2	0.0133		0.0023	0.0035
3	0.0204	0.0023		0.6393
4	0.0725	0.0035	0.6393	

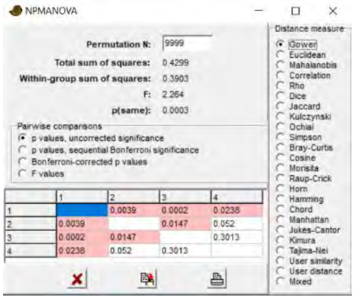
WSR



Permutation N: 9999
Total sum of squares: 15.49
Within-group sum of squares: 14.4
F: 1.697
p(same): 0.0349

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Bray-Curtis

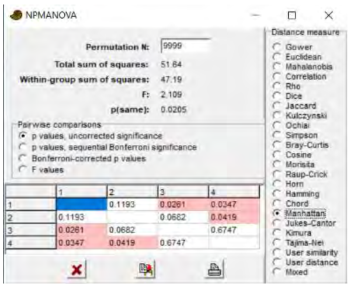
	1	2	3	4
1		0.1182	0.0283	0.0559
2	0.1182		0.0912	0.1
3	0.0283	0.0912		0.7211
4	0.0559	0.1	0.7211	



Permutation N: 9999
Total sum of squares: 0.4299
Within-group sum of squares: 0.3903
F: 2.264
p(same): 0.0003

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Gower

	1	2	3	4
1		0.0039	0.0002	0.0238
2	0.0039		0.0147	0.052
3	0.0002	0.0147		0.3013
4	0.0238	0.052	0.3013	

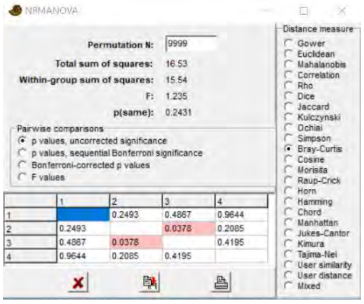


Permutation N: 9999
Total sum of squares: 51.64
Within-group sum of squares: 47.19
F: 2.109
p(same): 0.0205

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Manhattan

	1	2	3	4
1		0.1193	0.0261	0.0347
2	0.1193		0.0682	0.0419
3	0.0261	0.0682		0.6747
4	0.0347	0.0419	0.6747	

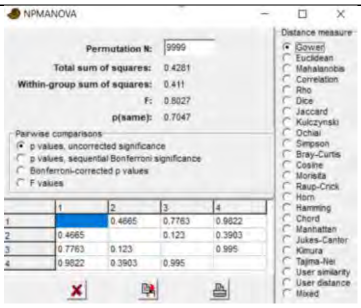
SCC – note that even although the Bray Curtis distance measures suggest that there is a significant difference between some seasons, this was not confirmed by the other distance measures used.



Permutation N: 9999
Total sum of squares: 16.53
Within-group sum of squares: 15.54
F: 1.235
p(same): 0.2431

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Bray-Curtis

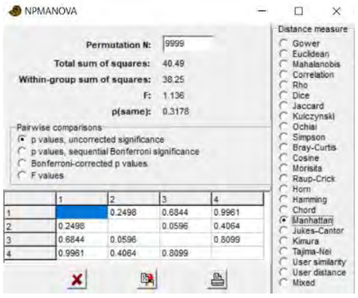
	1	2	3	4
1		0.2493	0.4867	0.9644
2	0.2493		0.0378	0.2085
3	0.4867	0.0378		0.4195
4	0.9644	0.2085	0.4195	



Permutation N: 9999
Total sum of squares: 0.4281
Within-group sum of squares: 0.411
F: 0.8027
p(same): 0.7047

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Gower

	1	2	3	4
1		0.4665	0.7763	0.9822
2	0.4665		0.123	0.3903
3	0.7763	0.123		0.995
4	0.9822	0.3903	0.995	

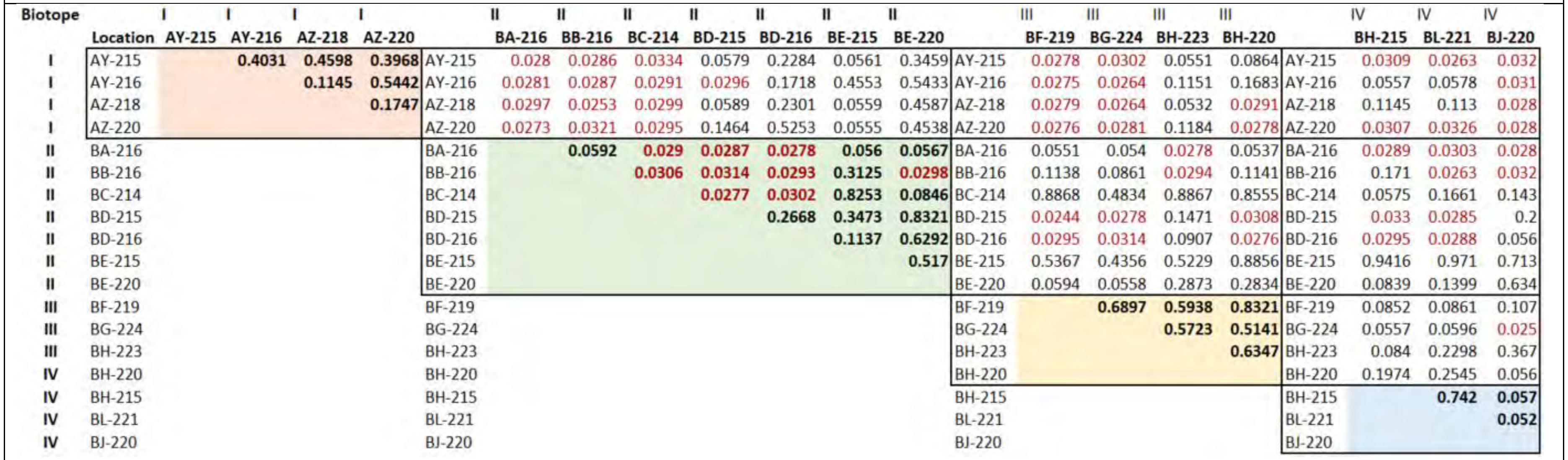


Permutation N: 9999
Total sum of squares: 40.49
Within-group sum of squares: 38.25
F: 1.136
p(same): 0.3178

Pairwise comparisons: ● p values, uncorrected significance
Distance measure: ● Manhattan

	1	2	3	4
1		0.2498	0.6844	0.9961
2	0.2498		0.0596	0.4064
3	0.6844	0.0596		0.8099
4	0.9961	0.4064	0.8099	

Supplementary Table 5.3: One way PERMANOVA (PAST) for all localities with biotopes and between biotopes with text in red indicating instances where a significant difference ($p < 0.05$) was observed in ichthyofauna MaxN.



Biotope		I	I	I	I		II	II	II	II	II	II	II		III	III	III	III		IV	IV	IV
	Location	**AY-215**	**AY-216**	**AZ-218**	**AZ-220**		**BA-216**	**BB-216**	**BC-214**	**BD-215**	**BD-216**	**BE-215**	**BE-220**		**BF-219**	**BG-224**	**BH-223**	**BH-220**		**BH-215**	**BL-221**	**BJ-220**
I	AY-215		**0.4031**	**0.4598**	**0.3968**	AY-215	0.028	0.0286	0.0334	0.0579	0.2284	0.0561	0.3459	AY-215	0.0278	0.0302	0.0551	0.0864	AY-215	0.0309	0.0263	0.032
I	AY-216			**0.1145**	**0.5442**	AY-216	0.0281	0.0287	0.0291	0.0296	0.1718	0.4553	0.5433	AY-216	0.0275	0.0264	0.1151	0.1683	AY-216	0.0557	0.0578	0.031
I	AZ-218				**0.1747**	AZ-218	0.0297	0.0253	0.0299	0.0589	0.2301	0.0559	0.4587	AZ-218	0.0279	0.0264	0.0532	0.0291	AZ-218	0.1145	0.113	0.028
I	AZ-220					AZ-220	0.0273	0.0321	0.0295	0.1464	0.5253	0.0555	0.4538	AZ-220	0.0276	0.0281	0.1184	0.0278	AZ-220	0.0307	0.0326	0.028
II	BA-216					BA-216		**0.0592**	**0.029**	**0.0287**	**0.0278**	**0.056**	**0.0567**	BA-216	0.0551	0.054	0.0278	0.0537	BA-216	0.0289	0.0303	0.028
II	BB-216					BB-216			**0.0306**	**0.0314**	**0.0293**	**0.3125**	**0.0298**	BB-216	0.1138	0.0861	0.0294	0.1141	BB-216	0.171	0.0263	0.032
II	BC-214					BC-214				**0.0277**	**0.0302**	**0.8253**	**0.0846**	BC-214	0.8868	0.4834	0.8867	0.8555	BC-214	0.0575	0.1661	0.143
II	BD-215					BD-215					**0.2668**	**0.3473**	**0.8321**	BD-215	0.0244	0.0278	0.1471	0.0308	BD-215	0.033	0.0285	0.2
II	BD-216					BD-216						**0.1137**	**0.6292**	BD-216	0.0295	0.0314	0.0907	0.0276	BD-216	0.0295	0.0288	0.056
II	BE-215					BE-215							**0.517**	BE-215	0.5367	0.4356	0.5229	0.8856	BE-215	0.9416	0.971	0.713
II	BE-220					BE-220								BE-220	0.0594	0.0558	0.2873	0.2834	BE-220	0.0839	0.1399	0.634
III	BF-219					BF-219								BF-219		**0.6897**	**0.5938**	**0.8321**	BF-219	0.0852	0.0861	0.107
III	BG-224					BG-224								BG-224			**0.5723**	**0.5141**	BG-224	0.0557	0.0596	0.025
III	BH-223					BH-223								BH-223				**0.6347**	BH-223	0.084	0.2298	0.367
IV	BH-220					BH-220								BH-220					BH-220	0.1974	0.2545	0.056
IV	BH-215					BH-215								BH-215					BH-215		**0.742**	**0.057**
IV	BL-221					BL-221								BL-221					BL-221			**0.052**
IV	BJ-220					BJ-220								BJ-220					BJ-220			

Supplementary Table 5.3 continued

Biotope		V	V	V	V	V	V		VI	VI	VI	VI	VI	VI		VII	VII	VII	VII	VII	VII
		CV-71	**CP-83**	**CQ-83A**	**CQ-84**	**CU-72**	**CR-71**		**CR-68**	**CR-70**	**CR-69**	**CV-70**	**CS-71**	**CU-69**		**CU-68**	**CT-68**	**CS-67**	**CR-84**	**CR-83A**	**CP-82**
I	AY-215	0.3199	0.2049	0.3154	0.0871	0.0303	0.0572	AY-215	0.4798	0.0282	0.0571	0.0307	0.2542	0.1366	AY-215	0.0298	0.0283	0.0266	0.5985	0.069	0.1465
I	AY-216	0.1445	0.1142	0.2915	0.0878	0.0586	0.0292	AY-216	0.0579	0.1106	0.0305	0.1153	0.0533	0.0602	AY-216	0.0292	0.0267	0.0258	0.6036	0.0641	0.0522
I	AZ-218	0.5757	0.43	0.6927	0.1181	0.2364	0.4515	AZ-218	0.7384	0.1684	0.4571	0.2023	0.9153	0.6566	AZ-218	0.057	0.0819	0.0575	0.396	0.1923	0.7352
I	AZ-220	0.0286	0.3105	0.3436	0.0293	0.0312	0.03	AZ-220	0.0898	0.0258	0.0266	0.0305	0.0292	0.0917	AZ-220	0.0295	0.0289	0.03	0.7985	0.0689	0.0561
II	BA-216	0.0567	0.0541	0.056	0.0549	0.0252	0.0268	BA-216	0.0281	0.0294	0.028	0.0298	0.0263	0.0297	BA-216	0.0271	0.0317	0.0272	0.2001	0.0672	0.0602
II	BB-216	0.0282	0.0291	0.0271	0.0286	0.0276	0.0265	BB-216	0.0295	0.0309	0.0305	0.0298	0.0291	0.0302	BB-216	0.029	0.0288	0.0278	0.199	0.0706	0.0316
II	BC-214	0.0874	0.0277	0.0585	0.0279	0.0578	0.0292	BC-214	0.0311	0.1692	0.0263	0.0853	0.0269	0.0312	BC-214	0.0297	0.0312	0.029	0.2011	0.0654	0.028
II	BD-215	0.0828	0.4938	0.2306	0.0297	0.0291	0.3968	BD-215	0.03	0.0276	0.029	0.03	0.0883	0.0531	BD-215	0.0278	0.0262	0.0267	0.2039	0.071	0.0281
II	BD-216	0.0882	0.7145	0.1992	0.0295	0.03	0.027	BD-216	0.0865	0.0276	0.0293	0.0283	0.0558	0.1175	BD-216	0.0276	0.03	0.0283	0.3958	0.0694	0.0266
II	BE-215	0.7989	0.3057	0.6027	0.3904	0.4619	0.6311	BE-215	0.0573	0.9429	0.0282	0.7714	0.1677	0.0557	BE-215	0.0274	0.0281	0.0305	0.3973	0.2015	0.0625
II	BE-220	0.3129	0.7384	0.6336	0.0821	0.0566	0.8829	BE-220	0.2496	0.1172	0.0252	0.1166	0.1427	0.114	BE-220	0.0275	0.0338	0.0303	0.3998	0.0596	0.0274
III	BF-219	0.0607	0.0814	0.0844	0.0242	0.0303	0.0282	BF-219	0.0278	0.0901	0.0331	0.0294	0.0279	0.029	BF-219	0.0286	0.0275	0.0257	0.2038	0.0697	0.0267
III	BG-224	0.0281	0.03	0.0269	0.0313	0.0311	0.0309	BG-224	0.0288	0.0319	0.03	0.03	0.0289	0.0292	BG-224	0.0285	0.031	0.0274	0.1938	0.0708	0.0314
III	BH-223	0.1448	0.2112	0.1759	0.0314	0.0568	0.1391	BH-223	0.0288	0.1661	0.0292	0.0858	0.0585	0.0575	BH-223	0.0304	0.0322	0.027	0.2061	0.0699	0.0606
IV	BH-220	0.084	0.0273	0.0562	0.0554	0.0274	0.0277	BH-220	0.0268	0.3728	0.0268	0.1483	0.0281	0.0279	BH-220	0.0269	0.0311	0.0302	0.3927	0.0653	0.0296
IV	BH-215	0.2567	0.0599	0.0847	0.3433	0.2614	0.0561	BH-215	0.0573	0.8835	0.0304	0.573	0.0253	0.0568	BH-215	0.0259	0.0291	0.0278	0.3902	0.1354	0.0303
IV	BL-221	0.5143	0.0816	0.2294	0.1905	0.1724	0.0883	BL-221	0.0252	0.8568	0.0314	0.4823	0.0544	0.061	BL-221	0.0296	0.028	0.0251	0.2056	0.069	0.027
IV	BJ-220	0.1123	0.2298	0.3173	0.0306	0.0302	0.4644	BJ-220	0.0296	0.0586	0.0261	0.0574	0.0562	0.0564	BJ-220	0.0294	0.0291	0.0259	0.206	0.068	0.0572
V	CV-71		**0.2061**	**0.5972**	**0.4007**	**0.602**	**0.3143**	CV-71	0.2526	0.5489	0.0883	0.6279	0.4247	0.1429	CV-71	0.0293	0.0258	0.0582	0.5002	0.2058	0.1062
V	CP-83			**0.8034**	**0.0999**	**0.0606**	**0.4084**	CP-83	0.0621	0.0588	0.0577	0.0552	0.1171	0.1181	CP-83	0.026	0.0832	0.0592	0.4967	0.1043	0.1007
V	CQ-83A				**0.0987**	**0.0576**	**0.4264**	CQ-83A	0.7195	0.1325	0.7179	0.1932	0.592	0.7665	CQ-83A	0.4596	0.7147	0.3636	0.7458	0.1965	0.704
V	CQ-84					**0.5036**	**0.0571**	CQ-84	0.089	0.2522	0.0282	0.37	0.03	0.059	CQ-84	0.0292	0.0296	0.0313	0.4947	0.4996	0.0977
V	CU-72						**0.0578**	CU-72	0.0565	0.3141	0.0286	0.8278	0.0586	0.0575	CU-72	0.0277	0.0326	0.0277	0.1982	0.0678	0.0299
V	CR-71							CR-71	0.0881	0.1156	0.0278	0.1714	0.2374	0.1089	CR-71	0.0266	0.0286	0.0265	0.397	0.0647	0.0308
VI	CR-68							CR-68		**0.0506**	**0.6003**	**0.1189**	**0.5095**	**0.7753**	CR-68	0.0305	0.0608	0.0838	0.3968	0.0682	0.3963
VI	CR-70							CR-70			**0.0282**	**0.69**	**0.0579**	**0.0546**	CR-70	0.0292	0.0285	0.0275	0.2048	0.1341	0.0297
VI	CR-69							CR-69				**0.0314**	**0.2294**	**0.9136**	CR-69	0.1458	0.3076	0.1455	0.396	0.0655	0.8302
VI	CV-70							CV-70					**0.1782**	**0.0861**	CV-70	0.0253	0.0274	0.0277	0.1911	0.1271	0.0305
VI	CS-71							CS-71						**0.3408**	CS-71	0.0283	0.0271	0.0562	0.4023	0.0646	0.1113
VI	CU-69							CU-69							CU-69	0.3083	0.317	0.1769	0.6093	0.0649	0.9743
VII	CU-68							CU-68							CU-68		**0.7213**	**0.229**	**0.3978**	**0.0674**	**0.8557**
VII	CT-68							CT-68							CT-68			**0.3997**	**0.5926**	**0.0738**	**0.7138**
VII	CS-67							CS-67							CS-67				**0.1939**	**0.0728**	**0.3326**
VII	CR-84							CR-84							CR-84					**0.3364**	**0.49**
VII	CR-83A							CR-83A							CR-83A						**0.097**
VII	CP-82							CP-82							CP-82						

Supplementary Table 5.4: Average ichthyofauna species abundance for all the biotopes

Biotope I	
Boopsoidea inornata	21.61
Sarpa salpa	15.62
Spondyliosoma emarginatum	13.42
Diplodus capensis	10.87
Cheimerius nufar	8.34
Pagellus natalensis	7.67
Rhabdosargus holubi	5.98
Diplodus hottentotus	2.86
Chrysoblephus laticeps	2.29
Pomadasys olivaceus	2.08
Myliobatis aquila	1.43
Haploblepharus fuscus	1.34
Poroderma pantherinum	1.13
Chirodactylus brachydactylus	1.1
Galeichthys ater	1.07
Poroderma africanum	0.79
Gymnocrotaphus curvidens	0.39
Amblyrhynchotes honckenii	0.31
Haploblepharus edwardsii	0.3
Cymatoceps nasutus	0.26
Pachymetopon aeneum	0.21
Pomatomus saltatrix	0.19
Bathytoshia brevicaudata	0.15
Mustelus palumbes	0.15
Lithognathus mormyrus	0.13
Cheilodactylus pixi	0.11
Chaetodon marleyi	0.07
Eptatretus hexatrema	0.04
Acanthistius sebastoides	0.03

Biotope VII	
Pagellus natalensis	48.34
Spondyliosoma emarginatum	12.43
Galeichthys ater	8.63
Cheimerius nufar	4.71
Haploblepharus edwardsii	4.39
Pomatomus saltatrix	3.8
Rhabdosargus holubi	3.24
Boopsoidea inornata	2.84
Raja miraletus	1.97
Sarpa salpa	1.73
Chrysoblephus laticeps	1.63
Poroderma africanum	1.13
Myliobatis aquila	0.9
Pomadasys olivaceus	0.83
Lithognathus mormyrus	0.58
Pachymetopon aeneum	0.53
Diplodus hottentotus	0.51
Rhabdosargus globiceps	0.32
Raja straeleni	0.26
Amblyrhynchotes honckenii	0.24
Sphyrna zygaena	0.24
Chirodactylus brachydactylus	0.16
Chrysoblephus gibbiceps	0.08
Diplodus capensis	0.08
Carcharias taurus	0.06

Biotope II	
Boopsoidea inornata	30.75
Spondyliosoma emarginatum	15.66
Chrysoblephus laticeps	10.02
Cheimerius nufar	6.64
Pagellus natalensis	5.81
Diplodus capensis	4.41
Sarpa salpa	3.73
Pachymetopon aeneum	3.66
Chirodactylus brachydactylus	2.18
Chrysoblephus cristiceps	2.1
Rhabdosargus holubi	1.85
Diplodus hottentotus	1.29
Poroderma pantherinum	1.16
Poroderma africanum	1.11
Gymnocrotaphus curvidens	0.82
Acanthistius sebastoides	0.77
Rhabdosargus globiceps	0.69
Mustelus palumbes	0.64
Galeichthys ater	0.55
Haploblepharus edwardsii	0.47
Myliobatis aquila	0.3
Bathytoshia brevicaudata	0.3
Triakis megalopterus	0.3
Chrysoblephus gibbiceps	0.3
Serranus cabrilla	0.28
Dasyatis chrysonota	0.28
Cheilodactylus fasciatus	0.22
Mustelus mustelus	0.12
Epinephelus marginatus	0.09

Biotope IV	
Boopsoidea inornata	40.14
Spondyliosoma emarginatum	16.01
Chrysoblephus laticeps	11.69
Pachymetopon aeneum	4.09
Pagellus natalensis	3.99
Chirodactylus brachydactylus	3.15
Cheimerius nufar	3.12
Rhabdosargus holubi	2.58
Diplodus hottentotus	2.01
Haploblepharus edwardsii	1.94
Diplodus capensis	1.38
Poroderma africanum	1.18
Serranus cabrilla	1.05
Chrysoblephus cristiceps	0.98
Acanthistius sebastoides	0.65
Rhabdosargus globiceps	0.65
Poroderma pantherinum	0.62
Epinephelus marginatus	0.39

Biotope III	
Boopsoidea inornata	50.3
Pachymetopon aeneum	6.22
Chrysoblephus cristiceps	6.16
Chrysoblephus laticeps	5.95
Rhabdosargus holubi	4.84
Spondyliosoma emarginatum	4.72
Cheimerius nufar	4.56
Sarpa salpa	3.58
Chirodactylus brachydactylus	2.79
Diplodus capensis	2.03
Myliobatis aquila	2
Diplodus hottentotus	0.7
Gymnocrotaphus curvidens	0.61
Oplegnathus conwayi	0.25

Biotope VI	
Pagellus natalensis	21.05
Spondyliosoma emarginatum	20.82
Boopsoidea inornata	14.55
Cheimerius nufar	10.57
Rhabdosargus holubi	5.79
Chrysoblephus laticeps	5
Pomatomus saltatrix	2.74
Sarpa salpa	2.47
Diplodus capensis	1.96
Lithognathus mormyrus	1.94
Pachymetopon aeneum	1.44
Chrysoblephus cristiceps	1.3
Haploblepharus edwardsii	1.06
Galeichthys ater	1.04
Poroderma africanum	0.91
Diplodus hottentotus	0.86
Chirodactylus brachydactylus	0.7
Myliobatis aquila	0.68

Biotope V	
Spondyliosoma emarginatum	25.39
Boopsoidea inornata	21.3
Chrysoblephus laticeps	9.46
Pagellus natalensis	6.87
Cheimerius nufar	5.68
Pachymetopon aeneum	5.32
Rhabdosargus globiceps	3.17
Sarpa salpa	2.89
Chirodactylus brachydactylus	2.88
Poroderma africanum	1.85
Pomatomus saltatrix	1.81
Rhabdosargus holubi	1.61
Diplodus hottentotus	1.56
Diplodus capensis	1.5
Acanthistius sebastoides	1.13
Galeichthys ater	0.85
Gymnocrotaphus curvidens	0.57
Carcharias taurus	0.54
Triakis megalopterus	0.39
Myliobatis aquila	0.32

Supplementary Table 5.5: List of species identified in Correlation analyses between fish species distribution and relative abundance and the complete set of biotic variables (n = 378) identified 23 variables show a strong correlation with the observed ichthyofauna (r = 0.711).

Amphisbetia orperculata (C0003)
Aplidiopsis sp. 004 (U0167)
Aplidium sp. 022 (U0180),
Arthrocardia carinata (M0017)
Ciocalypta sp. 001 (P0134)
Didemnum sp. 010 (U0135)
Eudendrium deciduum (C0019)
Eudendrium sp. 001 (C0058)
Eudistoma sp. 011 (U0010)
Eudistoma digitatum (U0068)
Eunicella papillosa (C0012)
Hemimycale sp. 003 (P0192)
Leptoclinides sp. 004 (U0137)
Leptogorgia barnardi (C0066)
Leptophytum foveatum (M0273
Mixed tufts of small hydroids (Bio-cns)
Ralfsia expansa (M0214)
Reteporella sp. 001 (B0019)
Sycozoa sp. 002 (U0151)
Synoicum sp. 003 (U0154),
Tedania stylonychaeta (P0055)
Trachycladus sp. 004 (P0143)
Wrightella sp. 001 (C0036)

Supplementary Table 5.6: Technical report for compact stereo Baited Underwater Video (sBRUV)

The development of the Baited Remote Underwater Video or BRUV system for BELTER arose from the need to collect fish distribution and abundance data from the benthic habitat, reducing in-water person-hours and general sampling cost. Two cameras mounted at an angle capture video imagery of the same object from slightly different viewpoints (stereo effect). This allowed, with the development of various software packages, relatively fast and accurate *in situ* measurement of the length of the object such as fish and invertebrates.

Shallow coastal BELTER necessitated the development of a small compact system that is easy to deploy and quickly retrievable in unpredictable conditions from even the wave-dominated inshore areas. The current systems can also be deployed in very shallow water bodies i.e. estuaries and rivers. The system is small and light and can be deployed and retrieved by a single person, by hand, quickly. It should however be durable and should not move once deployed and it should hold adequate bait.

In summary, the equipment is required to be:

- durable and robust,
- small, light, compact, stackable,
- it should offer little resistance against water movement, current and surge,
- it should have space to attach extra weight.

The external cage (Figure S5.7 A) includes rear diagonal support, a bait arm support and stacking hooks constructed from a solid 10 mm stainless-steel round bar. Side base sections (Figure S5.7 B) on the outer frame is elevated to enable more stable seating on an uneven substrate. The outer cage structure has a base width of 735 mm (Figure S5.7 B), base depth of 755 mm, total height of 430 mm, top width of 635 mm, top depth of 255 mm, a vertical bait support bar of 355 mm, an anterior and posterior bait arm position aperture (Figure S5.7 A).

The camera bar 700 mm (Figure S5.7 B and D) is attached to the frame and carried on (20 x 20mm) steel bars welded to the supporting sidebars of the frame. The square bars fit in polymer lined (Figure S5.7 D) square cradles and are secured by a bolt and nut. The ‘give’ provided by the polymer spacer (5 mm thick) is necessary to reduce torsion of the bar when the frame is deployed on an uneven surface e.g. reef.

Figure S5.7: sBruv frames side view, B) view from bottom, C) view from the top and D) camera base with polymer lined cradle.

The camera housings (Figure S5.8 A) are situated on the outer edge on the inside of the frame. This is done to maximize the distance between the camera units and provide protection for the camera housings during deployment and retrieval. The camera housings are attached at five degrees toward each other 500 mm apart (Figure S5.7B). The two flat plate-like camera housing cradles (Figure S5.8 C) with three of the four edges turned up 90 degrees are 140 x 120 mm and welded to the camera bar

(Figure S5.8 B). The cradle holds the round bullet-shaped camera housing (Figure S5.8 D). The camera support bar is 702 X 20 x 20 mm, held in place by a 6 mm in diametre stainless nut and bolt.

Figure S5.8: Camera housing A) front view, B) top view, C) from the base with a view of the cradle, D) attachment clamps, E) inner cavity and F) clamps that secures the detachable front form the rest of the housing.

The waterproof camera housings 155 x 120 mm (Figure S5.8 E) consist of hollow stainless steel units welded to a concave-shaped backplate with a working depth grading of 370 m. The front part of the housing is constructed of a stainless steel flange securing the camera window (Figure S5.8 A). The flange is aligned with the camera housing with a seating pin projecting from the housing into the flange. The door is secured with quick-release clamps holding (Figure S5.8 F) the lens caps in place (Figure S5.8 B). On the interior of the flange attached to the housing door is a moulded polymer seat that secures the camera in place with O-ring (Figure S5.8 E).

The 8 mm round steel rod bait arm holds a 200 x 80 mm bait canister. The bait arm (Figure S5.9 C) and bait canister (Figure S5.9 B) is removable and secured to the frame by anterior and posterior positioning apertures (Figure S5.7 A). The bait canister is held on the distal end of the bait arm by a cradle (Figure S5.9 B) secured by a nut and bolt. One end of the bait canister can be unscrewed (Figure S5.9 A) to access the interior.

Figure S5.9: A) Bait arm seat, B)arm and C) bait canister

In summary, the new compact sBRUV platform has a total weight of 12 kg, the bait canister holds 275 g to 350 g of bait (crushed *Sardinops sagax*). The entire structure is made from stainless steel, except for the polymer (PU) inserts, O-rings and bait canister. Go-Pro action cameras are inserted in custom made polymer moulds for the model to ensure inertia. The camera is secured with a tensioned O ring.

Chapter 6 Traits and indices for benthic biotopes and associated ichthyofauna in Algoa Bay

6.1 Objective

The purpose of this chapter is twofold. Firstly is the use of the biotope dataset to look at the importance and role that traits both of the habitat (sedimentary composition and topographical composition) and the species in the community assemblages (higher taxa that species belong to, the contribution of a predefined set of growth forms and attainable growth hight categories species within the community assemblages attain). This is done for the research localities with reference to the research stations and biotope types. The rationale for this is to show that in studies where species identification is not possible to the genus or species level a coarser level taxa assignment (phyla) and the use of morphological traits of species can be used to describe and identify biotope components that contribute to the larger seascape.

The second aspect involved the calculation and comparison of a suite of diversity indices for both the sessile benthic communities and the ichthyofauna species recorded for each of the biotopes. The reason for this was to evaluated functional indices that may be routinely calculated to allow for reporting on the status and possible changes in both the benthic invertebrate and ichthyofauna communities for the LTER stations both spatially and temporally.

6.1.1 Specific goals

- Convert the species dataset to a traits dataset,
- use this trait-based dataset to investigate the structural aspects of communities within biotopes for the research locations and research stations and
- identify a suite of diversity indices that can be used to report on change both spatially and temporally for the benthic invertebrate and ichthyofauna communities at LTER sampling localities, stations and for the defined biotopes.

6.2 Introduction

6.2.1 Traits

Information on and a description of the assemblages of species that contribute to a specific biotope is well-known (Costello 2009, Lombard et al. 2019). A community may have the same complement of species but due to environmental conditions, their growth forms and the physical structure of the community may present morphologically different or may change over time. This may affect how the benthic biota is utilised by its complement of intra- and supra-benthic ichthyofauna. Broaders taxonomic representations (generally phylum or group) and traits provide information that is important when assessing the effects of anthropogenic pressures on ecosystem structure and function (Jetz et al. 2019, Lombard et al. 2019). Ecological and biological traits are now an integral part of biodiversity databases (Costello et al. 2015) and readily used when focussing on large ecosystems including taxonomic composition (phylum, class orders or families), geographical distribution (e.g. country, locality), environment or seascape (e.g. freshwater, estuarine, marine, bay), habitat (e.g. consolidated, unconsolidated substrates) and guild (e.g. pelagic, benthic, epifauna, plankton) (Costello 2009). Other traits are associated with the organism itself and include growth form, reproduction, life history, method of feeding, diets and behaviour (Costello et al. 2015).

In the previous chapters, we assigned each organism to a species, known or unknown, or a bin (group) of organisms if they could not be distinguished individually. Species identification of benthic biota, especially when dependent on image-based data, is problematic owing to limited information on species identity or the large number of species not known or not described. Phenotypic plasticity and the presence of cryptic species is also problematic. To mitigate these challenges many studies use broad classes or depend on traits-based classification (Althaus et al. 2014, 2015, Davies et al. 2017, James et al. 2017, Langlois et al. 2018, 2020, Dames 2021). This may provide valuable insights into the higher taxonomic representation of the biota and give insight into the structural composition of communities and habitats.

