A COMMUNITY–WIDE TROPHIC STRUCTURE ANALYSIS IN INTERTIDAL ECOSYSTEMS ON THE SOUTH COAST OF SOUTH AFRICA

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MOLLINE NATANAH C. GUSHA

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ABSTRACT

Coastal ecosystems are more than microhabitats for marine species. Acting as atmospheric carbon filters, species in coastal environments are directly and/or indirectly associated with transferring organic carbon to species at higher trophic levels. However, the progressing change in global climatic conditions has created the need to assess the consequences of the shifting conditions on both direct and indirect interactions of physical and biological parameters at species and/or community levels. From these perturbations, the effects of biotic homogenization on ecosystem functioning and resilience can also be realised. Herein, I discuss the effects of temperature, nutrients, biotic interactions and habitat characteristics on community dynamics within intertidal rock pool systems on the south coast of South Africa using complementary qualitative and quantitative analytical methods. Seasonality had a significant impact on rock pool species with changes in composition and higher richness in winter than summer. The first two axes of the Canonical Correspondence Analysis (CCA) of the plant and animal communities each explained ~20% of the relationship between physico-chemical parameters and biological variables. The CCA highlighted that seasonal shifts in chlorophyll-*a*, conductivity, salinity, water depth, surface area and substratum type indirectly influenced species composition. For example, pools with heterogenous substratum comprising a mixture of sand and rock exhibited higher species diversity than homogenously bedded pools. Furthermore, a Bayesian analysis of community structure based on stable isotope ratios was used to assess how trophic pathways of carbon and nitrogen elements reflected community composition and richness. Isotopic biplots showed an increase in food web size, food chain length and the trophic positions of fish and some gastropods in winter compared to summer. There was greater dietary overlap among species in larger pools. In addition, while isotopic nearest neighbour distance and species evenness also showed a positive increase with pool size in summer, the same metrics were almost constant across all pool sizes in winter. These changes in food web packing and species evenness suggest seasonal preferences or migration of species in summer from small pools to larger pools with stable physico-chemical parameters. Furthermore, the presence of fish was seen to promote trophic diversity within some pools. The results from laboratory microcosm grazing experiments demonstrated

significant direct and indirect effects of temperature and nutrients within plankton communities. Copepod grazing had an indirect positive influence on phytoplankton biomass and size structure while the interactive effects of temperature and nutrients had contrasting effects on both phytoplankton communities and copepod biomass. Shifts in water chemistry and nutrient treatments were also observed in the presence of copepods. Phosphate addition had a recognisable impact on plankton communities. The presented synthesis of the literature mainly highlighted that positive effects at one trophic level do not always positively cascade into the next trophic level which is evidence of complex interactive biotic, habitat and water chemistry effects within these intertidal ecosystems. Thus, to further understand cascading effects or community structure functioning in general, there may be a need to incorporate and understand species functional traits and how they contribute to trophic diversity, community restructuring and functioning in coastal habitats.

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INTRODUCTION AND OVERVIEW

1.1 Coastal Ecosystems

The need to understand community dynamics in a continually changing environment has generated a plethora of hypotheses and models to explain the variation in trophic structure, biomass and diversity of organisms within coastal environments (Romanuk and Kolasa 2002; Harley et al. 2006; O'Connor et al. 2013; Kanamori et al. 2017). Some of the underlying factors leading to variation include oscillations in local oceanographic conditions, long term variability in climatic conditions and anthropogenic effects (Forister et al. 2010). These factors in addition to the ecological and socio-economic importance of coastal environments (Gibson 1982; Doney et al. 2011, Dias et al. 2014) have inspired a myriad of ecological studies (e.g. McQuaid and Branch 1984; McQuaid and Branch 1985; Bustamante et al 1995; Menge et al. 1997; Thompson et al. 2002; Bergamino et al. 2014, Dalu et al. 2014; Fica et al. 2017). However, the effects of microclimatic variability are still highly debated particularly due to the complexity of species interactions and habitat structure within these ecosystems (Wootton 2012).

Coastal ecosystems have been widely viewed as meta-communities (i.e. sets of communities linked by different species interacting directly and /or indirectly with each other; Wilson 1992, Leibold et al. 2004). Two of the major theoretical frameworks describing meta-community function are patch dynamics and species-sorting models (Loreau et al. 2003; Chase et al. 2005). The former explains how species within habitat patches (e.g. rock pools) are likely to have homogenous species composition patterns as a result of micro-scale spatial variations (Wilson 1992), and the latter, describes how individual species responses to physical environmental factors result in variation in species interactions, composition and abundances (Loreau et al. 2003). Because these two theoretical frameworks are mainly based on spatio-temporal variability, it has been demonstrated that coastal ecosystem function can be understood by focusing on processes occurring within localized communities experiencing the same ecological conditions (Menge et al. 2015). Estes et al. (2013) further suggested that species

interactions within meta-communities can be better understood by slightly manipulating ecosystem properties such as temperature and nutrients concentrations. This inclusion of assessing the effects of abiotic parameters e.g. temperature, energy, nutrient flow and other propagules has propelled the meta-community theory to be redefined as the meta-ecosystem concept (Menge et al. 2015; Guichard 2017).

1.2 Temperature and Nutrients

Temperature is regarded as the main abiotic factor influencing species distribution and community structure (McQuaid 1980; Harley et al. 2006; Olonscheck et al. 2013) within meta-ecosystems (Guichard 2017). When considered in isolation, temperature affects species metabolic rates (Sanford 2002; Wheeler 2017), behavioural traits (Nagelkerken and Munday 2016) and habitat choice (Bullock 1955; Roessig et al. 2004) and overall food web structure and functioning. For example, among winter flounders, compromised egg ratios, growth rates, size at hatch and larval mortality were observed as a result of warmer winters (Keller and Mac-Phee 2000). Moreover, within reef ecosystems, an increase in temperature of ~1°C has been associated with the initiation of cascading effects on species across different trophic levels (Parker and Dixon 1998).

Furthermore, within natural ecosystems, there is a significant correlation between nutrient dynamics and temperature effects (Winder and Schindler 2004). In recent years, the shifts in temperature and nutrient dynamics have been associated with altering phytoplankton community structure with significant alterations to trophic pathway and overall food chain length. Two types of trophic pathways have been recognized i.e. classical and microbial pathway. The former is dominated by large-sized phytoplankton cells while the latter is controlled by smaller sized phytoplankton cells forming complex and longer food chains (Cermeno et al. 2006).

In addition, although subject to concentration levels, location and species in question, nutrients present a connection between the environment and higher consumers through primary producers (Bakker et al. 2015). Behrenfeld et al. (2006), Boyce et al. (2010) and Polovina et al. (2008) proposed that effects of temperature and nutrient changes impose

cascading effects on zooplankton communities. Commonly known effects of such interactions concern how predators directly and/or indirectly alter community structure depending on metabolic demands, food availability and palatability (Carpenter et al. 2016).

1.3 Trophic Cascades

Trophic cascades reflect trait and density mediated indirect effects of predators on other species within an ecosystem (Shurin et al. 2002; Schmitz et al. 2004; Worm and Lenihan 2013). Trait-mediated effects can positively and/or negatively affect species by causing behavioural and/or morphological changes among other species such as altered foraging patterns (Trussell et al. 2003; Gravem and Morgan 2016) while density effects occur when predators indirectly affect the abundances of prey species through intermediary species (Wasserman et al. 2018). The occurrence of trophic cascades is associated with triggering imbalances in community structures with potential promotion and/or disruption of ecosystem function (Trussell et al. 2004)

An important digression concerns the history of trophic cascade theory. The indirect influence of predators on plants through herbivores was first introduced into the scientific discourse by Hairston et al. in 1960 (Pinnegar et al. 2000). The theory, initially termed the green world hypothesis, later became widely known as trophic cascades and is credited with bringing attention to the role of predators in shaping communities and delineating ecosystem complexity (Vinagre et al. 2015). The green world hypothesis was extended by Fretwell (1977), who suggested that predator effects will be influenced by food chain length. According to his work, food chains can have less or more than three trophic levels; in odd-numbered food chains primary productivity would proliferate with grazers being predator limited, while in even-numbered food chains grazers would become resource limited. Oksanen, et al. (1981) in the exploitation ecosystem hypothesis (EEH) further suggested that food chain length varied with net primary productivity. According to the EEH, environments with low primary productivity will contain less food to meet the metabolic carbon demands of higher level species, thus regulation of primary productivity is more bottom-up regulated, while in areas with high primary

productivity, trophic interactions are top-down controlled (Oksanen et al. 1981). Pace et al. (1999) highlighted that the impacts of top-down trophic cascades are highly consequential across the whole ecosystem. On the other hand, Ware and Thomson, (2005) proposed that bottom-up trophic cascades that had been previously overlooked, can significantly compromise food web functioning.

1.4 Food Webs

Food webs are nested designs of food chains that have turned out to be an important conceptual tool used for illustrating direct (Paine 1980) and indirect feeding interactions among populations (Hui 2012). First recognized by Elton in 1927, the concept of food web structure analysis was viewed as a basic descriptor of community structure (Paine 1988). However in subsequent years, the concept has yielded better understanding of some complex interactions between producers and consumers (bottom-up interactions) and predator-prey effects (top-down effects). Another key aspect of food web structure analysis has been its use in providing insights into food chain length and shape, from which ecosystem function and resilience can be inferred. However, the major limitation of confining our understanding of ecosystem dynamics and functioning to food web structure analysis is that the pathway of organic matter is not easily traceable in many cases, including coastal ecosystems (Riera et al. 1999).

1.5 Stable Isotopes

The use of naturally existing biomarkers such as stable isotope values to ascertain the pathway of primary production across successive trophic levels has gained momentum over recent years. This approach addresses the significant drawbacks associated with traditional methods of understanding community structure. The common elements used in stable isotope analyses are oxygen, sulphur, hydrogen, carbon and nitrogen. Although, the incorporation of sulphur stable isotopes has been recommended for coastal ecosystems to further differentiate between classical and microbial trophic pathways (Peterson 1999), its use has not gained much attention due to the laborious analytical techniques needed to isolate the element from its matrix (Mancinelli and Vizzini 2015). Hence, the most common natural isotopic biomarkers used in tracking

movement of key trophic elements in coastal ecosystems have been stable carbon and nitrogen isotopes (Peterson and Fry, 1987, Dalu et al. 2016).

Mean carbon and nitrogen isotope ratios of different species within a community can be presented in the form of biplots to provide visual impressions of trophic structure, such as food web shape and height within ecosystems (Peterson and Fry, 1987; Layman et al. 2007). Although this technique is useful in providing qualitative insights into trophic structure, more quantitative measures can be inferred from stable isotope data such as dietary preferences, species distribution, calculation of the species trophic positions, niche diversity and food chain length (Vander Zanden et al. 1997; Layman et al. 2007; Fry and Davis 2015).

1.6 Thesis Overview

Higher trophic level species in marine ecosystems are being affected by the changes in global phytoplankton productivity and biomass (Chavez et al. 2011; Yvon-Durocher et al. 2015;Laufkotter et al. 2015; Behrenfeld et al. 2016) while effects of shifts in productivity at regional and local scales are often overlooked (Menendez et al. 2006). Hence, I integrated manipulative, qualitative and quantitative analytical tools to assess the effects of seasonal variation in temperature and nutrients on species composition, trophic structure and species richness within a local coastal ecosystems i.e. intertidal rock pools along the south coast of South Africa.

The aim of Chapter 2 was to explore the extent to which seasonal variability in physical environmental factors influenced species composition and richness within intertidal communities. In Chapter 3, I used biplots based on isotope ratios to qualitatively assess the change in food web shape and height across two seasons. I also performed quantitative analyses to determine consumer trophic positions and ascertain possible shifts in food chain length due to differences in pool size, or changes in temperature and nutrients. Using a novel Bayesian approach on community-wide metrics based on the stable carbon and nitrogen isotopes, I assessed the effects of seasonality and pool morphometrics on trophic diversity, food web packing, dietary similarity and species

evenness with the aim of understanding intertidal community interactions and composition in response to seasonal variability. In Chapter 4, I was primarily interested in assessing the occurrence of cascades at species level within basal communities in marine ecosystems. This study demonstrated how plankton communities respond directly and indirectly to shifts in water chemistry parameters with a forecast of the potential effects of observed changes to higher level species. Phytoplankton size structure and their production dynamics were observed to a critical factor in marine food webs. Chapter 5, which is the general synthesis, summarises how trophic structure within intertidal ecosystems is affected by seasonal variation, habitat structure and direct and indirect biotic interactions with the aim of providing insights into how species within the south coast are likely to be affected/respond/contribute to localized changes in microclimatic conditions which are an indirect consequence of global climatic changes.

SPATIO-TEMPORAL VARIATION IN ROCK POOL SPECIES RICHNESS AND COMPOSITION ALONG THE SOUTH COAST OF SOUTH AFRICA

2.1 Introduction

Environmental variables in coastal habitats exhibit considerable variation in space and time (Bhadja et al. 2014; Castillo-Escrivà et al. 2017). This non-uniformity often results from the interaction of upwelling events (Madhupratap et al. 1990; Iriate and Gonzalez 2004; Lopez-Lopez et al. 2017), wave action (McQuaid and Branch 1984; Hewitt et al. 2016) and biological influences such as intra and interspecific resource competition (Cox et al. 2011). Examples of environmental parameters primarily structuring species distribution, composition and diversity in marine ecosystems (inclusive of intertidal habitats) include salinity, pH, nutrients and water temperature (Huggett and Griffiths 1986; Metaxas and Scheibling 1994; Genner et al. 2004; Clare et al. 2017; Sommer et al. 2017). These environmental stressors may trigger indirect interactions among individual and/or species with significant effects on the structure of the whole community. Denny and Gaines (2007) point out that a rise in ambient temperature and long-term shifts in salinity levels may expose ectothermic invertebrate and macroalgal species to osmotic stress. Bakker et al. (2015) further highlighted that high salinity levels may hinder the uptake of nitrogen, leading to slow growth and vigour, with an overall decrease in plant biomass.

In this study I primarily focused on rock pools due to their known ecological importance as microhabitats for marine organisms (Underwood 1980; Firth and Williams 2009; Jackson 2010; Anusa et al. 2012; White et al. 2015) Their geomorphological similarities render them ideal *in situ* 'laboratory' sites to study community structure, habitat preferences (Sebens 1991) and trophic interactions (Metaxas and Scheibling 1993; Johnson 2001). Although species are likely to respond individually to changes in environmental variables, effects of environmental perturbations are assumed to be more

pronounced in aggregate communities (Kennedy et al. 2002) for example in coastal rock pools (Brierley and Kingsford 2009). As such, the understanding of community structure and ecosystem in response for example to effects of climate change has been estimated by the use of traditional community descriptive methods (e.g. species richness and species evenness), Forister et al. (2010). Also applying a similar approach in this study, I assessed the interactive effects of variability in habitat complexity, nutrients and temperature based on rock pool species richness and composition.

Sampling took place along the Great Fish River rocky shore within the influence of the Port Alfred upwelling cell (Lutjehams 2006) on the south coast of South Africa. Due to the projected changes likely to occur within the Agulhas Current Large Marine Ecosystem (ACLME), the aim of this study was to test the species-energy theory at micro-scale gradients. According to this theory, species diversity increases with elevated temperature (Wright 1983; Brown 2014). Hence, it was hypothesised that higher species richness and composition would be recorded in summer than winter. I also assessed the correlation between species richness and rock pool surface area following the species-area assumptions of the single large or several small (SLOSS) debate of island biogeography theory by MacArthur and Wilson 1967 cited in Hamilton (1968) which suggests that several smaller environments often contain fewer species than one single environment of an equivalent size. Thirdly, based on the assumption that habitat heterogeneity influences species-area relationships (Greenstreet et al. 2007), I assessed the effects of substratum variability and pool size on rock pool species richness.

2.2 Materials and Methods

2.2.1 Study area

The study was conducted along the Great Fish River (GFR) mouth rocky shore area on the south coast of South Africa (33°34′06.29″–33°34′08.87″S, 27°00′33.39″–27°00′36.06″E). Rainfall in this area is highly variable, with mean annual precipitation of ~570mm. The mean annual ambient air temperature, ranges from 20-26 °C between July and February, with low winter temperatures of ~8°C. The wind mostly blows from the north-east and south-west resulting in a lowering of temperature and humidity across

the region during summer. Although minimally disturbed by anthropogenic activities, the area is prone to periodic freshwater intrusions from the Great Fish River.

Twelve rock pools were selected using the stratified random sampling technique. The pools were selected from approximately the same shore height at a mean between-pool distance of ±c.30m. Pool surface area/pool size (in m^2) was estimated from photographic images using ImageJ software version 1.47 (Free Software Foundation, Inc., USA). The first sampling period was conducted in winter (25–26 July, 2016) and the same pools were re-sampled in summer (1–2 December, 2016). All sampling was conducted during low tide.

2.2.2 Sampling

2.2.3 Ethics statement

Species were collected in terms of section 83 of the Marine Living Resource Act 1998 (Act No. 18 of 1998). All vertebrate species were collected in accordance to the Rhodes University Animal Ethics clearance (RU-LAD-16-08-0001).