6.2.2 Diversity indices

Diversity indices are important tools in observing, assessing and communicating the difference between or change in communities, spatially and temporally. The number of individuals and species recorded (species richness), density (Gotelli and Colwell 2011), Shannon-Weiner species diversity index (Engels 1974) and Simpson index, which measure community composition, richness and evenness, taxonomic diversity and distinctiveness, which take into account the relativeness of species, are commonly used in ecological community assessment. It should be noted that diversity indices are not diversities themselves but are indices of diversity, and many are nonlinear. Thus a small difference in the value of an index may, when correctly interpreted, equate to a large difference in reality. This means that indices values cannot always be directly compared, or provide the correct insight if directly compared (Jost 2006). In these cases, corresponding Hill numbers (Jost 2006, Chao et al. 2010), or the effective number of species, are also calculated (PRIMER). The reason for this is that after conversion, diversity is measured in units of numbers of species, irrespective of the unit used by the index, and allows comparison and interpretation of the calculated indices. The effective number of species is a useful tool for comparing diversities of different communities, even when different diversity indices were used in their assessment (Jost 2006, Chao et al. 2010). Phylogenetic diversity indices are important, as they take into account the inequality of species due to their taxonomic relatedness or distinctiveness (Clarke and Warwick 1998, 1999, Vellend et al. 2010) and a community of phylogenetically divergent species could be seen as more diverse than an assemblage of closely related species (Chao et al. 2010). In this chapter, we compute several indices and compare these for both benthic communities and the associated ichthyofauna assemblages identified within the broader biotopes.

6.3 Material and methods

The data collected from the two sample stations, White Sands Reef (WSR) and St Croix Complex (SCC) within Algoa Bay, consisted of 10 images at each of the 36 research localities, within which 216 point counts were made, thereby providing a 77 760 point dataset. In addition, a total of 35 teleosts and 15 elasmobranch species were identified in four seasonal sample events for the two stations. Relative abundance (MaxN) was obtained by examining the first 15 minutes of the 60-minute video collected (see Chapter 5). During this process, 5 917 teleost and elasmobranchs were identified to species level and counted.

The benthic species dataset, consisting of 375 benthic algal and invertebrate species, was used and transformed into a trait-based dataset. The traits considered here were used to assist in informing on habitat, the taxonomic relationship of broad groups of the benthic biota and on the morphological characteristics of species that would contribute to the general structure of the community. Firstly, the habitats, substrate composition and architecture were compared. Secondly, a trait-based dataset was constructed by placing all species within each of four categories:

i) higher taxonomic affiliation: Chlorophyta, Rhodophyta and Ochrophyta, Porifera, Cnidaria, Annelida, Bryozoa, Echinodermata and Ascidia;

ii) growth form: endopsammic, encrusting, tufts, erect and arborescent (classification of the organisms in morphological classes followed that proposed for sponges (Boury-Esnault and Rützler 1997) and were applied similarly to the other taxa);

iii) attainable height or reach into the water column above the substrate: 0, 5, 15, 30 and 50-centimetre classes; and

iv) a measure to indicate the resistance an organism would exert against the moving water column: flexible, resistant and rigid.

Thirdly, a dataset was constructed consisting of calculated diversity indices and lastly, a Linnaean taxonomic tree was constructed for all recorded species.

The analysis was conducted using various analytical tools in PRIMER6 (Clarke and Warwick 2001) and Paleontological Statistics Version 4.05 (PAST) (Hammer 2001). Multivariate PERMANOVA analysis (PAST) investigated the difference of trait datasets for the defined biotopes. The univariate diversity indices (PRIMER DIVERS analysis) include the number of species, number of individuals, (Shannon-Wiener index, Simpson Diversity index and Hill numbers), taxonomic diversity and distinctiveness indices. Species density was calculated as the product of two equations: i) species richness (number of species represented by the number (N) of individuals) and ii) total individual density (number of individuals (N), disregarding species in a set area (A) (James and Wamer 1982, Gotelli and Colwell 2011). The breakdown in the above equation shows that the number of species per sampling unit reflects both the underlying species richness and the total number of individuals sampled (James and Wamer 1982, Gotelli and Colwell 2011). A Linnaean tree of taxa identified and recorded in this study, both benthos and ichthyofauna, was constructed to allow the estimation of taxonomic diversity and distinctiveness between and within the stations, locations and biotopes.

6.4 Results

6.4.1 Traits

A comparison of substrate composition of sampled locations within the different biotopes indicates that the majority of sample locations are characterised by consolidated reef substrate (Figure 6.1 A) with the reef substrate generally characterised as flat reef or sandy plains (Figure 6.1 B). This was the result of sampling bias in that the selection of the localities depended, in part, on the success of the deployment of the sBRUV systems used to observe ichthyofauna. Investigation into the higher taxa and traits contribution of all 375 species in the dataset showed 34.4% of species were ascidian species, (55.0% encrusting and 45.0% erect), 30.7% sponge species (51.7% encrusting, 47.4% erect, 0.9% endopsammic), 12.8% cnidarian species (75.5% erect, 22.5% arborescent and 2.0% tufts), 8.0%

bryozoan species (93.3% erect, 6.7% encrusting), 1.1% annelid species (all were tube forming and classified as erect), 0.5% echinoderm species (two species of crinoids were regarded as sedentary and erect) and 12.5% macroalgae species (of which 76.6% Rhodophyta, 12.8% Ochrophyta, 10.6% Chlorophyta and 64.4% erect, 26.7% encrusting, 8.9% tufts) (Figure 6.1 C). Of all taxa, 56.8% were classified as erect, 38.7% encrusting, 2.9% arborescent, 1.3% as tufts and 0.3% as endopsammic (Figure 6.1 D). The height that a benthic organism penetrates the water column has implications for the ability of suspension feeders to access food in the water column, provide protection to other organisms and inadvertently allow benthic organisms to change the turbulence dynamics of the immediate water column (Margalef 1997). It furthermore offers insight into the structural height of the benthic community as a whole. A single endopsammic sponge was recorded at two of the localities, while 49.6% of species could access the water column up to 5 cm above the substrate (of which 38.7% were ascidians, 29.6% sponges and 14.0% cnidarians) and 43.2% of species could access up to 15 cm of the water column (again the majority were ascidians (33.3%), 28.4% were sponges and 9.3% cnidarians). Those species able to access the water column to 30 cm above the substrate were predominantly sponges (52.4%), followed by 28.6% cnidarians, with ascidians and macroalgae each accounting for 9.5%. Species with a reach of 50 cm into the water column consisted of 60.0% cnidarians (large sea fans) and 40.0% sponges (Figure 6.1 E).

As a measure of the structural integrity of the communities or resistance of individuals in the community to the movement of the water column, species were classified into three categories. These included those that were rigid or did not have any give (give: the capacity to bend or alter in shape under pressure), those that were firm and structurally resistant to movement of the water but with little give, and lastly, the flexible species that responded easily to movement in the water column, swaying readily with the current. Communities consisted mostly of structurally resistant species (72.5%), 47.1% of which were ascidians and 39.7% sponges. A smaller percentage of species (19.2%) were considered flexible, represented by 45.8% macroalgae and 40.3% cnidarians. Only 8.3% of species were structurally rigid, 61.3% being bryozoans, 16.1% macroalgae and 12.9% sponges (Figure 6.1 F).

Where the previous section assessed the composition and contribution of substrate and benthos as a whole, the next section draws comparisons between the biotopes (indicated by dotted lines in Figure 6.1). Statistical tests using Multivariate PERMANOVA analysis (PAST) compared the biotopes substrate characteristics, high taxonomic composition and the morphological traits identified for each biotope and shows that in general, the selected traits differ significantly between biotopes ($p < 0.05$) (Table 6.1 with detailed statistical results provided in Supplementary Table 6.2). Pairwise comparison between the different biotopes indicates that all biotopes differ significantly from each other in the higher taxa benthos. Biotope VII differs significantly (p < 0) from all other biotopes in substrate composition, architecture and morphological traits.

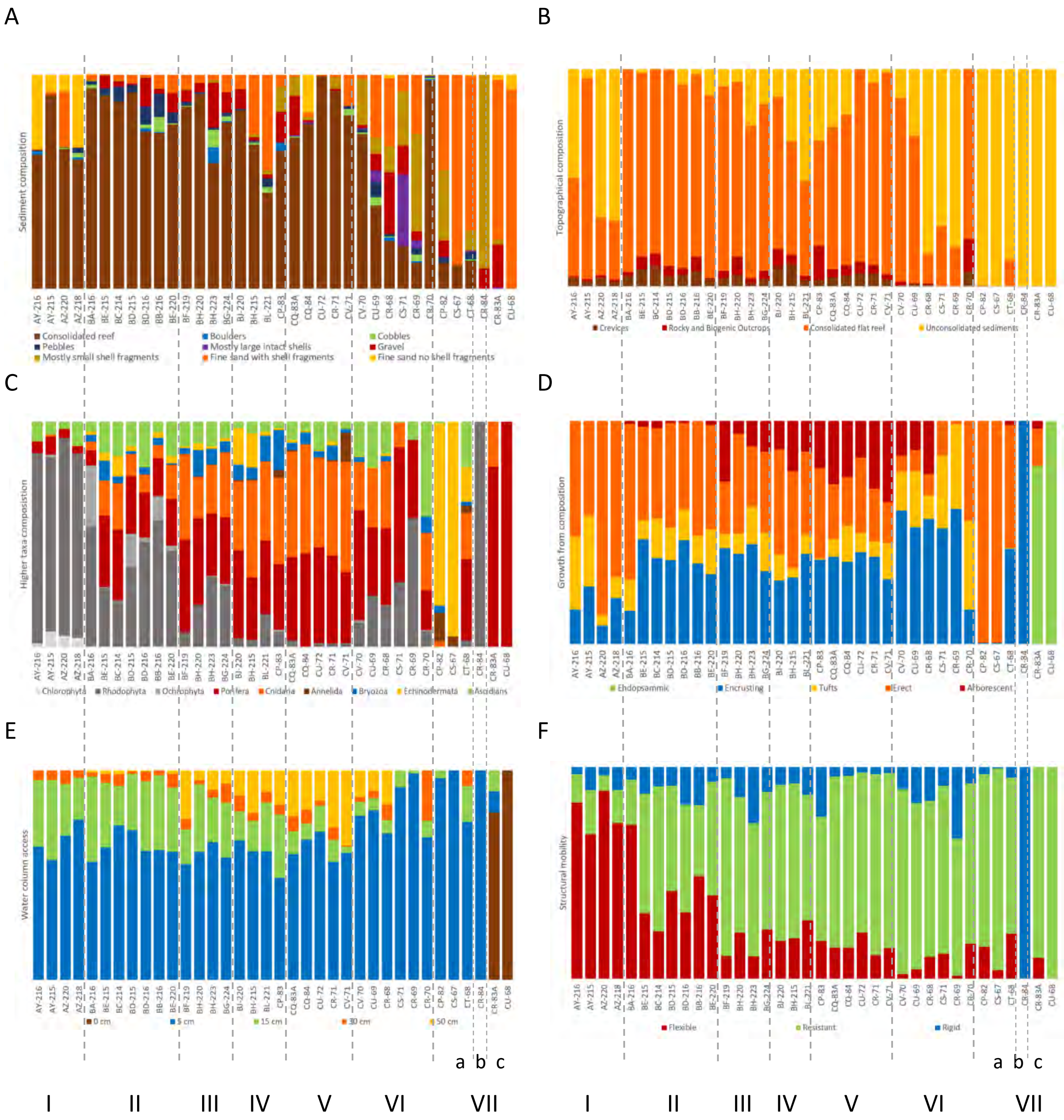


Figure 6.1: The contribution of individual recordings (point reads) to A) sedimentary composition; B) topographical composition; C) higher taxa to community composition; D) contribution of different growth forms to the community architecture; E) composition of species with different reach utilization of different zones of the water column above the habitat surface and F) structural rigidity of the species that contribute to the communities at the different localities. The grouping as suggested by CLUSTER analyses as given in Chapter 3 and Figure 3.4 is indicated by dotted lines and labelled at the bottom of the figure.

Biotope I is characterised prominently by consolidated substrate of which most is flat with only a small percentage of crevices and outcrops measured (Figure 6.1). It differs significantly in substrate composition from Biotope II and VII, and architecture from Biotope II and V. The biotic component is dominated by algae, the majority consisting of red algae (Rhodophyta 82.3%). Individuals are predominantly erect (61.0%), 65.8% able to access the water column up to 5cm above the substrate and 77.5% of the biota are classified as flexible, moving readily with the current. It differs significantly ($p < 0.05$) from all other biotopes in the growth form represented and the structural rigidity of the community (Table 6.1). The growth profile is significantly different ($p < 0.05$) from Biotope II, IV and V (Table 6.1).

Table 6.1: Multivariate PERMANOVA analysis (PAST) compared observed traits for each biotope with significant differences ($p < 0.05$ in bold). Substrate composition and surface topography (percentage cover) PERMANOVA computed with Euclidean distances, biotic traits (abundance) computed using Bray Curtis similarity index (see Supplementary Table 6.1 for detailed results).

		Substrate composition	**Surface topography**	**Higher taxa**	**Growth form**	**Height**	**Rigidity**
Biotope I	Biotope II	**0.0107**	**0.0257**	**0.0051**	**0.0334**	**0.0159**	**0.0189**
	Biotope III	0.0552	0.0814	**0.0286**	**0.0294**	0.1119	**0.0284**
	Biotope IV	0.1414	0.0558	**0.0265**	**0.0297**	**0.0267**	**0.0304**
	Biotope V	0.0716	**0.0190**	**0.0053**	**0.0047**	**0.0125**	**0.0054**
	Biotope VI	0.0904	0.9704	**0.0053**	**0.0390**	0.0668	**0.0004**
	Biotope VII	**0.0036**	**0.0039**	**0.0050**	**0.0036**	**0.0045**	**0.0048**
Biotope II	Biotope III	0.2957	0.3109	**0.0274**	**0.0093**	**0.0122**	**0.0358**
	Biotope IV	**0.0331**	0.5696	**0.0098**	**0.0088**	**0.0008**	0.0838
	Biotope V	0.3764	0.5315	**0.0004**	**0.0007**	**0.0007**	**0.0033**
	Biotope VI	**0.0100**	0.1297	**0.0005**	**0.0049**	**0.0001**	**0.0011**
	Biotope VII	**0.0011**	**0.0008**	**0.0004**	**0.0003**	**0.0004**	**0.0011**
Biotope III	Biotope IV	0.1705	0.2872	0.1166	0.144	0.1438	0.4228
	Biotope V	0.6584	0.5143	**0.0101**	0.1913	0.1081	0.3474
	Biotope VI	0.0982	0.5443	**0.0283**	0.0521	0.0584	0.1603
	Biotope VII	**0.0051**	**0.0050**	**0.0047**	**0.0044**	**0.0040**	**0.0047**
Biotope IV	Biotope V	0.0847	0.6435	**0.0371**	**0.0234**	0.2121	0.1682
	Biotope VI	0.3139	0.2597	**0.0483**	0.1066	0.2128	0.4591
	Biotope VII	0.0252	**0.0093**	**0.0490**	**0.0240**	**0.0239**	**0.0104**
Biotope V	Biotope VI	**0.0404**	0.1971	**0.0025**	**0.0019**	**0.0255**	0.0437
	Biotope VII	**0.0030**	**0.0102**	**0.0020**	**0.0023**	**0.0024**	**0.0030**
Biotope VI	Biotope VII	**0.0138**	**0.0020**	**0.0056**	**0.0031**	**0.0045**	**0.0026**

Biotope II has a predominantly consolidated reef habitat with crevices and outcrops. It differs significantly from Biotope I, IV and VI in the substrate composition as well as from Biotope I in its topography. The biotic component is well represented by red algae (40.0%), as well as porifera (21.7%), ascidians (11.7%) and cnidarians (11.1%). Erect growth forms dominate (48.3%) followed by encrusting forms (35.9%). The majority of individuals occupy the zone 5 cm above the substrate, and 30.9% reach up to 15 cm. Growth forms that dominate are resistant (47.5%) and flexible (41.3%).

Biotope II differs significantly ($p < 0.05$) from all other biotopes in growth form and the height represented in the community is also different from all but Biotope IV in its structural rigidity (Figure 6.1 and Table 6.1).

Biotope III habitat consists of a consolidated substrate with crevices, outcrops and some gravel. It does not differ significantly from Biotope I, II, IV, V and VI in its substrate composition and surface architecture (Table 6.1). The biotic component consists mostly of sponges (34.9%), cnidarians (26.9%) and Rhodophyta (20.1%). Most individuals are encrusting forms (40.3%) and arborescent growth forms (14.5%), distinguishing this biotope from biotope I and II, a characteristic shared with biotope IV, V and VI. The majority of individuals occupy the zone 5 cm into the water column (60.0%), with 24.3% reaching a height of 15 cm and occasional individuals reaching up to 50 cm (10.9%). This biotope differs significantly ($p < 0.05$) from all others in the growth height of the benthos and differs from Biotope I and VII in its growth forms and the structural rigidity of the community (Table 6.1).

Biotope IV is predominantly reef substrate, but fine sediment with shell fragments is also a prominent component of the habitat (Figure 6.1). The substrate composition differs significantly from Biotope II (Table 3.1). The biota is well represented by cnidarians (36.2%) and sponges (33.4%) consisting of 43.4% erect, 32.0% encrusting and 16.3% arborescent individuals. The largest proportion (63.6%) of individuals in the community attain a height of only about 5cm above the substrate, while taller individuals of up to 15 cm and 50 cm represent 16.4% and 14.3%, respectively, with most individuals (70.0%) categorised as resistant. The height and structural rigidity of the benthos in this biotope's community differ significantly ($p < 0.05$) from Biotope I and II (Figure 6.1).

Biotope V consist of rocky reef habitat. The biota is dominated by cnidarians (43.8%) and porifera (37.0%). A large part of the community is composed of encrusting (37.3%) species, with erect (26.9%) and arborescent (26.2%) components being well-represented. Most of the individuals (61.2%) project only 5 cm above the substrate, a smaller percentage (22.7%) to 50 cm and a large proportion have growth forms categorised as resistant (Figure 6.1). It differs significantly ($p < 0$) from all other biotopes except in its surface topography and the rigidity of the biota (Figure 6.1).

Biotope VI is characterised by a mixed substrate (Figure 6.1). This differs significantly from substrate composition in Biotopes II and V ($p < 0.05$) (Table 6.1). The biota is well represented by several groups, 35.1% porifera, 22.4% ascidians, 22.3% cnidarians and 14.5% red algae. The dominant growth form is encrusting (42.5%) with 28.3% forming tufts and 21.0% categorised as erect. The majority of individuals (76.9%) only utilise the immediate (5 cm) zone above the substrate with 6.6%, 10.2% and 6.3% in the 15, 30 and 50 cm categories, respectively. The majority (78.6%) provide some degree of structural integrity, while 12.5% have a rigid growth form. This biotope differs significantly ($p < 0.05$)

in all morphological traits from Biotope II and V in addition to the aforementioned Biotope VII (Figure 6.1).

As mentioned before, Biotope VII differs significantly ($p < 0.05$) from the other biotopes and tentatively consists of three subunits united primarily by the unconsolidated character of the habitats. Biotope VIIa bottom is dominated by fine sand with shell fragments with low, sand-covered, hard substrate providing attachment for typical reef biota, predominantly crinoids (56.8%) and porifera (14.9%), mostly extending 5 cm above the substrate surface (88.4%) (81.0% being erect), to 15 cm (8.6%) above the substrate (Figure 6.1) Biotope VIIb represents a single sample locality consisting mostly of small loose shell fragment habitat, the only biota recorded being encrusting red coralline algae. Biotope VIIc consists of unconsolidated substrate be made up of fine sand with shell fragments and a preliminarily identified endopsammic sponge species (Figure 3.4 and Figure 6.1).

6.4.2 Diversity indices

The number of species (S), the Shannon-Weiner index (N), Simpson diversity index (1-λ) and total phylogenic diversity (sPhi+) were selected and plotted for all quadrats collected and analysed. It shows clearly, in some cases, a large variation in the considered indices for quadrats collected from a single sample locality (Figure 6.2). Fine-scale heterogeneity of habitat and communities present in the immediate seascape where the quadrat images were collected (generally within a target area of 25 metres of the reference research location and in some cases only a metre apart) is evidenced by the difference in the number of individuals, species and diversity of species collected (Figure 6.2). An *a posteriori* analysis of the quadrat-derived data subsequently resulted in the identification of 44 distinct biotope sub-units which contribute in a varying degree to the overall character of the biotope and is a measure of the heterogeneity within the broader biotopes (Figure 4.6). A comparison of the diversity indices as per Figure 6.2 provides comparable insight into the variability of species and taxonomic composition of the community at each of the research locations (fine-scale) and shows that a comparison of indices at different temporal and spatial scales is essential to understand the organisational structure of abiotic and biotic components within the seascape (broad-scale).

Species diversity indices for the community dataset were used to compare the two stations (WSR and SCC) as well as the individual localities in this study (Figure 6.2). Species density was calculated as the product of two equations: i) species richness (number of species represented by some number of individuals) and ii) total individual density (the number of individuals in amount or area). This can be expressed as (species / (area A)) = (species / (N individuals)) x ((N individuals) / (area A)), as in James and Wamer (1982) and Gotelli and Colwell (2011). Owing to the non-linear character of most diversity

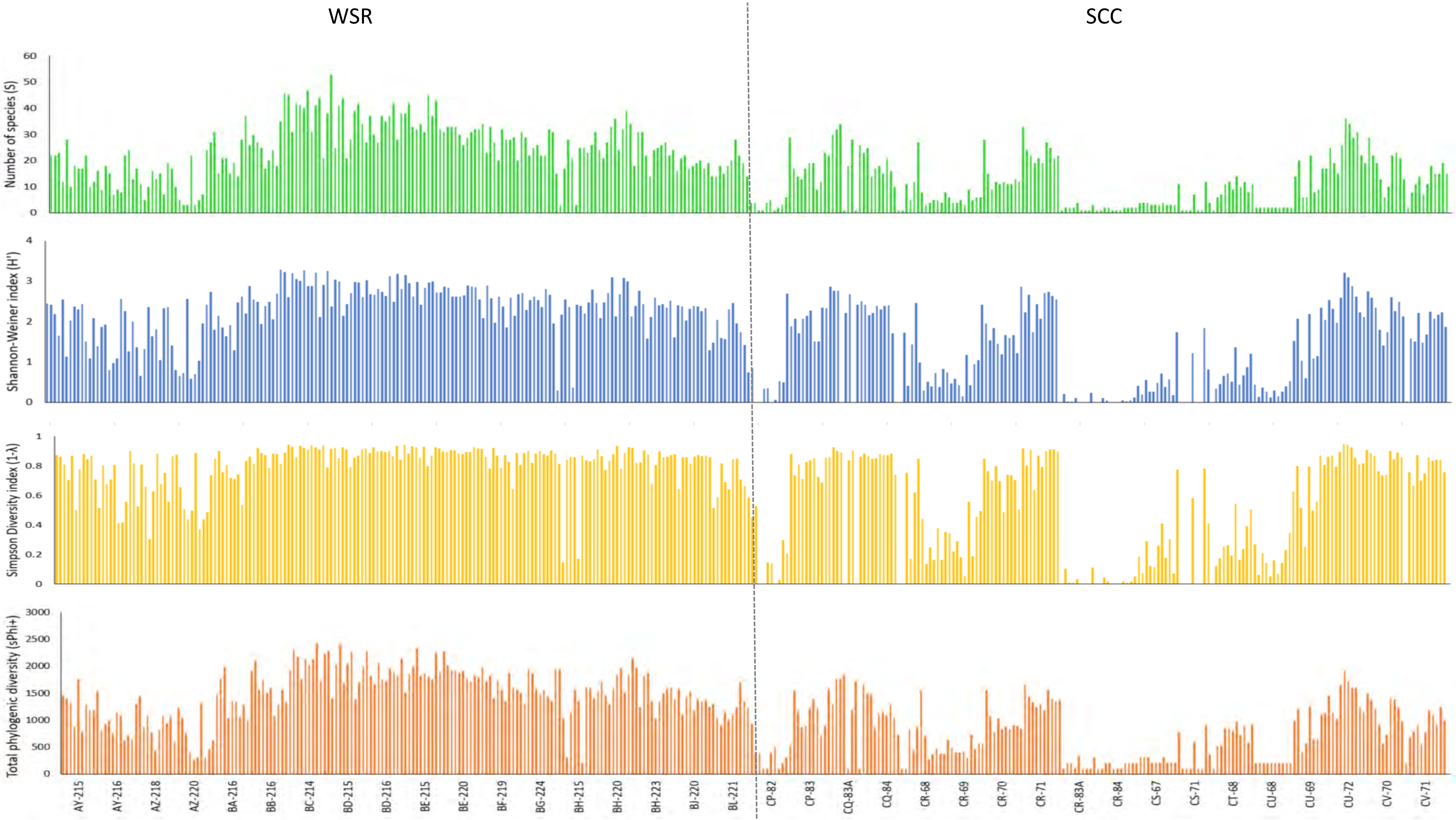


Figure 6.2: The diversity indices; Number of species, Shannon-Weiner index, Simpson Diversity index and Total phylogenic diversity of benthic sessile and sedentary biota for each of the sampled sites indicated by research location. The dashed line separates the stations White Sands Reef (WSR) and St Croix Complex (SCC).

indices, and thus to afford easier direct comparison between sampled units, the associated true diversity or Hill numbers (conversions equations for indices as given in Jost (2006)) are provided at the bottom of Table 6.2. Taxonomic diversity and distinctiveness indices were calculated with weights determined by taxon richness data (Clarke and Warwick 1998) (Table 6.2 with a visual comparison given in Figure 6.3). The differences identified and discussed in Chapters 3 and 4 are highlighted by the calculated indices for the sample stations and localities within the biotopes (Table 6.2). This supports the collection of LTER data from different stations within different ecosystems in the seascape to assess the difference between systems and the response of different systems to change.

The difference in the number of epibenthic species (species richness) as well as the abundance of algae and benthic invertebrates is clear between WSR and SCC (Table 6.2). This is especially prominent for Biotope VII, which is characterised by predominantly unconsolidated sediment. The overall density of organisms and species for each location (Figure 6.3 C and D) and biotope (Figure 6.4 A and B) (number of individual benthic organisms and the species (DS) per area (m^2)) were compared. In Biotope II more individuals and more species are present per area (Figure 6.4 A and B). Biotope VII has the least and Biotope V has a high density of organisms, but relative to other biotopes, has a low diversity of species per area (Figure 6.4 A and B).

A one-way ANOVA analysis, Kruskal-Wallis test for equal means and a non-parametric Mann-Whitney U test were conducted to determine the difference in species and taxonomic indices as calculated for benthic sessile organisms between biotopes. Levene’s test for homogeneity of variance and the Shapiro-Wilk test to determine if data are normally distributed as well as a box plot for the indices per biotope is provided in Supplementary Table 6.2 (all statistical analysis performed in PAST). All diversity indices calculated for benthic communities, except taxonomic distinctiveness, indicate significant differences between biotopes ($p < 0.05$) (Table 6.2). For additional details and pairwise comparison see Supplementary Table 6.2. Similar statistical analyses for ichthyofauna also indicate a significant difference for all diversity indices, but, in contrast to the benthos, no significant difference was found in the taxonomic diversity of the fish assemblages between the different biotopes. Taxonomic diversity and distinctiveness were proposed as indices to detect shifts in the hierarchy of relatedness above the species level that were not measured or detected by the other indices (Hall and Greenstreet 1998, Clarke and Warwick 1999). This is a valuable tool to identify changes in species composition when long-term datasets are available.

Table 6.2: Species diversity indices from the community dataset for and in each of the stations (WSR and SCC).

S = Number of species, N = Number of individuals, A = area (4.35 m^2), D_S = Species density in (s/m^2) H'(loge) = Shannon-Wiener index, (1-λ) = Simpson Diversity index and Hill number, calculated (as given at the bottom of this table). Taxonomic diversity and distinctiveness indices were calculated with weights determined by taxon richness data with Δ= Taxonomic diversity and Δ* = Taxonomic distinctiveness.

Station/Code	**S**	**N**	**S/N**	**N/A**	**D_S**	**H'(loge)**	**Hill H'(loge)**	**(1-λ)**	**Hill (1-λ)**	**Δ**	**Δ***
WSR	326	31 305	0.0104	399.808	4.163	3.886	48.7156	0.9546	22.0264	88.48	92.68
SCC	214	18 060	0.0119	230.651	2.733	3.644	38.2445	0.9476	19.0840	85.94	89.94
Localities											
AY-216(I)	39	1396	0.0279	320.920	8.966	2.309	10.0644	0.8260	5.7471	73.52	88.94
AY-215(I)	65	1955	0.0332	449.425	14.943	2.580	13.1971	0.8468	6.5274	77.08	90.98
AZ-220(I)	33	1421	0.0232	326.667	7.586	1.949	7.0217	0.6896	3.2216	50.48	73.15
AZ-218(I)	38	1410	0.0270	324.138	8.736	2.135	8.4570	0.7453	3.9262	62.19	83.38
BA-216(II)	72	2091	0.0344	480.690	16.552	2.479	11.9293	0.8155	5.4201	75.41	92.43
BE-215(II)	106	1996	0.0531	458.851	24.368	3.407	30.1746	0.9270	13.6986	86.18	92.92
BC-214(II)	120	1992	0.0602	457.931	27.586	3.617	37.2257	0.9476	19.0840	87.88	92.69
BD-215(II)	104	2041	0.0510	469.195	23.908	3.290	26.8429	0.9246	13.2626	86.14	93.12
BD-216(II)	111	1817	0.0611	417.701	25.517	3.358	28.7317	0.9258	13.4771	82.97	89.57
BB-216(II)	91	1871	0.0486	430.115	20.920	2.920	18.5413	0.8848	8.6806	78.72	88.92
BE-220(II)	90	1738	0.0518	399.540	20.690	3.276	26.4697	0.9262	13.5501	85.37	92.13
BF-219(III)	104	1874	0.0555	430.805	23.908	3.075	21.6499	0.8925	9.3023	80.19	89.8
BH-220(III)	95	1975	0.0481	454.023	21.839	3.304	27.2213	0.9172	12.0773	85.55	93.22
BH-223(III)	92	1600	0.0575	367.816	21.149	3.165	23.6887	0.9131	11.5075	84.63	92.63
BG-224(III)	82	1756	0.0467	403.678	18.851	3.239	25.5082	0.9327	14.8588	85.08	91.17
BJ-220(IV)	52	1808	0.0288	415.632	11.954	2.881	17.8321	0.9040	10.4167	83.33	92.12
BH-215(IV)	78	1478	0.0528	339.770	17.931	2.978	19.6485	0.9050	10.5263	82.51	91.11
BL-221(IV)	62	1086	0.0571	249.655	14.253	3.125	22.7599	0.9258	13.4771	84.51	91.2
CP-83(V)	65	1528	0.0425	351.264	14.943	3.226	25.1787	0.9392	16.4474	85.24	90.7
CQ-83A(V)	86	1539	0.0559	353.793	19.770	3.240	25.5337	0.9338	15.1057	80.85	86.53
CQ-84(V)	51	1662	0.0307	382.069	11.724	2.919	18.5228	0.9195	12.4224	78.76	85.61
CU-72(V)	90	2146	0.0419	493.333	20.690	3.315	27.5224	0.9371	15.8983	82.37	87.86
CR-71(V)	70	1995	0.0351	458.621	16.092	3.156	23.4765	0.9215	12.7389	81.03	87.89
CV-71(V)	42	1978	0.0212	454.713	9.655	2.488	12.0372	0.8545	6.8729	75.75	88.6
CV-70(VI)	52	1604	0.0324	368.736	11.954	2.772	15.9906	0.8957	9.5877	81.68	91.13
CU-69(VI)	46	1015	0.0453	233.333	10.575	2.720	15.1803	0.8852	8.7108	81.77	92.29
CR-68(VI)	34	534	0.0637	122.759	7.816	2.734	15.3943	0.9137	11.5875	83.34	91.04
CS-71(VI)	19	475	0.0400	109.195	4.368	2.248	9.4688	0.8381	6.1767	75.72	90.15
CR-69(VI)	13	399	0.0326	91.724	2.989	1.571	4.8115	0.7223	3.6010	70.67	97.6
CR-70(VI)	48	2130	0.0225	489.655	11.034	2.078	7.9885	0.7734	4.4131	72.74	94
CP-82(VIIa)	8	297	0.0269	68.276	1.839	0.712	2.0387	0.3302	1.4930	33.06	99.77
CS-67(VIIa)	3	169	0.0178	38.851	0.690	0.208	1.2317	0.0907	1.0997	9.122	100
CT-68(VIIIa)	34	329	0.1033	75.632	7.816	2.942	18.9537	0.9282	13.9276	85.55	91.88
CR-84(ViIb)	1	18	0.0556	4.138	0.230	0	1.0000	0.0000	1.0000	0	0
CU-68(VIIc)	1	212	0.0047	48.736	0.230	0	1.0000	0.0000	1.0000	0	0
CR-83A(VIIc)	5	30	0.1667	6.897	1.149	0.766	2.1518	0.3489	1.5359	35.17	97.46

Conversion equations for indices as given in (Jost 2006).

Index	**Index value**	**True diversity**
Species richness (S)	$x \equiv \sum_{i=1}^{S} p_i^0$	x
Shannon entropy (H)	$x \equiv \sum_{i=1}^{S} p_i^q \ln p_i$	$exp(x)$
Gini- Simpson index $(1 - \lambda)$	$x \equiv 1 - \sum_{i=1}^{S} p_i^2$	$1/(1-x)$

p_i = the proportion of individuals belonging to the *i*th species in the dataset

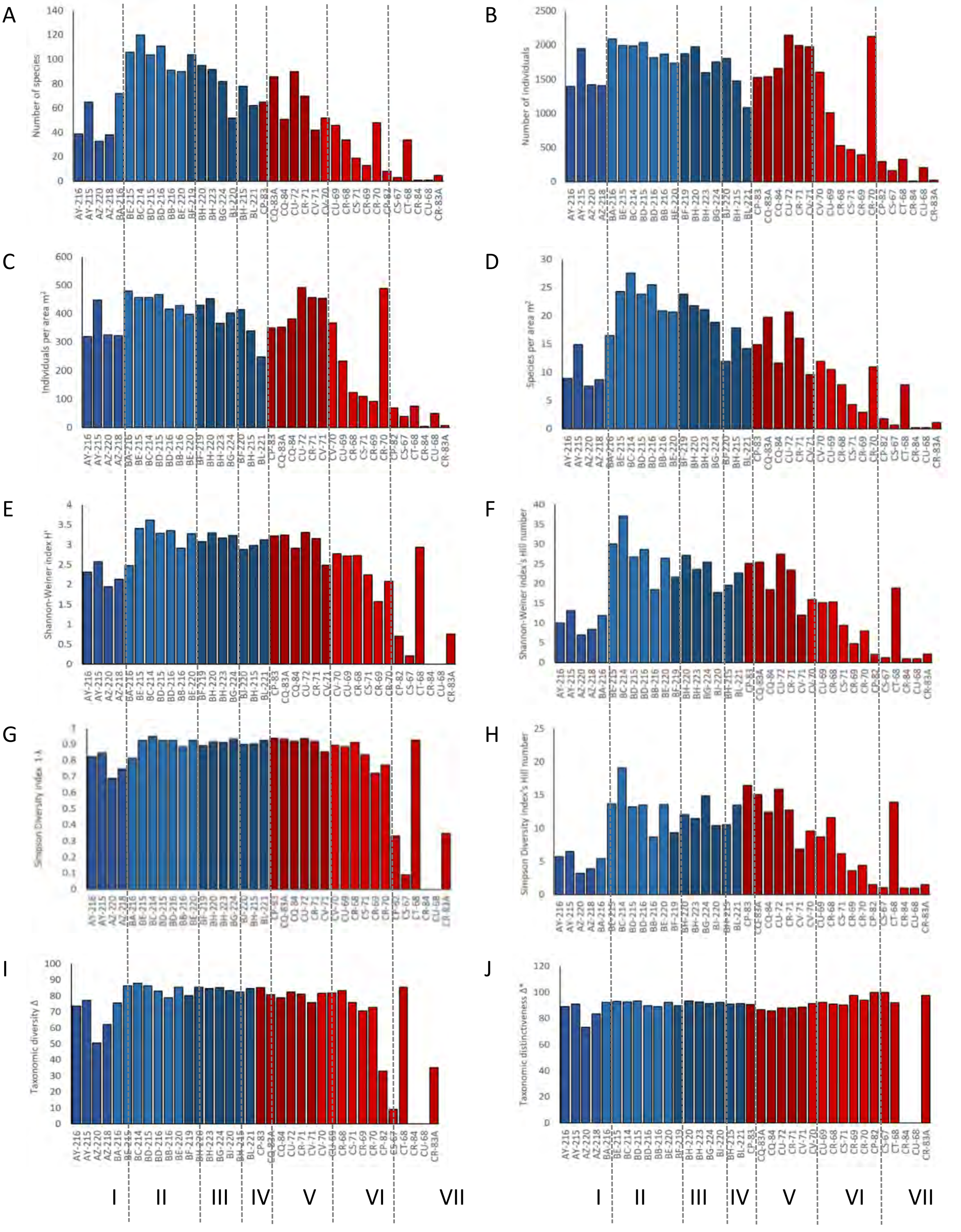


Figure 6.3: Species and taxonomic indices colour coded into biotopes for all locations sampled. Localities are colour coded blue for WSR and red for SCC stations and arranged per biotope group from left to right. A) Number of species, B) Number of individuals, C) Number of individuals per area, D) the number of species per area, E) Shannon-Weiner index, F) and its Hill number, G) Simpson Diversity index, H) and its hill number, I) taxonomic diversity and J) taxonomic distinctiveness.

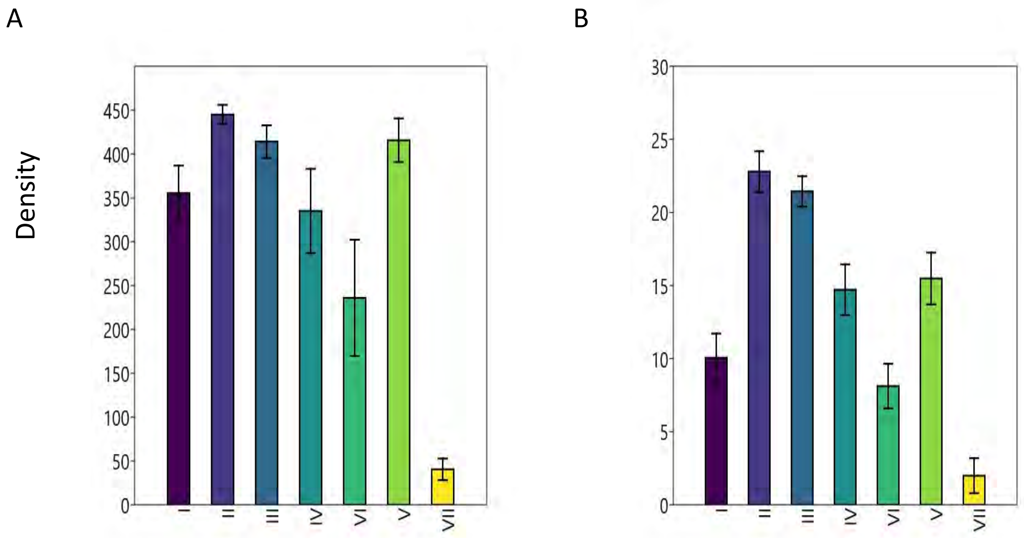


Figure 6.4: Box plot calculated for density of A) number individuals and B) number species per area (m^2) of benthos with standard error indicated by 95% interval whiskers for each biotope indicate on the x-axis.

Species diversity and taxonomic indices for the benthos and ichthyofauna were compared with Kernel density violin plots superimposed with box plots (Figure 6.6) and analysed statistically (in PAST) to determine the differences in indices for ichthyofauna between biotopes (see Supplementary Table 6.3). It is evident that although the benthic communities show differences in community composition, species richness and evenness, it is not as clearly observed for ichthyofauna between the biotopes (Figure 6.6 C and D). Biotope VII differs in ichthyofauna species diversity from all other biotopes, but not significantly ($p > 0.05$) in its abundance between any of the biotopes. The Shannon-Weiner index and the Simpson diversity index indicated a significant difference in fish assemblage composition, species richness and evenness between most biotopes (Supplementary Table 6.3).

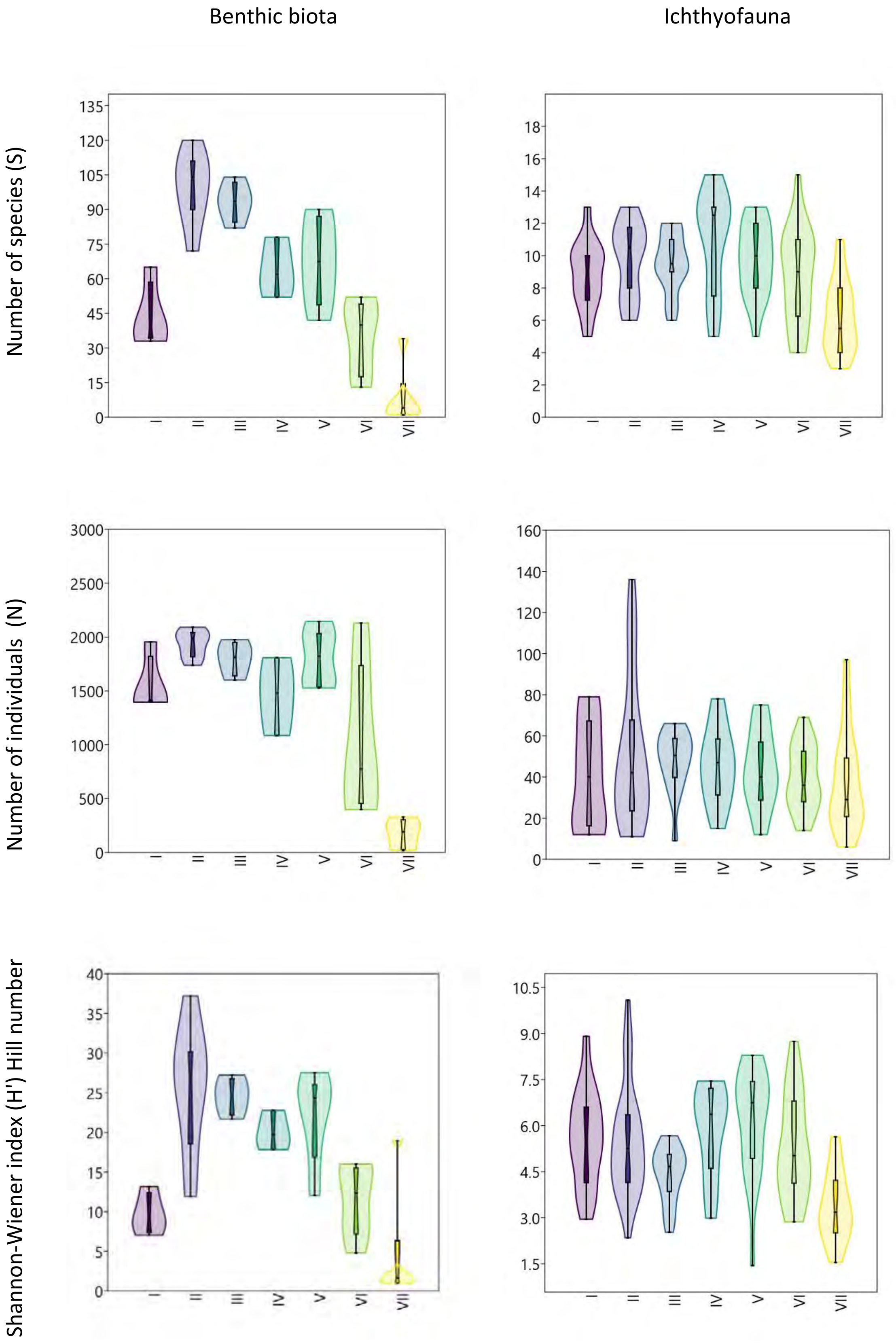


Figure 6.5: Kernel density violin with box plot superimposed for species and taxonomic indices calculated for all biotopes (for detailed statistical data see Supplementary Table 6.2 for the benthic biota and Supplementary Table 6.3 for the ichthyofauna). Please take note Biotope is given on the x-axes and value on the y-axes (the scale of which may differ between graphs).

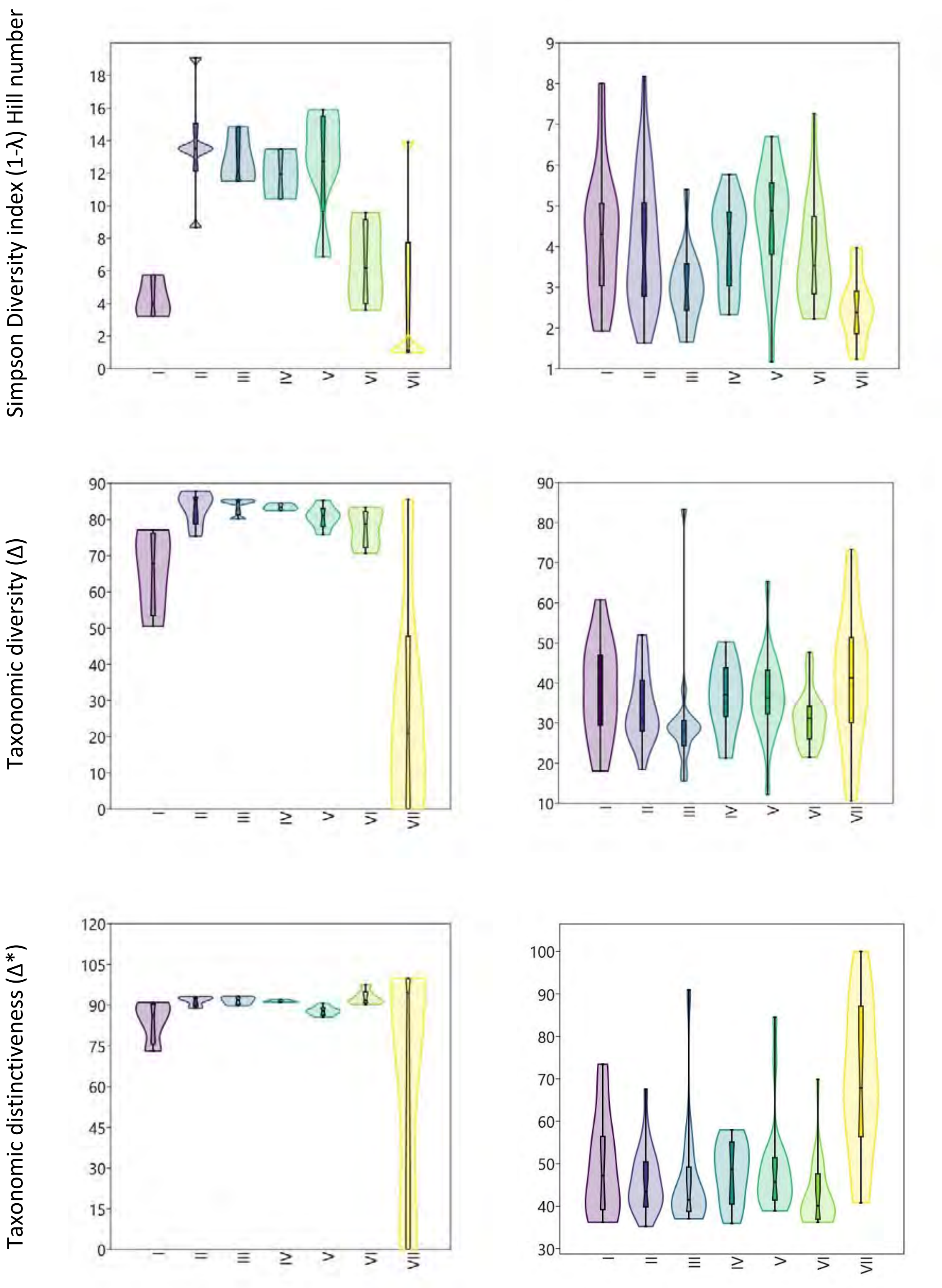


Figure 6.6 continued: Kernel density violin with box plot superimposed for species and taxonomic indices calculated for all biotopes (for detailed statistical data see Supplementary Table 6.2 for the benthic biota and Supplementary Table 6.3 for the ichthyofauna). Please take note Biotope is given on the x-axes and value on the y-axes (the scale of which may differ between graphs).

It is advantageous for long-term data collection facilities, such as SAEON, not to solely supply raw data to end users but to produce a set of easily digestible data products. Traits and relevant species indices should be used to develop easily digestible visual aids to inform on the ecosystem as a whole. Take for instance the identification of indicators by calculating indicator value (Dufrêne and Legendre 1997, Hammer 2001) (Equation 6.1 in the supplementary section). This can be calculated for a species or, in this case, traits. The graphic representation of the higher taxa to biotope community and morphological traits can easily characterise biotopes and distinguish one from the other. The estimation of indicator traits takes into account the representation of the trait in the group (in this case the biotope) and its fidelity to the group (biotope) given as a percentage. We can subsequently see that Biotope I contains green (Chlorophyta) and red (Rhodophyta) algae. The occurrence of green algae only in Biotope I makes it more significant as an indicator (indicated by the high indicator value) than the red algae which are found in several biotopes. The same can be done for morphological traits. Erect growth form and the flexibility of the growth form play a more important role in defining the biotope than how far the biota extends above the substrate, which contributes little to the identity or distinctness of this biotope (**Error! Reference source not found.**). This is in contrast with Biotope V where segmented worms (Annelida), bryozoans, cnidarians, sponges (Porifera), encrusting species and in particular arborescent growth forms, that may grow to 50 cm tall and do not readily bend but sway in currents, play a significant role in defining the biotope (**Error! Reference source not found.**).

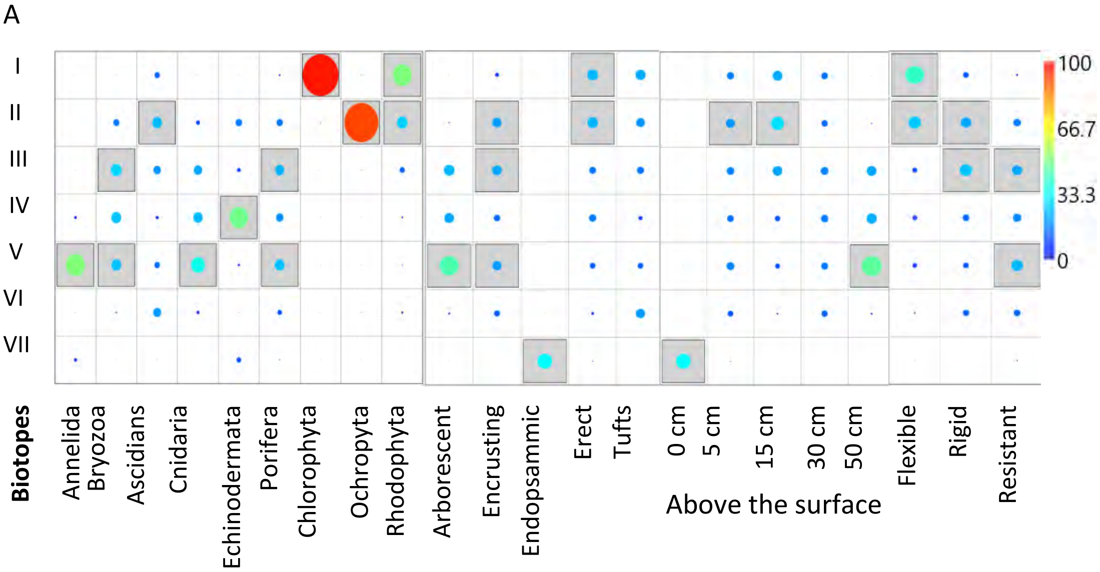


Figure 6.7: A) Indicator value of high taxa and traits within each biotope. Shaded boxes represent where traits are significantly different from others in their group ($p < 0.05$).

B

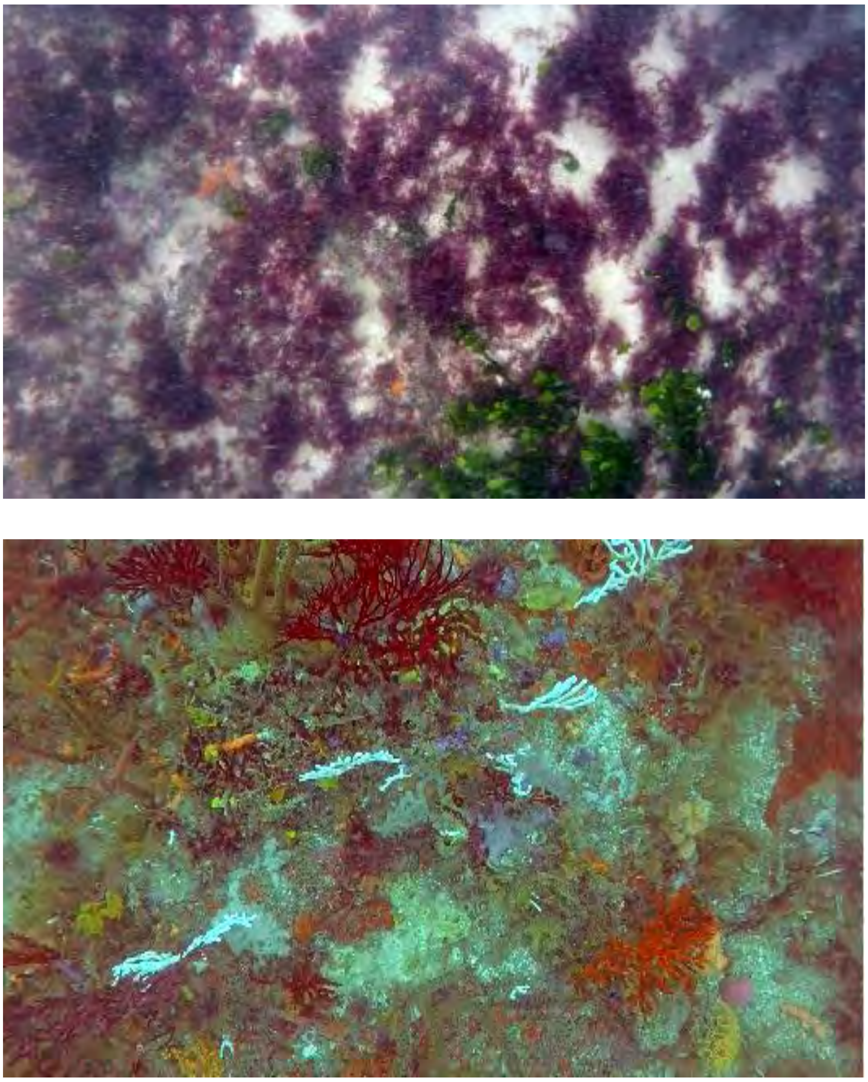


Figure 6.8: B) *In situ* examples of the substrate present in Biotope I (left) and Biotope V (right). Indicators species value is given in colour scale (0 to 100).

The same graphic illustration may be produced for fish (Figure 6.9). It is evident that santer (*Cheimerius nufar*), black tail (*Diplodus capensis*), zebra (*D. hottentotus*), brown shyshark (*Haploblepharus fuscus*), common eagle ray (*Myliobatis aquila*), cape stumpnose (*Rhabdosargus holubi*) and sterpie (*Sarpa salpa*) form a species indicator complex characteristic of Biotope I. With black tail and brown shyshark having high indicator species values. This is in contrast with Biotope V where koester (*Acanthistius sebastoides*), ragged tooth shark (*Carcharias taurus*), two-tone fingerfin (*Chirodactylus brachydactylus*), red roman (*Chrysoblephus laticeps*), blue hottentot (*Pachymetopon aeneum*), scotsman (*Polysteganus praeorbitalis*), white stumpnose (*Rhabdosargus globiceps*) and spotted gully shark (*Triakis megalopterus*), all with similar indicator species values, form an indicator species complex (Figure 6.9).

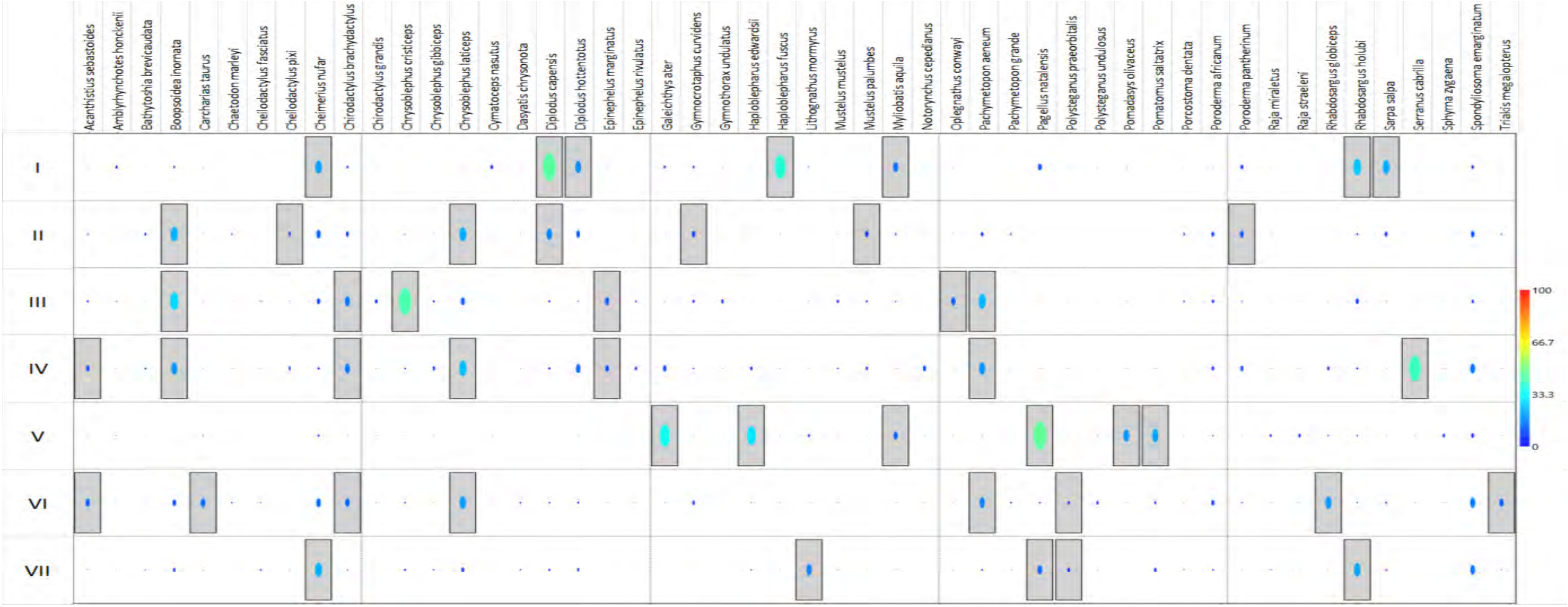


Figure 6.9: Indicator values for fish within each biotope. Shaded boxes represent where abundance (MaxN) is significantly different from others in their biotope ($p < 0.05$). The statistical significances (p values) of the indicator values are estimated by 9999 random reassignments (permutations) of locations across biotopes. Indicators species value is given in colour scale (0 to 100).

6.5 Discussion

6.5.1 Traits

The use of traits to further describe the habitat provides valuable insight into the composition and topography of the habitat. Using broader taxonomic group (phyla) and species-specific traits such as morphology, and growth form allow for comparing community and biotope structure. In the absence of detailed species-level indication, this can be used as a substitute to identify, describe and compare the characteristics of the biotope, the abiotic and biotic elements that contribute to its identity. The contributing traits of a community infer on its physical structure and can give valuable insight into the effect of environmental conditions e.g. current, sand inundation on the biota. It can provide valuable insight and explanation of how the resource is used by ichthyofauna.

White Sands Reef consists of biotopes predominantly characterised by consolidated flat reefs. The biota is dominated by algal beds sponges and cnidaria that have a flexible nature. This may be a direct response to the high energy character of this shallow dissipated flat reef system exposed to wave energy moving into the bay. Soft algae fronds such as those of *Plocamium corallorhiza, Amphiroa ephedraea* and *Hypnia spp*. are well adapted to high energy conditions. They provided a medium thickness three-dimensional environment that provide food and shelter to ichthyofauna. The constant water movement bringing nutrients and small food particles are retained in the biotic mat. These areas are especially important as nursery areas (Beckley and Buxton 1989) where juvenile fish use the spaces between the fronds as a refuge and feed on the small food particles constantly suspended in the water column (Margalef 1997).

In contrast, the St Croix Complex consists of two small islands situated deep in the embayment and more protected from the direct impact of bottom swell moving into the bay. However, the islands have a steep topography with high relief reef edges and shoulders levelling out on the sea bottom or abruptly ending in soft unconsolidated sediments. Exposure of the nearshore communities to environmental conditions such as current, swell, wave action and sand movement depend largely on the position of the habitat around the island, protected to more exposed, and the bottom character which could be a continuation of the rocky outcrop or may consist of plains of soft sediment. This means the St Croix Complex, consisting in this study of St Croix Island and Brenton Island, has a more varied and diverse habitat complement than White Sands Reef. High profile reef shoulder areas protected from the elements provide habitat colonised by erect arborescent species that contribute to the increased thickness of the three-dimensionality of the biotic layer and the volume of the adjacent water column used by the benthic sessile biota (Gili and Coma 1998). This provides more vertical resource use space for ichthyofauna. This is in stark contrast to areas in which the vertical walls (not included in the sampled regime) of the island terminate into soft or unconsolidated sediment like shell rubble or gravel that provide a very thin two-dimension benthic resource, especially for supra-benthic ichthyofauna.

Trait-based analysis information adds valuable insight into how the biotopes are used by other organisms. It should accompany species composition information as it informs on the functionality of the biotope. Understanding biotope composition and distribution within a seascape, the processes that connect habitat and community subunits, biotope, community and habitat heterogeneity lie central to understanding functionally of the larger ecosystem. Change due to anthropogenic impact, resource use and different management strategies are expected to have a local effect. But, in an interconnected system understanding the components and connectivity of these in the seascape is essential for effective ecosystem-based management.

6.5.2 Diversity indices

Diversity indices provide valuable insight into community composition because they take into account relative abundance and do not solely depend on species richness, but evenness as well. The effective Hill number (Jost 2006, Chao et al. 2010) of the Shannon-Weiner and Simpson Diversity indices are useful tools for comparing diversity in communities directly. It is evident for the calculated Hill numbers (also referred to as the effective number of species) that sample localities, biotopes and the stations, in general, differ with respect to benthic species diversity but do not differ greatly in species distinctiveness (Figure 6.3 E to H). The difference in species richness, abundance and composition could be in response to habitat type, niche availability and physical processes such as temperature, upwelling events, food availability and/or management and resource use.

The use of a suite of diversity indices that can detect changes in community composition species richness and taxonomic composition of the benthos and ichthyofauna allows for the comparison of these indices for permanent sample locations and defined biotopes over space and time. Phylogenetic diversity indices have shown to be of value and a useful tool in reporting on change, as they take into account the inequality of species due to their taxonomic relatedness or distinctiveness (Clarke and Warwick 1998, 1999, Vellend et al. 2010). This study showed that the Numbers of species, Numbers of Individuals and Shannon-Weiner index Hill numbers are especially useful in distinguishing the difference between biotopes and their biotic components.