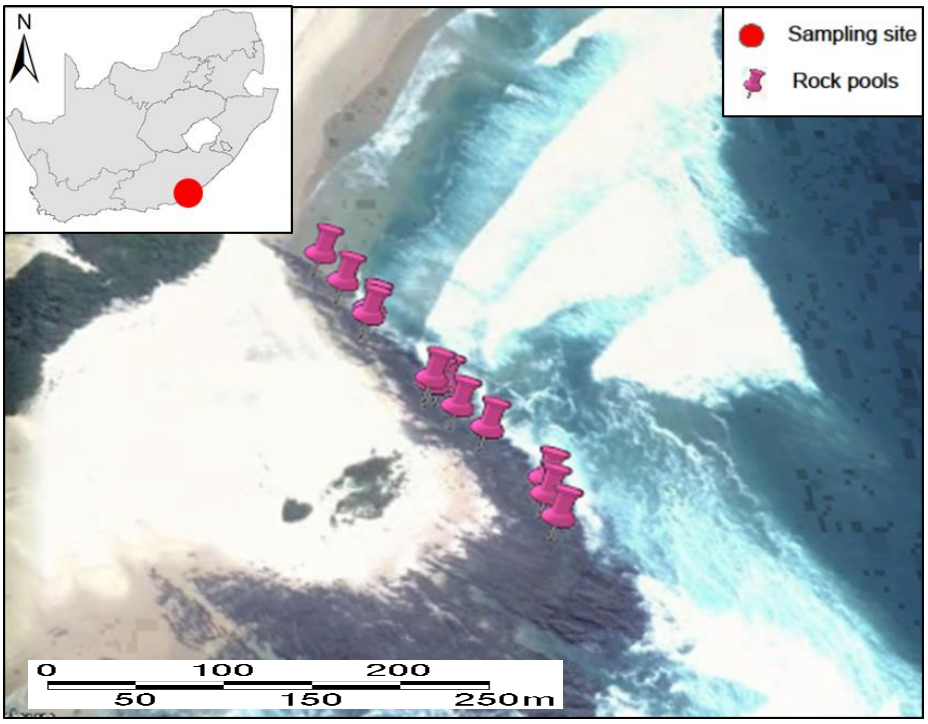

Figure 2. 1: Location of study site (red) along the south coast of South Africa (inset). The satellite image indicates (in magenta) the location of the 12 sampled pools.

2.2.4 Environmental parameters

A portable YSI 500 series multi-parameter water quality sonde (TTT Environmental Instruments & Supplies, USA) was used to measure the following pool environmental parameters *in situ*: total dissolved solids (TDS), conductivity, salinity, oxidation reduction potential (ORP), pH and water temperature. Pool images were captured using 16Mp cameras (Nikon AW130 and Olympus TG310). From the images, pool surface area (pool size) was calculated using ImageJ software by taking the mean of three estimated measurements. Mean water depth was estimated by taking three random measurements within each pool. Pool substratum embeddedness or substratum type (an estimate of how the rock pool bed is covered by fine sediment relative to other material in the rock pool bed e.g. rocks, pebbles, algae) was quantified according to the methods of Platts et al. (1983): (1) >75%; (2) 50–75%; (3) 25–50%; (4) 5–25%; and (5) <5% of surface covered by fine or homogenous sediment.

2.2.5 Nutrient analysis

Water samples (n = 2) for analysis of the two major limiting nutrients (phosphates and nitrates) in marine environments were collected in 250mL labelled polyethylene bottles from each pool. All samples were kept frozen and processed within 48h of collection. Phosphate and nitrate concentrations were measured using an HI 83203 multi-parameter photometer (Hanna Instruments Inc., Rhode Island). Prior to phosphate analysis, rock pool water samples from each pool were filtered through a 0.22µm cellulose acetate membrane syringe filter (Micron Separations Inc., USA) into a 10mL glass cuvette. The cuvette was wiped clean and inserted in the photometer reaction chamber and served as the blank. After the photometer highlighted a nought reading, the cuvette was removed from the reaction chamber, 10 drops of HI93717A-O Molybdate reagent A and one sachet of HI93717B-O Phosphate HR Reagent B (a powder) were added to the sub-sample. The cuvette was gently shaken until the reagents were completely dissolved. The cuvette was re-inserted into the photometer reaction chamber and after a five-minute count-down, readings of phosphate (PO^{3-}_4) concentration were recorded in mg/L. The photometer had a phosphate measuring range of 0–30 mg/L ±0.05. The cuvettes were rinsed three times with distilled water between samples to avoid contamination.

For nitrate analysis, filtered water samples were spectrophotometrically analysed for total oxidized nitrogen (nitrates and nitrites) using the reduced copper cadmium method as described by Bate and Heelas (1975). Copper cadmium is a reduction agent involved in the break-down of nitrates to nitrites in the water column (Patey et al. 2008). Initially, the reduction of copper cadmium was done by washing the cadmium powder with 100mL of 5% hydrochloric acid (HCl) solution then rinsing with deionized water. The cadmium was then rinsed from silver grey to dark grey using 500mL of 0.5% $CuSO_4$·5HCl (copper II sulfate pentahydrate). Immediately after the colour change, the copper cadmium was rinsed with 0.007N HCl containing 0.005 Na_2 EDTA (disodium ethylenediaminetetraacetic acid- used in metal ion sequestration). Washing was repeated several times and the supernatant containing the precipitated copper was decanted until the copper cadmium changed back to a silver-grey colour. A 5mM stock solution was made by dissolving 0.51g of potassium nitrate (KNO_3) in 1L of deionized water and this

solution was used to make several other standards. A pipette was used to transfer 3mL of the sample to glass vials after which 2mL of buffer solution 24.4g L NH_4Cl (ammonium chloride) adjusted to pH of 9.6 was added. Approximately 2g of copper cadmium was added to each of the vials and the mixture agitated for approximately 20min to ensure that all nitrogen present was converted to nitrate (NO_3). A 1mL sample was then withdrawn from each vial and placed into a separate vial. To each of these vials, 1mL sulfanimide solution (1g sulfanimide +100 mL1.5N HCl) and 1mL diamine hydrochloride solution (0.02g N1-naphthyl-diamine hydrochloride + 100mL deionized water) were added. Each of the samples and standards were read on a spectrophotometer at 540µm wavelength.

2.2.6 Macroinvertebrates

Four specimen samples from each observed macroinvertebrate species (>10mm e.g. dwarf cushion stars and snails) were handpicked, rinsed in seawater, transferred to ziplock bags and stored on ice for laboratory identification. Organisms such as limpets and anemones were scraped off rock surfaces using steel scrapers whilst loose rocks were overturned to collect chitons. Fish species were caught through active searching using hand nets and immediately euthanized with a few drops of clove oil (Anderson et al. 1997).

2.2.7 Macroalgae

Macroalgal samples were collected by randomly placing a number of 10 × 10cm quadrats in each rock pool (depending on the number of different species observed) and hand collecting all algae within the quadrats which was ~30g per sample. All samples were rinsed with sea water to remove excess sand between fronds before storage for later identification. All collected species were identified to species or genus level according to Branch et al. (2012).

2.2.8 Chlorophyll-a analysis

From each pool, 250mL water samples (n = 2) were collected in polyethylene containers for chlorophyll-*a* (chl-*a*) analysis and stored on ice. In the laboratory, water samples were filtered onto pre-combusted glass fibre filters (GF/F 47mm, 0.7µm pore size) using a

Chemvac (<4cm Hg) vacuum pump (Busch Vacuum, South Africa). The saturated filters were transferred into 15mL sterile Schott cuvettes containing 10mL, 90% acetone and stored in a dark box for chl-*a* extraction. After 24h, samples were centrifuged for 5min at 1000rpm (revolutions per minute) using a centrifuge (Heraeus Sepetech GmbH, Germany). Using the Turner-design 10AU fluorometer (Thyssen et al. 2015) calibrated to mg/L as the standard unit of measurement, chl-*a* concentration was measured by decanting 8mL of the centrifuged solution into a 10mL glass cuvette, readings were taken before and after addition of 1N HCl (hydrochloric acid). Approximately 1N HCl allows for the breakdown of chl-*a* into phaeopigments. All glass cuvettes were rinsed three times with 90% acetone between samples. Chl-*a* concentration was calculated following the EPA (Environmental Protection Agency) method 445.0 (Arar and Collins 1992):

$$\text{Chl-}a\ (\text{mg/L}) = (C_3H_60/V) \times (F_0 - F_a) \times 0.325$$

Where, Chl-*a* (mg/L) = chl-*a* concentration in mg/L,

C_3H_60 =quantity of acetone used for extraction in mL,

V = quantity of water filtered in mL,

F_0 = chl-*a* reading before acidification,

F_a = chl-*a* reading after acidification.

2.3 Data Analysis

Prior to statistical analyses, environmental variables were log (x+1) transformed except for pH. To test for differences between mean water chemistry parameters from each pool and season, a two-way ANOVA was performed. Furthermore, to assess the possibility of any relationship between between pool size and environmental variables (salinity, temperature, ORP, conductivity, TDS, pH, chl-*a* and substratum type), a Pearson's correlation analysis was used. A simple linear regression analysis was conducted to assess the relationship between pool size and species richness. A Welch's two-sample *t*-test was also used to compare total species richness between the seasons. These statistical tests were carried out in R version 3.4.2 at $p < 0.05$ (R Core Team, 2017).

In addition, a multivariate analytical tool, Canonical Correspondence Analysis (CCA) was used to explore the relationship between rock pool species composition and environmental variables between the 2 seasons. The presence/absence data were analysed separately for macroinvertebrates and macroalgal communities. The CCA selects the most influential environmental parameters mapping spatial distribution of biological communities. Prior to using the CCA, a DCA (Detrended Correspondence Analysis) was first conducted to test for heterogeneity in species composition. A gradient length of >4, indicates a unimodal distribution and a CCA is recommended while an RDA (Redundancy Analysis) is recommended for a gradient length of <3. In cases where the gradient length is between 3 and 4, an RDA or CCA is performed depending on whether the data are standardized. In this study, the data were standardised and the gradient length in both data sets was 3.1, thus I opted for CCA. All ordinations were performed in CANOCO version 5 (Šmilauer and Lepš 2014).

2.4 Results

2.4.1 Environmental variables

2.4.1.1 Intra and inter-seasonal variation in environmental parameters

The mean environmental variables measured in summer and winter are tabulated in **Appendix 1**. A two-way ANOVA indicated no significant differences among environmental parameters with change in pool size in either season or between the 2 seasons, ($F_{(1,21)}$=0.817, p>0.05) and ($F_{(1,21)}$=0.206, p>0.05), respectively.

2.4.1.2 Relationship between pool size and environmental variables

Although, there were no significant differences in the means of water chemistry parameters, using the Pearson's correlation coefficient analysis to test whether there was any form of relationship between pool size and the measured physico-chemical parameters, the Pearson's test indicated significant relationships between some physico-chemical parameters and season (**Table 2.1**). In winter, the parameters: water depth, salinity, substratum, conductivity and pH were correlated to surface area while in summer, the parameters; depth, substratum type, temperature and chl-*a* were correlated to surface area.

Table 2. 1: Summary of Pearson's correlation indicating the degree of association between pool size (surface area) and the environmental parameters measured. Significant correlation (*r*) and (*p*) values are indicated in bold.

	Winter		**Summer**	
Surface area	***r***	***p***	***r***	***P***
Water depth	**0.57**	**0.053**	**0.57**	**0.053**
Salinity	**0.60**	**0.037**	-0.24	0.456
Conductivity	**0.87**	**0.000**	-0.18	0.573
ORP	0.12	0.702	-0.29	0.364
Temperature	0.14	0.673	**-0.63**	**0.029**
pH	**0.82**	**0.001**	-0.19	0.563
Substratum type	**0.58**	**0.050**	**0.68**	**0.015**
Chl-*a*	-0.49	0.103	**0.56**	**0.049**

2.5.2 Species richness and community composition

A total of 47 species (7 fish, 23 macroinvertebrate and 17 macroalgal species) were collected from the 12 rock pools across both seasons. Among these, 3 fish species were caught in summer and 6 in winter. The average species richness ± SD in summer pools <1 m^2 was 5 ± 1 and for pools >1 m^2 was 11 ± 1.8 while in winter, the means were 7 ± 0.5 and 11 ± 2, respectively and a Welch's two sample t-test indicated no differences in species richness between the 2 seasons. Substantial differences in species counts were also observed in pools that exhibited heterogenous *vs* homogenous substratum. Across both seasons, the average richness for pools comprising homogenous substratum (i.e. comprising >75% of either rock or sand) was 7 ± 0.9 while heterogenous bedded pools (comprising <50% of different pool bed material) contained 10 ± 1.1 species. When all pools were categorised according to substratum type for each season, there was a gradual increase in species richness from a homogenous to a heterogenous substratum observed in winter, while in summer there was a much steeper linear relationship between species richness and substratum type (**Fig. 2.2**). Overall heterogenous bedded pools in summer had higher total species richness than winter.

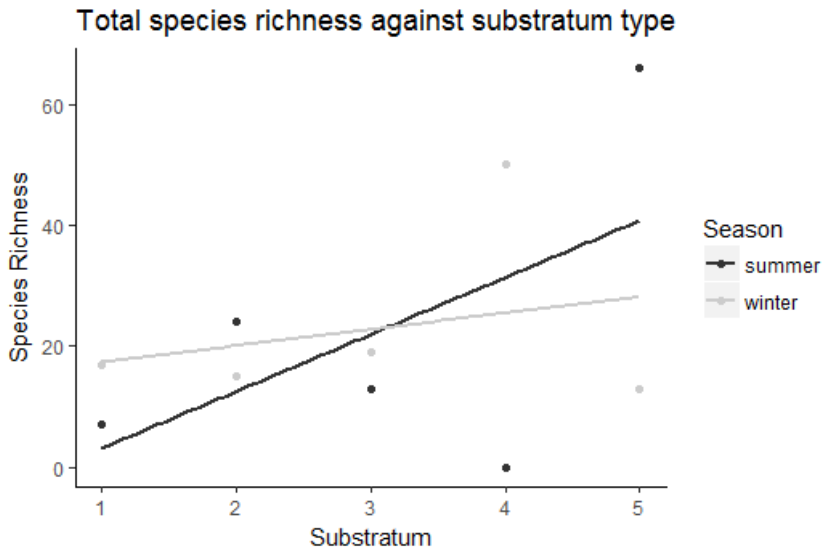

***Figure 2. 2**:* A plot indicating total species recorded in each substratum type for each season, 1 indicating >75% homogenous substratum and 5 representing <5% homogenous substratum.

Community composition exhibited notable variation between the two seasons. Species exclusive to each season are tabulated according to family name (**Table 2.2**). However, despite the differences in species composition, there were no significant differences in mean species richness between the two seasons ($t_{22} = 0.05$, $p = 0.956$).

Table 2. 2: List of species found exclusive to each season categorised according to family name.

Taxon	Season	Taxon	Season
FISH			
Clinidae		**Serranidae**	
Clinus superciliosus	Summer	*Epinephelus marginatus*	Winter
MACROINVERTEBRATES			
Siphonariidae		**Siphonariidae**	
Siphonaria anneae	Summer	*Siphonaria cochlear*	Winter
Siphonaria capensis	Summer		
Chitonidae		**Turbinidae**	
Acanthochitona garnoti	Summer	*Turbo sarmaticus*	Winter
Varunidae		**Chitonidae**	
Cyclograpsus punctatus	Summer	*Conus tulipa*	Winter
		Patellidae	
		Scutellastra granularis	Winter
MACROALGAE		*Scutellastra sp.*	Winter
Halymeniaceae		**Cystocloniaceae**	
Polyopes constrictus	Summer	*Hypnea spicifera*	Winter
Gelidiaceae		**Sargassaceae**	
Gelidium abbottiorum	Summer	*Sargassum sp*	Winter
Gelidium pristoides	Summer	**Plocamiaceae**	
Sargassaceae		*Plocamium suhrii*	Winter
Sargassum incisifolium	Summer	**Delesseriaceae**	
Cystocloniaceae		*Bartoniella sp*	Winter
Hypnea rosea	Summer		
Udoteaceae			
Chlorodesmis hilderbrandtii	Summer		

2.5.3 Relationship between environmental variables and community composition

The eigenvalues for the first 2 axes of the CCA highlighting the relationship between biological data and environmental variables were notably low in both the animal and the algal data sets, particularly in the case of the macroinvertebrate data (**Table 2.3**). The eigenvalues represent how much variation or inertia in species composition was explained by the different axes, with the first axis always explaining the highest variation. Explained variation is the percentage contribution of each axis to total variation within the data set, while pseudo-canonical correlation highlights the correlation strength between the species and the environment. Although the pseudo-canonical correlation value in this study was relatively high, it is worth noting that CCA

selects the factors that best explain variation so that values can seem relatively high as they are calculated in the context of the sampled parameters. The explained fitted variation expresses the amount of inertia explained by each axis as a fraction of the total inertia.

2.5.3.1 Macroinvertebrates

CCA axes 1 and 2 exhibited a cumulative variation of 13.5% with the two axes contributing 6.9% and 6.6%, respectively (**Fig 2.3a**). The results showed that of the sampled physico-chemical parameters, the macroinvertebrate community in GFR rock pools was mainly influenced by salinity, water depth, surface area and chl-*a*. **Fig 2.3a** indicates that species such as the limpet *Siphonaria capensis,* chitons (e.g. *Acanthochitona garnoti*) and the chilli pepper sponge (*Tedania anhelans*) were negatively affected by chl-*a.* Water depth also influenced gastropods such as *Turbo sarmaticus*, which exhibited an affinity for deeper pools. Surface area was significantly correlated to negative axis 1 attracting limpet species such as *Siphonaria anneae*. Low salinity negatively influenced species including the gastropod *Burnupena cincta* and limpets as shown by a negative correlation with both axes. The occurrence of ubiquitous species such as *Burnupena lagenaria* and *Oxystele tigrina* was not influenced by environmental variables and most were concentrated in pools of low water depth and surface area. This is indicated by the concentration of small pools in the upper right tetragon which can be identified as small in the pool size column in **Appendix 1**.