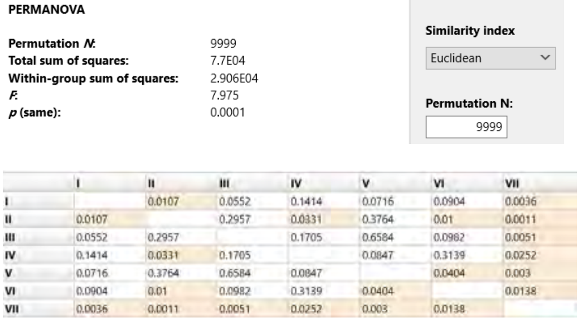
6.6 Conclusion

In this chapter, the value of trait-based characterization of the biotope component was highlighted. It informed on habitat contribution, three-dimensional structure and functionality of the habitat, communities and biotopes. Diversity indices are valuable tools in reporting on and comparing differences in species, community and biotope composition by assessing and comparing species richness, taxonomic diversity and distinctiveness. The Number of species, the Shannon-Wiener index Hill numbers and Taxonomic diversity showed especially useful in relating trends in the benthic biota to that observed for the ichthyofauna.

6.7 Supplementary material

Supplementary Table 6.1: One-way multivariate PERMANOVA (PAST) with significance for abiotic traits using Euclidean distance and biotic traits using Bray Curtis similarity index used to compute significant difference between biotopes. Shaded areas indicated a significant difference ($p < 0.05$). The heterogenic unconsolidated broader biotope VII is treated as a single entity.

Substrate composition



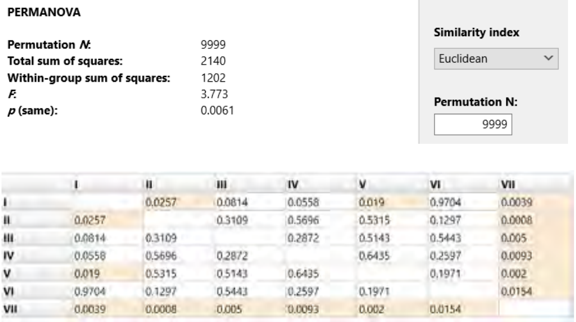
PERMANOVA

Permutation *N*: 9999
Total sum of squares: 7.7E04
Within-group sum of squares: 2.906E04
***F*:** 7.975
***p* (same):** 0.0001

Similarity index: Euclidean
Permutation N: 9999

	I	II	III	IV	V	VI	VII
I		0.0107	0.0552	0.1414	0.0716	0.0904	0.0036
II	0.0107		0.2957	0.0331	0.3764	0.01	0.0011
III	0.0552	0.2957		0.1705	0.6584	0.0982	0.0051
IV	0.1414	0.0331	0.1705		0.0847	0.3139	0.0252
V	0.0716	0.3764	0.6584	0.0847		0.0404	0.003
VI	0.0904	0.01	0.0982	0.3139	0.0404		0.0138
VII	0.0036	0.0011	0.0051	0.0252	0.003	0.0138	

Topography surface architecture



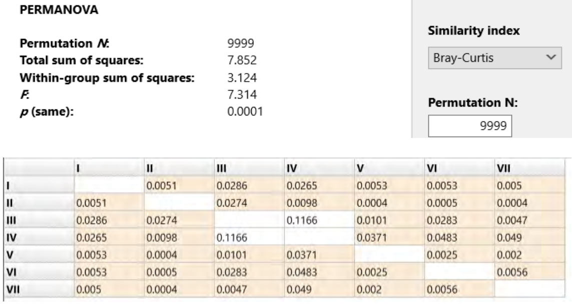
PERMANOVA

Permutation *N*: 9999
Total sum of squares: 2140
Within-group sum of squares: 1202
***F*:** 3.773
***p* (same):** 0.0061

Similarity index: Euclidean
Permutation N: 9999

	I	II	III	IV	V	VI	VII
I		0.0257	0.0814	0.0558	0.019	0.9704	0.0039
II	0.0257		0.3109	0.5696	0.5315	0.1297	0.0008
III	0.0814	0.3109		0.2872	0.5143	0.5443	0.005
IV	0.0558	0.5696	0.2872		0.6435	0.2597	0.0093
V	0.019	0.5315	0.5143	0.6435		0.1971	0.002
VI	0.9704	0.1297	0.5443	0.2597	0.1971		0.0154
VII	0.0039	0.0008	0.005	0.0093	0.002	0.0154	

Comparison in difference in higher taxa composition



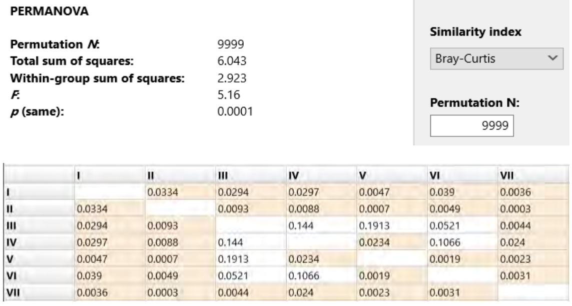
PERMANOVA

Permutation *N*: 9999
Total sum of squares: 7.852
Within-group sum of squares: 3.124
***F*:** 7.314
***p* (same):** 0.0001

Similarity index: Bray-Curtis
Permutation N: 9999

	I	II	III	IV	V	VI	VII
I		0.0051	0.0286	0.0265	0.0053	0.0053	0.005
II	0.0051		0.0274	0.0098	0.0004	0.0005	0.0004
III	0.0286	0.0274		0.1166	0.0101	0.0283	0.0047
IV	0.0265	0.0098	0.1166		0.0371	0.0483	0.049
V	0.0053	0.0004	0.0101	0.0371		0.0025	0.002
VI	0.0053	0.0005	0.0283	0.0483	0.0025		0.0056
VII	0.005	0.0004	0.0047	0.049	0.002	0.0056	

Comparison in difference in growth form



PERMANOVA

Permutation *N*: 9999
Total sum of squares: 6.043
Within-group sum of squares: 2.923
***F*:** 5.16
***p* (same):** 0.0001

Similarity index: Bray-Curtis
Permutation N: 9999

	I	II	III	IV	V	VI	VII
I		0.0334	0.0294	0.0297	0.0047	0.039	0.0036
II	0.0334		0.0093	0.0088	0.0007	0.0049	0.0003
III	0.0294	0.0093		0.144	0.1913	0.0521	0.0044
IV	0.0297	0.0088	0.144		0.0234	0.1066	0.024
V	0.0047	0.0007	0.1913	0.0234		0.0019	0.0023
VI	0.039	0.0049	0.0521	0.1066	0.0019		0.0031
VII	0.0036	0.0003	0.0044	0.024	0.0023	0.0031	

Comparison in difference growth heights

PERMANOVA

Permutation *N*: 9999
Total sum of squares: 5.304
Within-group sum of squares: 2.539
***F*:** 5.261
***p* (same):** 0.0001

Similarity index: Bray-Curtis
Permutation N: 9999

	I	II	III	IV	V	VI	VII
I		0.0159	0.1119	0.0267	0.0125	0.0668	0.0045
II	0.0159		0.0122	0.008	0.0007	0.001	0.0004
III	0.1119	0.0122		0.1438	0.1081	0.0584	0.004
IV	0.0267	0.008	0.1438		0.2121	0.2128	0.0239
V	0.0125	0.0007	0.1081	0.2121		0.0255	0.0024
VI	0.0668	0.001	0.0584	0.2128	0.0255		0.0045
VII	0.0045	0.0004	0.004	0.0239	0.0024	0.0045	

Comparison in difference structural rigidity

PERMANOVA

Permutation *N*: 9999
Total sum of squares: 1.695E07
Within-group sum of squares: 4.435E06
***F*:** 13.63
***p* (same):** 0.0001

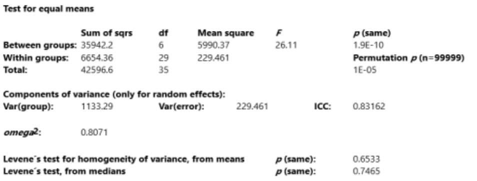
Similarity index: Bray-Curtis
Permutation N: 9999

	I	II	III	IV	V	VI	VII
I		0.0189	0.0284	0.0304	0.0045	0.004	0.0048
II	0.0189		0.0358	0.0838	0.0033	0.0011	0.0011
III	0.0284	0.0358		0.4228	0.3474	0.1603	0.0047
IV	0.0304	0.0838	0.4228		0.1682	0.4591	0.0104
V	0.0045	0.0033	0.3474	0.1682		0.0437	0.003
VI	0.004	0.0011	0.1603	0.4591	0.0437		0.0026
VII	0.0048	0.0011	0.0047	0.0104	0.003	0.0026	

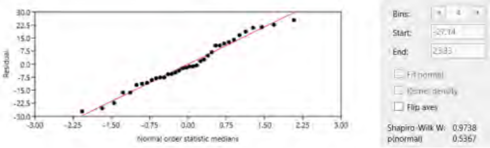
Supplementary Table 6.2: Diversity indices calculated in DIVERS (PRIMER) with one-way ANOVA analysis (PAST), Kruskal-Wallis test for equal means and a non-parametric Mann-Whitney U to determine the difference in species and taxonomic indices for benthic sessile organisms between biotopes (shaded areas show a significant difference between the two biotopes). Levene's test for homogeneity of variance and the Shapiro-Wilk test: If p < then 0.05 H_0 rejected = data tested not normally distributed. Box plot for the indices per biotope.

Number of Species (S)

One-way ANOVA

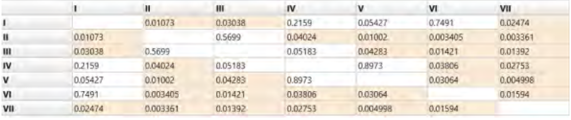


```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  35942.2       6     5990.37       26.11      1.9E-10
Within groups:   6654.36       29    229.461                  Permutation p (n=99999)
Total:           42596.6       35                             1E-05

Components of variance (only for random effects):
Var(group):      1133.29       Var(error):     229.461        ICC:   0.83162

omega2:          0.8071

Levene´s test for homogeneity of variance, from means   p (same):   0.6533
Levene´s test, from medians                             p (same):   0.7465
```

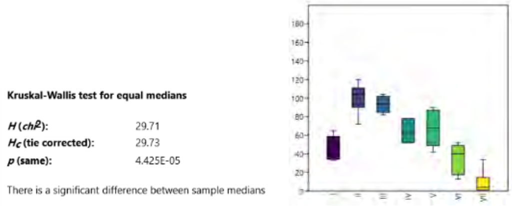


```
Bins:   4
Start:  -27.14
End:    23.33
☐ Fit normal
☐ Kernel density
☐ Flip axes
Shapiro-Wilk W:  0.9738
p(normal)        0.5367
```

Mann- Whitney U test (PAST)



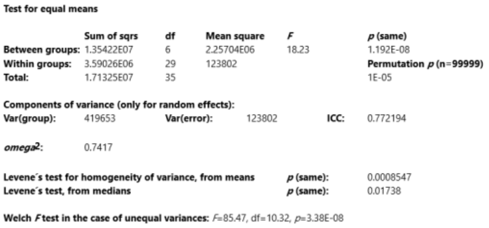
	I	II	III	IV	V	VI	VII
I		0.01073	0.03038	0.2159	0.05427	0.7491	0.02474
II	0.01073		0.5699	0.04024	0.01002	0.003405	0.003361
III	0.03038	0.5699		0.05183	0.04283	0.01421	0.01392
IV	0.2159	0.04024	0.05183		0.8973	0.03806	0.02753
V	0.05427	0.01002	0.04283	0.8973		0.03064	0.004998
VI	0.7491	0.003405	0.01421	0.03806	0.03064		0.01594
VII	0.02474	0.003361	0.01392	0.02753	0.004998	0.01594	



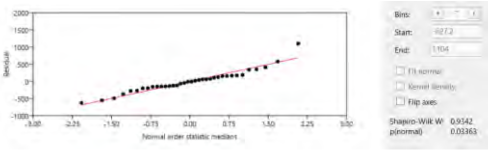
```
Kruskal-Wallis test for equal medians

H (chi2):              29.71
Hc (tie corrected):    29.73
p (same):              4.425E-05

There is a significant difference between sample medians
```

Number of Individuals (N)

One-way ANOVA

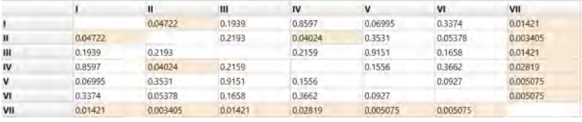


```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  1.35422E07    6     2.25704E06    18.23      1.192E-08
Within groups:   3.59026E06    29    123802                   Permutation p (n=99999)
Total:           1.71325E07    35                             1E-05

Components of variance (only for random effects):
Var(group):      419653        Var(error):     123802         ICC:   0.772194

omega2:          0.7417

Levene´s test for homogeneity of variance, from means   p (same):   0.0008547
Levene´s test, from medians                             p (same):   0.01738

Welch F test in the case of unequal variances: F=85.47, df=10.32, p=3.38E-08
```

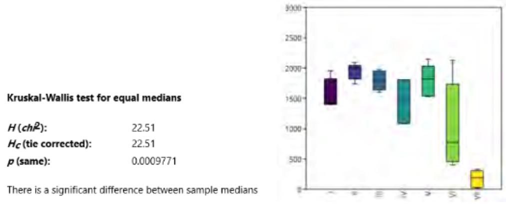


```
Bins:
Start:  -927.2
End:    1104
☐ Fit normal
☐ Kernel density
☐ Flip axes
Shapiro-Wilk W:  0.9342
p(normal)        0.03363
```

Mann- Whitney U test (PAST)



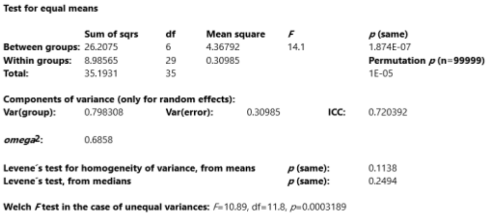
	I	II	III	IV	V	VI	VII
I		0.04722	0.1939	0.8597	0.06995	0.3374	0.01421
II	0.04722		0.2193	0.04024	0.3531	0.05378	0.003405
III	0.1939	0.2193		0.2159	0.9151	0.1658	0.01421
IV	0.8597	0.04024	0.2159		0.1556	0.3662	0.02819
V	0.06995	0.3531	0.9151	0.1556		0.0927	0.005075
VI	0.3374	0.05378	0.1658	0.3662	0.0927		0.005075
VII	0.01421	0.003405	0.01421	0.02819	0.005075	0.005075	



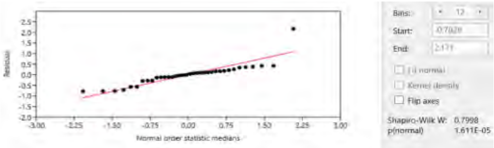
```
Kruskal-Wallis test for equal medians

H (chi2):              22.51
Hc (tie corrected):    22.51
p (same):              0.0009771

There is a significant difference between sample medians
```

Shannon-Wiener index's

One-way ANOVA

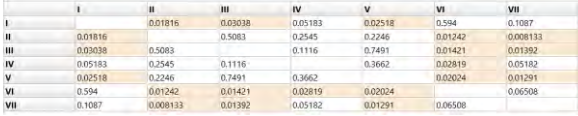


```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  26.2075       6     4.36792       14.1       1.874E-07
Within groups:   8.98565       29    0.30985                  Permutation p (n=99999)
Total:           35.1931       35                             1E-05

Components of variance (only for random effects):
Var(group):      0.798308      Var(error):     0.30985        ICC:   0.720392

omega2:          0.6858

Levene´s test for homogeneity of variance, from means   p (same):   0.1138
Levene´s test, from medians                             p (same):   0.2494

Welch F test in the case of unequal variances: F=10.89, df=11.8, p=0.0003189
```

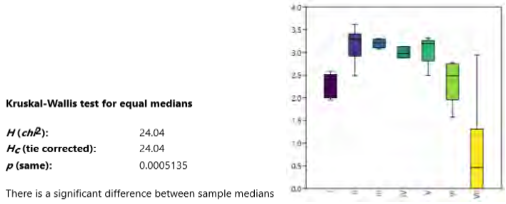


```
Bins:   12
Start:  -0.7028
End:    2.171
☐ Fit normal
☐ Kernel density
☐ Flip axes
Shapiro-Wilk W:  0.7998
p(normal)        1.611E-05
```

Mann- Whitney U test (PAST)



	I	II	III	IV	V	VI	VII
I		0.01816	0.03038	0.05183	0.02518	0.594	0.1087
II	0.01816		0.5083	0.2545	0.2246	0.01242	0.008133
III	0.03038	0.5083		0.1116	0.7491	0.01421	0.01392
IV	0.05183	0.2545	0.1116		0.3662	0.02819	0.05182
V	0.02518	0.2246	0.7491	0.3662		0.02024	0.01291
VI	0.594	0.01242	0.01421	0.02819	0.02024		0.06508
VII	0.1087	0.008133	0.01392	0.05182	0.01291	0.06508	



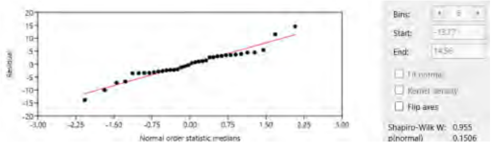
```
Kruskal-Wallis test for equal medians

H (chi2):              24.04
Hc (tie corrected):    24.04
p (same):              0.0005135

There is a significant difference between sample medians
```

Supplementary Table 6.2 continued

Shannon-Wiener index’s Hill number

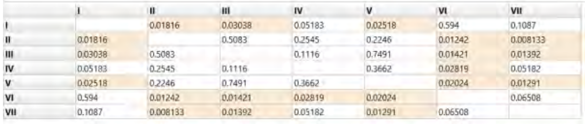
One-way ANOVA

```
Test for equal means

                 Sum of sqrs   df   Mean square   F       p (same)
Between groups:  2286.25       6    381.042       11.19   1.875E-06
Within groups:   987.805       29   34.0622               Permutation p (n=99999)
Total:           3274.06       35                         1E-05

Components of variance (only for random effects):
Var(group):      68.2583       Var(error):    34.0622     ICC:   0.667103

omega2:          0.6293

Levene´s test for homogeneity of variance, from means     p (same):   0.3361
Levene´s test, from medians                               p (same):   0.7558

Welch F test in the case of unequal variances: F=14.71, df=11.87, p=7.058E-05
```



Shapiro-Wilk W: 0.955
p(normal) 0.1506

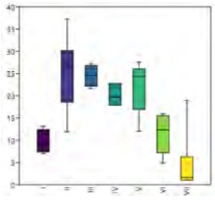
Mann- Whitney U test



	I	II	III	IV	V	VI	VII
I		0.01816	0.03038	0.05183	0.02518	0.594	0.1087
II	0.01816		0.5083	0.2545	0.2246	0.01242	0.008133
III	0.03038	0.5083		0.1116	0.7491	0.01421	0.01392
IV	0.05183	0.2545	0.1116		0.3662	0.02819	0.05182
V	0.02518	0.2246	0.7491	0.3662		0.02024	0.01291
VI	0.594	0.01242	0.01421	0.02819	0.02024		0.06508
VII	0.1087	0.008133	0.01392	0.05182	0.01291	0.06508	

Kruskal-Wallis test for equal medians

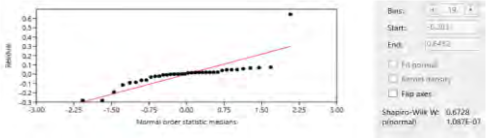
```
H (chi2):              24.04
Hc (tie corrected):    24.04
p (same):              0.0005135

There is a significant difference between sample medians
```



Simpson Diversity index ((1-λ))

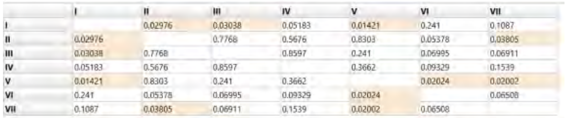
One-way ANOVA

```
Test for equal means

                 Sum of sqrs   df   Mean square   F       p (same)
Between groups:  1.85313       6    0.308855      13.11   3.92E-07
Within groups:   0.682963      29   0.0235504             Permutation p (n=99999)
Total:           2.53609       35                         0.0003

Components of variance (only for random effects):
Var(group):      0.0561255     Var(error):    0.0235504   ICC:   0.704422

omega2:          0.6688

Levene´s test for homogeneity of variance, from means     p (same):   0.001667
Levene´s test, from medians                               p (same):   0.003651

Welch F test in the case of unequal variances: F=4.998, df=12.11, p=0.008545
```



Shapiro-Wilk W: 0.6728
p(normal) 1.087E-07

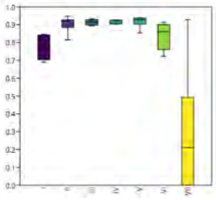
Mann- Whitney U test



	I	II	III	IV	V	VI	VII
I		0.02976	0.03038	0.05183	0.01421	0.241	0.1087
II	0.02976		0.7768	0.5676	0.8303	0.05378	0.03805
III	0.03038	0.7768		0.8597	0.241	0.06995	0.06911
IV	0.05183	0.5676	0.8597		0.3662	0.09329	0.1539
V	0.01421	0.8303	0.241	0.3662		0.02024	0.02002
VI	0.241	0.05378	0.06995	0.09329	0.02024		0.06508
VII	0.1087	0.03805	0.06911	0.1539	0.02002	0.06508	

Kruskal-Wallis test for equal medians

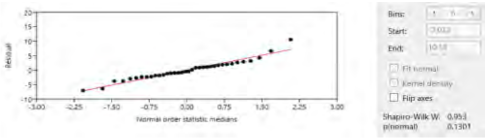
```
H (chi2):              18.4
Hc (tie corrected):    18.41
p (same):              0.005288

There is a significant difference between sample medians
```



Simpson Diversity index’s Hill number

One-way ANOVA

```
Test for equal means

                 Sum of sqrs   df   Mean square   F       p (same)
Between groups:  519.768       6    86.6281       6.494   0.0002004
Within groups:   386.858       29   13.3399               Permutation p (n=99999)
Total:           906.626       35                         0.00025

Components of variance (only for random effects):
Var(group):      14.4173       Var(error):    13.3399     ICC:   0.519408

omega2:          0.478

Levene´s test for homogeneity of variance, from means     p (same):   0.6059
Levene´s test, from medians                               p (same):   0.9505

Welch F test in the case of unequal variances: F=8.217, df=11.74, p=0.001184
```



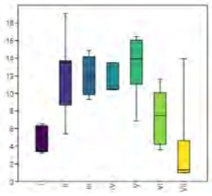
Shapiro-Wilk W: 0.953
p(normal) 0.1301

Mann- Whitney U test

	I	II	III	IV	V	VI	VII
I		0.02976	0.03038	0.05183	0.01421	0.241	0.1087
II	0.02976		0.7768	0.5676	0.8303	0.05378	0.03805
III	0.03038	0.7768		0.8597	0.241	0.06995	0.06911
IV	0.05183	0.5676	0.8597		0.3662	0.09329	0.1539
V	0.01421	0.8303	0.241	0.3662		0.02024	0.02002
VI	0.241	0.05378	0.06995	0.09329	0.02024		0.06508
VII	0.1087	0.03805	0.06911	0.1539	0.02002	0.06508	

Kruskal-Wallis test for equal medians

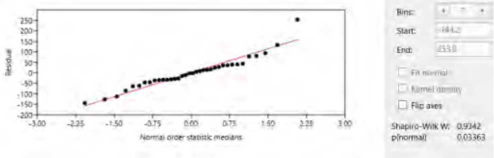
```
H (chi2):              18.4
Hc (tie corrected):    18.41
p (same):              0.005288

There is a significant difference between sample medians
```



Individuals per area (N/m^2)

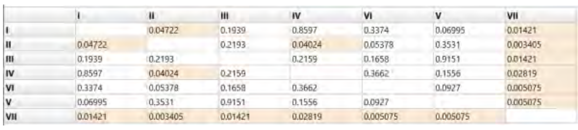
One-way ANOVA

```
Test for equal means

                 Sum of sqrs   df   Mean square   F       p (same)
Between groups:  715668        6    119278        18.23   1.192E-08
Within groups:   189735        29   6542.59               Permutation p (n=99999)
Total:           905404        35                         1E-05

Components of variance (only for random effects):
Var(group):      22177.5       Var(error):    6542.59     ICC:   0.772194

omega2:          0.7417

Levene´s test for homogeneity of variance, from means     p (same):   0.0008547
Levene´s test, from medians                               p (same):   0.01738

Welch F test in the case of unequal variances: F=85.47, df=10.32, p=3.38E-08
```



Shapiro-Wilk W: 0.9342
p(normal) 0.03363

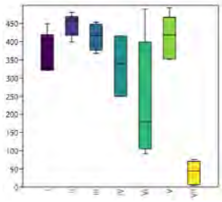
Mann- Whitney U test



	I	II	III	IV	VI	V	VII
I		0.04722	0.1939	0.8597	0.3374	0.06995	0.01421
II	0.04722		0.2193	0.04024	0.05378	0.3531	0.003405
III	0.1939	0.2193		0.2159	0.1658	0.9151	0.01421
IV	0.8597	0.04024	0.2159		0.3662	0.1556	0.02819
VI	0.3374	0.05378	0.1658	0.3662		0.0927	0.005075
V	0.06995	0.3531	0.9151	0.1556	0.0927		0.005075
VII	0.01421	0.003405	0.01421	0.02819	0.005075	0.005075	

Kruskal-Wallis test for equal medians

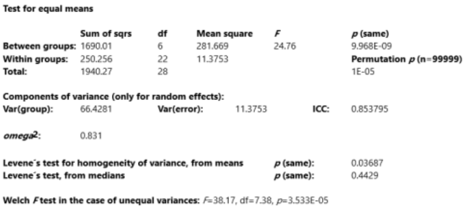
```
H (chi2):              22.51
Hc (tie corrected):    22.51
p (same):              0.0009771

There is a significant difference between sample medians
```



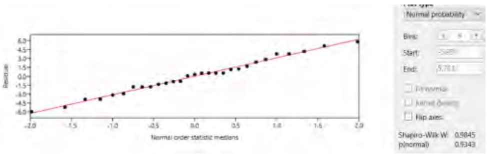
Supplementary Table 6.2 continued

Species per area(S/m^2)

One-way ANOVA

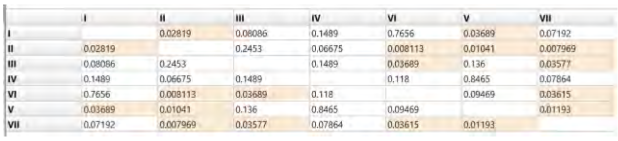


```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  1690.01       6     281.669       24.76      9.968E-09
Within groups:   250.256       22    11.3753                  Permutation p (n=99999)
Total:           1940.27       28                             1E-05

Components of variance (only for random effects):
Var(group):      66.4281       Var(error):     11.3753   ICC:   0.853795

omega2:          0.831

Levene´s test for homogeneity of variance, from means     p (same):   0.03687
Levene´s test, from medians                               p (same):   0.4429

Welch F test in the case of unequal variances: F=38.17, df=7.38, p=3.533E-05
```



Shapiro-Wilk W: 0.9845
p(normal) 0.9343

Mann- Whitney U test

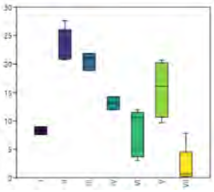


	I	II	III	IV	VI	V	VII
I		0.02819	0.08086	0.1489	0.7656	0.03689	0.07192
II	0.02819		0.2453	0.06675	0.008113	0.01041	0.007969
III	0.08086	0.2453		0.1489	0.03689	0.136	0.03577
IV	0.1489	0.06675	0.1489		0.118	0.8465	0.07864
VI	0.7656	0.008113	0.03689	0.118		0.09469	0.03615
V	0.03689	0.01041	0.136	0.8465	0.09469		0.01193
VII	0.07192	0.007969	0.03577	0.07864	0.03615	0.01193	

Kruskal-Wallis test for equal medians

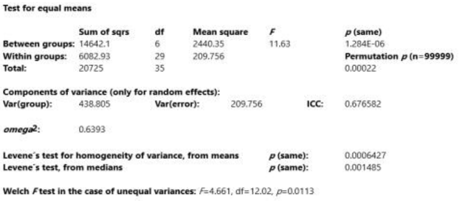
***H* (chi²):** 24.43
***Hc* (tie corrected):** 24.45
***p* (same):** 0.0004311

There is a significant difference between sample medians

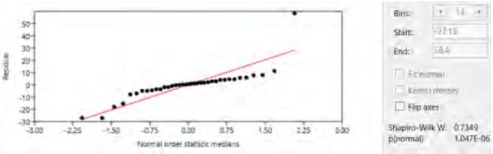


Taxonomic diversity (Δ)

One-way ANOVA



```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  14642.1       6     2440.35       11.63      1.284E-06
Within groups:   6082.93       29    209.756                  Permutation p (n=99999)
Total:           20725         35                             0.00022

Components of variance (only for random effects):
Var(group):      438.805       Var(error):     209.756   ICC:   0.676582

omega2:          0.6393

Levene´s test for homogeneity of variance, from means     p (same):   0.0006427
Levene´s test, from medians                               p (same):   0.001485

Welch F test in the case of unequal variances: F=4.661, df=12.02, p=0.0113
```



Shapiro-Wilk W: 0.7349
p(normal) 1.047E-06

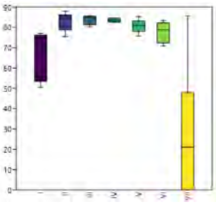
Mann- Whitney U test

	I	II	III	IV	V	VI	VII
I		0.01816	0.03038	0.05183	0.02518	0.1658	0.1087
II	0.01816		0.7768	0.6485	0.2246	0.07415	0.01826
III	0.03038	0.7768		0.3768	0.241	0.06995	0.08616
IV	0.05183	0.6485	0.3768		0.1556	0.09329	0.1539
V	0.02518	0.2246	0.241	0.1556		0.4712	0.06508
VI	0.1658	0.07415	0.06995	0.09329	0.4712		0.06508
VII	0.1087	0.01826	0.08616	0.1539	0.06508	0.06508	

Kruskal-Wallis test for equal medians

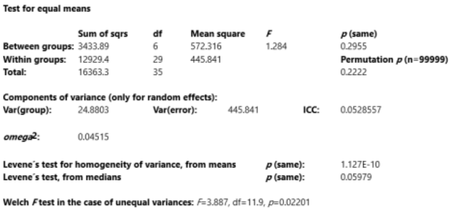
***H* (chi²):** 17.18
***Hc* (tie corrected):** 17.18
***p* (same):** 0.008634

There is a significant difference between sample medians

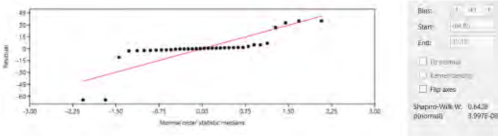


Taxonomic distinctiveness (Δ*)

One-way ANOVA

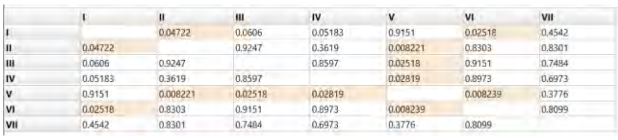


```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  3433.89       6     572.316       1.284      0.2955
Within groups:   12929.4       29    445.841                  Permutation p (n=99999)
Total:           16363.3       35                             0.2222

Components of variance (only for random effects):
Var(group):      24.8803       Var(error):     445.841   ICC:   0.0528557

omega2:          0.04515

Levene´s test for homogeneity of variance, from means     p (same):   1.127E-10
Levene´s test, from medians                               p (same):   0.05979

Welch F test in the case of unequal variances: F=3.887, df=11.9, p=0.02201
```



Shapiro-Wilk W: 0.6428
p(normal) 3.997E-08

Mann- Whitney U test

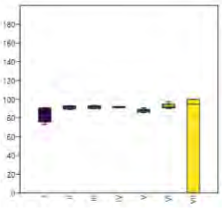


	I	II	III	IV	V	VI	VII
I		0.04722	0.0606	0.05183	0.9151	0.02518	0.4542
II	0.04722		0.9247	0.3619	0.008221	0.8303	0.8301
III	0.0606	0.9247		0.8597	0.02518	0.9151	0.7484
IV	0.05183	0.3619	0.8597		0.02819	0.8973	0.6973
V	0.9151	0.008221	0.02518	0.02819		0.008239	0.3776
VI	0.02518	0.8303	0.9151	0.8973	0.008239		0.8099
VII	0.4542	0.8301	0.7484	0.6973	0.3776	0.8099	

Kruskal-Wallis test for equal medians

***H* (chi²):** 12.93
***Hc* (tie corrected):** 12.93
***p* (same):** 0.04419

There is a significant difference between sample medians

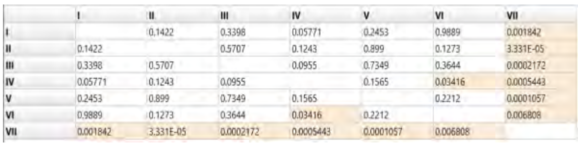


Supplementary Table 6.3: Diversity indices calculated in DIVERS (PRIMER) with one-way ANOVA analysis (PAST), Kruskal-Wallis test for equal means and a non-parametric Mann-Whitney U to determine the difference in species and taxonomic indices for the relative abundance of ichthyofauna between biotopes (shaded areas show a significant difference between the two biotopes). Levene's test for homogeneity of variance and the Shapiro-Wilk test: If p < then 0.05 then H_0 rejected = data tested not normally distributed. Box plot for the indices per biotope.

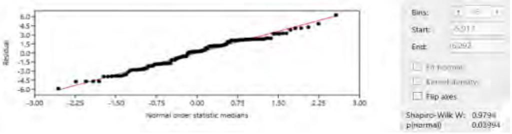
Number of species (S)

One-way ANOVA

```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  225.334       6     37.5557       6.411      6.383E-06
Within groups:   743.92        127   5.85763                  Permutation p (n=99999)
Total:           969.254       133                            2E-05

Components of variance (only for random effects):
Var(group):      1.6749        Var(error):      5.85763       ICC:   0.222355

omega2:          0.195

Levene´s test for homogeneity of variance, from means      p (same):   0.08758
Levene´s test, from medians                                p (same):   0.3283

Welch F test in the case of unequal variances: F=6.449, df=51.06, p=4.176E-05
```



	I	II	III	IV	V	VI	VII
I		0.1422	0.3398	0.05771	0.2453	0.9889	0.001842
II	0.1422		0.5707	0.1243	0.899	0.1273	3.331E-05
III	0.3398	0.5707		0.0955	0.7349	0.3644	0.0002172
IV	0.05771	0.1243	0.0955		0.1565	0.03416	0.0005443
V	0.2453	0.899	0.7349	0.1565		0.2212	0.0001057
VI	0.9889	0.1273	0.3644	0.03416	0.2212		0.006808
VII	0.001842	3.331E-05	0.0002172	0.0005443	0.0001057	0.006808	

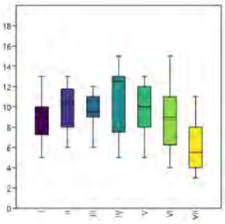


Shapiro-Wilk W: 0.9794
p(normal) 0.03994

Kruskal-Wallis test for equal medians

***H* (*chi*2):**	27.76
***Hc* (tie corrected):**	28.13
***p* (same):**	8.893E-05

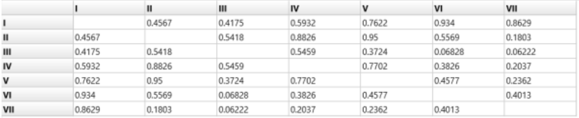
There is a significant difference between sample medians



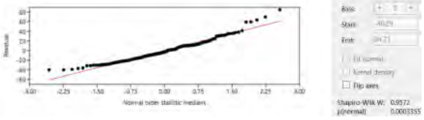
Number of individuals (N)

One-way ANOVA

```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  3169.53       6     528.255       0.907      0.4922
Within groups:   73968.5       127   582.429                  Permutation p (n=99999)
Total:           77138         133                            0.4918

Components of variance (only for random effects):
Var(group):      -2.86251      Var(error):      582.429       ICC:   -0.00493906

omega2:          0

Levene´s test for homogeneity of variance, from means      p (same):   0.0008576
Levene´s test, from medians                                p (same):   0.01299

Welch F test in the case of unequal variances: F=0.8945, df=51.37, p=0.506
```



	I	II	III	IV	V	VI	VII
I		0.4567	0.4175	0.5932	0.7622	0.934	0.8629
II	0.4567		0.5418	0.8826	0.95	0.5569	0.1803
III	0.4175	0.5418		0.5459	0.3724	0.06828	0.06222
IV	0.5932	0.8826	0.5459		0.7702	0.3826	0.2037
V	0.7622	0.95	0.3724	0.7702		0.4577	0.2362
VI	0.934	0.5569	0.06828	0.3826	0.4577		0.4013
VII	0.8629	0.1803	0.06222	0.2037	0.2362	0.4013	

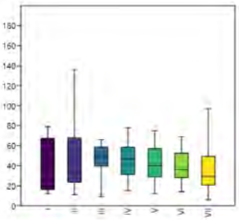


Shapiro-Wilk W: 0.9572
p(normal) 0.0003355

Kruskal-Wallis test for equal medians

***H* (*chi*2):**	4.868
***Hc* (tie corrected):**	4.87
***p* (same):**	0.5606

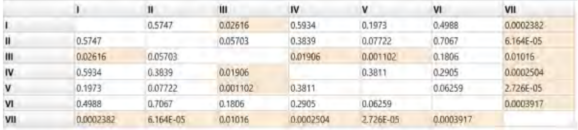
There is no significant difference between sample medians



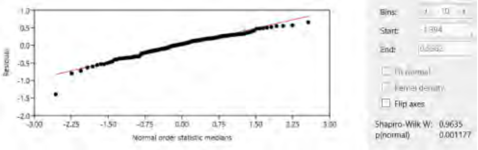
Shannon-Wiener index's

One-way ANOVA

```
Test for equal means

                 Sum of sqrs   df    Mean square   F          p (same)
Between groups:  4.68349       6     0.780582      7.348      9.29E-07
Within groups:   13.4917       127   0.106234                 Permutation p (n=99999)
Total:           18.1752       133                            1E-05

Components of variance (only for random effects):
Var(group):      0.035632      Var(error):      0.106234      ICC:   0.251166

omega2:          0.2213

Levene´s test for homogeneity of variance, from means      p (same):   0.8447
Levene´s test, from medians                                p (same):   0.835

Welch F test in the case of unequal variances: F=6.346, df=51.55, p=4.779E-05
```



	I	II	III	IV	V	VI	VII
I		0.5747	0.02616	0.5934	0.1973	0.4988	0.0002382
II	0.5747		0.05703	0.3839	0.07722	0.7067	6.164E-05
III	0.02616	0.05703		0.01906	0.001102	0.1806	0.01016
IV	0.5934	0.3839	0.01906		0.3811	0.2905	0.0002504
V	0.1973	0.07722	0.001102	0.3811		0.06259	2.726E-05
VI	0.4988	0.7067	0.1806	0.2905	0.06259		0.0003917
VII	0.0002382	6.164E-05	0.01016	0.0002504	2.726E-05	0.0003917	

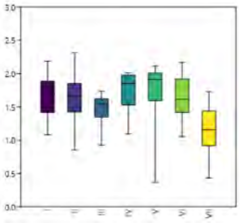


Shapiro-Wilk W: 0.9635
p(normal) 0.001177

Kruskal-Wallis test for equal medians

***H* (*chi*2):**	33.7
***Hc* (tie corrected):**	33.7
***p* (same):**	7.673E-06

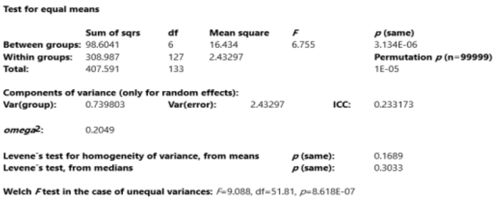
There is a significant difference between sample medians



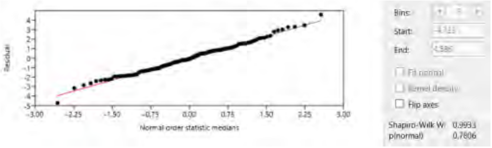
Supplementary Table 6.3 continued

Shannon-Wiener index’s Hill number

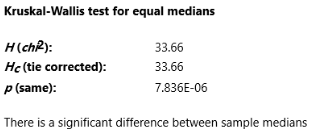
One-way ANOVA



```
Test for equal means

                  Sum of sqrs   df    Mean square   F        p (same)
Between groups:   98.6041       6     16.434        6.755    3.134E-06
Within groups:    308.987       127   2.43297                Permutation p (n=99999)
Total:            407.591       133                          1E-05

Components of variance (only for random effects):
Var(group):       0.739803      Var(error):   2.43297    ICC:   0.233173

omega2:           0.2049

Levene´s test for homogeneity of variance, from means   p (same):   0.1689
Levene´s test, from medians                             p (same):   0.3033

Welch F test in the case of unequal variances: F=9.088, df=51.81, p=8.618E-07
```



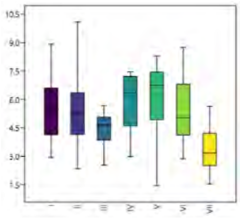
	I	II	III	IV	V	VI	VII
I		0.5747	0.02747	0.5934	0.1973	0.4988	0.0002382
II	0.5747		0.05865	0.3839	0.07722	0.7067	6.164E-05
III	0.02747	0.05865		0.01906	0.001102	0.1806	0.01016
IV	0.5934	0.3839	0.01906		0.3811	0.2905	0.0002504
V	0.1973	0.07722	0.001102	0.3811		0.06428	2.726E-05
VI	0.4988	0.7067	0.1806	0.2905	0.06428		0.0003917
VII	0.0002382	6.164E-05	0.01016	0.0002504	2.726E-05	0.0003917	



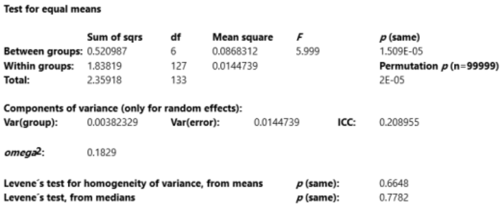
Kruskal-Wallis test for equal medians

***H* (*chi*2):**	33.66
***Hc* (tie corrected):**	33.66
***p* (same):**	7.836E-06

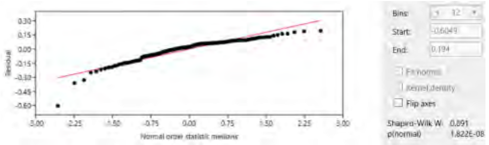
There is a significant difference between sample medians

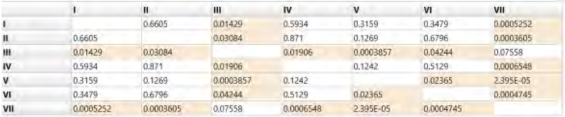


Simpson Diversity index ((1-λ))

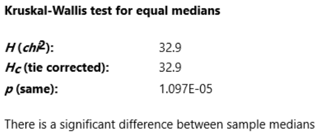


```
Test for equal means

                  Sum of sqrs   df    Mean square   F        p (same)
Between groups:   0.520987      6     0.0868312     5.999    1.509E-05
Within groups:    1.83819       127   0.0144739              Permutation p (n=99999)
Total:            2.35918       133                          2E-05

Components of variance (only for random effects):
Var(group):       0.00382329    Var(error):   0.0144739    ICC:   0.208955

omega2:           0.1829

Levene´s test for homogeneity of variance, from means   p (same):   0.6648
Levene´s test, from medians                             p (same):   0.7782
```





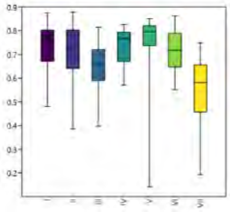
	I	II	III	IV	V	VI	VII
I		0.6605	0.01429	0.5934	0.3159	0.3479	0.0005252
II	0.6605		0.03084	0.871	0.1269	0.6796	0.0003605
III	0.01429	0.03084		0.01906	0.0003857	0.04244	0.07558
IV	0.5934	0.871	0.01906		0.1242	0.5129	0.0006548
V	0.3159	0.1269	0.0003857	0.1242		0.02365	2.395E-05
VI	0.3479	0.6796	0.04244	0.5129	0.02365		0.0004745
VII	0.0005252	0.0003605	0.07558	0.0006548	2.395E-05	0.0004745	



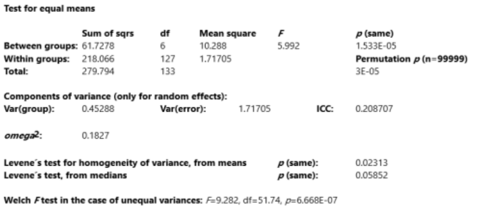
Kruskal-Wallis test for equal medians

***H* (*chi*2):**	32.9
***Hc* (tie corrected):**	32.9
***p* (same):**	1.097E-05

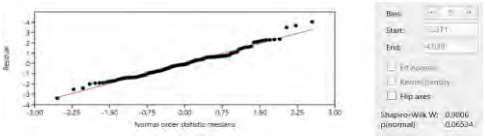
There is a significant difference between sample medians

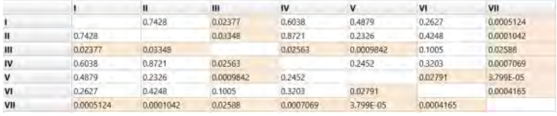


Simpson Diversity index’s Hill number

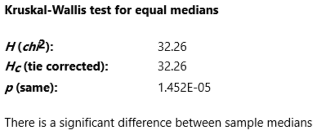


```
Test for equal means

                  Sum of sqrs   df    Mean square   F        p (same)
Between groups:   61.7278       6     10.288        5.992    1.533E-05
Within groups:    218.066       127   1.71705                Permutation p (n=99999)
Total:            279.794       133                          3E-05

Components of variance (only for random effects):
Var(group):       0.45288       Var(error):   1.71705    ICC:   0.208707

omega2:           0.1827

Levene´s test for homogeneity of variance, from means   p (same):   0.02313
Levene´s test, from medians                             p (same):   0.05852

Welch F test in the case of unequal variances: F=9.282, df=51.74, p=6.668E-07
```





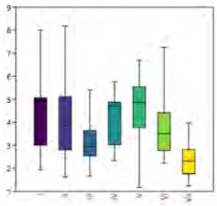
	I	II	III	IV	V	VI	VII
I		0.7428	0.02377	0.6038	0.4879	0.2627	0.0005124
II	0.7428		0.03348	0.8721	0.2326	0.4248	0.0001042
III	0.02377	0.03348		0.02563	0.0009842	0.1005	0.02588
IV	0.6038	0.8721	0.02563		0.2452	0.3203	0.0007069
V	0.4879	0.2326	0.0009842	0.2452		0.02791	3.799E-05
VI	0.2627	0.4248	0.1005	0.3203	0.02791		0.0004165
VII	0.0005124	0.0001042	0.02588	0.0007069	3.799E-05	0.0004165	



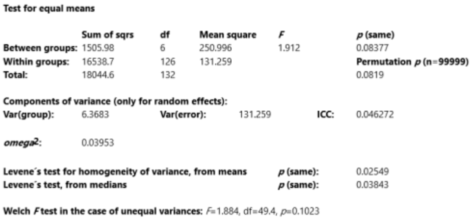
Kruskal-Wallis test for equal medians

***H* (*chi*2):**	32.26
***Hc* (tie corrected):**	32.26
***p* (same):**	1.452E-05

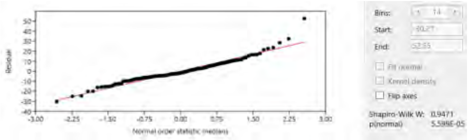
There is a significant difference between sample medians



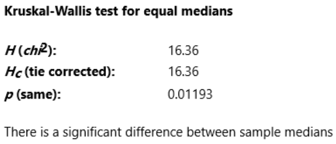
Taxonomic diversity (Δ)



```
Test for equal means

                  Sum of sqrs   df    Mean square   F        p (same)
Between groups:   1505.98       6     250.996       1.912    0.08377
Within groups:    16538.7       126   131.259                Permutation p (n=99999)
Total:            18044.6       132                          0.0819

Components of variance (only for random effects):
Var(group):       6.3683        Var(error):   131.259    ICC:   0.046272

omega2:           0.03953

Levene´s test for homogeneity of variance, from means   p (same):   0.02549
Levene´s test, from medians                             p (same):   0.03843

Welch F test in the case of unequal variances: F=1.884, df=49.4, p=0.1023
```



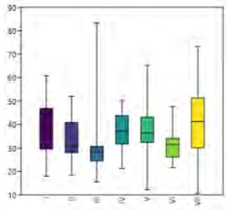
	I	II	III	IV	V	VI	VII
I		0.2427	0.0226	0.7628	0.7143	0.05861	0.6169
II	0.2427		0.09475	0.3858	0.2678	0.3037	0.1024
III	0.0226	0.09475		0.013	0.00358	0.1992	0.01986
IV	0.7628	0.3858	0.013		0.9845	0.07811	0.4588
V	0.7143	0.2678	0.00358	0.9845		0.01674	0.3274
VI	0.05861	0.3037	0.1992	0.07811	0.01674		0.01521
VII	0.6169	0.1024	0.01986	0.4588	0.3274	0.01521	



Kruskal-Wallis test for equal medians

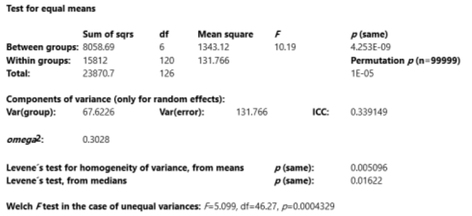
***H* (*chi*2):**	16.36
***Hc* (tie corrected):**	16.36
***p* (same):**	0.01193

There is a significant difference between sample medians



Supplementary Table 6.3 continued

Taxonomic distinctiveness (Δ*)



Test for equal means

	Sum of sqrs	**df**	**Mean square**	***F***	***p* (same)**
Between groups:	8058.69	6	1343.12	10.19	4.253E-09
Within groups:	15812	120	131.766		**Permutation *p* (n=99999)**
Total:	23870.7	126			1E-05

Components of variance (only for random effects):

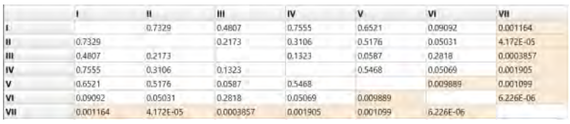
Var(group): 67.6226 **Var(error):** 131.766 **ICC:** 0.339149

***omega2*:** 0.3028

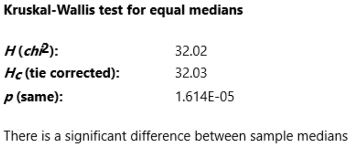
Levene´s test for homogeneity of variance, from means ***p* (same):** 0.005096

Levene´s test, from medians ***p* (same):** 0.01622

Welch *F* test in the case of unequal variances: *F*=5.099, df=46.27, *p*=0.0004329



	I	II	III	IV	V	VI	VII
I		0.7329	0.4807	0.7555	0.6521	0.09092	0.001164
II	0.7329		0.2173	0.3106	0.5176	0.05031	4.172E-05
III	0.4807	0.2173		0.1323	0.0587	0.2818	0.0003857
IV	0.7555	0.3106	0.1323		0.5468	0.05069	0.001905
V	0.6521	0.5176	0.0587	0.5468		0.009889	0.001099
VI	0.09092	0.05031	0.2818	0.05069	0.009889		6.226E-06
VII	0.001164	4.172E-05	0.0003857	0.001905	0.001099	6.226E-06	



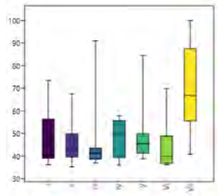
Kruskal-Wallis test for equal medians

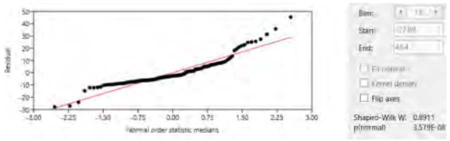
***H* (*chi2*):** 32.02

***Hc* (tie corrected):** 32.03

***p* (same):** 1.614E-05

There is a significant difference between sample medians





Shapiro-Wilk W: 0.8911

p(normal) 3.579E-08

Notes: Shapiro-Wilk test: If p < then 0.05 then H_0 rejected = data tested not normally distributed

---

Equation 6.1: Equation for determining Indicator species as per (Dufrêne and Legendre 1997, Hammer 2001)

For each group *i* and *j*:

define the specificity as

$$A_{ij} = N_{ij}/N_i$$

where N_{ij} is the mean number of individuals of species *i* across sites in group *j*, and N_i is the sum of the mean number of individuals of species I over all groups

define the fidelity

$$B_{ij} = Nsite_{ij} / Nsite_j$$

where $Nsite_{ij}$ is the number of sites in group *j* where species *i* is present, and $Nsite_j$ is the total number of sites in group *j*

The indicator value of species *i* in group *j* is then a value from 0 to 100 (percentage)

$$INDVAL_{ij} = 100\, A_{ij}B_{ij}$$

The statistical (*p* value) of the indicator values are estimated by 9999 random reassignment (permutations) of sites across groups.

Chapter 7 Conclusion

7.1 Rational supporting the establishment of SAEON's Benthic Ecosystem Long-Term Ecological Research (BELTER) programme

The increasing dependence of man on natural marine resources, the growing demands on coastal ichthyofauna resources and uncertainties associated with climate change (Clark 2006, Sink et al. 2018) highlight the need for the inclusion of benthic biotope and its associated ichthyofauna into long-term research programmes (Bennett 2007, Bernard 2012). It furthermore highlights the necessity for the development of comprehensive integrated management strategies that would take into account economic development, protection and conservation of natural resources for the benefit of the people of Algoa Bay and South Africa. Mapping of the marine benthic environment assists in the identification of priority protection areas to meet sustainable development and conservation goals (Douglass et al. 2014, Anderson et al. 2017, NDP 2030 2019). Fine to broad-scale long-term ecological data series (Harvey et al. 2020), information on physical, geochemical and biological variables (Chalmers 2012, Dorrington et al. 2018, Retzlaff and LeBleu 2018) and the description, classification and mapping of the benthic environment are essential building blocks for Marine Spatial Planning (Livingstone et al. 2018), Ecosystem-Based management (EBM) (Ehler and Douvere 2009, Brown et al. 2011, Chalmers 2012, Buhl-Mortensen et al. 2020) and the development of relevant algorithms and models that increase our ability to predict future changes and impacts (Thomson et al. 2014, Tyberghein et al. 2019).

The sessile nature of the benthos and their ability to tolerate short-term fluctuation or changes in the environment make them good indicators of long-term change (Chalmers 2012). Long-term change is induced by changes in environmental variables such as global temperature and shifts in the frequency and amplitude of extreme conditions (Meehl et al. 2007). Organisms forming the benthic boundary layer between the substrate and the water column are impacted by animals that utilize them. Infra- and supra-benthic fishes use benthic environments for shelter and food but can move from the area when conditions become unfavourable. Long-term changes in fish assemblage composition, i.e. due to fishing pressure and seawater temperature rise, are believed to alter interspecific competition and change species distributions (Götz et al. 2009a, 2009b). This drives shifts in species and trophic interactions, subsequently altering the species composition of the benthos (Smith et al. 2020). To understand the response of the benthic biota to environmental change one needs to also observe the associated ichthyofauna. The effect of multiple complex feedback responses to climate change is difficult to predict, but detailed long-term information on the physical environment, the benthos and the overarching pelagic ecosystem, as well as their connectivity and interaction in the seascape, will allow for the construction of complex algorithms and the development of predictive models that could assist in the preparation for and mitigation of global climate change (Griffiths et al. 2017).

7.2 Long-Term Ecological Research (LTER)

To ensure continuity and longevity of Long-Term Ecological Research (LTER) activities require that:

- the data collected should be able to record change,
- the equipment used should be easy to handle, calibrate and deploy,
- the equipment should be cost-effective, easily serviced, repaired and replaced,
- the equipment should be robust,
- data collection should not be dependent on expensive infrastructure such as large vessels,
- the system should allow quick data retrieval, cleaning and analysis and
- the data collected should have significance for secondary research investigations and be available for analysis by interested stakeholders, as this will encourage collaboration, data and platform use and increase the value of the information.

Although the primary goal of LTER programmes is the collection of long-term data several shortcomings have been identified by data users. These includes:

- delays in data dissemination,
- the limited scope of data products provided by LTER programmes (initial analysis of the collected data done by the LTER team are for rapid reporting purposes and although the data collected may be available to interested parties, a full analysis and stakeholder specific data products may not).

The delay in data dissemination may be due to several issues. This includes the time *in situ* instrumentation is deployed and the subsequent delay in data retrieval. This could be addressed by observatories that allow for the live streaming or near-real-time delivery of recorded data. Delays in data availability may also depend on the time and manpower required to clean and package the collected data for dissemination. The improvement of infrastructure would address the latter. Improved communication with stakeholders would address the type of data products in addition to data collected made available for use. This would include a clear understanding by data users that purpose fit data products may need project-specific analysis of collected datasets.

7.3 Baseline description of the Benthic Biotopes for two Long-Term Ecological Research (LTER) stations in Algoa Bay, Agulhas ecoregion, South Africa

This is the first study in South Africa that describes habitat, benthic community structure and infra- and supra-benthic ichthyofauna for biotopes. It illustrated that broader biotopes are constructed from distinct subunits indicative of the heterogeneous nature of the Algoa Bay seascape. This pilot study makes a preliminary baseline assessment using subsets of the BELTER datasets collected in the implementation phase of the new research platform. In this work habitat types were described, reference libraries for the identification of substrate types, species and biotope subunits were constructed. Comprehensive species lists were compiled for biotopes and biotope subunits. Ichthyofauna assemblages were identified for the biotopes. These were described and compared indicating that assemblages differ for different biotopes. The data was also able to record seasonal change, especially between winter and summer, in the assemblage composition.

The results presented in this thesis on habitats, benthic communities and fish assemblages, demonstrate the value of observed essential environmental and biological variables. Accurate taxa assignment and specimen identification, even to higher taxonomic groups, the phylum to family level, can be problematic and plague many publications. Collaboration with researchers skilled in species identification is important to ensure the integrity of the research done. Identification of genus and species levels is more difficult. Many species are cryptic or present similar morphological characteristics, especially those in the same genus. A comprehensive image library that references different species morphotypes is pivotal the achieve the best possible outcome. The link between collected and curators specimens, species identification and comprehensive image libraries for image-based species identification is essential and allow for the generation of accurate species lists.

Many of these hurdles can be circumvented by the use of trait-based classification systems. Trait-based assessment of biotope information collected for samples, locations and research stations in this study was able to highlight differences in habitat composition, the broad-scale taxonomic composition of and the structural morphological characteristics for benthic assemblages. Diversity indices were successfully used to highlighting the difference between biotopes and allowed for comparison between benthic biota and ichthyofauna for selected indices.

The work clearly shows the value of the data collected and its ability to detect change both spatially and temporally. During the development of this programme, the local research requirements and demands in the context of the global LTER initiatives was accounted for and the new BELTER platform is predicted to respond to the needs of the scientific community, natural marine resource managers and policymakers and provide valuable information on global climate change and impact for the South African shallow marine coastal system.

This proof of concept investigation was a valuable exercise and served as a preliminary audit of the potential research impact of the platform. It demonstrates the efficacy of the sampling equipment, the methodologies and analyses used in the implementation of BELTER while identifying acknowledged limitations, caveats and biases. This SAEON BELTER research platform was successfully realized in the Algoa Bay Sentinel Site and implementation in other sentinel and satellite sentinel LTER sites along the South African coast will provide comprehensive datasets on essential biodiversity variables (EBV).

7.4 Recommendations for future research

Critical shortcomings identified in this study include the availability of detailed bottom geology and topography. Future mapping using the Multi-beam Echosounder (MBES) Sound Navigation, Ranging (SoNAR) and Light Detection and Ranging (LiDAR) scanner platforms will provide valuable information and will permit the construction of biotope, habitat and community distribution maps at various scales (Brock et al. 2004, Wedding et al. 2008, Costa et al. 2009, Pittman and Brown 2011, Pillay et al. 2021b). Big data collection, handling and analysis is labour intensive and time-consuming. Near-real-time analysis of large datasets will become commonplace as Machine Learning data processing applications are developed and implemented (MacLeod et al. 2010, Mohamed et al. 2018, Gómez-Ríos et al. 2019, González-Rivero et al. 2020, Pillay et al. 2021a, 2021b). Automation should be implemented as soon as possible. In the interim, it is prudent to develop and use snapshot analytical methods that allow for quick evaluation of the data and produce workable indices to track change. The development and population of image-based libraries to assist in species, habitat and community unit identification are essential.

Only a subset of the data collected during the initial stage of BELTER was used in this study. Valuable information would be gained through additional investigations. These could include:

- the investigation of the benthic species associations in a heterogeneous seascape,
- intra-annual change and composition of ichthyofauna assemblages,
- size-frequency composition differences in ichthyofauna species composition within and between LTER stations investigating the effect of biotope character and management strategies,

- an investigation of the relationship between benthic community structure and the water column including an assessment of the link between localised upwelling events, plankton composition and abundance and the benthic filter and suspension feeders communities.

The appeal of using imagery derived datasets is that data can be collected remotely, safely, and is largely non-destructive thereby minimally impacting the observed ecosystems and organisms. Well curated image data, supplemented by comprehensive metadata, can be kept in perpetuity and readily allow reanalysis as new analytical techniques arise. It provides a reliable account of the state of the systems at the point in time the image was collected.

The method developed and used in this BELTER does not come without biases and caveats. Several have been discussed and highlighted throughout this work. The biotope habitat mapping use images that focus solely on epibenthic species. The contrast in the biotic diversity recorded between consolidated and unconsolidated is not necessarily indicative of total biotope species richness. Comparisons in the study were made solely based on epifauna and does not include infauna.

However, to obtain a holistic understanding of benthic species distribution, abundance and associated bentho-pelagic coupling, BELTER would benefit from the collection of macro-infauna species data. This would however include invasive sampling techniques and the extraction of organisms. Frequent removal of species from a permanent positioned sample site may introduce data output bias that needs to be carefully considered before implementation. The sample methodology, as used for the collection of JC images collection, the collection of samples from random sample points around a predefined reference sample location, may mitigate the impact. As would a longer period between subsequent sample collection. The addition of infauna LTER in BELTER should be considered.

7.5 SAEON Elwandle Coastal Nodes multi-layers approach to LTER

The multidisciplinary cross-boundary approach of SAEON especially by its Elwandle Coastal Node which includes estuarine, pelagic (PELTER) and benthic (BELTER) LTER platforms allow for a holistic approach to the interpretation, understanding and description of the connectivity, linkage and dependence of different processes in a complex seascape (Figure 7.1). It is believed and supported by the outcome of this study, that the BELTER data products will become an integral part of the SAEON SMCRI toolbox.