2.5.3.2 Macroalgae

CCA indicated that the first two axes had contributions of 7% and 6.3% of cumulative variation respectively (**Fig 2.3b**). The macroalgal communities were mainly influenced by salinity, pool depth, conductivity and substratum type. Species such as *Hypnea spicifera* and *Gelidium pteridifolium* were positively associated with high salinity and conductivity (positive axis 1 and 2). Furthermore, the results indicated that depth was positively associated with the second axis while substratum type was negatively correlated to axis 1, influencing the occurrence of opportunistic species such as *Plocamium suhrii*. Species such as *Ulva fasciata* and *Codium extricatum* were observed in most of the pools.

Table 2.3: Summary of the first two axes of CCA plots results explaining how environmental variables influence species composition (animals and plants) within rock pools along GFR mouth rock pools.

Statistic	Animals		Plants	
	CCA 1	CCA 2	CCA 1	CCA 2
Eigen values	0.29	0.28	0.399	0.275
Explained variation (cumulative %)	6.83	13.5	9.5	16.05
Pseudo-canonical correlation	0.91	0.91	0.86	0.78
Explained fitted variation (cumulative %)	34.43	68.19	41.22	69.63

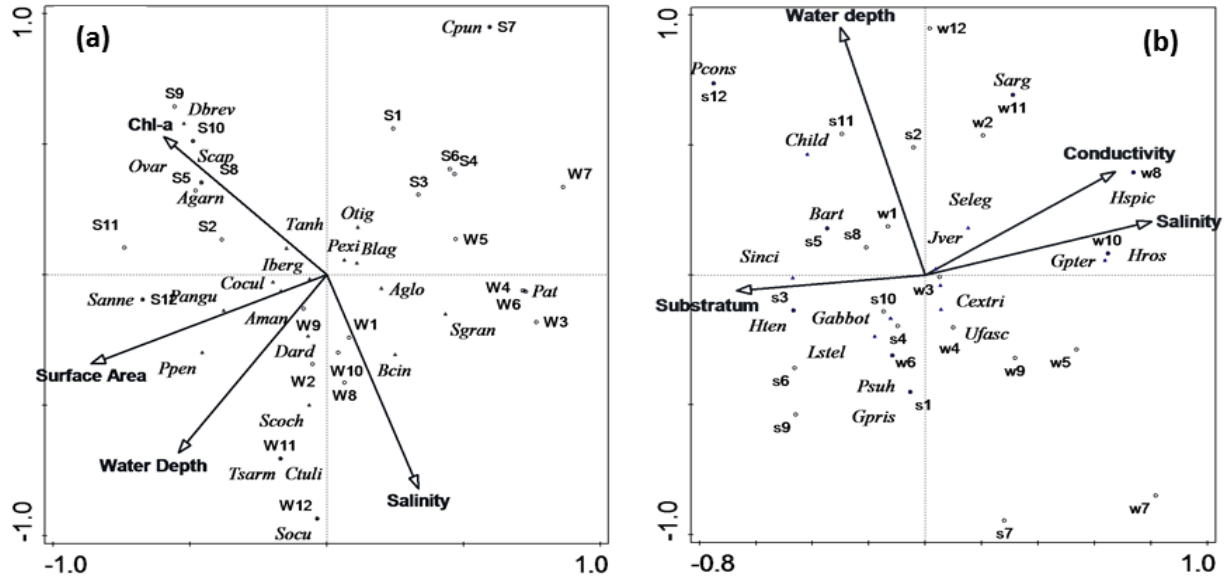

Figure 2. 3: CCA triplots illustrating the relationship between rock pool species and the most significant environmental variables: (**a**) indicates macroinvertebrate communities and (**b**) represents the macroalgal communities. Pool are labelled with a pool number and season code e.g. s10, s8, s1 – summer, w9, w8, w4 – winter pools. Quantitative environmental variables are indicated by arrows. The species names for macroinvertebrates (**Fig 2.3a**)*:* Agarn – *Acantochitona garnoti,* Aman – *Actinia equina*; Blag – *Burnupena lagenaria,* Bcin – *Burnupena cincta,* Cocul – *Cymbula oculus,* Cpun – *Cyclograpsus punctatus, ,* Ctuli – *Conus tulipa,* Dard – *Dardanus arrosor,* Dbrev – *Diogenes brevirostris,* Iberg – *Ischnochiton bergoti*, Otig – *Oxystele tigrina,* Ovar – *Oxystele variegata,* Ppen – *Palaemon peringueyi,* Pangu – *Parechinus angulosus,* Pexi – *Parvulastra exigua,* Pat-*Patiriella sp,* Sgran – *Scutellastra granularis ,* Scoch – *Scutellastra cochlear,* Scap – *Siphonaria capensis,*Tanh – *Tedania anhelans,* Limp –*Scutellastra sp,* Socu – *Siphonaria oculus,* Tsarm – *Turbo sarmaticus.* The species names for macroalgae (**Fig 2.3b**): Bart – *Bartoniella sp,* Cextr – *Codium extricatum,* Hten – *Hypnea tenuis,* Gabbot – *Gelidium abbottiorum,* Gpter – *Gelidium pteridifolium,*Hros – *Hypnea rosea,* Hspic – *Hypnea spicifera, ,* Lstel – *Lyengaria stellata,* Psuh – *Plocamium suhrii,* Pcons – *Polyopes constrictus,* Seleg – *Sargassum elegans,* Sarg-*Sargassum sp,* Sinci – *Sargassum incissifolium,* Ufasc – *Ulva fasciata,*

2.6 Discussion

The aim of this study was to investigate the influence of seasonal variation in nutrient variability and physico-chemical parameters on species richness and composition in rock pool ecosystems. The results of this study showed the impacts of seasonality on rock pool species composition and richness. Contrary to my hypothesis, the summer season had lower species richness than winter.

2.6.1 Effects of pool size on water chemistry parameters

The Pearson's correlation analysis highlighted a significant correlation between pool size and water chemistry parameters which may have been responsible for the differences in species richness among pools. However, due tominimal spatial variation and the fact that the pools are inundated with water from the same sources i.e. the sea and the periodic inflow of fresh water from the Great Fish River may have further explained the lack of significant differences between water chemistry among pools or between the seasons observed in the two-way ANOVA.

2.6.2 Effects of physico-chemical variables on rock pool species richness and composition

Following the assumptions made based on the theory of island biogeography (IBT) predicting a direct correlation between species diversity and habitat size, results of this study indicate the effects of surface area and water depth on rock pool communities. Small and shallow pools were reduced to species such as ribbon sea lettuce (*Ulva fasciata*), sand shrimps (*Palaemon peringueyi*) and plum anemones *Actinia equina*. It is speculated that low species richness in the small pools was a consequence of lack of habitat suitability, poor environmental buffering capacities, edge effects and trait-mediated indirect effects of predators. This is also supported by supplementary evidence provided by gut content analysis performed on fish from which remains of sand shrimp were observed. A visual comparison between small shallow and small deep pools indicated that the latter had more macroinvertebrates suggesting that pool depth may increase niche diversity. Furthermore, deeper pools were associated with greater habitat heterogeneity, supporting more benthic species and hiding spots for cryptic species. For

example, for gastropods such as *Turbo sarmaticus*, deeper pools served as refuge habitats from anthropogenic predation as suggested by Rouhani and Cowley (2016). These findings provide evidence on the effects of habitat structure consistent with Mgaya (1992) and Martins et al. (2007). Moreover contrary to my hypothesis, predictions based on the single large or several small (SLOSS) model were not evident in this study.

Although many common species were observed in both seasons, macroinvertebrates observed in both seasons including gastropods (*Scutellastra cochlear, Siphonaria capensis, Oxystele tigrina, Burnupena cinta, Burnupena lagenaria*), cnidarians (*Actinia equina*), echinoderms (*Parechinus angulosus* and *Parvulastra exigua*) and crustaceans (*Dardanus arrosor*) and a few rare species such as *Conus tulipa* and *Turbo sarmaticus,* there were also changes in composition (**Table 2.2**). Changes in community composition were attributed to seasonal shifts in substratum type. Some opportunistic winter species such as *Plocamium suhrii* and sandy bottom loving species such as *Hypnea tenuis* and *Gelidium abbottiorum* in summer are assumed to have taken advantage of the shifts in substratum. These findings are consistent with McQuaid and Dower (1990), Sylte and Fischenich (2002) Nejrup and Pedersen (2012) who identified substratum type as a key component in the proliferation of certain macroalgal species and it is known that the amount of sand in the intertidal varies seasonally on this coast (Zardi et al. 2006). In addition, substratum shifts are associated with changes in water chemistry. For example, a sandy substratum can lead to plant smothering due to reduced light. On the other hand, an exposed rocky substratum with <5 % fine sediment cover (following methods by Platts et al. 1983) can negatively affect species with a root system that requires anchorage. In addition, a shift in macroalgal species may have been merely a response seasonal variation as suggested by McQuaid (1980). The results of this study confirm the importance of substratum type highlighted by Johnson et al. (1968), McQuaid (1980) and Greenstreet et al. (2007). It is also predicted that substratum type can result in bottom-up trophic cascades firstly by positively and/or negatively affecting macroalgal communities and secondly by providing refuges and nursery beds for higher trophic level species (e.g. fish and macroinvertebrates).

2.7 Conclusion and Recommendations

It was evident that temperature per se did not have direct effects on species richness as most of these species have evolved to tolerate seasonal fluctuations in temperature. However, it was observed that variations in temperature were associated with changes in other physico-chemical parameters (e.g. depth, salinity, conductivity, substratum, chl-*a* and surface area) in turn contributing to species composition along the south coast. The findings of this study support work by Martin et al. (2007) and White et al. (2015) who observed significant influences of micro-climatic conditions in contributing to species richness and composition within coastal habitats.

Moreover, although traditional community descriptors provide insights into species responses to environmental parameters, a considerable degree of variation remains unexplained. This unexplained variation may have been due to the limited number of physico-chemical parameters measured in this study. Thus, some physical factors that may significantly impact micro-climatic conditions that affect species richness and composition as well as aspects of water chemistry were not addressed in this study. These include the angle of pool relative to the ocean, pool shape and edge effects. Moreover, because community descriptors only provide a snapshot of the influences of sampled parameters relative to the species' sampled to thoroughly understanding the underlying factors and interactions requires methods which can show spatio-temporal changes, biotic interactions and their effects on species richness and composition. Some techniques useful to community ecology studies which can be employed are food web structure analyses using natural biomarkers such as fatty acids and stable isotopes.

A STABLE ISOTOPE-BASED COMMUNITY METRICS APPROACH ASSESSING VARIATION IN INTERTIDAL POOL TROPHIC STRUCTURE

3.1 Introduction

The concept of food web structure analysis was initially aimed at complementing traditional community descriptors (e.g. species richness, composition and abundance estimates) which often failed to decipher the complex feeding interactions driving ecosystems (Abrantes et al. 2014; Perkins et al. 2014; Sokolowski et al. 2014; Coll and Lotze 2016). Over the years, the concept of food web structure analysis has been broadly defined as estimating the number of energy or trophic levels in an ecosystem and/or the degree of trophic complexity within a food web network (Vander Zanden et al. 2006). The examination of trophic structure within food webs targets elucidating how communities remain ecologically functional despite spatio-temporal variation, the effects of changes in food chain length and the transfer of carbon and nutrients across trophic levels (Polis and Strong 1996; Austin 2002; Naeem and Wright 2003; Edwards et al. 2013; Beauchard et al. 2017).

To date, stable isotope techniques based on the selective assimilation of heavier over lighter isotopes (which, in the case of carbon and nitrogen, are lost through respiration and excretion, respectively) allow for the assessment of assimilated matter and clarification of trophic complexity over time and space (Cabana and Rasmussen 1996; Renones et al. 2002; Persic et al. 2004; Kupfer et al. 2006; Boecklen et al. 2011). Carbon ($\delta^{13}C/\delta^{12}C$) and nitrogen ($\delta^{15}N/\delta^{14}N$) stable isotopes (hereafter $\delta^{13}C$ and $\delta^{15}N$, respectively) display a stepwise enrichment of the heavier isotope between prey and predator tissue and have been extensively employed to decipher food web structure (Catry et al. 2016; Drazen and Sutton 2017). The stable isotopes allow for the construction of general community trophic structure by identifying feeding and energy flow patterns, dietary overlaps and the estimation of species' niches (Vander Zanden et al. 1997; Abrantes and Sheaves 2009).

Based on change in carbon and nitrogen values between source and consumers, known as the trophic enrichment factor (TEF), species' trophic positions can be estimated (France and Peters 1997; Zanden and Rasmussen 2001; Moore and Semmens 2008). In recent years, a novel Bayesian statistical approach to the Layman metrics (a 6-component community-wide measure of trophic diversity based on the mean $\delta^{13}C$ and $\delta^{15}N$ values of individual species within a food web) was developed to quantitatively assess community structure repeatedly over time and/or across environmental gradients (Layman et al. 2007; Jackson et al. 2011; Catry et al. 2016). This novel approach includes an additional metric (SEA_c); i.e. the corrected measure of total diversity allows one to minimise overestimation of trophic diversity by calculating the realised niche.

In the present study, I was interested in a quantitative analysis of intertidal rock pool trophic structure. Coastal habitats, particularly intertidal rock pools, provide refuge, food and nursery sites to a range of marine organisms. Although many studies have been done to understand the concept of trophic structure in various ecosystems (Trussel et al. 2003; Casini et al. 2008; Carpenter et al. 2016), the major challenge exists in accounting for and/or forecasting trophic structure in an ever changing ecosystem. I hypothesized that trophic diversity would significantly increase in summer following the assumptions of the species energy theory (Wright, 1983), which states that species richness is likely to increase with habitat size and increases in physical environmental factors such as temperature. This hypothesis also led to my next hypothesis that in summer rock pool food chain length (FCL) would increase as diversity in food sources increases. The supporting hypothesis (FCL theory) suggests that an increase in bottom up elements such as nutrients positively increases the number of energy transfers from the base to the top of a food web (Samuelsson et al. 2002). Lastly, following the 'species-area' effect, of the island biogeography theory predicting an increase in species richness in larger areas by MacArthur and Wilson 1967, (Hamilton, 1968), I predicted that an increase in pool size would promote higher trophic diversity and shifts in consumer trophic positions. Based on these assumptions, I primarily expected that trophic diversity and food chain length would increase in summer and in larger pools

3.2 Materials and Methods

3.2.1 Sampling

Seasonal sampling of physico-chemical parameters, basal food sources (macroalgae, macrophytes, suspended particulate organic matter (SPOM), phytobenthos) and consumers (invertebrates, fish) was conducted at the Great Fish River rocky intertidal area on the south coast of South Africa. Sampling was performed on the same pools (n = 12) as in Chapter 2 during winter (July 2016) and summer (December 2016). Refer to Chapter 2 for detailed methods.

3.2.2 Stable isotope sample collection and preparation

3.2.2.1 Macroinvertebrate and fish collection

From each of the 12 pools, 4 specimens of each observed species such as cushion stars (*Parvulastra* and *Patiriella* spp.), gastropods (*Burnupena* spp.) and hermit crabs (*Diogenes brevirostris*) were handpicked and stored separately in labelled jars. Extreme care was taken during collection of Cape sea urchins (*Parechinus angulosus*) and sea anemones (*Actinia equina*) due to their sharp spines and fragility, respectively. In the laboratory, all taxa were rinsed in distilled water, placed in filtered seawater for 24h to allow gut clearance and sacrificed by freezing (Schaal et al. 2010). Prior to drying, shelled organisms were removed from their shells and only muscle tissue was dried to avoid overestimation of carbon values (Yokoyama et al. 2005; Dalu et al. 2016); fish muscle tissue was excised from the lower lateral line of the organism. Each specimen was placed in a labelled pre-combusted (450°C, 24h) aluminium foil sleeve and oven-dried at 60°C for 72h. For most animal samples, only muscle tissue was analysed as it is less variable in carbon and nitrogen (Yokoyama et al. 2005) while for species such as sea anemones, dwarf cushion stars, sand shrimps and hermit crabs the whole body was dried for analysis.

3.2.2.2 Macroalgae

Approximately 20 g of all observed macroalgal species were hand-collected, rinsed with pool water and stored on ice in labelled ziplock bags. In the laboratory, samples were identified to species level (Branch et al. 2012). Samples were further rinsed in distilled

water to remove any epiphytes, placed in pre-combusted aluminium foil sleeves and oven-dried (72h, 60°C).

3.2.2.3 Phytobenthos and particulate organic matter

Phytobenthos and particulate organic matter (SPOM) samples (n = 4) were collected in 250mL polyethylene bottles from each pool. Phytobenthos samples were brushed off loose rock substrata and from fronds of macroalgae using a toothbrush, rinsed in sea water and transferred into storage containers. Water samples for SPOM were collected by horizontally towing the sample bottles at the water surface. Samples were immediately stored on ice in the field and upon arriving in the laboratory, the samples were filtered onto pre-combusted (450°C, 4h) Whatman glass fibre filters (GF/F) under pressure (≤ 4cm Hg). The saturated filters (phytobenthos and SPOM) were folded in half and placed into aluminium sleeves and oven dried (60°C, 72h) and packaged for stable isotope analysis (SIA). Fish, macroinvertebrate and macroalgal samples were each ground into fine homogenous powder using a pestle and mortar and sent for isotope analysis at the Mammal Research Institute Stable Isotope Laboratory at the University of Pretoria.