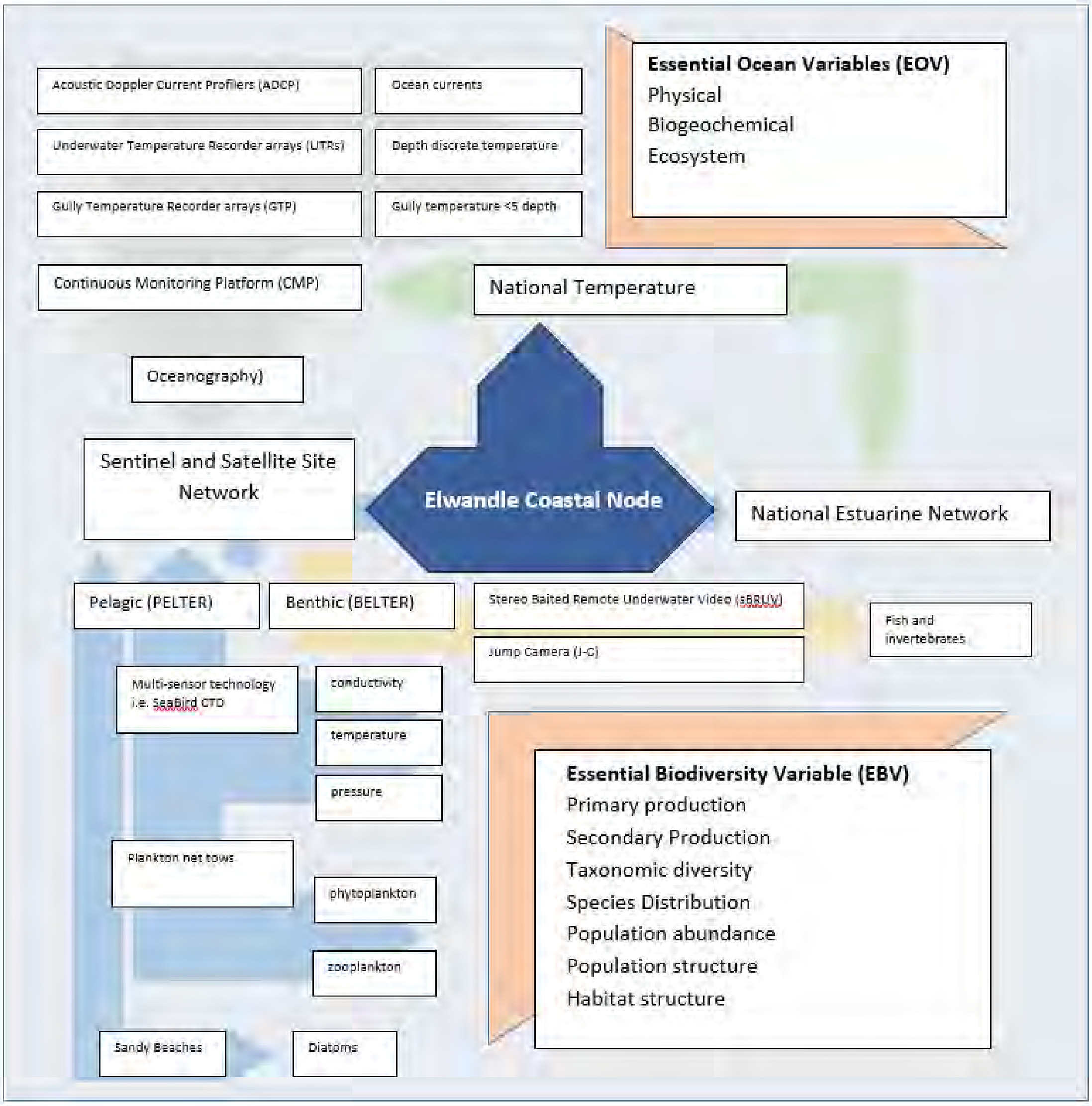


Figure 7.1: Emended organogram of science activities at the Elwandle Coastal Node (from SAEON Elwandle Node Science Plan: 2016-2018) to illustrate the multi-disciplinary data collection and long-term research activities.

Chapter 8 References

Adams LA, Maneveldt GW, Green A, Karenyi N, Parker D, Samaai T, Kerwath S 2020. Rhodolith Bed Discovered off the South African Coast. *Diversity* 12: 125.

Adeniji AO, Okoh OO, Okoh AI 2019. Distribution pattern and health risk assessment of polycyclic aromatic hydrocarbons in the water and sediment of Algoa Bay, South Africa. *Environmental Geochemistry and Health* 41: 1303–1320.

Al-qaness MAA, Ewees AA, Fan H, Aziz MA El, Abd El Aziz M 2020. Optimization Method for Forecasting Confirmed Cases of COVID-19 in China. *Journal of Clinical Medicine* 9: 674.

Alley RB 2000. Ice-core evidence of abrupt climate changes. *Proceedings of the National Academy of Sciences of the United States of America* 97: 1331–1334.

Althaus F, Hill N, Ferrari R, Edwards L, Przeslawski R, Schönberg CHL, Stuart-Smith R, Barrett N, Edgar G, Colquhoun J, et al. 2015. A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: The CATAMI classification scheme. *PLoS ONE* 10: 1–18.

Althaus F, Hill N, Rees T, Jordan A, Industries P, Colquhoun J, Sch C, Case M, Scott F, Edgar G, et al. 2014. CATAMI classification scheme for scoring marine biota and substrata in underwater imagery. *http://catami.org/classification* 1–24.

Anderson K, Ryan B, Sonntag W, Kavvada A, Friedl L 2017. Earth observation in service of the 2030 Agenda for Sustainable Development. *Geo-Spatial Information Science* 20: 77–96.

Anderson NJ, Engstrom DR, Leavitt PR, Flood SM, Heathcote AJ 2020. Changes in coupled carbon–nitrogen dynamics in a tundra ecosystem predate post-1950 regional warming. *Communications Earth & Environment* 1.

Anderson RJ, Bolton JJ, Stegenga H 2009. Using the biogeographical distribution and diversity of seaweed species to test the efficacy of marine protected areas in the warm-temperate Agulhas Marine Province, South Africa. *Diversity and Distributions* 15: 1017–1027.

Anderson RJ, McKune C, Bolton JJ, DeClerck O, Tronchin E 2005. Patterns in subtidal seaweed communities on coral-dominated reefs at Sodwana Bay on the KwaZulu-Natal coast, South Africa. *African Journal of Marine Science* 27: 529–537.

Anderson RJJ, Stegenga H 1989. Subtidal Algal Communities at Bird Island, Eastern Cape, South Africa. *Botanica Marina* 32: 299–311.

Arntz WE, Gili JM, Reise K 1999. Unjustifiably Ignored: Reflections on the Role of Benthos in Marine Ecosystems. *Biogeochemical Cycling and Sediment Ecology*. Dordrecht: Springer Netherlands. pp 105–124.

Atkinson L, Field J, Hutchings L 2011. Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages. *Marine Ecology Progress Series* 430: 241–255.

Attwood CG, Bennett BA 1995. Modelling the effect of marine reserves on the recreational shore-fishery of the South-Western Cape, South Africa. *South African Journal of Marine Science* 16: 227–240.

Awad AA, Griffiths CL, Turpie JK 2002a. Distribution and endemicity patterns of benthic marine invertebrates in South Africa applied to the selection of priority conservation areas. *Diversity and Distributions* 8: 129–145.

Awad AAA, Griffiths CLL, Turpie JKK 2002b. Distribution of South African marine benthic invertebrates applied to the selection of priority conservation areas. *Distribution and Distributions* 8: 129–145.

Bach LL, Saunders BJ, Newman SJ, Holmes TH, Harvey ES 2019. Cross and long-shore variations in reef fish assemblage structure and implications for biodiversity management. *Estuarine, Coastal and Shelf Science* 218: 246–257.

Bai X, Dawson RJ, Ürge-Vorsatz D, Delgado GC, Salisu Barau A, Dhakal S, Dodman D, Leonardsen L, Masson-Delmotte V, Roberts DC, et al. 2018. Six research priorities for cities and climate change. *Nature* 555: 23–25.

Barnes H 1952. Under-Water Television and Marine Biology. *Nature* 169: 477–479.

Bastian M, Heymann S, Jacomy M 2009. Gephi: an open source software for exploring and manipulating networks. International AAAI Conference on Weblogs and Social Media. *International AAAI Conference on Weblogs and Social Media* 361–362.

Baudoin M-AA, Ziervogel G 2017. What role for local organisations in climate change adaptation? Insights from South Africa. *Regional Environmental Change* 17: 691–702.

Beal LM, Chereskin TK, Lenn YD, Elipot S 2006. The sources and mixing characteristics of the Agulhas Current. *Journal of Physical Oceanography* 36: 2060–2074.

Beal LM, De Ruijter WPM, Biastoch A, Zahn R, Cronin M, Hermes J, Lutjeharms J, Quartly G, Tozuka T, Baker-Yeboah S, et al. 2011. On the role of the Agulhas system in ocean circulation and climate. *Nature* 472: 429–436.

Bearzi G, Agazzi S, Gonzalvo J, Costa M, Bonizzoni S, Politi E, Piroddi C, Reeves RR 2008. Overfishing and the disappearance of short-beaked common dolphins from western Greece. *Endangered Species Research* 5: 1–12.

Beckley L, Buxton C 1989. Underwater Observations of Reef Fish in and around Algoa Bay, South Africa. *Transactions of the Royal Society of South Africa* 47: 29–38.

Beckley LE 1984. Shallow-Water Trawling Off the Swartkops Estuary, Algoa Bay. *South African Journal of Zoology* 19: 248–250.

Beckley LE 1985. *Coastal zone utilization by juvenile fish in the Eastern Cape, South Africa*. PhD. Department of Biological Sciences. University of Cape Town. pp 103.

Beckley LE 1986. The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. *South African Journal of Zoology* 21: 244–252.

Beckley LE, McLachlan A 1979. Studies on the littoral seaweed epifauna of St Croix Island I Physical and biological features of the littoral zone. *South African Journal of Zoology* 14: 175–182.

Beckley LE, McLachlan A 1980. Studies on the littoral seaweed epifauna of 8t Croix Island 2. Composition and summer standing stock. *African Zoology* 15: 170–176.

Bell JJ 2008. The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science* 79: 341–353.

Bennett K, Wilson SK, Shedrawi G, McLean DL, Langlois TJ 2016a. Can diver operated stereo-video surveys for fish be used to collect meaningful data on benthic coral reef communities? *Limnology and Oceanography: Methods* 14: 874–885.

Bennett RH 2007. *Optimisation of a sampling protocol for long-term monitoring of temperate reef fishes*. MSc. Rhodes University. pp 154.

Bennett RH, Cowley PD, Childs AR, Attwood CG, Swart L, Næsje TF 2017. Movement patterns of an endangered fishery species, Lithognathus lithognathus (Sparidae), and the role of no-take marine protected areas as a management tool. *African Journal of Marine Science* 39: 475–489.

Bennett S, Wernberg T, Connell SD, Hobday AJ, Johnson CR, Poloczanska ES 2016b. The 'Great Southern Reef': Social, ecological and economic value of Australia's neglected kelp forests. *Marine and Freshwater Research* 67: 47.

Benson A, Brooks CM, Canonico G, Duffy E, Muller-Karger F, Sosik HM, Miloslavich P, Klein E 2018. Integrated observations and informatics improve understanding of changing marine ecosystems. *Frontiers in Marine Science* 5: 1–8.

Bernard ATF 2012. *Towards a Cost - Efficient & Standardised Monitoring Protocol for Subtidal Reef Fish in the Agulhas Ecoregion of South*. PhD. Rhodes University. pp. 325.

Bernard ATF, Götz A 2012. Bait increases the precision in count data from remote underwater video for most subtidal reef fish in the warm-temperate Agulhas bioregion. *Marine Ecology Progress Series* 471: 235–252.

Bernard ATF, Götz A, Parker D, Heyns ER, Halse SJ, Riddin NA, Smith MKS, Paterson AW, Winker H, Fullwood L, et al. 2014. New possibilities for research on reef fish across the continental shelf of South Africa. *South African Journal of Science* 110: 1–5.

Berov D, Hiebaum G, Vasilev V, Karamfilov V 2016. An optimised method for scuba digital photography surveys of infralittoral benthic habitats: A case study from the SW Black Sea Cystoseira-dominated macroalgal communities. *Underwater Technology* 34: 11–20.

Biermann F, Kim RE 2020. The boundaries of the planetary boundary framework: A critical appraisal of approaches to define a ‘safe operating space’ for humanity. *Annual Review of Environment and Resources* 45: 497–521.

Biggs HC, Kerley GIH, Tshiguvho T 1999. A South African long-term ecological research network: a first for Africa? *South African Journal of Science* 95: 244–246.

Binning K, Baird D 2001. Survey of heavy metals in the sediments of the Swartkops River estuary, Port Elizabeth South Africa. *Water SA* 27: 461–466.

Blamey LK, Bolton JJ 2018. The economic value of South African kelp forests and temperate reefs: Past, present and future. *Journal of Marine Systems* 188: 172–181.

Blamey LK, Branch GM, Reaugh-Flower KE 2010. Temporal changes in kelp forest benthic communities following an invasion by the rock lobster Jasus lalandii. *African Journal of Marine Science* 32: 481–490.

Bolton JJ, Stegenga H 2002. Seaweed species diversity in South Africa. *South African Journal of Marine Science* 24: 9–18.

Bornman TG 2016. SAEON Elwandle Node Science Plan: 2016-2018.

Bornt KR, McLean DL, Langlois TJ, Harvey ES, Bellchambers LM, Evans SN, Newman SJ 2015. Targeted demersal fish species exhibit variable responses to long-term protection from fishing at the Houtman Abrolhos Islands. *Coral Reefs* 34: 1297–1312.

Bosman AL, Du Toit JT, Hockey PAR, Branch GM 1986. A field experiment demonstrating the influence of seabird guano on intertidal primary production. *Estuarine, Coastal and Shelf Science* 23: 283–294.

Boury-Esnault N, Rützler K 1997. Thesaurus of sponge morphology. *Smithsonian Contributions to Zoology* 1–55.

Bouveroux TN, Caputo M, Froneman PW, Plön S 2018. Largest reported groups for the Indo-Pacific bottlenose dolphin (Tursiops aduncus) found in Algoa Bay, South Africa: Trends and potential drivers. *Marine Mammal Science* 34: 645–665.

Branch GM, Clark BM 2006. Fish stocks and their management: The changing face of fisheries in South Africa. *Marine Policy* 30: 3–17.

Brash JM 2006. *Zonation of benthic communities on the subtropical Aliwal Shoal.* MSc. University of KwaZulu-Natal. p. 105.

Bremner JM 1991a. Properties of Surficial sediment in Algoa Bay. *Geological Survey Bulletin* 100: 23–73.

Bremner JM 1991b. Meteorology and hydrography in the vicinity of Algoa Bay. *Geological Survey Bulletin* 100: 19–22.

Brock JC, Wright CW, Clayton TD, Nayegandhi A 2004. LIDAR optical rugosity of coral reefs in Biscayne National Park, Florida. *Coral Reefs* 23: 48–59.

Bromley CL, Parker-Nance S, De La Mare J-A, Edkins AL, Beukes DR, Davies-Coleman MT 2013. Halogenated oxindole and indoles from the South African marine ascidian Distaplia skoogi. *South African Journal of Chemistry* 66: 64–68.

Brooks EJ, Sloman KA, Sims DW, Danylchuk AJ 2011. Validating the use of baited remote underwater video surveys for assessing the diversity, distribution and abundance of sharks in the Bahamas. *Endangered Species Research* 13: 231–243.

Brouwer SL, Griffiths MH 2004. Age and growth of Argyrozona argyrozona (Pisces: Sparidae) in a marine protected area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark-recapture. *Fisheries Research* 67: 1–12.

Brouwer SL, Griffiths MH 2005. Reproductive biology of carpenter seabream (Argyrozona argyrozona) (Pisces: Sparidae) in a marine protected area. *Fisheries Bulletin* 103: 258–269.

Brown AC 1999. Marine invertebrate systematics and zoogeography in southern africa: An historical overview. *Transactions of the Royal Society of South Africa* 54: 21–30.

Brown E, Cox E, Jokiel P, Rodgers K, Smith W, Tissot B, Coles SL, Hultquist J 2004. Development of benthic sampling methods for the Coral Reef Assessment and Monitoring Program (CRAMP) in Hawai'i. *Pacific Science* 58: 145–158.

Brown PC 1992. Spatial and seasonal variation in chlorophyll distribution in the upper 30 m of the photic zone in the southern Benguela/Agulhas ecosystem. *South African Journal of Marine Science* 12: 515–525.

Bruford MW, Brummitt N, Butchart SHM, Cardoso AC, Coops NC, Dulloo E, Pereira HM, Ferrier S, Walters M, Geller GN, et al. 2013. Essential Biodiversity Variables. *Science* 339: 277–278.

Buhl-Mortensen P, Dolan MFJ, Ross RE, Gonzalez-Mirelis G, Buhl-Mortensen L, Bjarnadóttir LR, Albretsen J 2020. Classification and Mapping of Benthic Biotopes in Arctic and Sub-Arctic Norwegian Waters. *Frontiers in Marine Science* 7: 1–15.

Burger LF 1990. *The distribution patterns and community structure of the Tsitsikamma rocky littoral ichthyofauna*. MSc. Rhodes University. pp. 121.

Buxton CD 1984. Feeding biology of the roman Chrysoblephus laticeps (Pisces: Sparidae). *South African Journal of Marine Science* 2: 33–42.

Buxton CD, Allen JC 1989. Mark and recapture studies of two reef sparids in the Tsitsikamma Coastal National Park. *Koedoe* 32: 39–45.

Buxton CD, Clarke JR. 1986. Age, growth and feeding of the blue hottentot Pachymetopon aeneum (Pisces: Sparidae) with notes on reproductive biology. *African Zoology* 21: 33–38.

Buxton CD, Garratt PA 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). *Alternative life-history styles of fishes* 28: 113–124.

Buxton CD, Smale MJ 1984. A preliminary investigation of the Marine Ichthyofauna in the Tsitsikamma Coastal National Park. *Koedoe* 27: 13–24.

Buxton CD, Smale MJ 1989. Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape coast. *Journal of Applied Ecology* 26: 441–451.

Byrne MP, O'Gorman PA 2018. Trends in continental temperature and humidity directly linked to ocean warming. *Proceedings of the National Academy of Sciences of the United States of America* 115: 4863–4868.

Caley T, Kim JH, Malaizé B, Giraudeau J, Laepple T, Caillon N, Charlier K, Rebaubier H, Rossignol L, Castañeda IS, et al. 2011. High-latitude obliquity as a dominant forcing in the Agulhas current system. *Climate of the Past* 7: 1285–1296.

Campbell EE, Bate GC 1998. Tide-induced pulsing of nutrient discharge from an unconfined aquifer into an Anaulus australis-dominated surf-zone. *Water SA* 24: 365–370.

Campbell EE, Parker-Nance T, Bate GC 1992. A Compilation of Information on the Magnitude, Nature and Importance of Coastal Aquifers in Southern Africa. *Institude for Coastal Research, University of Port Elizabeth* 1–192.

Campbell MD, Pollack AG, Gledhill CT, Theodore S, Devries SDA, Campbell MD, Pollack AG, Gledhill CT, Switzer TS, Devries DA 2015. Comparison of relative abundance indices calculated from two methods of generating video count data. *Fisheries Research* 170: 125–133.

Canonico G, Buttigieg PL, Montes E, Muller-Karger FE, Stepien C, Wright D, Benson A, Helmuth B, Costello M, Sousa-Pinto I, et al. 2019. Global observational needs and resources for marine biodiversity. *Frontiers in Marine Science* 6: 1–20.

Cao Y, Liang S, Chen X, He T, Wang D, Cheng X 2017. Enhanced wintertime greenhouse effect reinforcing Arctic amplification and initial sea-ice melting. *Scientific Reports* 7: 1–9.

Carleton JH, Done TJ 1995. Quantitative video sampling of coral reef benthos: large-scale application. *Coral Reefs* 14: 35–46.

Carlos-Júnior LA, Spencer M, Neves DM, Moulton TP, Pires D de O, Castro CB, Ventura CRR, Ferreira CEL, Serejo CS, Oigman-Pszczol S, et al. 2019. Rarity and beta diversity assessment as tools for guiding conservation strategies in marine tropical subtidal communities. *Diversity and Distributions* 25: 743–757.

Carroll A, Althaus F, Beaman R, Friedman A, Ierodiaconou I, Ingleton T, Jordan A, Linklater M, Monk J, Post A, et al. 2018. Marine sampling field manual for towed underwater camera systems. In: Field Manuals for Marine Sampling to Monitor Australian Waters. 131–152.

Celliers L, Schleyer MH 2008. Coral community structure and risk assessment of high-latitude reefs at Sodwana Bay, South Africa. *Biodiversity and Conservation* 17: 3097–3117.

Celliers L, Mann BQ, Macdonald AHH, Schleyer MH 2007. A benthic survey of the rocky reefs off Pondoland, South Africa. *African Journal of Marine Science* 29: 65–77.

Chalmers R 2012. *Systematic marine spatial planning and monitoring in a data poor environment: A case study of Algoa Bay, South Africa.* PhD Thesis, Department of Ichthyology and Fisheries Science, Rhodes University, South Africa.

Chao A, Chiu CH, Jost L 2010. Phylogenetic diversity measures based on Hill numbers. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 3599–3609.

Chase JM, Myers JA 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2351–2363.

Chen X, Zhang X, Church JA, Watson CS, King MA, Monselesan D, Legresy B, Harig C 2017. The increasing rate of global mean sea-level rise during 1993-2014. *Nature Climate Change* 7: 492–495.

Clark BM 2006. Climate change: A looming challenge for fisheries management in southern Africa. *Marine Policy* 30: 84–95.

Clarke KR, Gorley RN 2015. Clarke, K.R. and Gorley, R.N., 2015. Getting started with PRIMER v7. PRIMER-E. 300.

Clarke KR, Warwick RM 1998. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* 35: 523–531.

Clarke KR, Warwick RM 1999. The taxonomic distinctness measure of biodiversity: Weighting of step lengths between hierarchical levels. *Marine Ecology Progress Series* 184: 21–29.

Clarke KR, Warwick RM 2001. *Change in marine communities. An approach to statistical analysis and interpretation.* (2 nd edn). Plymouth Marine Laboratory, UK.

Clarke KR, Somerfield PJ, Chapman MG 2006. On resemblance measures for ecological studies, including taxonomic dissimilarity and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* 330: 55–80.

Clarke KR, Somerfield PJ, Gorley RN 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *Journal of Experimental Marine Biology and Ecology* 366: 56–69.

Clarke TM, Whitmarsh SK, Fairweather PG, Huveneers C 2019. Overlap in fish assemblages observed using pelagic and benthic baited remote underwater video stations. *Marine and Freshwater Research* 70: 870–880.

Coa J, Strohmeier R, Mjwara P, Sullivan K 2015. *GEO Strategic Plan 2016-2025: Implementing GEOSS*.

Cockcroft AC, McLachlan A 1986. Distribution of juvenile and adult penaeid prawns Macropetasma africanus (Balss) in Algoa Bay. *South African Journal of Marine Science* 4: 245–255.

Coetzee PS 1986. Diet composition and breeding cycle of blacktail, Diplodus sargus capensis (Pisces: Sparidae), caught off St Croix Island, Algoa Bay, South Africa. *African Zoology* 21: 237–243.

Coetzee PS, Baird D 1981. Age, growth and food of Cheimerius nufar (Ehrenberg, 1820) (Sparidae), collected off St Croix Island, Algoa Bay . *African Zoology* 16: 137–143.

Collins M, Knutti R, Arblaster J, Dufresne J-L, Fichefet T, Friedlingstein P, Gao X, Gutowski WJ, Johns T, Krinner G, et al. 2013. Long-term climate change: Projections, commitments and irreversibility. In: Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia VB and PMM (ed.), *Climate Change 2013 the Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (9781107057 vol.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. pp 1029–1136.

Collins SL, Carpenter SR, Swinton SM, Orenstein DE, Childers DL, Gragson TL, Grimm NB, Morgan GJ, Harlan SL, Kaye JP, et al. 2011. An integrated conceptual framework for long-term social-ecological research. *Frontiers in Ecology and the Environment* 9: 351–357.

Colton MA, Swearer SE 2012. Locating faunal breaks in the nearshore fish assemblage of Victoria, Australia. *Marine and Freshwater Research* 63: 218–231.

Compton TJ, Morrison MA, Leathwick JR, Carbines GD 2012. Ontogenetic habitat associations of a demersal fish species, Pagrus auratus, identified using boosted regression trees. *Marine Ecology Progress Series* 462: 219–230.

Connolly-Boutin L, Smit B 2016. Climate change, food security, and livelihoods in sub-Saharan Africa. *Regional Environmental Change* 16: 385–399.

Connor DW, Allen JH, Golding N, Howell KL, Lieberknecht LM, Northen KO, Reker JB 2004. The marine habitat classification for Britain and Ireland version 04.05. *JNCC, Peterborough* 1–49.

Coppin RM 2017. *Ecklonia maxima kelp forests along a thermal gradient : community composition and recovery from disturbance*. MSc. Department of Biodiversity and Conservation Biology. University of the Western Cape. pp. 87.

Costa BM, Battista TA, Pittman SJ 2009. Comparative evaluation of airborne LiDAR and ship-based multibeam SoNAR bathymetry and intensity for mapping coral reef ecosystems. *Remote Sensing of Environment* 113: 1082–1100.

Costalago D, Potter P, Pattrick P, Strydom NA 2018. Influence of environmental variables on the larval stages of anchovy, Engraulis encrasicolus, and sardine, Sardinops sagax, in Algoa Bay, South Africa. *Environmental Biology of Fishes* 101: 225–236.

Costello MJ 2009. Distinguishing marine habitat classification concepts for ecological data management. *Marine Ecology Progress Series* 397: 253–268.

Costello MJ, Claus S, Dekeyzer S, Tyler-walters H 2015. Biological and ecological traits of marine species. *PeerJ* 3: 1–29.

Cottrell RS, Fleming A, Fulton EA, Nash KL, Watson RA, Blanchard JL 2018. Considering land–sea interactions and trade-offs for food and biodiversity. *Global Change Biology* 24: 580–596.

Cowley PD, Brouwer SL, Tilney RL 2002. The role of the Tsitsikamma National Park in the management of four shore-angling fish along the south-eastern Cape coast of South Africa. *South African Journal of Marine Science* 7615: 27–35.

Crawford RJM, Altwegg R, Barham BJ, Barham PJ, Durant JM, Dyer BM, Geldenhuys D, Makhado AB, Pichegru L, Ryan PG, et al. 2011. Collapse of South Africa ’ s penguins in the early 21st century. *African Journal of Marine Science* 37–41.

Crawford RJM, Davis SA, Harding RT, Jackson LF, Leshoro TM, Meÿer MA, Randall RM, Underhill LG, Upfold L, Van Dalsen AP, et al. 2000. Initial impact of the treasure oil spill on seabirds off Western South Africa. *South African Journal of Marine Science* 7615: 157–176.

Cresswell AK, Edgar GJ, Stuart-Smith RD, Thomson RJ, Barrett NS, Johnson CR 2017. Translating local benthic community structure to national biogenic reef habitat types. *Global Ecology and Biogeography* 26: 1112–1125.

Cundy ME, Santana-Garcon J, Ferguson AM, Fairclough D V., Jennings P, Harvey ES 2017. Baited remote underwater stereo-video outperforms baited downward-facing single-video for assessments of fish diversity, abundance and size composition. *Journal of Experimental Marine Biology and Ecology* 497: 19–32.

Dahl F 1908. Grundsätze und Grundbegriffe der biocönotischen Forschung. *Zoologischer Anzeiger* 33: 349–353.

Dames V, Bernard A, Floros C, Mann B, Speed C, Maggs J, Laing S, Meekan M, Olbers J 2020. Zonation and reef size significantly influence fish population structure in an established marine protected area, iSimangaliso Wetland Park, South Africa. *Ocean & Coastal Management* 185: 105040.

Dames VA 2021. *The effect of habitat and spatial management on reef fish assemblages in an established marine protected area*. MSc. Rhodes University. pp 209.

Dando JW 2020. *A baited remote underwater video survey of the Goukamma Marine Protected Area's ichthyofauna and a subsequent community structure comparison with the Betty's Bay, Stilbaai, and Tsitsikamma Marine Protected Areas*. University of Cape Town.

Datta RT, Tedesco M, Agosta C, Fettweis X, Kuipers Munneke P, van den Broeke MR 2018. Melting over the East Antarctic Peninsula (1999-2009): evaluation of a high-resolution regional climate model. *The Cryosphere Discussions* 12: 2901–2922.

Davies JS, Guillaumont B, Tempera F, Vertino A, Beuck L, Ólafsdóttir SH, Smith CJ, Fosså JH, van den Beld IMJ, Savini A, et al. 2017. A new classification scheme of European cold-water coral habitats: Implications for ecosystem-based management of the deep sea. *Deep-Sea Research Part II: Topical Studies in Oceanography* 145: 102–109.

Davis SE, Boucek R, Castañeda-Moya E, Dessu S, Gaiser E, Kominoski J, Sah JP, Surratt D, Troxler T 2018. Episodic disturbances drive nutrient dynamics along freshwater-to-estuary gradients in a subtropical wetland. *Ecosphere* 9: 1–19.

Dencausse G, Arhan M, Speich S 2010. Spatio-temporal characteristics of the Agulhas Current retroflection. *Deep Sea Research Rat 1: Oceanographic Research Papers* 57: 1392–1405.

Department of Environmental Affairs 2004. Notice Declaring The Bird Island Group Marine Protected Area Under Section 43 of the Marine Living Resources Act, 18 or 1998. *South Africa Government Gazette* 696: 1–4.

Department of Environmental Affairs 2019a. Marine Spatial Planning Act, 2018: Act No. 16 or 2018. *South Africa Government Gazette* 641: 1–16.

Department of Environmental Affairs 2019b. National Environmental Management: Protected Areas Act - Declaration of Marine Protected Areas, 2019. *South Africa Government Gazette* 42478: 1–48.

Department of Environmental Affairs 2019c. National Environmental Management: Protected Areas ACT, 2003 (Act NO. 57 of 2003) Regulations for the management of the Addo Elephant National Park Marine Protected Area. *South Africa Government Gazette* 42479: 4–25.

Department of Science and Technology 2016a. South African Research Infrastructure Roadmap. South African Department of Science and Technology (DST). Pretoria. pp 66.

Department of Science and Technology 2016b. *Research Infrastructure Roadmap*. Department of Science and Technology. pp 36.

Dethier MN, Graham ES, Cohen S, Tear LM 1993. Visual versus random-point percent cover estimations: ‘objective’ is not always better. *Marie Ecology Progress Series* 96: 93–100.

Dicken ML, Booth AJ 2013. Surveys of white sharks (Carcharodon carcharias) off bathing beaches in Algoa Bay, South Africa. *Marine and Freshwater Research* 64: 530–539.

Dicken ML, Bradshaw M, Smale MJ 2013. White shark (Carcharodon carcharias)-inflicted bite wounds observed on cape fur seals (Arctocephalus pusillus pusillus) at Black Rocks, Algoa Bay, South Africa. *African Zoology* 48: 418–426.

Dodds WK, Robinson CT, Gaiser EE, Hansen GJA, Powell H, Smith JM, Morse NB, Johnson SL, Gregory S V., Bell T, et al. 2012. Surprises and insights from long-term aquatic data sets and experiments. *BioScience* 62: 709–721.

Donovan MK, Adam TC, Shantz AA, Speare KE, Munsterman KS, Rice MM, Schmitt RJ, Holbrook SJ, Burkepile DE 2020. Nitrogen pollution interacts with heat stress to increase coral bleaching across the seascape. *Proceedings of the National Academy of Sciences of the United States of America* 117: 5351–5357.

Dorman SR, Harvey ES, Newman SJ 2012. Bait effects in sampling coral reef fish assemblages with stereo-BRUVs. *PLoS ONE* 7: 1–12.

Dorrington RA, Lombard AT, Bornman TG, Adams JB, Cawthra HC, Deyzel SHP, Goschen WS, Liu K, Mahler-Coetzee J, Matcher GF, et al. 2018. Working together for our oceans: A marine spatial plan for Algoa Bay, South Africa. *South African Journal of Science* 114: 2–7.

Douglass LL, Turner J, Grantham HS, Kaiser S, Constable A, Nicoll R, Raymond B, Post A, Brandt A, Beaver D 2014. A Hierarchical Classification of Benthic Biodiversity and Assessment of Protected Areas in the Southern Ocean. 9: e100551.