3.3 Stable isotope analysis

Aliquots of ~1–1.1mg of macroalgae ~0.5–0.6mg of ground macroinvertebrate and fish samples and ~20–25mg of particulate organic matter and phytobenthos filters were weighed into tin capsules pre-sterilised with toluene. Isotopic analysis was performed on a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (Thermo Fischer, Bremen, Germany). Two laboratory running standards (Merck Gel: $\delta^{13}C$ = –20.26‰, $\delta^{15}N$ = 7.89‰, C% = 41.28, N% = 15.29, and DL-Valine: $\delta^{13}C$ = –10.57‰, $\delta^{15}N$ = –6.15‰, C% = 55.50, N% = 11.86) were used and a blank sample was run after every 12 unknown samples. These running standards were calibrated against the international standards of National Institute of Standards & Technology (NIST): NIST 1557b (bovine liver), NIST 2976 (mussel tissue) and NIST 1547 (peach leaves). Data corrections were done using the values obtained for the Merck Gel standards during each run. The values for the DL-Valine standard provided the standard error for each run. All results were referenced

against Vienna Pee-Dee Belemnite, and air for carbon and nitrogen isotope values respectively (Feuchtmayr and Grey 2003). Results were expressed in delta notation using a per mille scale using the standard equation:

$$\delta X\ (‰) = [(R_{sample} - R_{standard})/R_{standard} - 1] \times 1000$$

Where X= ^{15}N or ^{13}C and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively.

The trophic positions (TP) of consumers within the GFR rock pools were determined using $\delta^{15}N$ values following the formula proposed by McCutchan et al. (2003), with a baseline of a primary consumer:

$$TP = (\delta^{15}N_{consumer} - \delta^{15}N_{base}) / 3 + 2$$

Where TP = trophic position, $\delta^{15}N_{consumer}$ = mean measured $\delta^{15}N$ of consumer, $\delta^{15}N_{base}$ = mean $\delta^{15}N$ of the chilli pepper sponge (*Tedania anhelans*).

In the present study, a mean $\delta^{15}N$ TEF value of 3‰ was used following McCutchan et al. (2003). Assuming primary producers are represented as trophic level 1, *T. anhelans* would be placed in trophic level 2. Furthermore, to capture possible spatio-temporal variation at the base of the food web in a particular location, the baseline selection was based upon a species with limited mobility as suggested by Di Camillo et al. (2012) and Bergamino et al. (2015).

3.4 Data analysis

Seven quantitative Layman metrics based on stable isotope data were calculated to reveal key aspects of GFR rock pool trophic structure. Using the Stable Isotope Analysis in R (SIAR) model, the Layman metrics were calculated based on consumer isotope data for each pool. The results for each pool comprised the dNr ($\delta^{15}N$ range) defined as the trophic height of the food web; dCr ($\delta^{13}C$ range), the breadth of basal resources; total area (TA) or size of the food web in isotopic space; centroid distance (CD), explained as trophic diversity within a food web; mean nearest neighbour distance (MNND) i.e. the mean Euclidean distance to each species' closest neighbour in bi-plot space, this is a measure of food web packing; standard deviation of nearest neighbour distance (SDNND) i.e. the measure of species evenness, a low value indicating a highly uniform

distribution of trophic niches (Layman et al. 2007); and the Standard Ellipse Area correction (SEA_c), defined as the bivariate measure of mean core isotopic niche width (i.e. realised niche) which is used as an estimate of dietary similarity among populations (Jackson et al. 2012). To measure mean core isotopic niche overlap (SEA_c), consumer isotope data from both seasons were analysed using the SIBER model (Jackson et al. 2011). All metric calculations were bootstrapped (n = 9999) to allow for comparisons among species with different sample sizes. A Pearson's correlation analysis was performed to assess the relationship between the trophic components measured using Layman metrics among the rock pools across the two seasons. Biplots of carbon and nitrogen isotope ratios for all species in each pool across both seasons (including SPOM and phytobenthos) were plotted in SigmaPlot v 12.5 (Systat Software Inc., San Jose California USA). All other statistical analyses were performed in R version 3.4.2 (R Core Team 2017).

3.5 Results

3.5.1 Intertidal rock pool trophic diversity

Overall species richness increased between summer and winter, with a total catch of 27 and 34 species respectively. In both seasons, rock pool communities were numerically dominated by herbivorous macroinvertebrates, with fish occupying the highest trophic position (**Fig 3.1**, **Appendix 3**). An increase in trophic position of some fish and some macroinvertebrate species such as the hermit crab (*Diogenes brevirostris*) and gastropods (*Oxystele tigrina*) was observed in winter in comparison to summer (**Appendix 3)**. Furthermore, there was a general increase in trophic diversity with pool size especially in winter (compare same pools juxtaposed from different seasons e.g. panel u & v, o & p in **Fig 3.1**). Within primary producer communities, two-way ANOVA indicated no significant interactions between pool size and season on SPOM or phytobenthos isotope values. However, season had a main effect on both variables (**Table 3.1**).

Table 3. 1: Two-way ANOVA summary of results on the effects of season and pool size on SPOM and phytobenthos

Factor		**SPOM**		**Phytobenthos**	
	Df	***F***	***p***	***F***	***p***
Season	1,44	12.923	**0.0001**	4.481	**0.04**
Pool size	1,44	0.932	0.339	1.485	0.23
Season× Pool size	1,44	2.99	0.091	1.132	0.293

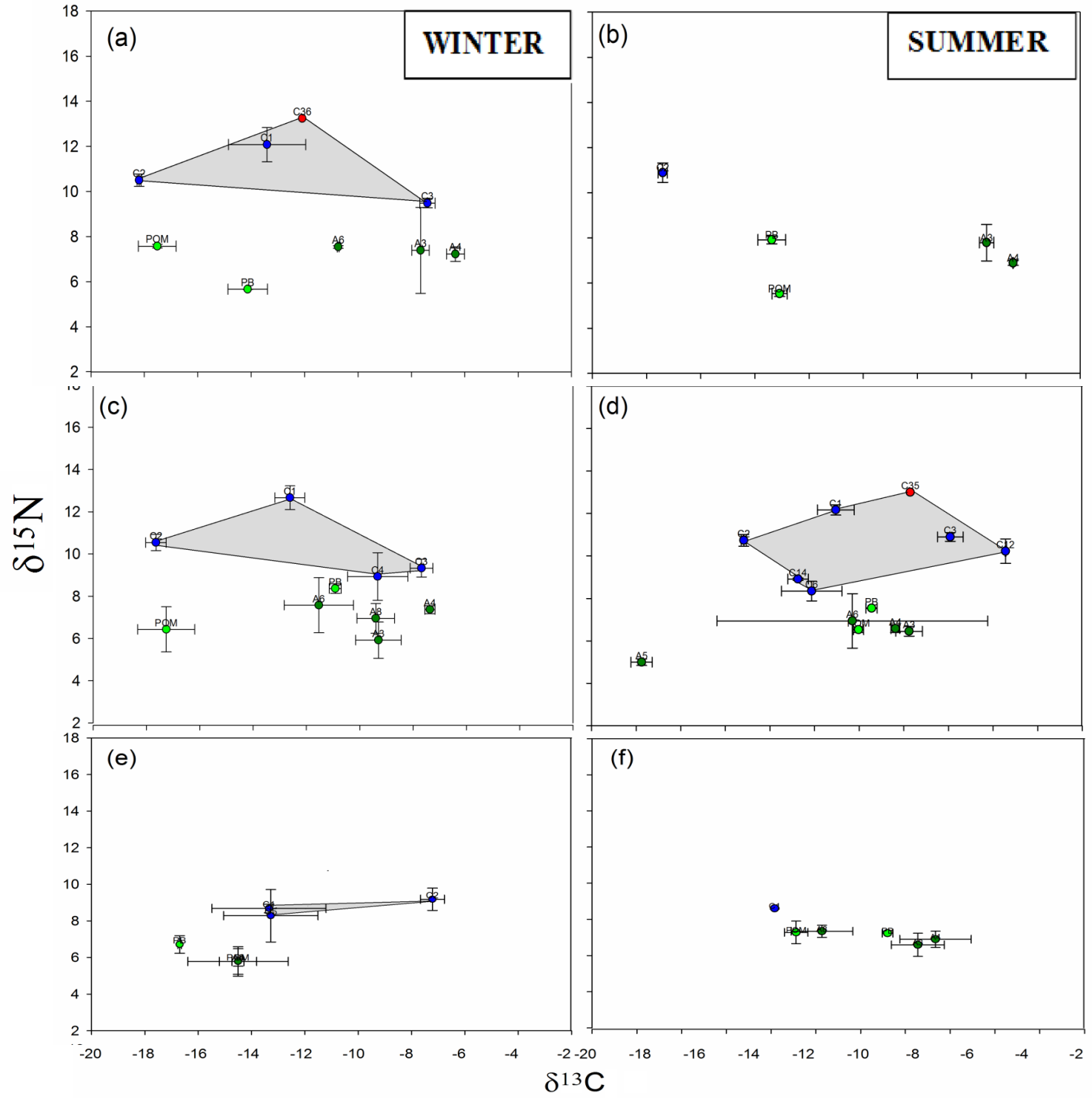

Figure 3. 1: **(a-f):** Stable isotope-based biplots of rock pool food web diversity inferred from $\delta^{15}N$ vs $\delta^{13}C$ across 12 rock pools sampled in 2 seasons. Paired plots (e.g. a, b; c, d etc.) represent different seasons for the same pool. Each sample point represents mean $\delta^{15}N$ and $\delta^{13}C$ isotope values with error bars indicated standard deviations. SPOM and phytobenthos – light green circles, macroalgae – dark green circles, macroinvertebrates – dark blue circles, and fish – red circles. Shaded regions indicate the size of food web in isotopic space. For abbreviation for taxon codes refer to **Appendix 3**.

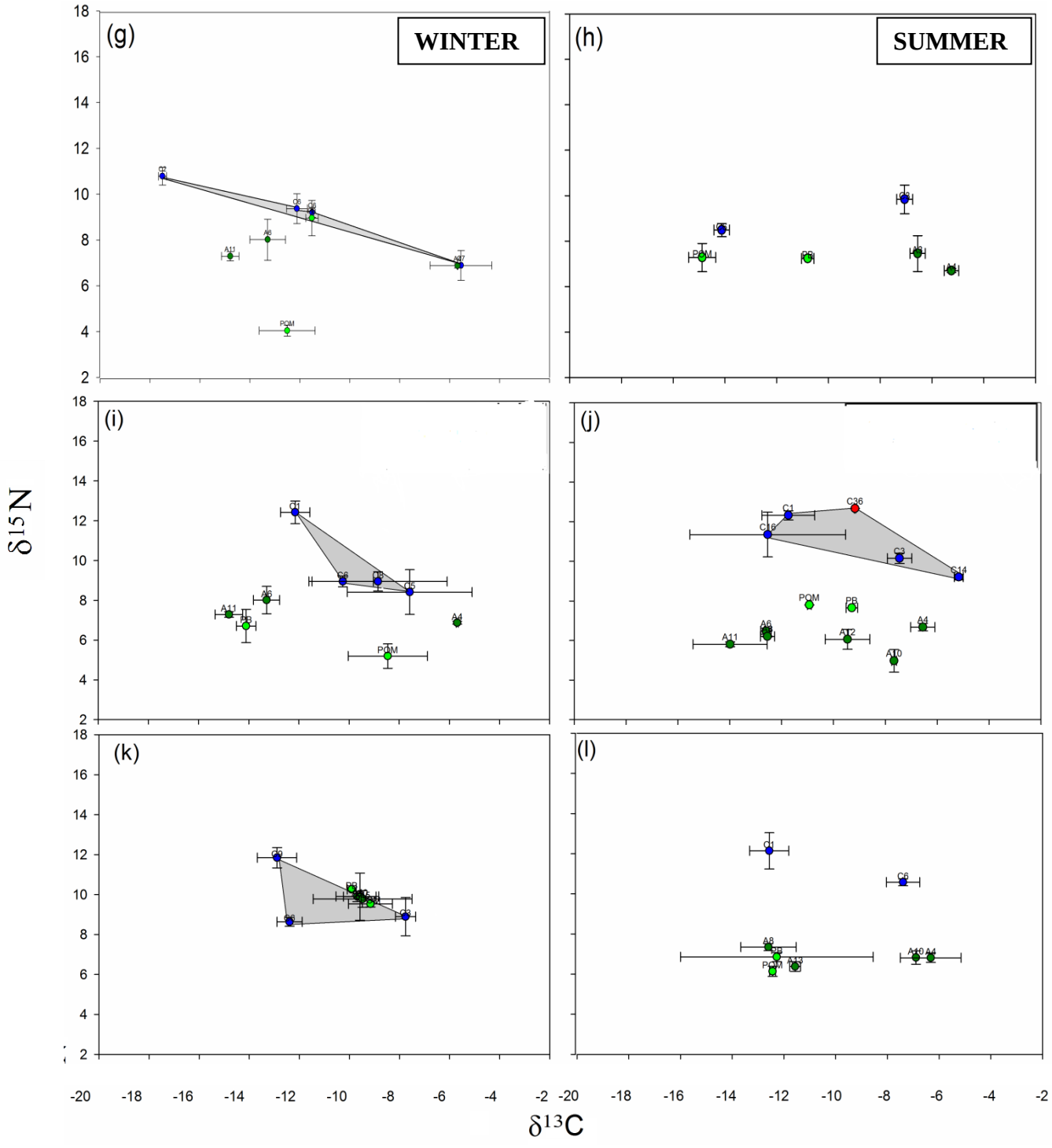

Figure 3. 1 **(g-l):** Stable isotope-based biplots of rock pool food web diversity inferred from $\delta^{15}N$ vs $\delta^{13}C$ across 12 rock pools sampled in 2 seasons. Paired plots (e.g. a, b; c, d etc.) represent different seasons for the same pool.Each sample point represents mean $\delta^{15}N$ and $\delta^{13}C$ isotope values with error bars indicated standard deviations. SPOM and phytobenthos – light green circles, macroalgae – dark green circles, macroinvertebrates – dark blue circles, and fish – red circles. Shaded regions indicate the size of food web in isotopic space. For abbreviations for taxon codes refer to **Appendix 3**.

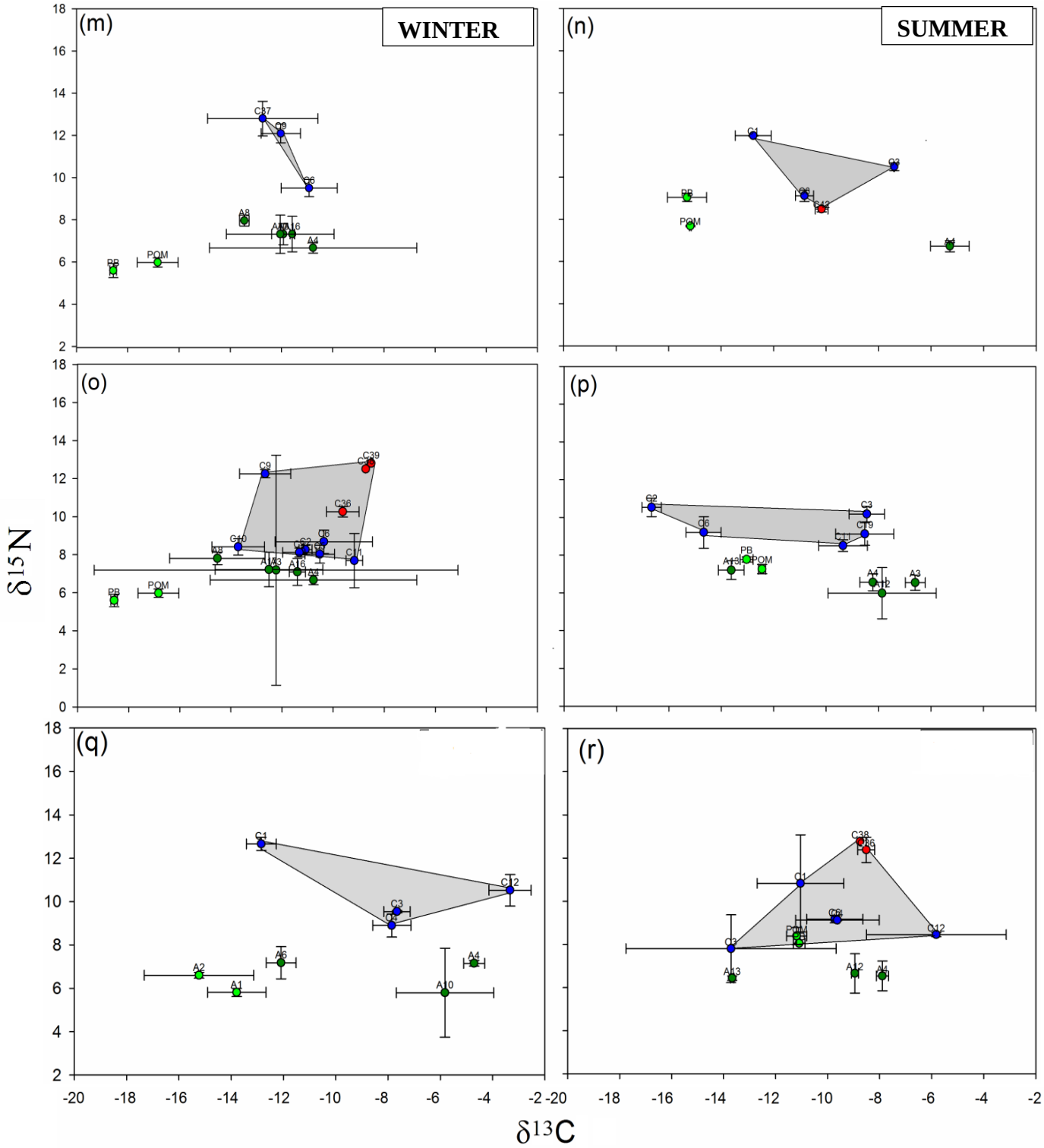

***Figure 3.1*: (m-r):** Stable isotope-based biplots of rock pool food web diversity inferred from $\delta^{15}N$ vs $\delta^{13}C$ across 12 rock pools sampled in 2 seasons. Paired plots (e.g. a, b; c, d etc.) represent different seasons for the same pool . Each sample point represents mean $\delta^{15}N$ and $\delta^{13}C$ isotope values with error bars indicated standard deviations. SPOM and phytobenthos – light green circles, macroalgae – dark green circles, macroinvertebrates – dark blue circles, and fish – red circles. Shaded regions indicate the size of food web in isotopic space. For abbreviations for taxon codes refer to **Appendix 3**.

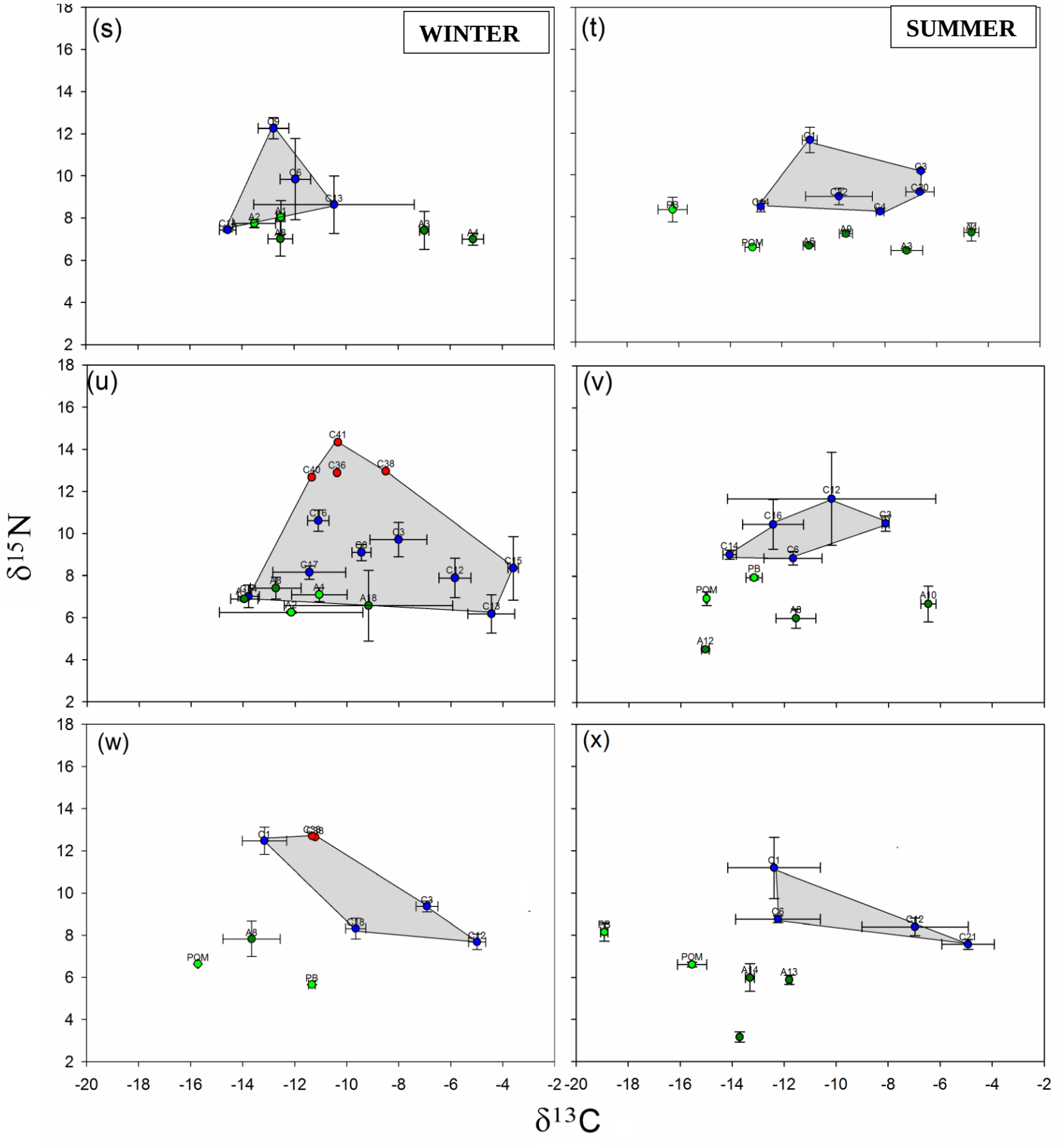

Figure 3.1: **(s-x):** Stable isotope-based biplots of rock pool food web diversity inferred from $\delta^{15}N$ vs $\delta^{13}C$ across 12 rock pools sampled in 2 seasons. Paired plots (e.g. a, b; c, d etc.) represent different seasons for the same pool. Each sample point represents mean $\delta^{15}N$ and $\delta^{13}C$ isotope values with error bars indicated standard deviations. SPOM and phytobenthos – light green circles, macroalgae – dark green circles, macroinvertebrates – dark blue circles, and fish – red circles. Shaded regions indicate the size of food web in isotopic space. For abbreviations for taxon codes refer to **Appendix 3**.

Table 3. 2: Seasonal community-wide rock pool trophic structure analysis calculated based on Bayesian Layman metrics; dNr indicates the nitrogen ($\delta^{15}N$) range, dCr is the carbon ($\delta^{13}C$) range, TA is total area in isotope space, CD (centroid distance) the mean distance of species to central mean N and C value, MNND - mean nearest neighbor distance, SDNND (standard deviation of nearest neighbor distance)-trophic redundancy and SEA_c (Standard Ellipse Area corrected)-a measure of dietary similarity, area- pool size measured in m^2.

SUMMER

Pool	Code	Area	dNr		dCr		TA		CD		MNND		SDNND		SEA_c	
			Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
1	a	0.89	4.37	4.38-4.54	9.50	7.5-10.9	24.1	20.8-28.2	2.85	2.7-3.1	0.38	0.3-0.5	0.72	0.5-0.9	12.86	11.1-14.6
2	c	1.709	4.20	3.99-4.49	11.45	11.7-11.9	27.6	25.1-30.6	3.39	3.1-3.7	0.29	0.2-0.4	0.54	0.4-0.7	15.91	14.6-17.3
3	e	0.464	0.05	0.04-0.05	0.01	0	0.0	0	0.02	0	0.02	0.014	0.02	0.02-0.03	0.00	0
4	g	1.359	1.97	1.8-2.32	7.26	7.3-7.7	4.6	3.6-5.6	3.05	2.9-3.5	0.34	0.2-0.3	0.60	0.2-0.4	4.78	3.5-6
5	i	1.47	0.71	0.69-0.91	0.26	0.1-0.4	0.1	0	0.32	0.3-0.4	0.19	0.1-0.3	0.23	0.1-0.3	0.14	0
6	k	0.377	2.15	2.32.34	5.67	5.7-6.1	2.5	1.8-3.7	2.44	2.3-2.7	0.40	0.2-0.6	0.55	0.3-0.6	2.91	2.2-3.4
7	m	0.471	3.81	3.82-4.1	5.71	5.6-5.9	12.8	11.7-14.2	2.30	2.1-2.5	0.24	0.2-0.3	0.40	0.3-0.5	8.10	7.4-9
8	o	1.874	2.64	2.46-2.89	9.31	9-9.8	17.3	15.8-19	3.18	2.9-3.5	0.33	0.3-0.4	0.55	0.5-0.7	9.21	8.2-10.3
9	q	2.586	6.09	6.04-6.37	11.28	10.9-12.3	37.1	34.5-41.6	2.97	2.7-3.3	0.36	0.3-0.4	0.67	0.5-0.8	17.49	15-20
10	s	2.075	4.43	4.4-4.63	6.74	6.8-7	18.3	17.2-20.2	2.43	2.3-2.6	0.29	0.2-0.4	0.52	0.4-0.6	10.23	9-11.5
11	u	2.468	4.58	3.29-5.68	7.45	6.8-8	18.9	13.4-24.7	2.62	2.4-2.8	0.39	0.3-0.5	0.73	0.5-1.1	10.69	6.9-13.5
12	w	1.909	4.64	4.66-4.93	9.66	9.7-10	24.4	22.2-26.9	3.33	3.1-3.6	0.45	0.3-0.6	0.73	0.6-0.9	14.23	12.5-15.9

Table 3.2: Seasonal community-wide rock pool trophic structure analysis calculated based on Bayesian Layman metrics; dNr indicates the nitrogen ($\delta^{15}N$) range, dCr is the carbon ($\delta^{13}C$) range, TA is total area in isotope space, CD (centroid distance) the mean distance of species to central mean N and C value, MNND - mean nearest neighbor distance, SDNND (standard deviation of nearest neighbor distance)-trophic redundancy and SEA_c (Standard Ellipse Area corrected)-a measure of dietary similarity, area- pool size measured in m^2.

WINTER

Pool	Code	Area	dNr		dCr		TA		CD		MNND		SDNND		SEA_c	
			Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
1	b	0.89	5.23	4.91-5.96	7.02	6.8-7.9	13.8	11.5-16.6	2.49	2.2-2.8	0.51	0.3-0.7	0.83	0.6-1.1	9.36	7.7-11.4
2	d	1.709	3.87	3.86-4.1	10.24	10.2-10.8	19.2	18.2-21.7	3.73	3.4-4.1	0.40	0.2-0.5	0.74	0.4-1.3	16.92	15.3-19.3
3	f	0.464	1.92	1.89-2.09	6.66	6.6-6.9	6.2	4.3-7.9	2.35	2.1-2.6	0.35	0.2-0.5	0.59	0.4-0.8	4.55	3.3-5.6
4	h	1.359	1.94	1.81-2.06	10.03	10.1-1.04	10.3	8.1-12.4	3.15	2.8-3.6	0.31	0.2-0.4	0.52	0.3-0.6	6.62	5.2-8
5	j	1.47	3.57	3.34-3.92	10.43	10.7-11.2	16.3	14.4-20.6	3.63	3.2-3.6	0.59	0.4-0.8	1.06	0.7-1.5	15.95	13.5-19.9
6	l	0.377	3.70	3.75-3.94	5.82	5.6-6.2	14.1	11.3-14.1	2.56	2.4-2.8	0.38	0.3-0.5	0.65	0.4-0.9	10.32	9.3-11.8
7	n	0.471	3.88	3.62-4.45	3.53	2.9-4.2	6.9	5.6-8.9	1.67	1.5-1.8	0.40	0.3-0.5	0.61	0.5-0.7	5.16	4.3-6.1
8	p	1.874	6.06	5.25-6.62	9.61	9.3-10.1	36.8	34.3-39.8	3.22	3.1-3.4	0.29	0.2-0.3	0.52	0.4-0.6	17.69	16.3-1.9
9	r	2.586	4.71	4.53-5.13	10.41	10.1-11.1	21.8	19.5-25.6	3.02	2.6-3.5	0.39	0.3-0.5	0.75	0.4-0.9	13.97	11.5-16.9
10	t	2.075	5.09	4.94-5.09	6.12	3.6-8	15.0	8.9-20.4	2.29	2-2.6	0.43	0.2-0.7	0.88	0.3-1.4	11.94	6.9-16.1
11	v	2.468	10.43	9.2-12.07	12.12	10.6-13.3	69.8	58.5-69.8	3.58	3.3-3.9	0.42	0.3-0.5	0.78	0.6-0.9	24.09	20.7-27.3
12	x	1.909	5.37	5.34-5.51	8.84	8.7-9.3	19.1	18-20.8	3.21	2.9-3.5	0.29	0.2-0.4	0.49	0.4-0.6	10.86	9.7-11.3

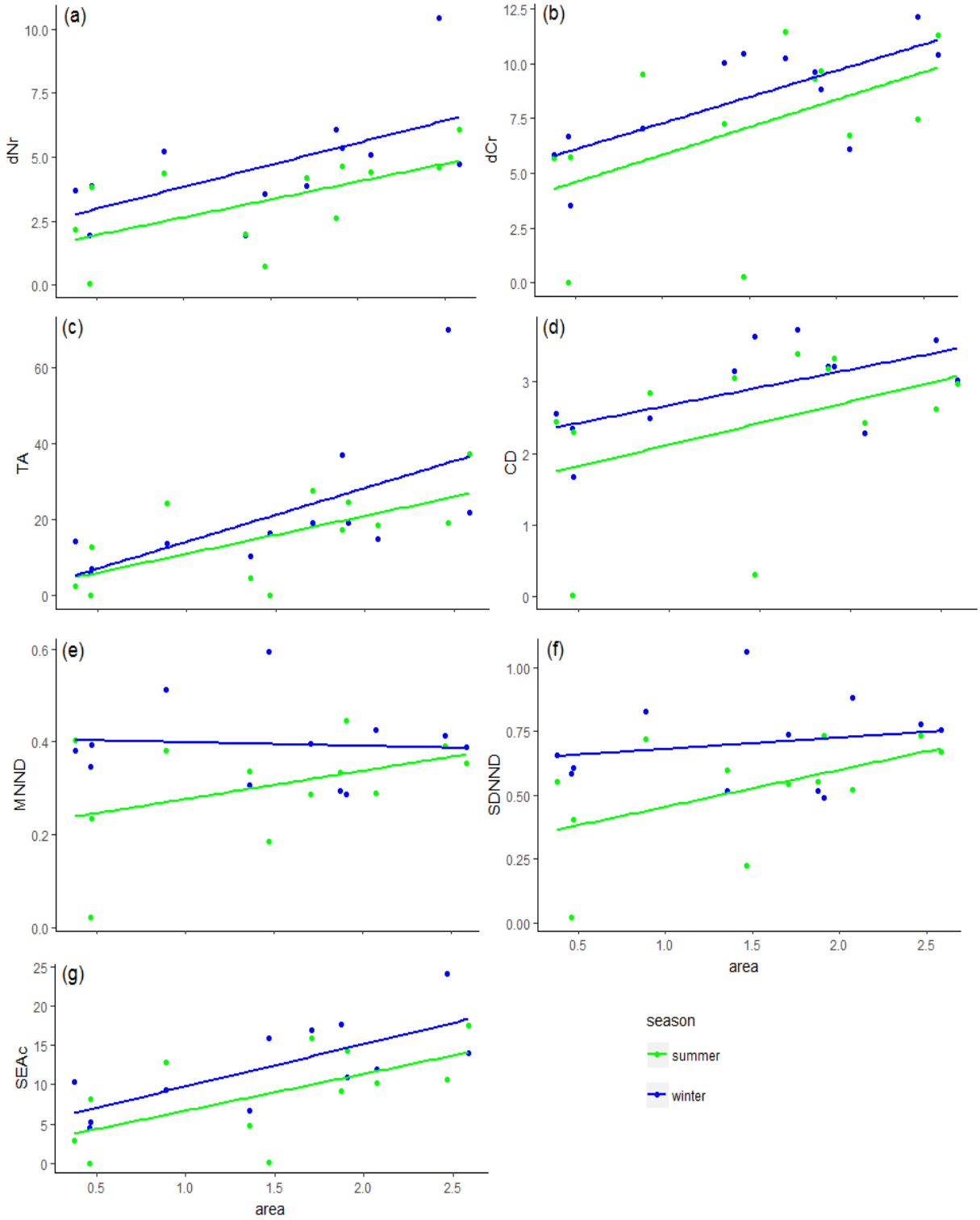

***Figure 3.2* (a-g):** Layman metrics results for consumer communities from the 12 rock pools repeatedly sampled in summer and winter. Summer is indicated by green and winter by blue. a= $\delta^{15}N$ range (dNr), b=$\delta^{13}C$ range (dCr), c= trophic diversity (TA), d=mean distance to centroid (CD), e= mean nearest neighbour distance (MNND), f= species evenness across populations (SDNND), g= the realized niche (SEA_c), area =pool size in m^2.

3.5.2 Community-wide trophic diversity in rock pool food web structure

The Layman community-wide trophic metrics exhibited notable variation in species diversity among pools across the 2 seasons (**Table 3.2**). With the exception of MNND and SDNND, the metrics (dNr, dCr, TA, CD, SEA_c) were positively correlated with pool size (**Table 3.3**). A comparison of these metrics across both seasons indicated that winter was trophically more diverse (**Fig 3.2 a-d, g**, **Table 3.2** -e.g. pools 5, 9, 11) than summer. On the other hand, of the 7 metrics only SDNND and MNND were significantly correlated with season (**Table 3.3**). SDNND increased across both seasons with increase in pool size (**Fig 3.2f)** while MNND was relatively constant in winter across all pools, exhibiting a gradual increase with increased pool size in summer (**Fig 3.2e**).

A two-way ANOVA indicated no significant interaction between pool size and season on these Layman metrics, however pool size exhibited a main factor effect on all the 5 metrics ($F_{(1,20)}$ =15.871, p<0.0001), while MNND and SDNND were significantly influenced by season ($F_{(1,20)}$ =16.31, p<0.0001) and ($F_{(1,20)}$ =5.59, p=0.02), respectively. A post hoc test revealed that the realized niche (SEA_c) differed significantly between seasons in pools 3, 6 and 8, while CD differed significantly only in pool 3.

Table 3.3: Summary of Pearson's correlation analysis indicating the degree of association of season and area (pool size) with the Layman metrics calculated for each pool. Significant correlation (r) and (p) values are indicated in bold.