Dufrêne M, Legendre P 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

Durham BD, Pauw JC (eds) 2000. *Summary Marine Biodiversity Status Report for South Africa: At the end of the 20th Century*. Pretoria: National Research Foundation. pp 51.

Ehler C, Douvere F 2009. *Marine spatial planning: a step-by-step approach towards Ecosystem-based Management*. Intergovermental Pceanographic Commission and Man and the Bioshhere Programme (IOC) Maunual and Guides No. 53. ICAM Dossier NO. 6 .UNESCO. pp 99.

Ehler CN 2003. Indicators to measure governance performance in integrated coastal management. *Ocean and Coastal Management* 46: 335–345.

Eidens C, Hauffe T, Bayraktarov E, Wild C, Wilke T 2015. Multi-scale processes drive benthic community structure in upwelling-affected coral reefs. *Frontiers in Marine Science* 2: 1–11.

Ellis E, Maslin M, Boivin N, Bauer A 2016. Involve social scientists in defining the Anthropocene. *Nature* 540: 192–193.

Emilie Villar, Gregory K. Farrant, Michael Follows, Laurence Garczarek, Sabrina Speich, Stéphane Audic, Lucie Bittner, Bruno Blanke, Jennifer R. Brum, Christophe Brunet, et al. 2015. Environmental characteristics of Agulhas rings affect interocean plankton transport. *Science* 348: 1–26.

Engels P 1974. Comparing Species Diversity and Evenness Indices. *Journal of the Marine Biological Association of the United Kingdom* 54: 559–563.

Ensair HAM 2019. *The biology of Boopsoidea inornata (Castelnau, 1861) and life history comparisons within the Sparidae*. PhD. Marine Research Institute, Department of Biological Sciences. University of Cape Town. pp. 195.

Erbe C, Marley SA, Schoeman RP, Smith JN, Trigg LE, Embling CB 2019. The Effects of Ship Noise on Marine Mammals—A Review. *Frontiers in Marine Science* 6: 1–21.

Etnoyer PJ, Wood J, Shirley TC 2010. How Large Is the Seamount Niome? *Oceanography* 23: 206–209.

Evans RD, Wilson SK, Field SN, Moore JAY 2014. Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. *Marine Biology* 161: 599–607.

Field JG 1971. A numerical analysis of changes in the soft-bottom fauna along a transect across false bay, South Africa. *Journal of Experimental Marine Biology and Ecology* 7: 215–253.

Fischer A, Gunn J, Heslop E, Tanhua T 2019. *The Global Ocean Observation System 2030 Strategy*. IOC Brochure 2019-5 (IOC/BRO/2019/5 rev.). Paris. pp 24.

Fitzpatrick BM, Harvey ES, Heyward AJ, Twiggs EJ, Colquhoun J 2012. Habitat Specialization in Tropical Continental Shelf Demersal Fish Assemblages. *PLoS ONE* 7: e39634.

Fobert EK, Reeves SE, Swearer SE 2020. Ontogenetic shifts in social aggregation and habitat use in a temperate reef fish. *Ecosphere* 11: e03300.

Foley MM, Halpern BS, Micheli F, Armsby MH, Caldwell MR, Crain CM, Prahler E, Rohr N, Sivas D, Beck MW, et al. 2010. Guiding ecological principles for marine spatial planning. *Marine Policy* 34: 955–966.

Folpp H, Lowry M, Gregson M, Suthers IM 2013. Fish Assemblages on Estuarine Artificial Reefs: Natural Rocky-Reef Mimics or Discrete Assemblages? *PLoS ONE* 8: e63505.

Fong CR, Gaynus CJ, Carpenter RC 2020. Extreme rainfall events pulse substantial nutrients and sediments from terrestrial to nearshore coastal communities: a case study from French Polynesia. *Scientific Reports* 10: 1–8.

Fox L, Stukins S, Hill T, Miller CG 2020. Quantifying the Effect of Anthropogenic Climate Change on Calcifying Plankton. *Scientific Reports* 10: 1–9.

Funke, N., Claasen, M., Maissner, R., Nortje K (ed.) 2014. *Reflections on State of Research and Technology in South Africa's Marine and Maritime Sectors*. The Council for Scientific and Industrial Research(CSIR). Pretoria. pp. 322.

Gagnon K, Rothäusler E, Syrjänen A, Yli-Renko M, Jormalainen V 2013. Seabird Guano Fertilizes Baltic Sea Littoral Food Webs. *PLoS ONE* 8: e61284.

Garner CJ 2013. *Charactrisation and biotic Classification of Eastern Cape mixed substrate shores*. PhD. Botany Department. Nelson Mandela Metropolitain University. pp 395.

Geijzendorffer IR, Regan EC, Pereira HM, Brotons L, Brummitt N, Gavish Y, Haase P, Martin CS, Mihoub J-B, Secades C, et al. 2016. Bridging the gap between biodiversity data and policy reporting needs: An Essential Biodiversity Variables perspective. *Journal of Applied Ecology* 53: 1341–1350.

Gibbons MJ 1999. The taxonomic richness of South Africa's marine fauna: A crisis at hand. *South African Journal of Science* 95: 8–12.

Gili J-M, Coma R 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology & Evolution* 13: 316–321.

Gills B, Morgan J 2020. Global Climate Emergency: after COP24, climate science, urgency, and the threat to humanity. *Globalizations* 17: 885–902.

Gissi E, Manea E, Mazaris AD, Fraschetti S, Almpanidou V, Bevilacqua S, Coll M, Guarnieri G, Lloret-Lloret E, Pascual M, et al. 2021. A review of the combined effects of climate change and other local human stressors on the marine environment. *Science of the Total Environment* 755: 142564.

Gladstone W, Lindfield S, Coleman M, Kelaher B 2012. Optimisation of Baited Remote Underwater Video Sampling Designs for Estuarine Fish Assemblages 1 William Gladstone. *Journal of Experimental Marine Biology and Ecology* 429: 28–35.

Goff A 2012. The first portable digital camera – cassette included. *New Scientist* 213: 28–29.

Gómez-Ríos A, Tabik S, Luengo J, Shihavuddin ASM, Herrera F 2019. Coral species identification with texture or structure images using a two-level classifier based on Convolutional Neural Networks. *Knowledge-Based Systems* 184.

González-Rivero M, Beijbom O, Rodriguez-Ramirez A, Bryant DEP, Ganase A, Gonzalez-Marrero Y, Herrera-Reveles A, Kennedy E V., Kim CJS, Lopez-Marcano S, et al. 2020. Monitoring of coral reefs using artificial intelligence: A feasible and cost-effective approach. *Remote Sensing* 12: 1–22.

Goschen WS, Schumann EH 2011. The physical oceanographic processes of Algoa Bay , with emphasis on the western coastal region. *South African Environmental Observation Network (SAEON), Internal Report* 1–85.

Goschen WS, Bornman TG, Deyzel SHP, Schumann EH 2015. Coastal upwelling on the far eastern Agulhas Bank associated with large meanders in the Agulhas Current. *Continental Shelf Research* 101: 34–46.

Gotelli NJ, Colwell RK 2011. Estimating species richness. In Biological diversity: frontiers in measurement and assessment. In: Magurra, A and McGill B (eds) (ed.), *Biological diversity: frontiers in measurement and assessment.* Oxford University Press. pp 39–54.

Götz A 2005. *Assessment of the effect of Goukamma Marine Protected Area on community structure and fishery dynamics*. PhD. Rhodes University. pp232.

Götz A, Cowley PD, Winker H 2008. Selected fishery and population parameters of eight shore-angling species in the Tsitsikamma National Park no-take marine reserve. *African Journal of Marine Science* 30: 519–532.

Götz A, Kerwath SE, Attwood CG, Sauer WHH 2009a. Effects of fishing on a temperate reef community in South Africa 1: ichthyofauna. *African Journal of Marine Science* 31: 241–251.

Götz A, Kerwath SE, Attwood CG, Sauer WHH 2009b. Effects of fishing on a temperate reef community in South Africa 2: benthic invertebrates and algae. *African Journal of Marine Science* 31: 253–262.

Götz A, Kerwath SE, Samaai T, da Silva C, Wilke CG 2014. An Exploratory Investigation of the Fish Communities Associated with Reef in the Central Alghulas Bank, South Africa. *African Zoology* 49: 253–264.

Griffith AW, Gobler CJ 2020. Harmful algal blooms: A climate change co-stressor in marine and freshwater ecosystems. *Harmful Algae* 91: 101590.

Griffiths CL, Robinson TB, Lange L, Mead A 2010. Marine Biodiversity in South Africa: An Evaluation of Current States of Knowledge. *PLoS ONE* 5: e12008.

Griffiths JR, Kadin M, Nascimento FJA 2017. The importance of benthic – pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology* 23: 2179–2196.

Guidetti P, Bianchi CN, Chiantore M, Schiaparelli S, Morri C, Cattaneo-Vietti R 2004. Living on the rocks: Substrate mineralogy and the structure of subtidal rocky substrate communities in the Mediterranean Sea. *Marine Ecology Progress Series* 274: 57–68.

Gumede SV 2001. *A study of Benthic Invertebrate community structure in selected areas on the Continental Shelf off KwaZulu/Natal, South Africa.* MSc. University of Cape Town. pp 140.

Haase P, Tonkin JD, Stoll S, Burkhard B, Frenzel M, Geijzendorffer IR, Häuser C, Klotz S, Kühn I, McDowell WH, et al. 2018. The next generation of site-based long-term ecological monitoring: Linking essential biodiversity variables and ecosystem integrity. *Science of the Total Environment* 613–614: 1376–1384.

Hale R, Calosi P, Mcneill L, Mieszkowska N, Widdicombe S 2011. Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. *Oikos* 120: 661–674.

Hall SJ, Greenstreet SP 1998. Taxonomic distinctness and diversity measures: responses in marine fish communities. *Marine Ecology Progress Series* 166: 227–229.

Hammer Ø 2001. PAST: Paleontological Statistics software package for education and data analaysis. *Palaeontologia Electronica* 4: 9p.

Hampton SE, Strasser CA, Tewksbury JJ, Gram WK, Budden AE, Batcheller AL, Duke CS, Porter JH 2013. Big data and the future of ecology. *Frontiers in Ecology and the Environment* 11: 156–162.

Hanekom N, Hutchings L, Joubert PA, Van Der Byl PCN 1989. Sea temperature variations in the tsitsikamma coastal national park, South Africa, with notes on the effect of cold conditions on some fish populations. *South African Journal of Marine Science* 8: 145–153.

Harasti D, Malcolm H, Gallen C, Coleman MA, Jordan A, Knott NA 2015. Appropriate set times to represent patterns of rocky reef fishes using baited video. *Journal of Experimental Marine Biology and Ecology* 463: 173–180.

Harasti D, Williams J, Mitchell E, Lindfield S, Jordan A 2018. Increase in Relative Abundance and Size of Snapper Chrysophrys auratus Within Partially-Protected and No-Take Areas in a Temperate Marine Protected Area. *Frontiers in Marine Science* 5: 1–12.

Hardinge J, Harvey ES, Saunders BJ, Newman SJ 2013. A little bait goes a long way: The influence of bait quantity on a temperate fish assemblage sampled using stereo-BRUVs. *Journal of Experimental Marine Biology and Ecology* 449: 250–260.

Harley CDGG, Hughes AR, Hultgren KM, Miner BG, Sorte CJBB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL, Randall Hughes A, et al. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9: 228–241.

Harmer RW 2014. *Diversity and distribution of the subtidal soft-bottom macrofauna of the iSimangaliso Wetland Park, South Africa*. MSc. University of KwaZulu-Natal. pp 82.

Harris PT 2014. Shelf and deep-sea sedimentary environments and physical benthic disturbance regimes: A review and synthesis. *Marine Geology* 353: 169–184.

Harris PT, Macmillan-Lawler M, Rupp J, Baker EK 2014. Geomorphology of the oceans. *Marine Geology* 352: 4–24.

Harvey CJ, Fisher JL, Samhouri JF, Williams GD, Francis TB, Jacobson KC, deReynier YL, Hunsicker ME, Garfield N 2020. The importance of long-term ecological time series for integrated ecosystem assessment and ecosystem-based management. *Progress in Oceanography* 188: 102418.

Harvey ES, McLean D, Frusher S, Haywood MDE, Newman SJ, Williams A 2013. *The use of BRUVs as a tool for assessing marine fisheries and ecosystems: a review of the hurdles and potential.* University of Western Australia. p. 202.

Hays GC, Richardson AJ, Robinson C 2005. Climate change and marine plankton. *Trends in Ecology and Evolution* 20: 337–344.

Heagney EC, Lynch TP, Babcock RC, Suthers IM 2007. Pelagic fish assemblages assessed using mid-water baited video: Standardising fish counts using bait plume size. *Marine Ecology Progress Series* 350: 255–266.

Heiskanen A-S, Berg T, Uusitalo L, Teixeira H, Bruhn A, Krause-Jensen D, Lynam CP, Rossberg AG, Korpinen S, Uyarra MC, et al. 2016. Biodiversity in Marine Ecosystems—European Developments toward Robust Assessments. *Frontiers in Marine Science* 3: 1–20.

Heymans JJ, Bundy A, Christensen V, Coll M, de Mutsert K, Fulton EA, Piroddi C, Shin YJ, Steenbeek J, Travers-Trolet M 2020. The Ocean Decade: A True Ecosystem Modeling Challenge. *Frontiers in Marine Science* 7: 1–5.

Heyns-Veale ER, Bernard ATF, Götz A, Mann BQ, Maggs JQ, Smith MKS 2019a. Community-wide effects of protection reveal insights into marine protected area effectiveness for reef fish. *Marine Ecology Progress Series* 620: 99–117.

Heyns-Veale ER, Bernard ATF, Richoux NB, Parker D, Langlois TJ, Harvey ES, Götz A 2016. Depth and habitat determine assemblage structure of South Africa’s warm-temperate reef fish. *Marine Biology* 163: 158.

Heyns-Veale ER, Richoux NB, Bernard ATF, Götz A 2019b. Protected nearshore shallow and deep subtidal rocky reef communities differ in their trophic diversity but not their nutritional condition. *African Journal of Marine Science* 41: 103–114.

Heyns ER 2015. *Community structure and trophic ecology of shallow and deep rocky reefs in a well-established marine protected areas*. Springer Berlin Heidelberg.

Heyns ER, Bernard ATF, Richoux NB, Götz A 2016. Depth-related distribution patterns of subtidal macrobenthos in a well-established marine protected area. *Marine Biology* 163: 1–15.

Hierro LA, Garzón AJ, Atienza Montero P, Márquez JL 2020. Predicting Clinical Needs Derived from the COVID-19 Pandemic: The Case of Spain. *The Lancet* D-20-05254: 1–23.

Hill NA, Barrett N, Ford JH, Peel D, Foster S, Lawrence E, Monk J, Althaus F, Hayes KR 2018. Developing indicators and a baseline for monitoring demersal fish in data-poor, offshore Marine Parks using probabilistic sampling. *Ecological Indicators* 89: 610–621.

Hofmann M, Schellnhuber H 2009. Oceanic acidification affects marine carbon pump. *PNAS* 106: 3017–3022.

Horton T, Marsh L, Bett BJ, Gates AR, Jones DOB, Benoist N, Pfeifer S, Simon-Lledó E, Durden J, Vandepitte L, et al. 2021. Recommendations for the standardisation of open taxonomic nomenclature for image-based identifications. *Frontiers in Marine Science* 8: 62.

Innovation D of S and 2018. Draft: White Paper on Science, Technology and Innovation.

Ivanova S V., Kessel ST, Espinoza M, McLean MF, O'Neill C, Landry J, Hussey NE, Williams R, Vagle S, Fisk AT 2020. Shipping alters the movement and behavior of Arctic cod (Boreogadus saida), a keystone fish in Arctic marine ecosystems. *Ecological Applications* 30: 1–13.

Van Jaarsveld AS, Biggs HCC 2000. Broad participation enhances initial steps towards a South African ecosystem observatory system (LTER). *SouthAfrican Journal of Science* 96: 63–66.

James L, Marzloff M, Barrett N, Friedman A, Johnson C 2017. Changes in deep reef benthic community composition across a latitudinal and environmental gradient in temperate Eastern Australia. *Marine Ecology Progress Series* 565: 35–52.

Jetz W, McGeoch MA, Guralnick R, Ferrier S, Beck J, Costello MJ, Fernandez M, Geller GN, Keil P, Merow C, et al. 2019. Essential biodiversity variables for mapping and monitoring species populations. *Nature Ecology and Evolution* 3: 539–551.

Jin S 2020. COVID-19, Climate Change, and Renewable Energy Research: We Are All in This Together, and the Time to Act Is Now. *ACS Energy Letters* 5: 1709–1711.

Joshua TJ, Toefy R, Sparks C, Kirkman SP, Samaai T 2018. Macro-benthic invertebrate assemblages in the Betty's Bay Marine Protected Area (Kogelberg region South Africa). *Regional Studies in Marine Science* 22: 1–8.

Jost L 2006. Entropy and diversity. *Oikos* 113: 363–375.

Jürgens N, Schmiedel U, Haarmeyer DH, Dengler J, Finckh M, Goetze D, Gröngröft A, Hahn K, Koulibaly A, Luther-Mosebach J, et al. 2012. The BIOTA Biodiversity Observatories in Africa-a standardized framework for large-scale environmental monitoring. *Environmental Monitoring and Assessment* 184: 655–678.

Kalinski J-CJJCJ, Waterworth SCSC, Noundou XSXS, Jiwaji M, Parker-Nance S, Krause RWMRWM, McPhail KLKL, Dorrington RARA 2019. Molecular networking reveals two distinct chemotypes in pyrroloiminoquinone-producing tsitsikamma favus sponges. *Marine Drugs* 17: 1–16.

Karasti H, Baker KS, Halkola E 2006. Enriching the notion of data curation in e-Science: Data managing and information infrastructuring in the Long Term Ecological Research (LTER) network. *Computer Supported Cooperative Work* 15: 321–358.

Karczmarski L, Cockcroft VG, McLachlan A 2000. Habitat use and preferences of Indo-Pacific humpback dolphins Sousa chinensis in Algoa Bay, South Africa. *Marine Mammal Science* 16: 65–79.

Karenyi N 2014. *Patterns and drivers of benthic macrofauna to support systematic conservation planning for marine unconsolidated sediment ecosystems*. PhD. Nelson Mandel Metropolitain University. p. 252.

Katona S, Polsenberg J, Lowndes J, Halpern B, Pacheco E, Mosher L, Kilponen A, Papacostas K, Mora AGG-, Farmer G, et al. 2017. Navigating the seascape of ocean management: waypoints on the voyage toward sustainable use. *OpenChannels: Forum for Ocean Planning and Management.* 44.

Kerwath SE, Götz A, Attwood CG, Cowley PD, Sauer WHH 2007. Movement pattern and home range of Roman Chrysoblephus laticeps. *African Journal of Marine Science* 29: 93–103.

Kim E-SS 2006. Development, potentials, and challenges of the International Long-Term Ecological Research (ILTER) Network. *Ecological Research* 21: 788–793.

Kirkman S 2016. Spatial characterisation of the Benguela ecosystem for ecosystem-based Spatial characterisation of the Benguela ecosystem for ecosystem-based management. *African Journal of Marine Science* 1–18.

Kissling WD, Ahumada JA, Bowser A, Fernandez M, Fernández N, García EA, Guralnick RP, Isaac NJBB, Kelling S, Los W, et al. 2018a. Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. *Biological Reviews* 93: 600–625.

Kissling WD, Hardisty A, García EA, Santamaria M, De Leo F, Pesole G, Freyhof J, Manset D, Wissel S, Konijn J, et al. 2015. Towards global interoperability for supporting biodiversity research on essential biodiversity variables (EBVs). *Biodiversity* 16: 99–107.

Kissling WD, Walls R, Bowser A, Jones MO, Kattge J, Agosti D, Amengual J, Basset A, van Bodegom PM, Cornelissen JHC, et al. 2018b. Towards global data products of Essential Biodiversity Variables on species traits. *Nature Ecology & Evolution* 2: 1531–1540.

Klages NTW, Willis AB, Ross GJ 1992. Variability in the diet of the cape gannet at Bird Island, Algoa Bay, South Africa. *South African Journal of Marine Science* 12: 761–771.

Klein E, Appeltans W, Provoost P, Saeedi H, Benson A, Bajona L, Peralta AC, Bristol RS 2019. OBIS Infrastructure, Lessons Learned, and Vision for the Future. *Frontiers in Marine Science* 6: 1–7.

Kohler KE, Gill SM 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32: 1259–1269.

Koper RP, Plön S 2016. Interspecific interactions between cetacean species in Algoa Bay, South Africa. *Aquatic Mammals* 42: 454–461.

Kröner N, Kotlarski S, Fischer E, Lüthi D, Zubler E, Schär C 2017. Separating climate change signals into thermodynamic, lapse-rate and circulation effects: theory and application to the European summer climate. *Climate Dynamics* 48: 3425–3440.

Kruger N, Branch GM, Griffiths CL, Field JG 2005. Changes in the epibenthos of Saldanha Bay, South Africa, between the 1960s and 2001: An analysis based on dredge samples. *African Journal of Marine Science* 27: 471–477.

Lange L, Griffiths CL 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: 111–124.

Langlois T, Goetze J, Bond T, Monk J, Abesamis RA, Asher J, Barrett N, Bernard ATF, Bouchet PJ, Birt MJ, et al. 2020. A field and video annotation guide for baited remote underwater stereo-video surveys of demersal fish assemblages. *Methods in Ecology and Evolution* 11: 1401–1409.

Langlois T, Williams J, Monk J, Bouchet P, Currey L, Goetze J, Harasti D, Huveneers C, Ierodiaconou D, Malcolm H, et al. 2018. Marine Sampling Field Manual for Benthic Stereo BRUVS (Baited Remote Underwater Video). In: Przeslawski R, Foster S (eds), *Field Manuals for Marine Sampling to Monitor Australian Waters*. National Environmental Science Programme (NESP). p. 23.

Lasiak T a 1981. Nursery grounds of juvenile teleosts: evidence from the surf zone of King's Beach, Port Elizabeth. . *South African Journal of Science* 77: 388–390.

Lasiak TA 1984. Aspects of the biology of three benthic-feeding teleosts from King's Beach, Algoa Bay. *South African Journal of Zoology* 19: 51–56.

Lasiak TA 1986. Juveniles, food and the surf zone habitat: implications for teleost nursery areas. *South African Journal of Zoology* 21: 51–56.

Lemley DA, Adams JB, Bornman TG, Campbell EE, Deyzel SHP 2019. Land-derived inorganic nutrient loading to coastal waters and potential implications for nearshore plankton dynamics. *Continental Shelf Research* 174: 1–11.

Lescroël A, Bost CA 2006. Recent decrease in gentoo penguin populations at Iles Kerguelen. *Antarctic Science* 18: 171–174.

Li Y, Yu M, Xu M, Yang J, Sha D, Liu Q, Yang C 2020. Big Data and Cloud Computing. *Manual of Digital Earth*. pp 229–277.

Lindenmayer DB, Likens GE, Franklin JF 2018. Earth Observation Networks (EONs): Finding the Right Balance. *Trends in Ecology & Evolution* 33: 1–3.

Lindstrom E, Gunn J, Fischer A, McCurdy A, Glover LK, Members TT 2012a. A Framework for Ocean Observing. By theTask Team for an Integrated Framework for Sustained ocean Observing. *Unesco 2012, Ioc/Inf-1284* 1–28.

Lindstrom E, Gunn J, Fischer A, McCurdy A, Glover LK, Members TT 2012b. A Framework for Ocean Observing.

Liquete C, Cid N, Lanzanova D, Grizzetti B, Reynaud A 2016. Perspectives on the link between ecosystem services and biodiversity: The assessment of the nursery function. *Ecological Indicators* 63: 249–257.

Liu Y, Qiu M, Liu C, Guo Z 2017. Big data challenges in ocean observation: a survey. *Personal and Ubiquitous Computing* 21: 55–65.

Livingstone T-C, Harris JM, Lombard AT, Smit AJ, Schoeman DS 2018. Classification of marine bioregions on the east coast of South Africa. *African Journal of Marine Science* 40: 51–65.

Lombard A, Strauss T, Harris J, Sink K, Attwood C, Hurchings L 2004. *South African National Biodiversity Assessment 2004 Technical Report Volum 4: Marine Component*. South African National Biodiversity Institute. Pretoria. p. 101.

Lombard AT, Dorrington RA, Reed JR, Ortega-cisneros K, Penry GS, Pichegru L, Smit KP, Vermeulen EA, Witteveen M, Sink KJ, et al. 2019. Key Challenges in Advancing an Ecosystem-Based Approach to Marine Spatial Planning Under Economic Growth Imperatives. *Frontiers in Marine Science* 6: 1–11.

Long RD, Charles A, Stephenson RL 2015. Key principles of marine ecosystem-based management. *Marine Policy* 57: 53–60.

Lourenço CR, Nicastro KR, McQuaid CD, Krug LA, Zardi GI 2020. Strong upwelling conditions drive differences in species abundance and community composition along the Atlantic coasts of Morocco and Western Sahara. *Marine Biodiversity* 50: 15.

Lunney D, Dickman CR, Predavec M 2018. The critical value of long-term field studies and datasets: An editorial perspective. *Australian Zoologist* 39: 559–567.

Lustenberger F 2010. the Problem of Water in Southern Africa and in Particular the Management of Water in South Africa. 1–27.

Lutjeharms JRE 1976. The Agulhas Current System During the Northeast Monsoon Season. 6: 665–670.

Lutjeharms JRE 2007. Three decades of research on the greater Agulhas Current. *Ocean Science* 3: 129–147.

Lutjeharms JRE, Bornman TG 2010. The importance of the greater agulhas currentis increasingly being recognized. *South African Journal of Science* 106: 1–4.

Lutjeharms JRE, Roberts HR 1988. The Natal Pulse: An Extreme Transient on the Algulhas Current. *Journal of Geophysical Reasearch* 93: 631–645.

Lutjeharms JRE, Meyer AA, Ansorge IJ, Eagle GA, Orren MJ 1996. The nutrient characteristics of the Agulhas bank. *South African Journal of Marine Science* 17: 253–274.

MacLeod N, Benfield M, Culverhouse P 2010. Time to automate identification. *Nature* 467: 154–155.

Maduna SM 2017. *Macrobenthos Used to Validate Multi-Criteria Derived Marine Biodiversity Spatial Zones in KwaZulu-Natal, South Africa*. University of KwaZulu-Natal. pp. 227.

Magurran AE, Baillie SR, Buckland ST, Dick JM, Elston DA, Scott EM, Smith RI, Somerfield PJ, Watt AD 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution* 25: 574–582.

Makwela MS 2017. *An investigation of benthic epifauna to support classification and mapping of outer shelf ecosystems in KwaZulu-Natal*. University of the Western Cape. pp. 108.

Makwela MS, Kerwath SE, Götz A, Sink K, Samaai T, Wilke CG 2016. Notes on a remotely operated vehicle survey to describe reef ichthyofauna and habitats – Agulhas Bank, South Africa. *Bothalia* 46: 1–7.

Malan DE, McLachlan A 1985. Vertical gradients of meiofauna and bacteria in subtidal sandy sediments from two high-energy surf zones in Algoa Bay, South Africa. *South African Journal of Marine Science* 3: 43–53.

Mallet D 2014. *Underwater Rotating Video System To Study the Ichthyofauna: Applications to spatial and temporal variations in the lagoon of New Caledonia*. Université de la Nouvelle-Calédonie. pp. 263.

Mallet D, Pelletier D 2014. Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). *Fisheries Research* 154: 44–62.

Maluleke R 2016. *Provincial profile: Eastern Cape Community Survey 2016*.

Mann BQ, Buxton CD 1992. Diets of Diplodus sargus capensis and D. cervinus hottentotus (Pisces: Sparidae) on the Tsitsikamma coast, South Africa. *Koedoe* 35: 27–36.

Mann BQ, Celliers L, Fennessy ST, Bailey S, Wood AD 2006. Towards the declaration of a large marine protected area: A subtidal ichthyofaunal survey of the Pondoland coast in the Eastern Cape, South Africa. *African Journal of Marine Science* 28: 535–551.

Mann BQ, Cowley PD, Dunlop SW, Potts WM 2018. Is catch-and-release shore angling compatible with the conservation goals of marine protected areas? A case study from the iSimangaliso Wetland Park in South Africa. *Fisheries Research* 208: 179–188.

Margalef R 1997. Turbulance and marine life. *Scientia Marina* 61: 109–123.

Masikane N 2011. *Nearshore subtidal soft-bottom macrozoobenthic community structure in the western sector of Algoa Bay,South Africa*. MSc. Nelson Mandela Metropolitan University. pp. 183.

Matobole RM, Van Zyl LJ, Parker-Nance S, Davies-Coleman MT, Trindade M 2017. Antibacterial Activities of Bacteria Isolated from the Marine Sponges Isodictya compressa and Higginsia bidentifera Collected from Algoa Bay, South Africa. *Marine Drugs* 15.

Matona T 2019. *South Africa's Implementation of the 2030 Agenda for Sustainable Development.*

Mbambo 2006. *Scale of variability of phytoplanktion composition and biomass in Algoa Bay*.

McClain CR, Barry JP 2010. Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons. *Ecology* 91: 964–976.

McCleland D 2020. Port Elizabeth of Yore: Construction of the Breakwater. Accessed from http://thecasualobserver.co.za/.

Mclachlan A 1977. Studies on the Psammolittoral Meiofauna of Algoa Bay, South Africa. *Zoologica Africana* 12: 33–60.

McLachlan A, Erasmus T, Dye AH, Wooldridge T, Van der Horst G, Rossouw G, Lasiak TA, McGwynne L 1981. Sand beach energetics: An ecosystem approach towards a high energy interface. *Estuarine, Coastal and Shelf Science* 13: 11–25.

McLachlan A, Winter PED, Botha L 1977. Vertical and horizontal distribution of sub-littoral meiofauna in Algoa Bay, South Africa. *Marine Biology* 40: 355–364.

McPhail KL, Davies-Coleman MT, Starmer J 2001. Sequestered chemistry of the Arminacean nudibranch Leminda millecra in Algoa Bay, South Africa. *Journal of Natural Products* 64: 1183–1190.

McQuatters-Gollop A, Mitchell I, Vina-Herbon C, Bedford J, Addison PFE, Lynam CP, Geetha PN, Vermeulan EA, Smit K, Bayley DTI, et al. 2019. From Science to Evidence – How Biodiversity Indicators Can Be Used for Effective Marine Conservation Policy and Management. *Frontiers in Marine Science* 6: 1–16.

Mdlalose S 2019. *Determinants of a Competitive Bunkering Service: a South African Model*. Nelson Mandela University. pp. 226.

von der Meden CEO, Atkinson LJ, Branch GM, Asdar S, Ansorge IJ, van den Berg M 2017. Long-term change in epibenthic assemblages at the Prince Edward Islands: a comparison between 1988 and 2013. *Polar Biology* 40: 2171–2185.

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, et al. 2007. Global Climate Projections. In: Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt MT and HLM (ed.), *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Solomon, S., D. Qin, M. Manning, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. P 747-845.

Melly BL 2011. *The zoogeography of the cetaceans in Algoa Bay*. PhD. Rhodes University. pp 203.

Melly BL, McGregor G, Hofmeyr GJG, Plön S 2018. Spatio-temporal distribution and habitat preferences of cetaceans in Algoa Bay, South Africa. *Journal of the Marine Biological Association of the United Kingdom* 98: 1065–1079.

Michener WK, Jones MB 2012. Ecoinformatics: Supporting ecology as a data-intensive science. *Trends in Ecology and Evolution* 27: 85–93.

Miloslavich P, Bax NJ, Simmons SE, Klein E, Appeltans W, Aburto-Oropeza O, Andersen Garcia M, Batten SD, Benedetti-Cecchi L, Checkley DM, et al. 2018. Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. *Global Change Biology* 24: 2416–2433.