	Season		**Area (pool size)**	
	r	***p***	***R***	***p***
dNr	-0.33	0.11	**0.56**	**0.004**
dCr	-0.22	0.3	**0.58**	**0.003**
TA	-0.18	0.4	**0.62**	**0.001**
CD	-0.28	0.18	**0.45**	**0.021**
MNND	**-0.41**	**0.04**	0.18	0.391
SDNND	**-0.43**	**0.03**	0.34	0.105
SEA_c	-0.29	0.16	**0.64**	**0.001**

3.5.3 Consumer trophic niche diversity

A representation of trophic diversity was plotted in SIBER showing the fundamental (thick lines) and realised (ellipses) niches of the consumers within the south coast intertidal rock pools (**Fig 3.3**). The graph illustrates a slightly more diverse consumer trophic structure in winter over summer. Both seasons exhibited a trapezoid shaped food web with a notably broader food web structure along both axes in winter. Carbon sources ($\delta^{13}C$) for animals were more diverse in winter ranging from -18.26 to -0.74‰ as compared to a summer range of -17.67 to -3.92‰. A Tukey HSD post hoc test further indicated significant seasonal differences between the trophic height (dNr) of pool 11 (panel v in **Fig 3.1**) and pool 3 (panel e). The winter food web exhibited an increase in food chain length and trophic position (highest TP-winter=4 *vs* TP-summer=3, **Appendix 3**). Although the overall food chain height ($\delta^{15}N$) was greater in winter (2.27 - 14.34‰) *versus* a slightly lower summer range (6.86 - 14.23‰), a two-way ANOVA indicated no significant interactions in the overall Layman metrics between the 2 seasons or among pools within each season.

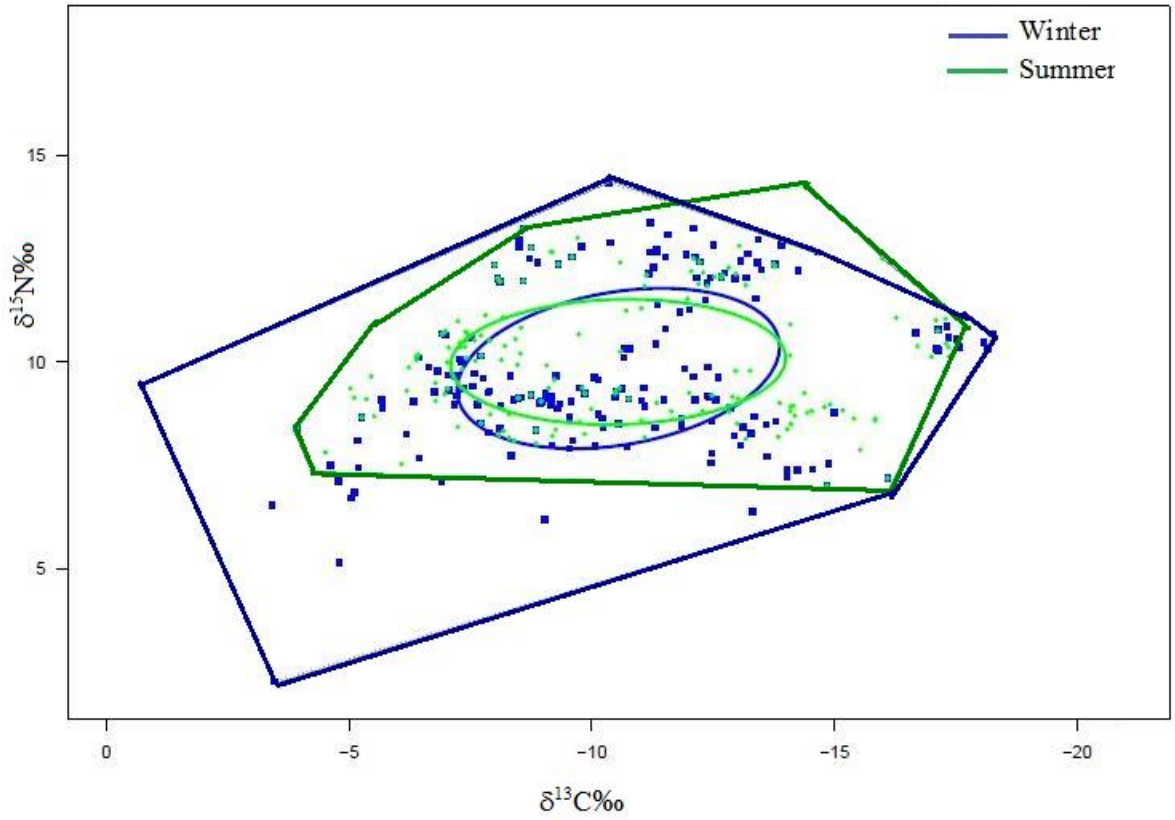

***Figure 3.3*:** Seasonal rock pool community-wide metrics based on seasonal $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures of consumer taxa. Blue indicates winter while green shows the summer season. The thick lines indicate the convex hulls of all consumer species recorded in each season in isotopic space. The ellipses encompass the SEA_c or realized niche of consumer species within each season.

3.6 Discussion

Given the global decline in species within communities, the attention of most community ecologists has now diverted to understanding the effects of species habitat shifts and biodiversity decay at community and ecosystem levels. Changes in trophic dynamics have been attributed to shifts in environmental conditions among other factors. In this study, an integrative approach based on descriptive and quantitative methods was used to estimate species interactions and changes in trophic structure in response to spatio-temporal variability within coastal ecosystems. The results obtained indicated notable shifts in trophic diversity (TA, dNr) with seasonal change.

3.6.1 Spatio-temporal variation in rock pool trophic diversity

Although seasonal effects were expected, the obtained results contrasted with the initial hypothesis, results showed an increase in trophic diversity in winter compared to summer. A qualitative biplot analysis based on the stable carbon and nitrogen isotope ratios illustrated a positive increase in food web size and length within some pools (compare **Fig 3.1** panels a *vs* b, o *vs* p, u *vs* v;) in winter as compared to summer. The Layman metrics (dNr, dCr, TA and CD) validated these results by indicating an increase in trophic diversity in winter (**Fig 3.2a-d**). These differences in trophic diversity between the two seasons also substantiate my earlier findings documented in this thesis (Chapter 2) which demonstrated the potential indirect effects of temperature on other water quality parameters which affected species richness and composition.

As hypothesised, there was an increase in trophic diversity (TA and SEA_c) marked by an increasing trophic height (dNr), carbon range (dCr) and centroid distance (CD) with increase in pool size across both seasons (**Fig 3.2a-g**, **Appendix 3**) suggesting surface area may have promoted species colonization. These results substantiate the widely accepted predictions of the species-area effect hypothesis of island biogeography theory suggesting that larger areas often support more species. Furthermore, from the assumptions of the ecological niche differentiation theory (Vandermeer 1972) stating that no 2 species can occupy the same niche, it is postulated that the trophic redundancy observed in the pools was a result of coexistence through partitioning of niche resources, which may also have been influenced by habitat heterogeneity. In addition, the high trophic redundancy observed in some pools may have been promoted by dietary similarity (as seen with increased SEA_c). Thus, it is speculated that if food becomes limiting in such communities (i.e. in communities experiencing high coexistence and dietary similarity), the possible occurrence of trait and/or density mediated indirect cascades will be elevated. Moreover, the low SEA_c in smaller pools potentially demonstrates that fewer consumers within a community lower the possibility of intra-specific competition for resources.

However, despite the seemingly higher carbon source breadth in macroalgal communities in summer (-26.22 to -4.16‰) as compared to winter (-16.88 to -3.8‰), species richness was lower in summer; hence it is assumed that a broad carbon source does not necessarily support higher trophic diversity. This interpretation must however be made cautiously because stable isotope ratios in primary producers are determined by photosynthetic reactions which are based on factors such as irradiance, often affected by seasonality. As such, the observed variations in $\delta^{13}C$ may reflect different photosynthetic pathways, growth conditions and irradiance levels inducing variations in isotopic values of different primary producers, at the same time, these may be assimilated with different efficiencies.

Although it would follow that an increase in trophic diversity with pool size observed in both seasons would promote food web packing and trophic redundancy calculated as MNND and SDNND respectively, the results obtained suggested otherwise. Both indices steadily increased with pool size in summer, while remaining relatively constant in winter across all pools. An explanation for this is that increased temperature promotes oxygen depletion potentially causing species migration. Furthermore, minimal differences in physico-chemical parameters (particularly temperature) across pools in winter may have promoted an even distribution of species across the sampled pools as evidenced by a constant MNND slope. The increase in SDNND with pool size also provides evidence of effects of habitat and the ability of species to coexist in promoting community structure. **Fig 3.3** also suggests greater niche overlap or dietary similarity in level 2 and 3 species (e.g. limpets and gastropods) which are mostly ubiquitous in the intertidal zone.

3.6.2 Seasonal effects on food chain length

Trophic positions have been assumed to be a good indicator of niche positions among macroinvertebrate species. The estimation of trophic position following the methods of McCutchan et al. (2003) revealed a shift in food web length from 3 trophic levels in summer to 4 in winter. Fish occupied the highest trophic position in winter, while in

summer there was co-dominance by fish and gastropods (e.g. *Burnupena lagenaria*). A shift in trophic positions between common species such as *Oxystele tigrina* and *Diogenes brevirostris* was also observed between the 2 seasons. This shift in trophic positions indicates the degree of generality in feeding patterns and dietary overlaps among rock pool grazer species. Moreover, the seasonal changes observed in carbon sources, macroalgal species composition and different assimilation efficiencies may have influenced the changes in consumer isotope ratios explaining the shifts in trophic positions. Another observation made was that smaller pools exhibited a 2-level food chain length, indicating the direct influence of habitat size on trophic structure. Based on the exploitation ecosystems hypothesis (EEH) which suggests that food chain lengths are often longer when there is a broader food base (Oksanen et al. 1981, Morris 2008), the shorter food chains observed in smaller pools may have been influenced by unfavourable environmental conditions hindering overall species colonization.

Contrary to the study expectations, the presence of fish exhibited a significant positive effect on overall food web structure in both seasons. Most pools that contained fish exhibited a relatively more diverse trophic structure (**Fig 3.1** u, t, w).These results are consistent with Paine (1980), who observed that the presence of a top predator within rock pool communities promoted trophic diversity. Layer et al. (2011) also observed that food webs with fish exhibited greater trophic packing than those without fish. Because rock pool fishes are highly territorial species, I assume their presence may have a repelling effect on other potential predators of other species within the same pools.

Furthermore, because fish are highly agile species and are always difficult to capture unless destructive methods such as use of rotenone are employed, it is difficult to conclusively account for the changes in fish species composition across the seasons. However, in summer, there was one common species, (*Caffrogobius* spp.) while in winter two additional species were observed (*Clinus* and *Epinephelus* spp.). Based on these observations, seasonality was assumed to have likely had a role in influencing fish composition in the rock pools under investigation particularly because there was a consistent shift in trophic positions in pools containing fish. In support of the findings of

this study was Willis and Roberts (1996) who highlighted that seasonality may cause significant variation in fish and other species abundances and composition. In addition, complementary data obtained from stomach content analysis affirms the possible role of fish in shaping community structure. It was observed that among the klip fishes (*Clinus* spp), the most commonly preyed upon species were sand shrimps (*Palaemon peringueyi*) and these prey items were found aggregated in small, shallow pools which in my opinion may have been a trait-mediated response, possibly habitat preference.

3.6.3 Consumer trophic niche diversity

Trophic diversity was higher in winter than summer as shown by the larger trapezoid (**Fig 3.3**). However, because overall trophic diversity is sensitive to the size of sample (i.e. it is biased towards large populations), SEA_c has been increasingly used to give a more accurate measure of trophic niche area (the realized niche). From the SEA_c, the consumer trophic composition was relatively similar across all pools indicating high dietary overlap. The significant overlap may have been because the species possessed sufficient trait differences to minimize competition on shared resources following the Gauseian maxim stating that no 2 species occupy the same ecological niche, a theory supported by Terbogh (2015). The similarities (compare **Fig 3.2** e *vs* f) in dietary preferences can also be explained by minimal to no variability in zonation. These deductions are also supported by the patch dynamics theoretical framework of meta-communities. Furthermore, the subtle differences observed in species composition may have been a result of seasonal fluctuations in physical environmental factors as supported by the species sorting models of meta-communities confirming the influence of habitat size, structure and seasonal variability in shaping rock pool community structure. The observed differences in trophic structure also show how slight changes in habitat type at smaller spatial scales may interact differently with biological variables as suggested by Byers et al. (2017).

3.7 Conclusion

Although, the results of this study did not contrast to what was expected, particularly with regards to the effects of pool size on trophic diversity; interesting trends were observed with food web packing and trophic redundancy (i.e. MNND and SDNND,

respectively) across all pools in the 2 seasons. This implies that in cooler seasons, rock pool species are presumably more likely to be evenly distributed across spatial gradients. The increase in SDNND with increase in pool size suggests possible species emigration to larger and more environmentally stable pools. Hence, it can be assumed that motile rock pool species may shift between pools of different sizes in search of cooler temperatures as illustrated by Perry et al. (2005). Furthermore, in these pools there is an increased level of dietary similarity evidenced by increase in SEA_c, which could significantly affect species composition through resource competition over time.

It was also observed that the presence of fish seemed to have a notable effect on community structure; pools containing fish exhibited high level of trophic redundancy. Although the high species counts could essentially mean functional insurance, the stability of such communities is highly dependent on species ability to partition resources and also the palatability of the present food sources. Furthermore, depending on species composition, high species diversity may cause positive and/or negative cascading effects. In addition, seasonal shifts in primary productivity could lead to shifts in consumer feeding strategies, shifts in trophic positions and niche roles with possible consequences of distorting community structure and functioning. This also has the potential of triggering trait mediated cascading effects on specialist feeders while in grazer dominated communities, primary productivity can be significantly compromised.

There was a reasonable interaction between species composition and abiotic factors in shaping community size and structure in this study. However, due to the high level of isotopic overlap observed particularly among trophic level 2 and 3 species; because of design of this study, I did not manage to identify feeding preferences solely based on basic stable carbon and nitrogen isotope analyses. It is also crucial to note that within rock pools there exist more trophic links than observed in this particular study, meaning there may have been other factors influencing the trophic structure. This may call for more in-depth measures of carbon sources containing information on mode of carbon acquisition and pathway such as incorporate stable carbon isotopes of essential amino acids ($\delta^{13}C_{AA}$).

ASSESSING CASCADING EFFECTS ON PLANKTON COMMUNITIES IN COASTAL WATERS: A LABORATORY MICROCOSM EXPERIMENT

4.1 Introduction

Coastal ecosystem function and resilience are linked to complex food webs formed from the direct or indirect effects of interactions among species and the environment (Lewandowska et al. 2014; Murphy et al. 2016). The direct effects of temperature may lead to shifts in organism physiology, demographic traits and behaviour, leading to effects on species richness, distribution and composition (Doney et al. 2011; Rousseaux and Gregg 2015). Although direct effects of biological and physico-chemical parameters can affect community structure, there has been mounting evidence suggesting that indirect effects may be more influential in promoting community restructuring than previously predicted (Winder and Schindler 2004).

In pelagic systems, the indirect effects of nutrients on higher trophic levels occur through zooplankton grazing on phytoplankton (Mousseau 1998; Calbet et al. 2000; Montoya-Maya and Strydom 2009). Zooplankton species such as calanoid copepods are critical in marine ecosystem function and productivity because their high abundances transfer organic carbon from primary to tertiary trophic levels (Reiss and Kröncke 2005; Pagano et al. 2006; Calliari et al. 2008; Jagadeesan et al. 2017). This influence of copepods and their support of marine trophic structure has been directly correlated to phytoplankton community size structure and discriminatory feeding preferences, especially for larger sized prey (Bergquist and Carpenter 1986; Nejstgaard et al. 2001; Jang et al. 2010; Boersma et al. 2015). Stoecker and Egloff (1987) and Froneman (2004), showed that calanoid copepods feed predominantly on particle sizes ranging from 2-200µm. Typically, it is assumed that communities dominated by nano- and microplankton have a greater ability of exporting organic carbon to upper trophic levels via short, classical food chains (Cermeno et al. 2006). However, this seemingly simple food chain concept

has been associated with significant cascading effects across the marine food web, promoting and/or mitigating ecosystem resilience.

Given the identified importance of phytoplankton size in plankton community dynamics, particularly their direct contribution to zooplankton biomass and their critical role in the fate of biogenic carbon within pelagic ecosystems (Cermeno et al. 2006; Cáceres et al. 2017), feeding studies often characterise phytoplankton communities based on size structure (Hunt et al., 2017). The three main size classes recognised are picoplankton (0.2-2µm), nanoplankton 2-20 (µm) and microplankton (>20µm), (Azam et al. 1983, Hunt et al. 2017). The ongoing elevation in temperature and decrease in nutrients due to climate change are assumed to favour the proliferation of picoplankton over microplankton promoting microbial over classic food chains. However, because of spatio-temporal variability, impacts are not always universal thus I assessed the importance of temperature and nutrient availability on phytoplankton size structure and its implications for a key copepod species from a warm-temperate region. This was done using a microcosm approach, which allows for control of key variables and the mitigation of potential confounds (Gonzales 2000).

Along the south coast of South Africa is a habitat of an ecologically important calanoid copepod species (*Pseudodiaptomus hessei*) frequently encountered in estuarine and shallow nearshore environments (Isla and Perrissinotto 1991; Jerling and Wooldridge 1991). Several studies (e.g. Kleppel et al. 1996; Froneman 2000, Wollrab et al. 2015; Almeda et al. 2016; Lopes et al. 2016) assessed different aspects of the ecology of this species, including its distribution patterns and feeding behaviour while interactive effects of physico-chemical parameters and phytoplankton size structure have largely been overlooked. Thus, using laboratory microcosms, the study comprised a temporally staggered experiment aimed at assessing three complimentary components. Firstly, I was interested in the role of temperature, nutrients and their emergent effects on determining phytoplankton biomass and size structure. Secondly, the implications of these outcomes on time-delayed zooplankton inoculates were assessed. Finally, the role of zooplankton responses in mitigating the initially observed bottom-up effects was assessed.