Miloslavich P, Seeyave S, Muller-Karger F, Bax N, Ali E, Delgado C, Evers-King H, Loveday B, Lutz V, Newton J, et al. 2019. Challenges for global ocean observation: the need for increased human capacity. *Journal of Operational Oceanography* 12: S137–S156.

Mirtl M, T. Borer E, Djukic I, Forsius M, Haubold H, Hugo W, Jourdan J, Lindenmayer D, McDowell WHH, Muraoka H, et al. 2018. Genesis, goals and achievements of Long-Term Ecological Research at the global scale: A critical review of ILTER and future directions. *Science of the Total Environment* 626: 1439–1462.

Misa WFXE, Richards BL, DiNardo GT, Kelley CD, Moriwake VN, Drazen JC 2016. Evaluating the effect of soak time on bottomfish abundance and length data from stereo-video surveys. *Journal of Experimental Marine Biology and Ecology* 479: 20–34.

Mohamed H, Nadaoka K, Nakamura T 2018. Assessment of machine learning algorithms for automatic benthic cover monitoring and mapping using towed underwater video camera and high-resolution satellite images. *Remote Sensing* 10: 1–17.

Mons B, Neylon C, Velterop J, Dumontier M, da Silva Santos LOB, Wilkinson MD 2017. Cloudy, increasingly FAIR; revisiting the FAIR Data guiding principles for the European Open Science Cloud. *Information Services & Use* 37: 49–56.

Muller-Karger FE, Miloslavich P, Bax NJ, Simmons S, Costello MJ, Sousa Pinto I, Canonico G, Turner W, Gill M, Montes E, et al. 2018. Advancing Marine Biological Observations and Data Requirements of the Complementary Essential Ocean Variables (EOVs) and Essential Biodiversity Variables (EBVs) Frameworks. *Frontiers in Marine Science* 5: 1–15.

Munilla I, Arcos JM, Oro D, Álvarez D, Leyenda PM, Velando A 2011. Mass mortality of seabirds in the aftermath of the Prestige oil spill. *Ecosphere* 2.

Navarrete SA, Wieters EA, Broitman BR, Castilla JC 2005. Scales of benthic – pelagic coupling and the intensity of species interactions : From recruitment limitation to top-down control. *PNAS* 102: 18046–18051.

Nel L, Strydom NA, Bouwman H 2015. Preliminary assessment of contaminants in the sediment and organisms of the Swartkops Estuary, South Africa. *Marine Pollution Bulletin* 101: 878–885.

Niekerk L Van, Taljaard S, Adams JB, Fundisi D, Huizinga P, Lamberth S, Mallory S, Snow G, Turpie J, Whitfield A, et al. 2015. *Desktop Provisional Ecoclassification of the Temperate Estuaries of South Africa*.

Nowogrodzki A 2020. Eleven tips for working with large data sets. *Nature* 577: 439–440.

O'Connor TG 2010. Understanding Environmental Change in Complex Systems: SAEON Core Science Framework. Pretoria.

O'Garra T 2017. Economic value of ecosystem services, minerals and oil in a melting Arctic: A preliminary assessment. *Ecosystem Services* 24: 180–186.

Olbers JM, Celliers L, Schleyer MH 2009. Zonation of benthic communities on the subtropical Aliwal shoal, Durban, KwaZulu-Natal, South Africa. *African Zoology* 44: 8–23.

Olenin S, Ducrotoy J-PP 2006. The concept of biotope in marine ecology and coastal management. *Marine Pollution Bulletin* 53: 20–29.

Olsgard F, Somerfield PJ, Carr MR 1997. Relationships between taxonomic resolution and data transformations in analyses of a macrobenthic community along an established pollution gradient. *Marine Ecology Progress Series* 149: 173–181.

Olson DB, Evans RH 1986. Rings of the Agulhas current. *Deep Sea Research Part A, Oceanographic Research Papers* 33: 27–42.

Ortega-Cisneros K, Yokwana S, Sauer W, Cochrane K, Cockcroft A, James NC, Potts WM, Singh L, Smale M, Wood A, et al. 2018. Assessment of the likely sensitivity to climate change for the key marine species in the southern Benguela system. *African Journal of Marine Science* 40: 279–292.

Osgood GJ, McCord ME, Baum JK 2020. Chondrichthyans as an umbrella species-complex for conserving South African biodiversity. *African Journal of Marine Science* 42: 81–93.

Parker D 2015. *An Evaluation of Sampling and Statistical methods for long-term monitoring of subtidal reef fishes: A case study of Tsitsikamma National Park Marine Protected Area.* Phd. Rhodes University. pp 178.

Pattrick P 2013. *Assemblage dynamics of larval fishes associated with various shallow water nursery habitats in Algoa Bay, South Africa*. PhD. Nelson Manela Metropolitan University. pp 253.

Pattrick P, Strydom NA 2008. Composition, abundance, distribution and seasonality of larval fishes in the shallow nearshore of the proposed Greater Addo Marine Reserve, Algoa Bay, South Africa. *Estuarine, Coastal and Shelf Science* 79: 251–262.

Pattrick P, Strydom N, Goschen W 2013. Shallow-water, nearshore current dynamics in Algoa Bay, South Africa, with notes on the implications for larval fish dispersal. *African Journal of Marine Science* 35: 269–282.

Pearlman J, Pearlman F, Ferdinand O, Zielinski O, Delory E, Meme S, Hareide NR, Kvalsund K, del Río J, Toma DM, et al. 2017. NeXOS, developing and evaluating a new generation of in-situ ocean observation systems. *OCEANS 2017 - Aberdeen* June.

Pearson R, Stevens T 2015. Distinct cross-shelf gradient in mesophotic reef fish assemblages in subtropical eastern Australia. *Marine Ecology Progress Series* 532: 185–196.

Pelletier D, Leleu K, Mallet D, Mou-Tham G, Hervé G, Boureau M, Guilpart N 2012. Remote High-Definition Rotating Video Enables Fast Spatial Survey of Marine Underwater Macrofauna and Habitats. *PLoS ONE* 7: e30536.

Penven P, Lutjeharms JRE, Marchesiello P, Roy C, Weeks SJ 2001. Generation of cyclonic eddies by the Agulhas Current in the lee of the Agulhas Bank. *Geophysical Research Letters* 28: 1055–1058.

Peters DPC, Havstad KM, Cushing J, Tweedie C, Fuentes O, Villanueva-Rosales N 2014. Harnessing the power of big data: Infusing the scientific method with machine learning to transform ecology. *Ecosphere* 5: 1–15.

Petit JR, Raynaud D, Basile I, Chappellaz J, Davisk M, Ritz C, Delmotte M, Legrand M, Lorius C, Pe L, et al. 1999. Climate and atmospheric history of the past 420 , 000 years from the Vostok ice core , Antarctica. *Nature* 399: 429–436.

Pichegru L, Ryan PG, Le Bohec C, Van Der Lingen CD, Navarro R, Petersen S, Lewis S, Van Der Westhuizen J, Grémillet D 2009. Overlap between vulnerable top predators and fisheries in the benguela upwelling system: Implications for marine protected areas. *Marine Ecology Progress Series* 391: 199–208.

Pickett STA, Cadenasso ML 1995. Landscape Ecology: Spatial Heterogeneity in Ecological Systems. *Science, New Series* 269: 331–334.

Picone F, Buonocore E, Claudet J, Chemello R, Russo GF, Franzese PP 2020. Marine protected areas overall success evaluation (MOSE): A novel integrated framework for assessing management performance and social-ecological benefits of MPAs. *Ocean and Coastal Management* 198: 105370.

Pillay T, Cawthra HC, Lombard AT 2020. Characterisation of seafloor substrate using advanced processing of multibeam bathymetry, backscatter, and sidescan sonar in Table Bay, South Africa. *Marine Geology* 429: 106332.

Pillay T, Cawthra HC, Lombard AT 2021a. Integration of machine learning using hydroacoustic techniques and sediment sampling to refine substrate description in the Western Cape, South Africa. *Marine Geology* 440: 106599.

Pillay T, Cawthra HC, Lombard AT, Sink K 2021b. Benthic habitat mapping from a machine learning perspective on the Cape St Francis inner shelf, Eastern Cape, South Africa. *Marine Geology* 440: 106595.

Pitcher G, Jiménez B, Kudela R, Reguera B 2017. Harmful Algal Blooms in Eastern Boundary Upwelling Systems: A GEOHAB Core Research Project. *Oceanography* 30: 22–35.

Pitcher GC, Cembella AD, Krock B, Macey BM, Mansfield L, Probyn TA 2014. Identification of the marine diatom Pseudo-nitzschia multiseries (Bacillariophyceae) as a source of the toxin domoic acid in Algoa Bay, South Africa. *African Journal of Marine Science* 36: 523–528.

Pittman SJ, Brown KA 2011. Multi-scale approach for predicting fish species distributions across coral reef seascapes. *PLoS ONE* 6: e20583.

Popova E, Yool A, Byfield V, Cochrane K, Coward AC, Salim SS, Gasalla MA, Henson SA, Hobday AJ, Pecl GT, et al. 2016. From global to regional and back again: Common climate stressors of marine ecosystems relevant for adaptation across five ocean warming hotspots. *Global Change Biology* 22: 2038–2053.

Porri F, Jackson JM, Von der Meden CEO, Weidberg N, McQuaid CD 2014. The effect of mesoscale oceanographic features on the distribution of mussel larvae along the south coast of South Africa. *Journal of Marine Systems* 132: 162–173.

Porter SN, Schleyer MH 2017. Long-term dynamics of a high-latitude coral reef community at Sodwana Bay, South Africa. *Coral Reefs* 36: 369–382.

Porter SN, Branch GM, Sink KJ 2013. Biogeographic patterns on shallow subtidal reefs in the western Indian Ocean. *Marine Biology* 160: 1271–1283.

Porter SN, Branch GM, Sink KJ 2017a. Changes in shallow-reef community composition along environmental gradients on the East African coast. *Marine Biology* 164: 101.

Porter SN, Branch GM, Sink KJ 2017b. Sand-mediated divergence between shallow reef communities on horizontal and vertical substrata in the western Indian Ocean. *African Journal of Marine Science* 39: 121–127.

Porter SN, Kaehler S, Branch GM, Sink KJ 2014. Riverine subsidies for inshore filter-feeder communities: potential influences on trophic patterns among bioregions. *Marine Ecology Progress Series* 498: 13–26.

Post AL, Lavoie C, Domack EW, Leventer A, Shevenell A, Fraser AD 2017. Environmental drivers of benthic communities and habitat heterogeneity on an East Antarctic shelf. *Antarctic Science* 29: 17–32.

Potter CP 2013. Anchovy and sardine in Algoa Bay and their relationship with response variables in two threatened avian predators. 105.

Rahmstorf S 2017. Rising hazard of storm-surge flooding. *Proceedings of the National Academy of Sciences of the United States of America* 114: 11806–11808.

Randall RM, Randall BM, Batchelor AL, Ross GJB 1971. The Status of Seabirds associated with Island in Algoa Bay, South Africa, 1973-1981. *Cormorant* 9: 85–104.

van Rein HB, Brown CJ, Quinn R, Breen J 2009. A review of sublittoral monitoring methods in temperate waters: a focus on scale. *Underwater Technology* 28: 99–113.

Reis-Filho JA, Schmid K, Harvey ES, Giarrizzo T 2019. Coastal fish assemblages reflect marine habitat connectivity and ontogenetic shifts in an estuary-bay-continental shelf gradient. *Marine Environmental Research* 148: 57–66.

Retzlaff R, LeBleu C 2018. Marine Spatial Planning: Exploring the Role of Planning Practice and Research. *Journal of Planning Literature* 33: 466–491.

Riegl B, Schleyer MH, Cook PJ, Branch GM 1995. Structure of Africa's southernmost coral communities. *Bulletin of Marine Science* 56: 676–691.

Roberson L, Winker H, Attwood C, De Vos L, Sanguinetti C, Götz A 2015. First survey of fishes in the Betty's Bay Marine Protected Area along South Africa's temperate south-west coast. *African Journal of Marine Science* 37: 543–556.

Roberts L, Pérez-Dominguez R, Elliot M 2016. Use of baited remote underwater video (BRUV) and motion analysis for studying the impacts of underwater noise upon free ranging fish and implications for marine energy management. *Marine Pollution Bulletin* 112: 75–85.

Roberts MJ 2010. Coastal currents and temperatures along the eastern region of Algoa Bay, South Africa, with implications for transport and shelf-bay water exchange. *African Journal of Marine Science* 32: 145–161.

Rockström J, Steffen W, Noone K, Persson Å, Chapin FS, Lambin EF, Lenton TM, Scheffer M, Folke C, Schellnhuber HJ, et al. 2009. A Safe operating space for humanity. *Nature* 461: 472–475.

Roelfsema C, Phinn S, Jupiter S, Comley J, Albert S 2013. Mapping coral reefs at reef to reef-system scales, 10s-1000s km2, using object-based image analysis. *International Journal of Remote Sensing* 34: 6367–6388.

Ruhl HA, Bahr FL, Henson SA, Hosking WB, Espinola B, Kahru M, Daniel P, Drake P, Edwards CA 2020. Understanding the remote influences of ocean weather on the episodic pulses of particulate organic carbon flux. *Deep-Sea Research Part II: Topical Studies in Oceanography* 173: 104741.

De Ruijter WPM, Biastoch A, Drijfhout SS, Lutjeharms JRE, Matano RP, Pichevin T, Van Leeuwen PJ, Weijer W 1999. Indian-Atlantic interocean exchange: Dynamics, estimation and impact. *Journal of Geophysical Research: Oceans* 104: 20885–20910.

Sagi T, Lehahn Y, Bar K 2020. Artificial intelligence for ocean science data integration: Current state, gaps, and way forward. *Elementa* 8: 1–20.

Sallée JB 2018. Southern ocean warming. *Oceanography* 31: 52–62.

Sanguinetti C 2013. *Patterns in reef fish assemblages as determinated by bated remote underwater video (BRUV) along the wastern side of False Bay: effect of site, septh, and protection status.* MSc. Percy FiszPatrick Institute of African Ornihology. University of Cape Town. pp 77.

Sbragaglia V, Nuñez JD, Dominoni D, Coco S, Fanelli E, Azzurro E, Marini S, Nogueras M, Ponti M, del Rio Fernandez J, et al. 2019. Annual rhythms of temporal niche partitioning in the Sparidae family are correlated to different environmental variables. *Scientific Reports* 9: 1–11.

Schlacher TA, Schlacher-Hoenlinger MA, Williams A, Althaus F, Hooper JNA, Kloser R 2007. Richness and distribution of sponge megabenthos in continental margin canyons off southeastern Australia. *Marine Ecology Progress Series* 340: 73–88.

Schleyer MH, Celliers L 2005. Modelling reef zonation in the Greater St Lucia Wetland Park, South Africa. *Estuarine, Coastal and Shelf Science* 63: 373–384.

Schleyer MH, Heikoop JM, Risk MJ 2006. A benthic survey of Aliwal Shoal and assessment of the effects of a wood pulp effluent on the reef. *Marine Pollution Bulletin* 52: 503–514.

Schmeller DS, Weatherdon L V., Loyau A, Bondeau A, Brotons L, Brummitt N, Geijzendorffer IR, Haase P, Kuemmerlen M, Martin CS, et al. 2018. A suite of essential biodiversity variables for detecting critical biodiversity change. *Biological Reviews* 93: 55–71.

Schumann EH, Illenberger WK, Goschen WS 1991. Surface winds over Algoa Bay, South Africa. *South African Journal of Science* 87: 202–207.

Schumann EH, Perrins LA, Hunter IT 1982. Upwelling along the South Coast of the Cape Province, South Africa. *South African Journal of Science* 78: 238–242.

Schumann EH, Ross GJB, Goschen WS 1988. Cold water events in Algoa Bay and along the Cape south coast, South Africa, in March/April 1987. *South African Journal of Science* 84: 579–584.

Scott R 2018. Biogeographical patterns of southern African marine invertabrates. *Journal of Chemical Information and Modeling* 53: 227.

Seager J 2008. TransectMeasure, EventMeasure and CAL SeaGIS Pty. Ltd., Bacchus Marsh, Victoria, Australia.

Shah A 2018. *Distribution of epifauna in offshore benthic environments along the west and south coast of South Africa*. Minor Dissertaion. University of Cape Town. pp 77.

Shears NT 2007. Biogeography, community structure and biological habitat types of subtidal reefs on the South Island West Coast, New Zealand. *Science for Conservation* 1–53.

Shears NT, Babcock RC 2007. Quantitative description mainland New Zealand’s shallow subtidal reef communities. *Science for Conservation* 280: 1–126.

Sherman K 1991. The large marine ecosystem concept: research and management strategy for living marine resources. *Ecological Applications* 1: 349–360.

Shihavuddin ASM, Gracias N, Garcia R, Gleason ACR, Gintert B 2013. Image-based coral reef classification and thematic mapping. *Remote Sensing* 5: 1809–1841.

Sikorska J, Hau AM, Anklin C, Parker-Nance S, Davies-Coleman MT, Ishmael JE, McPhail KL 2012. Mandelalides A-D, cytotoxic macrolides from a new Lissoclinum species of South African tunicate. *Journal of Organic Chemistry* 77.

Sink KJ, Atkinson LJ, Kerwath S, Samaai T 2010. *Assessment of offshore benthic biodiversity on the Agulhas Bank and the potential role of petroleum infrastructure in offshore spatial management*. Report prepared for WWF South Africa and PetroSA. pp 77.

Sink KJ, van der Bank MG, Majiedt PA, Harris LR, Atkinson LJ, Kirkman SP, Karenyi N 2018. *National Biodiversity Assessment 2018*. South African National Biodiversity Institute, Pretoria. pp 597.

Sink KJ, van der Bank MG, Majiedt PA, Harris LR, Atkinson LJ, Kirkman SP, Karenyi N 2019. South African National Biodiversity Assessment 2018 Technical Report Volume 4: Marine Realm. Pretoria.

Sink KJ, Boshoff W, Samaai T, Timm PG, Kerwath SE, Bosnoff W, Samaai T, Timm PG, Kerwath SE 2006. Observations of the habitat and biodiversity of the submarine canyons at Sodwana Bay. *South African Journal of Science* 102: 466–474.

Sink KJ, Holness S, Harris L, Majiedt PA, Atkinson L, Robinson T, Kirkman S, Hutchings L, Leslie R, Lamberth S, et al. 2012. National Biodiversity Assessment 2011: Technical Report. Volume 4: Marine and Coastal Component. Pretoria: South African National Biodiversity Institute. *Volume* 4: 325.

Skelton PHH 2014. *A National Marine Reseach Plan for South Africa, 2014+*. Prepared for The Department of Science and Technology. pp 61.

Skowno AL, Poole CJ, Raimondo DC, Sink KJ, Van Deventer H, Van Niekerk L, Harris LR, Smith-Adao LB, Tolley KA, Zengeya TA, et al. 2019. *Divesity Assessment 2018: The status of South Africa's ecosystems and biodiversity. Synthesis Report.* South African National Biodiversity Institute, an entity of the Department of Environment, Forestry and Fisheries. Pretoria.

Slater D, Felikson D, Straneo F, Goelzer H, Little C, Morlighem M, Fettweis X, Nowicki S 2019. 21st century ocean forcing of the Greenland Ice Sheet for modeling of sea level contribution. *The Cryosphere Discussions* September: 1–34.

Smale DA, Kendrick GA, Harvey ES, Langlois TJ, Hovey RK, Van Niel KP, Waddington KI, Bellchambers LM, Pember MB, Babcock RC, et al. 2012. Regional-scale benthic monitoring for ecosystem-based fisheries management (EBFM) using an autonomous underwater vehicle (AUV). *ICES Journal of Marine Science* 69: 1108–1118.

Smale MJ 1986. The feeding biology of four predatory reef fishes off the south-eastern Cape coast, South Africa. *African Zoology* 21: 111–130.

Smale MJ 1991. Occurrence and feeding of three shark species, carcharhinus brachyurus, C. Obscurus and sphyrna zygaena, on the eastern Cape Coast of South Africa. *South African Journal of Marine Science* 11: 31–42.

Smit AJ, Bolton JJ, Anderson RJ 2017. Seaweeds in two oceans: Beta-diversity. *Frontiers in Marine Science* 4: 1–15.

Smit KP, Bernard ATF, Lombard AT, Sink KJ 2021. Assessing marine ecosystem condition: A review to support indicator choice and framework development. *Ecological Indicators* 121: 107148.

Smith MKS 2007. *Towards a new approach for coastal governance with an assessment of the Plettenberg Bay linefisheries*. Rhodes University.

Smith MKS, King CM, Sauer WHH, Cowley PD 2007. Development of fishery indicators for local management initiatives — a case study for Plettenberg Bay, South Africa. *African Journal of Marine Science* 29: 511–525.

Smith S, Malcolm H, Marzinelli E, Shultz A, Steinberg P, Verges A 2020. 17 years of tropicalisation and kelp loss shift trophic composition and lead to more winners than losers in a fish community. *Authorea* October: 1–5.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, et al. 2007. Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience* 57: 573–583.

Sterne TK, Retchless D, Allee R, Highfield W 2020. Predictive modelling of mesophotic habitats in the north-western Gulf of Mexico. *Aquatic Conservation: Marine and Freshwater Ecosystems* 30: 846–859.

Stevens N, Bond WJ, Hoffman MT, Midgley GF 2015. *Change is in the air: Ecological trends and their drivers in South Africa*. SAEON and Department of Science and Technology. pp 33.

Struthers DP, Danylchuk AJ, Wilson ADM, Cooke SJ 2015. Action cameras: Bringing aquatic and fisheries research into view. *Fisheries* 40: 504–512.

Swanepoel E, Sauka S 2019. African perspectives Global insights Ecosystem-based Adaptation in South African Coastal Cities. *Policy Briefing* 1–10.

Tang KHD 2020. Impact of Climate Change on Impact of Climate Change on Marine Biodiversity Marine Biodiversity. *Global Journal of Agriculture and Soil Science* 1: 1–6.

Tanhua T, Pouliquen S, Hausman J, O'Brien K, Bricher P, de Bruin T, Buck JJH, Burger EF, Carval T, Casey KS, et al. 2019. Ocean FAIR Data Services. *Frontiers in Marine Science* 6: 1–17.

Taylor MD, Baker J, Suthers IM 2013. Tidal currents, sampling effort and baited remote underwater video (BRUV) surveys: Are we drawing the right conclusions? *Fisheries Research* 140: 96–104.

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F, Tielbörger K, Wichmann MC, Schwager M, et al. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* 31: 79–92.

Thrush SF, Hewitt JE, Cummings VJ, Norkko A, Chiantore M 2010. β-diversity and species accumulation in Antarctic coastal benthos: Influence of habitat, distance and productivity on ecological connectivity. *PLoS ONE* 5: e11899.

Tilney RL, Nelson G, Radloff SE, Buxton CD 1996. Ichthyoplankton distribution and dispersal in the Tsitsikamma National Park marine reserve, South Africa. *South African Journal of Marine Science* 17: 1–14.

Topál D, Ding Q, Mitchell J, Baxter I, Herein M, Haszpra T, Luo R, Li Q 2020. An internal atmospheric process determining summertime Arctic sea ice melting in the next three decades: Lessons learned from five large ensembles and multiple CMIP5 climate simulations. *Journal of Climate* 33: 7431–7454.

Trebilco R, Dulvy N, Stewart H, Salomon A 2015. The role of habitat complexity in shaping the size structure of a temperate reef fish community. *Marine Ecology Progress Series* 532: 197–211.

Tréguer P, Bowler C, Moriceau B, Dutkiewicz S, Gehlen M, Aumont O, Bittner L, Dugdale R, Finkel Z, Iudicone D, et al. 2018. Influence of diatom diversity on the ocean biological carbon pump. *Nature Geoscience* 11: 27–37.

Truter HJ 2019. *Epibenthic biodiversity , habitat characterisation and anthropogenic pressure mapping of unconsolidated sediment habitats in Algoa Bay , South Africa*. Nelson Mandela University.

Tuckett PA, Ely JC, Sole AJ, Livingstone SJ, Davison BJ, Melchior van Wessem J, Howard J 2019. Rapid accelerations of Antarctic Peninsula outlet glaciers driven by surface melt. *Nature Communications* 10: 1–8.

Turner JA, Hitchin R, Verling E, van Rein H, Hitchen R, Verling E, van Rein H 2016. Epibiota Remote Monitoring from Digital Imagery: Interpretation Guidelines.

Turpie JK, Beckley LE, Katua SM 2000. Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biological Conservation* 92: 59–72.

UNEP 2010. The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets Adopted. Nagoya.

United Nations 2016a. 2030 Agenda and the SDGs: Indicator framework, monitoring and reporting. U.N. Resolution A/RES/71/313.

United Nations 2016b. Transforming our world: The 2030 agenda for sustainable development. A/RES/70/1. 1–41.

Urquhart C 2007. *Algoa Bay in the Age of Sail (1488-1917): a Maritime Story*. Bluecliff Publishing.

Vallès H, Oxenford HA, Henderson A 2019. Switching between standard coral reef benthic monitoring protocols is complicated: Proof of concept. *PeerJ* 2019: 1–24.

Vanderbilt K, Gaiser E 2017. The international long term ecological research network: A platform for collaboration. *Ecosphere* 8: e01697.

Vellend M, Cornwell WK, Magnuson-Ford K, Mooers AØ 2010. OUP CORRECTED PROOF – FINAL Measuring phylogenetic biodiversity. *Biological Diversity: Frontiers in Measurement and Assessment* 194–207.

Vergés A, Doropoulos C, Malcolm HA, Skye M, Garcia-Pizá M, Marzinelli EM, Campbell AH, Ballesteros E, Hoey AS, Vila-Concejo A, et al. 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proceedings of the National Academy of Sciences* 113: 13791–13796.

Visbeck M 2018. Ocean science research is key for a sustainable future. *Nature Communications* 9: 1–4.

De Vos L 2012. *Baited remote underwater video survey of reef fish in the Stilbaai marine protected area, with an assessment of monitoring requirements.* MSc. University of Cape Town. pp 92.

De Vos L, Götz A, Winker H, Attwood CG 2014. Optimal BRUVs (baited remote underwater video system) survey design for reef fish monitoring in the Stilbaai Marine Protected Area. *African Journal of Marine Science* 36: 1–10.

Vousden D, Stapley J 2013. Evolving new Governance approaches for the Agulhas and Somali Current Large Marine Ecosystems through Dynamic Management Strategies and partnerships. *Environmental Development* 7: 32–45.

Wahab MAA, Radford B, Cappo M, Colquhoun J, Stowar M, Depczynski M, Miller K, Heyward A 2018. Biodiversity and spatial patterns of benthic habitat and associated demersal fish communities at two tropical submerged reef ecosystems. *Coral Reefs* 37: 327–343.

Wakefield CB, Lewis PD, Coutts TB, Fairclough D V., Langlois TJ 2013. Fish Assemblages Associated with Natural and Anthropogenically-Modified Habitats in a Marine Embayment: Comparison of Baited Videos and Opera-House Traps. *PLoS ONE* 8: 1–10.

Walters M 2012. *GEO Task US-09-01a : Critical Earth Observations Priorities Group on Earth Observations*.

Wang P, Du Y, Yu W, Algeo TJ, Zhou Q, Xu Y, Qi L, Yuan L, Pan W 2020. The chemical index of alteration (CIA) as a proxy for climate change during glacial-interglacial transitions in Earth history. *Earth-Science Reviews* 201: 1–23.

Washington H 2020. Ecosystem Services - Key Step Forward or Anthropocentrism’s 'Trajan Horse" in Concervation? In: Kopnina H, Washington H (eds), *Conservayion. Integrating Scial and Ecological Justice*. Springer Nature Switzerland. pp 1–236.

Watanabe YW, Li BF, Wakita M 2018. Long-Term Trends of Direct and Indirect Anthropogenic Effects on Changes in Ocean pH. *Geophysical Research Letters* 45: 9106–9113.

Waters CN, Steffen W, Waters CN, Zalasiewicz J, Zalasiewicz J, Summerhayes C, Summerhayes C, Barnosky AD, Barnosky AD, Poirier C, et al. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351: aad2622–aad2622.

Webb P, Wooldridge T 1990. Diel horizontal migration of Mesopodopsis slabberi (Crustacea: Mysidacea) in Algoa Bay, southern Africa. *Marine Ecology Progress Series* 62: 73–77.

Wedding LM, Friedlander AM, McGranaghan M, Yost RS, Monaco ME 2008. Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. *Remote Sensing of Environment* 112: 4159–4165.

Weilgart LS 2018. *The Impact of Ocean Noise Pollution on Marine Biodiversity*. Sinopsis. Dalhousie University. pp 36.

Whitfield AK, Pattrick P 2015. Habitat type and nursery function for coastal marine fish species, withemphasis on the Eastern Cape region, South Africa. *Estuarine, Coastal and Shelf Science* 160: 49–59.

Whitmarsh SK, Fairweather PG, Huveneers C 2017. What is Big BRUVver up to? Methods and uses of baited underwater video. *Reviews in Fish Biology and Fisheries* 27: 53–73.

Wicks ECC, Longsta BJ, Fertig B, Dennison WCWC, Longstaff BJ, Fertig B, Dennison WCWC 2010. Chapter 5: Ecological Indicators. Assessing Ecosystem Health Using Metrics. *Integrating and Applying Science: A practical handbook for effective coastal ecosystem assessment.* pp 1–18.

Wilkinson MD, Dumontier M, Aalbersberg IjJ, Appleton G, Axton M, Baak A, Blomberg N, Boiten J-WW, da Silva Santos LB, Bourne PE, et al. 2016. The FAIR Guiding Principles for scientific data management and stewardship. *Scientific Data* 3: 160018.

Williams J, Jordan A, Harasti D, Davies P, Ingleton T 2019. Taking a deeper look: Quantifying the differences in fish assemblages between shallow and mesophotic temperate rocky reefs. *PLOS ONE* 14: e0206778.

Winther J-G, Dai M, Douvere F, Fernandes L, Halpin P, Hoel AH, Juinio-Meñez MA, Li Y, Morrissey K, Rist T, et al. 2020. Integrated Ocean Management.

Wong P., Losada IJ, Gattuso J-P, Hinkel J, Khattabi A, McInnes K, Saito Y, Sallenger A 2014. Chapter 5: Coastal Systems and Low-Lying Areas. In: Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea and LLW (ed.), *Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, US. pp 361–409.

Woodworth-Jefcoats PA, Blanchard JL, Drazen JC 2019. Relative impacts of simultaneous stressors on a pelagic marine ecosystem. *Frontiers in Marine Science* 6: 1–16.

Wootton JT 1991. Direct and indirect effects of nutrients on intertidal community structure: variable consequences of seabird guano. *Journal of Experimental Marine Biology and Ecology* 151: 139–153.

Worm B, Barbier EB, Beaumont N, Duffy E, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, et al. 2006. Impact of Biodiversity Loss on Ocean Ecosystem Services. *Science* 314: 787–790.

Wu H, Shen C, Wang Q, Aronson RB, Chen C, Xue J 2019. Survivorship characteristics and adaptive mechanisms of phytoplankton assemblages in ballast water. *Journal of Oceanology and Limnology* 37: 580–588.

Wu PPY, Mengersen K, McMahon K, Kendrick GA, Chartrand K, York PH, Rasheed MA, Caley MJ 2017. Timing anthropogenic stressors to mitigate their impact on marine ecosystem resilience. *Nature Communications* 8: 1–10.

Yaghmour F 2019. Are oil spills a key mortality factor for marine turtles from the eastern coast of the United Arab Emirates? *Marine Pollution Bulletin* 149: 110624.

Yeager LA, Layman CA, Allgeier JE 2011. Effects of habitat heterogeneity at multiple spatial scales on fish community assembly. *Oecologia* 167: 157–168.

Zscheischler J, Martius O, Westra S, Bevacqua E, Raymond C, Horton RM, van den Hurk B, AghaKouchak A, Jézéquel A, Mahecha MD, et al. 2020. A typology of compound weather and climate events. *Nature Reviews Earth & Environment* 1: 333–347.