4.2 Materials and Methods

4.2.1 Experimental set-up

The microcosm experiments were run at 2 different temperatures: 17 and at 24 ±1°C (see set-up in **Fig 4.1**) with a 12:12 light:dark regime. For each temperature regime, naturally occurring phytoplankton communities were collected from the shallow (< 0.4m) regions within lower reaches of the Kowie estuary on the south coast of South Africa, <100m from sea, in 20L containers. To retain microphytoplankton, while also eliminating mesozooplankton, the collected seawater was passively filtered through a 41µm. From the filtrate, size fractionated chl-*a* analysis (see standard procedure in Chapter 2) was performed through a 20 µm Nitex nylon mesh filter (microplankton > 20 µm), a 2 µm Millipore isopore membrane filter (nanoplankton 2–20 µm) and a 0.7 µm Whatman GF/F filter (picoplankton 0.7–2 µm. Two litre experimental bottles (n = 24) were filled with the filtered sea water and placed in a controlled environment (CE) room (**Fig 4.1**). Treatments (NP, N, P and C; n = 6 replicates) were assigned randomly to the individual bottles. The N treatment received a nitrate enrichment of 10µM L^{-1} every 48h; NP contained 10µM L^{-1} and 15µM L^{-1} of nitrates and phosphates, respectively; P contained 15µM L^{-1} and C was the control with no nutrients added. For each microcosm with the exception of the controls, 1000µL L^{-1} of each respective nutrient working stock solution was added every 48h to maintain elevated nutrient levels. The NP treatment contained 1000µL L^{-1} of both nutrients.

Prior to copepod addition, phytoplankton assemblages were allowed to respond to the different nutrient treatments for 14 days after which the experiments ran in the presence of copepods for another 21 days, totalling to 35 days. The second experiment was run 3 days after the termination of the first following the same procedure.

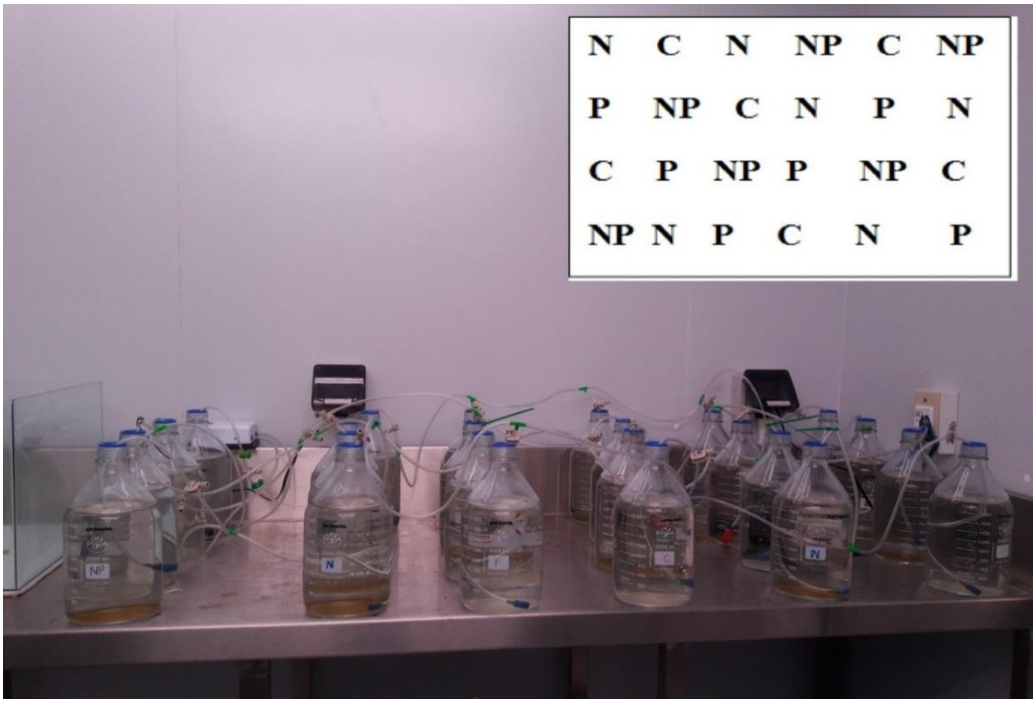

***Figure 4. 1*:**Laboratory microcosm set-up for copepod grazing experiment

4.2.2 Treatments and nutrient stock preparation

The nitrate (N) and phosphate (P) working stock solutions used in the microcosms had a concentration of 10µM and 15µM, respectively (Gobler et al. 2002). For the N treatment, 25.4g of sodium nitrate ($NaNO_3$) was dissolved in 100mL deionized water using a FMH model STR-M H-180 magnetic stirrer (B and M Scientific CC, South Africa) for 10mins. Next, 5mL of the primary solution was pipetted into a bottle containing 1L of autoclaved water (~140°C, 24h) giving a working stock solution of 1.27g L^{-1} of N. To produce a 15µM concentration of P, a dilution procedure similar to the N stock solution was done using 20.7g of potassium phosphate (KH_2PO_4). From this solution, 1mL was pipetted into 1L deionized water giving a working stock solution of 0.207g L^{-1}. The working stock solutions were kept refrigerated.

4.2.3 Zooplankton sampling

Field sampling was conducted in the lower reaches of the estuary at dusk when zooplankton migrated to the upper water layer from the sediment-water interface. *In situ* temperature and salinity were measured using a multi-parameter YSI 500 sonde meter prior to sampling. Zooplankton samples were collected following methods consistent

with Christoffersen and Jerspersen (1986) and Froneman (2004) and involved towing a 200µm mesh plankton net for replicated 10m distances at a depth of 0.5m. For each temperature regime, the zooplankton samples were transported from the field in 20L containers and upon arrival at the laboratory, were transferred into 35L gently aerated aquariums and left for 24h to acclimate to the experimental temperatures in the CE room. A total of 15 male and 5 female adult copepods were isolated under a dissecting microscope in a petri dish and transferred into the experimental bottles using a pasteur pipette cut ~2cm from the tip to avoid damage of appendages. This 3:1 ratio was maintained to minimize egg cannibalism (Lavens and Sorgeloos 1996). Microcosms were topped up with distilled water every 48h to maintain constant water salinity.

4.3 Data acquisition

As a standard protocol to avoid sample contamination, at day 34 of the experiment, 4L (n = 4) glass beakers to be used to hold the phytoplankton sample filtrate were acid washed with 1% HCl and rinsed 10 times with distilled water (He et al. 2015; Jagadeesan 2017). The beakers were labelled following the treatment labels (NP, N, P and C) and for all 6 replicates of each treatment, the corresponding beaker was repeatedly used. Each beaker was rinsed 3 times in between samples. At day 35, all microcosms were manually shaken to ensure homogeneity of samples (He et al. 2015), after which water chemistry parameters were recorded (**Appendix 4**). Subsequently, copepods were collected by passive filtration through a 41µm mesh. Using a squeeze bottle, the retained copepods were washed with 70% ethanol into 50mL labelled sample jars and stored for later quantification. From the filtrate, 250mL was sub-sampled for size fractionated chl-*a* analysis and nutrient analysis. During the filtration process, each saturated filter size class was routinely checked for potential copepodites that may have been filtered out. Total copepod abundances were counted using a dissecting microscope (Bioscope, USA). Due to the diverse stages of nauplii and copepodites present, the first size category contained the 6 nauplius stages, referred to as nauplii, and the second size class included all copepodites and the adult stage. The above procedures were performed for both temperatures.

4.3.1 Specific growth rate

The specific growth rate (SGR) is an important parameter derived from population growth studies. SGR is a measure of the suitability of different conditions to species productivity. In the present study, to quantify the influences of different nutrient treatments and temperature on copepod productivity, SGR was calculated separately for each replicate based on the formula following Viayeh and Mohammadi, (2012).

$$\text{Specific Growth Rate (SGR)} = \frac{\ln N_t - \ln N_0}{T}$$

Where; N_t= population density after duration of experiment

N_0 = population density at the start of the experiment

T = duration of grazing experiment (21 days)

4.3.2 Copepod egg production

Species egg production is a direct index of organism condition (Hagiwara et al. 2001). To characterise the effects of experimental conditions on egg production, the ratio of egg count to total number of females is usually performed (Viayeh and Mohammadi 2012). Copepod egg ratio was estimated as the number of eggs divided by the number of females sampled in each treatment in both temperature regimes. Prior to commencement of the grazing experiment ~24 female copepods were selected from the aquaria for egg counts. The mean value from 3 repeated egg counts was recorded for each copepod. After termination of the experiment, from each microcosm, the mean value from 3 repeated egg counts from 4 copepods from each microcosm was recorded. At the end an assessment was made between copepods freshly caught from the wild *versus* after the experiments.

4.4 Data Analysis

Prior to analysis, all data were tested for normality using the Shapiro test and were found to be normal. To assess the differences in total phytoplankton biomass recorded at days 0, 14 and 35 across the two temperatures, a repeated measures ANOVA was conducted. Three separate multivariate analyses of variance (MANOVA) tests were then performed

on size-fractionated phytoplankton biomass based on the three filters (20, 2, 0.7μm) in response to temperature and nutrient treatment. In addition, a two-way ANOVA was conducted to assess variation in combined phytoplankton biomass with treatment and nutrients. ANOVA tests were also performed for copepod abundances with temperature and nutrients as fixed factors. The copepod abundances were categorised as combined counts (adults + nauplii), then as separate counts of adults and nauplii. Separate repeated measures ANOVA were also done to assess the differences in phytoplankton size structure before and after grazing. Where significant effects were observed a Tukey's HSD test was performed to determine the location of differences within the data set. Effects of temperature and nutrients on copepod egg ratios, adult SGR and nauplius SGR were analysed using two-way ANOVA. All analyses were performed in R version 3.4.2 (R Core Team 2017).

4.5 Results

4.5.1 Phytoplankton biomass and size structure

There was an increase in total phytoplankton biomass particularly at 24°C between day 0 and day 14 prior to grazer presence while after the addition of copepods, phytoplankton biomass increased at 17°C and decreased at 24°C (**Fig 4.2**). However, a two-way ANOVA indicated no significant differences in overall phytoplankton biomass over time or between temperatures. The NP treatment maintained a high phytoplankton biomass before and after copepod addition with the control having the least irrespective of temperature. A two-way ANOVA indicated no significant interaction between temperature and treatment on total phytoplankton biomass at day 35, however treatment had a main effect. A repeated measures ANOVA indicated significant differences in phytoplankton size structure (with treatment as the error term) between day 14 and 35. Overall, the MANOVA tests (**Table 4.1**) indicated a significant interaction between temperature and nutrient treatment ($F_{(3,40)}$=12.3, p<0.001) on picoplankton, while temperature had a positive influence on microplankton communities ($F_{(1,40)}$=19.043, p<0.001; **Fig 4.3a**), while nanoplankton communities were influenced by nutrient treatments ($F_{(3,40)}$=2.975, p=0.045).

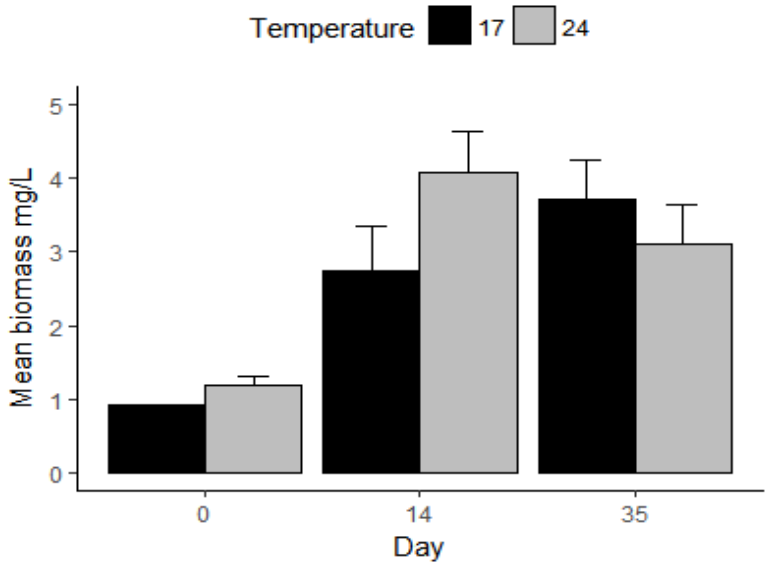

Figure 4. 2: Mean (+SD) total phytoplankton biomass before and after the addition of copepods on day 14.

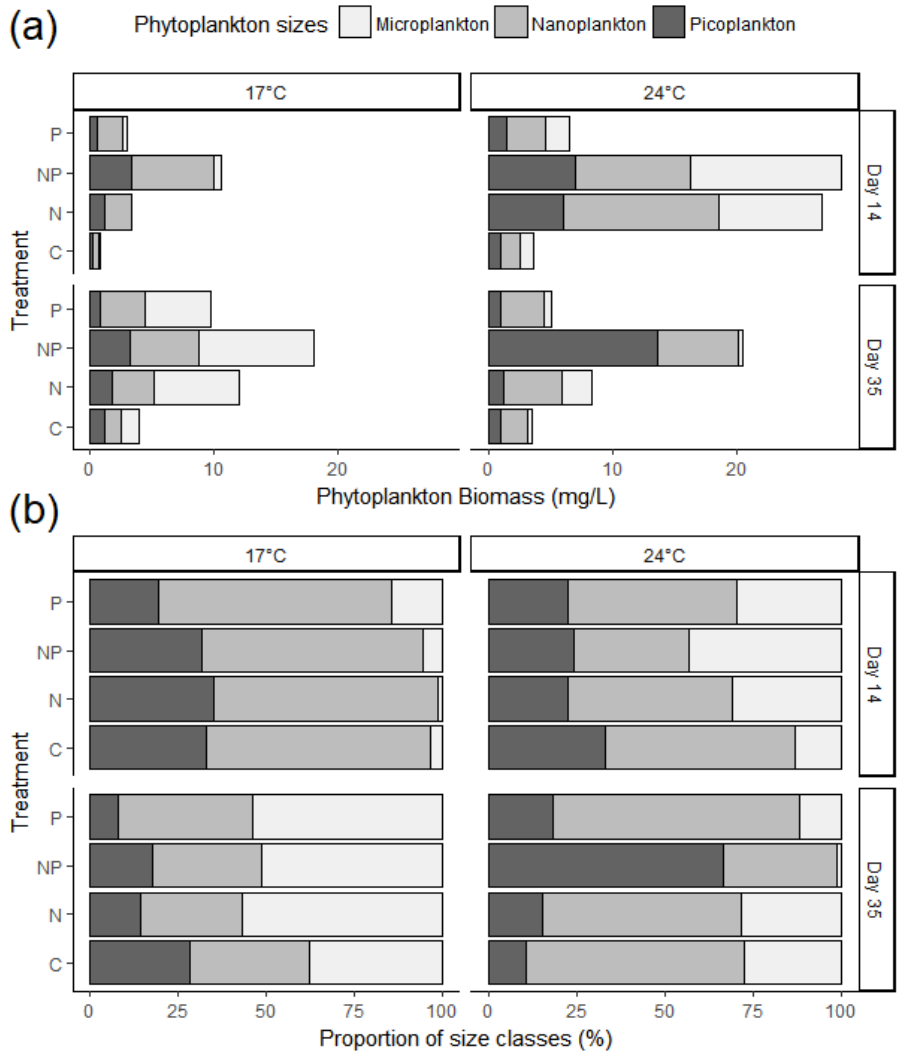

Figure 4. 3:Phytoplankton (**a**) densities and (**b**) proportion of size classes observed with different nutrient treatments and at different temperatures. Day 14 and 35 indicate the start and end of the grazing experiments, respectively.

Table 4. 1*:* Results from the MANOVA of size-fractionated phytoplankton responses to treatment and temperature regimes, significant results indicated in bold.

Source	**Microplankton**			**Nanoplankton**		**Picoplankton**	
	Df	***F***	***p***	***F***	***p***	***F***	***p***
Treatment	3,40	2.340	0.087	2.975	**0.042**	23.565	**<0.001**
Temperature	1,40	19.043	**<0.001**	0.579	0.451	10.854	**0.002**
Treatment × Temperature	3,40	2.549	0.069	0.091	0.964	12.300	**<0.001**

4.5.2 Copepod abundances

There was a significant interaction between temperature and nutrients on adult copepods ($F_{(3,40)}$ = 4.15, p < 0.05; **Table 4.2**). Temperature had no effect as a main factor, while nutrients affected total copepods abundances ($F_{(3,40)}$ = 6.42, p < 0.001) and nauplius abundances ($F_{(3,40)}$ =5.35, p = 0.003). Higher copepod abundances were recorded in the NP and N treatments, while the P and control treatments recorded the least across both temperature levels (**Fig 4.4)**. A Tukey's post hoc test revealed significant differences in total copepod abundances between NP and control treatments at 17°C (p < 0.05) while the same treatments were significantly different between 17°C and 24°C (p < 0.01).

Table 4. 2: Multivariate ANOVA summary of results of microcosm experiments on the effects temperature and nutrients (treatment) on copepod abundances separated into 3 categories (totals, adults and nauplii).

Factor	***Df***	**Totals**		**Adults**		**Nauplii**	
		F	***p***	***F***	***p***	***F***	***p***
Treatment	3,40	6.421	**0.001**	5.582	**<0.001**	5.350	**0.003**
Temperature	1,40	0.523	0.473	0.330	0.568	0.498	0.484
Temperature × Treatment	3,40	1.278	0.294	4.153	**0.011**	0.395	0.756

4.5.3 Specific growth rate

There were notable differences in SGR between adults and nauplii populations (**Table 4.3**). Although there were no significant interactions between temperature and treatment on total copepod SGR, treatment had significant main effect on the SGR of nauplii (**Table 4.4**) while temperature and treatment independently influenced adult copepod SGR. Post hoc tests showed that NP and N treatments were significantly different from the P treatment and the control in the case of nauplii.

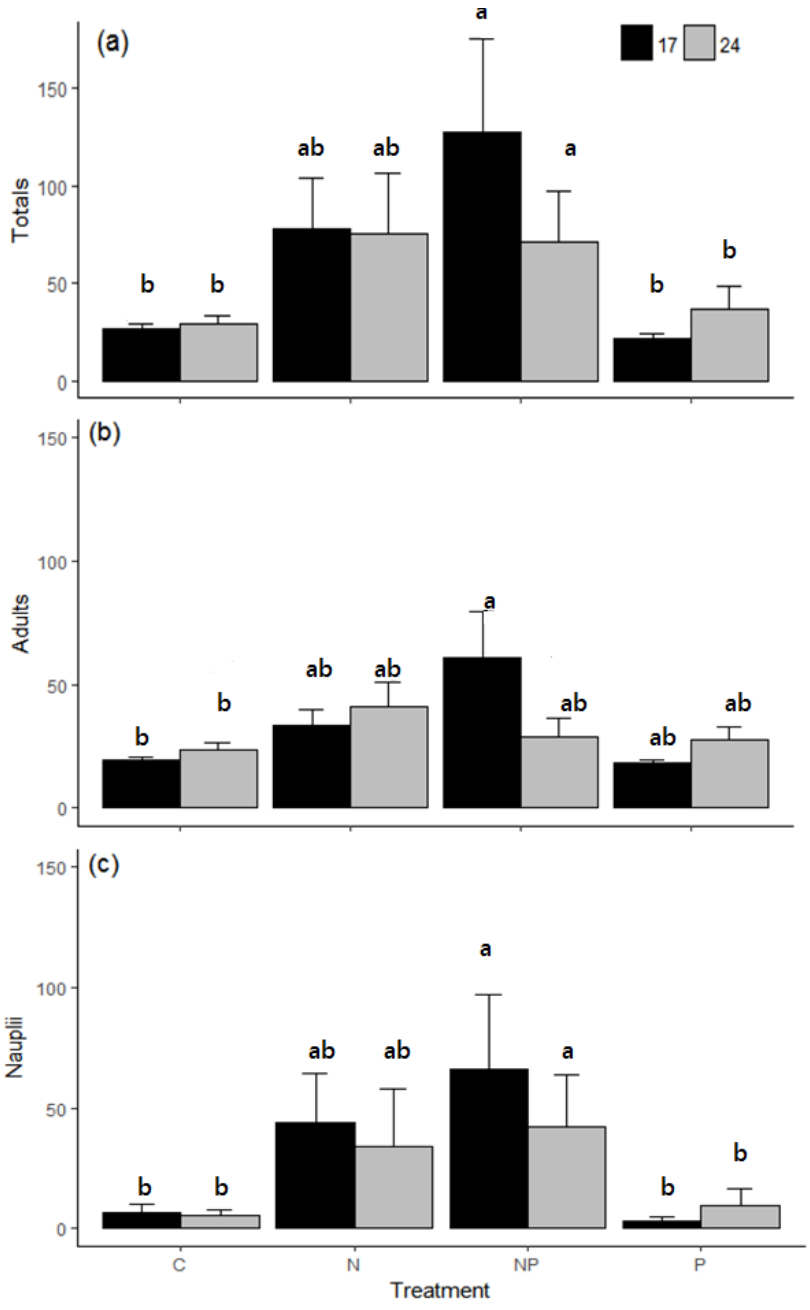

Figure 4. 4: Mean copepod abundances at different nutrient and temperature treatments. Letters indicate homogenous groups.

Table 4. 3: Mean (±SE) copepods' specific growth rates.

	Adults SGR		**Nauplii SGR**	
Variable	**17°C**	**24°C**	**17°C**	**24°C**
	Mean± SE	**Mean ±SE**	**Mean± SE**	**Mean ±SE**
NP	0.1±0.02	0.05±0.00	0.22±0.02	0.17±0.03
N	0.07±0.02	0.05±0.01	0.21±0.02	0.17±0.02
Control	0.025±0.01	0.01±0.01	0.09±0.03	0.06±0.03
P	0.026±0.00	0.02±0.00	0.06±0.03	0.07±0.03
Overall SGR	0.08±0.02	0.03±0.01	0.35±0.03	0.33±0.03

Table 4. 4: Two-way ANOVA summary of results on the effects of temperature and nutrients on copepod specific growth rates.

Factor		**Adult SGR**		**Nauplius SGR**	
	Df	***F***	***p***	***F***	***p***
Treatment	3,88	3.52	**0.018**	7.039	**0.0002**
Temperature	1,88	4.35	**0.039**	1.846	0.177
Treatment× Temperature	3,88	1.66	0.179	0.119	0.948

4.5.4 Copepod egg ratio

A two-way ANOVA of copepod egg ratios indicated no significant interaction between treatment and temperature, while treatment had a main effect (**Fig 4.5**, **Table 4.5**). Post hoc tests further indicated significant differences among start values and values pooled for all treatments and also differences among treatments ($p < 0.05$).

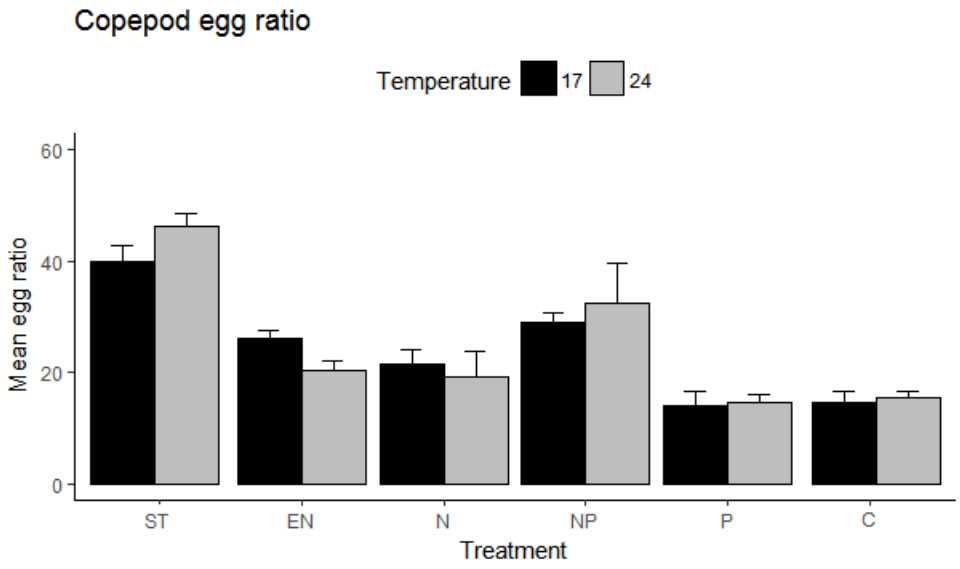

***Figure 4. 5*:** Mean copepod egg ratios recorded at the start, end and within treatments, where C,N,NP and P represent the nutrient treatments, EN indicates overall egg ratio at the end of experiments and ST shows the mean copepod egg ratio before incubation.

Table 4. 5: Summary of two-way ANOVA on the effects of temperature and nutrients on copepod egg ratios.

Variable	***Df***	***F***	***p***
Treatment	5,78	34.086	**0.0001**
Temperature	1,78	0.044	0.865
Treatment × Temperature	5,78	1.861	0.111

4.6 Discussion

In this chapter, I investigated the shifts in plankton community structure (i.e. phytoplankton size structure, biomass, copepod abundances and growth rates) as a result of changes in temperatures and nutrients. This study was based on a three-part assumption that copepod feeding and biomass would be directly influenced by phytoplankton sizes and biomass, while the phytoplankton communities would be affected by nutrient treatment and possibly temperature. The results demonstrated direct, indirect and contrasting influences of temperature and nutrients on plankton communities.

4.6.1 Interactive effects of temperature and nutrients on phytoplankton biomass and size structure

Because of known temperature and nutrients effects on phytoplankton metabolism, the initial hypothesis was that elevated temperature and nutrient addition would result in an increase in phytoplankton biomass in the absence of grazers. The results obtained highlighted a positive increase in mean total phytoplankton biomass between days 0 and 14 at both temperatures when all treatments were pooled. However, there was a notable shift in phytoplankton size structure irrespective of temperature, potentially due to interaction between temperature and nutrient treatments. On day 14 after nutrient addition in the absence of copepods, there was a more pronounced increase in microplankton at 24°C in comparison to 17°C (**Fig 4.3a**); these findings are consistent with Puccinelli et al. (2016). At low temperatures, pico- and nanoplankton were visibly dominant in comparison to microplankton, suggesting the greater competitive advantage of smaller celled communities at low temperature consistent with Agawin et al. (2000). The results from MANOVA analysis indicated that temperature and nutrients had contrasting effects on each of the phytoplankton size classes (**Table 4.1).** This demonstrates significant interactive effects of temperature and nutrients in structuring phytoplankton communities within coastal habitats.

Although nutrient impacts may differ with location (Tyrrell 1999, Howarth and Marino 2006), nutrients have been regarded as primary controllers of phytoplankton biomass and structure (Hill and McQuaid, 2008; Hilligsøe et al. 2011; Tahezardeh et al. 2017). In this study, I was interested in assessing the relative strengths of the effects of nitrates (N) and phosphates (P) on plankton communities in the south coast. The presence of N in the NP and N treatments exhibited a consistently stronger stimulatory effect on the whole phytoplankton community as compared to P after 14 days of nutrient addition across both temperatures. These results demonstrate the potential for N to impose the law of minimum effect in the proliferation of coastal primary productivity. Consistent with the study outcomes are Schluter (1998) and Sundareshwar et al. (2003), who reported significant effects of N on phytoplankton growth and abundance in coastal ecosystems.

4.6.2 Effects of copepods on phytoplankton communities and size structure

Across both temperatures, the presence of grazers brought about significant changes to phytoplankton abundances and size structure (**Figs 4.2**, **4.3**). The addition of copepods brought about positive shifts in phytoplankton abundances at 17°C, but a decline at 24°C while size structure differed between the temperatures. At low temperature, selective feeding by copepods is assumed to have contributed to nanoplankton depletion (**Fig 4.3b**) consequently creating a niche gap then occupied by microplankton. The results further suggest a feeding shift from nanoplankton to microplankton at 24°C as indicated by the significant drop in microplankton communities. It is assumed, this shift was prompted by a metabolic demand for food with higher carbon content, leading to copepods favouring larger cells and the release of picoplankton from grazing pressure with the opposite holding true at low temperature.

Furthermore, it is assumed the presence of zooplankton may have indirectly led to changes in water chemistry parameters such as oxygen reduction potential (ORP), nutrients and pH, potentially influencing phytoplankton communities and sizes, a finding consistent with Haney (1987) and Winder and Sommer (2012). The higher nutrient content (e.g. in N and NP treatments, **Appendix 4**) observed at the end of the grazing experiment is evidence that copepods may have contributed to nutrient regeneration through faecal matter deposition in the water column demonstrating a biogeochemical cycle typical in the open ocean. Furthermore, the increase in nutrients could have been because copepods sequester less N in the water column in comparison to other zooplankton species such as cladocerans Sommer and Sommer (2006).

4.6.3 Effects of temperature and nutrients on copepod turnover

Specific growth rate (SGR) is regarded as a comprehensive parameter that yields valuable insights into the suitability of water chemistry parameters for a given species (Viayeh and Mohammadi, 2012). The non-significant differences in copepod SGR and abundances between the two temperature regimes (**Tables 4.2**, **4.3**) suggest that temperature was not particularly influential in copepod reproduction and biomass, in contrast to the findings of Froneman (2001). This is attributed to the physiological

adaptions of zooplankton to changes in habitat conditions (Saiz and Calbet, 2011). None the less, a visual assessment of the raw data showed a slightly higher copepod turnover at 17°C. Lavens and Sorgeloos (1996) conclude that the optimum temperature for calanoid copepod growth and development is 16±2°C which could also explain the increased copepod abundances recorded in this study.

Although there were no significant temperature effects on copepod growth rates, the indirect effects of nutrients on copepods were manifested through differences among treatments in egg ratio. The results indicate that copepods in the N and NP were reproductively more fecund than in other treatments (P and control; **Table 4.3**). These observations portray how shifts in nutrient availability can significantly initiate cascading effects along the trophic chain by influencing the numbers of copepods developing into adults. However, although nutrients can have significant positive effects on plankton communities, He et al. (2015) highlighted that an increase in nutrients may promote the production of dinotoxins by some dinoflagellate species, causing detrimental effects on other higher-level species within the ecosystem. While this could partially explain the variations in copepod abundances observed in the microcosms, the concept cannot be examined here as phytoplankton species were not identified.

4.7 Conclusion and Recommendations

One of the major concerns experienced in the microcosm experiments which may have been due to the artificial habitat was the significant drop in egg ratios between freshly caught and experimental copepods, indicating an experimental artefact. While these may be drawbacks with laboratory microcosms, experiments including microorganisms are often difficult to perform in the wild. As such, manipulative experiments that contain a prey assemblage closest to the natural prey community have been associated with giving estimates of trophic interactions *in situ*. Hence, from this study, the indirect effects of temperature on plankton communities were recognised. Both top-down (grazing) and bottom-up (nutrient availability) effects proved to be important determinants of plankton community structure and abundance.

The significant effects of nutrients on nauplius abundances irrespective of temperature (**Table 4.2**; **Fig 4.4**) can initiate significant cascading effects across the ecosystem. Furthermore, although no effects of nauplii on picoplankton biomass were evident, they are assumed to have significant effects on phytoplankton abundances particularly in the euphotic as they do not exhibit diel vertical migration. Thus, to fully estimate their feeding effects on phytoplankton community structure, it may be necessary to conduct feeding experiments based on different known phytoplankton densities.

The importance of a preference for larger sized food particles by copepods cannot be overstated. From this study, it is understood that copepods preferentially fed more on microplankton at 24°C than at 17°C. However, the actual species preferred are still yet to be clarified, thus it would be meaningful to consider phytoplankton identification to allow for the identification of potential species which may have allelopathic effects on other phytoplankton species. Furthermore, it will be worth assessing the metabolic carbon demand of copepods and the carbon content of phytoplankton at different temperatures. It is thus suggested that the carbon content of phytoplankton assemblages before and after incubation experiment be measured to better understand the effects of temperature on copepod feeding preferences.

In conclusion, although gut fluorescence and evacuation experiments may could been implemented to minimise experimental artefacts, the chosen incubation experiments provided valuable predictions into the interactive effects of temperature and nutrients and how they influence plankton growth rates and biomass. Due to the paucity of knowledge on the effects of sex on feeding preferences, it is also strongly recommended that feeding experiments involving the separation of males and females be used to assess trophic cascade strength in coastal ecosystems of South Africa.

GENERAL SYNTHESIS

Concerns among community ecologists have shifted from the extinction of specialist species to the effects on communities of domination by the remaining, resilient species in the ecosystem (McKinney and Lockwood, 1999; Olden et al. 2004; Olden and Rooney, 2006; Clavel et al. 2010). Although strongly assumed to be driven by anthropogenic effects, this phenomenon, referred to as biotic homogenization (Smart et al. 2006, Velle et al. 2014), recognises the potential effects of within species interactions in addition to physical factors in shaping community structure and composition. However, the complexities of interactions among these factors make understanding species responses to local environmental and global climate change more difficult. The results of this study highlight the contributions and effects of these two factors within rock pools along the south coast of South Africa.

5.1 Species diversity and community structure in rock pool ecosystems

Species richness was an important indicator of how seasonal changes in abiotic factors contribute to species proliferation and composition within rock pools. The large difference in species richness between small and large pools in summer *versus* the small difference in richness between these pool sizes in winter is an indication of species responses to changes in physico-chemical parameters at micro-scales (100's m). Although temperature did not directly affect species richness, its effects manifested through seasonal changes in salinity, conductivity and pH. With substratum and water depth shifts, I was also able to observe the effects of seasonal variability in intertidal species composition. The effects of habitat size proved influential in controlling water chemistry parameters directly and indirectly affecting richness and composition.

The seasonal analysis of stable carbon and nitrogen isotope values provided a snapshot of within species interactions and also the influence of physical factors on the size and trophic structure of intertidal communities over space and time. The changes in food

chain length, size and trophic positions observed in this study are evidence of the impacts and/or extent of localized environmental and ecosystem shifts. Shifts in trophic positions may essentially mean a change in diet and ecosystem restructuring which might initiate cascading effects. For example, the shift between an odd and an even length food chain with dominance by secondary consumers may over time determine spatial structuring in intertidal ecosystems as supported by van der Heide et al. (2012).

5.2 Trophic cascades within coastal communities

5.2.1 Top-down trophic control in plankton communities

The addition of copepods, demonstrated direct and indirect top-down effects on phytoplankton. Copepod grazing is assumed to have created niche gaps within phytoplankton communities allowing for compensatory growth of both the grazed and ungrazed or unpalatable material. The addition of copepods is also assumed to have indirectly affected phytoplankton through changes in water chemistry and nutrients as they have been known to sequester less nitrates in the water column in comparison to other zooplankton, such as cladocerans as found by Sommer and Sommer (2006). This demonstrates that the presence of copepods' affects nutrient concentrations, which in turn (i.e. the nutrient concentrations) directly affect phytoplankton biomass and community structure while also having indirect consequences on higher trophic level species.

The presence of copepods is assumed to have initiated a shift in phytoplankton size structure across both temperatures. It is known that copepods feed on a broad spectrum of phytoplankton (e.g. Stoecker and Egloff 1987; Froneman 2000). However, in this study I was able to observe that the preferred range was between 2-20µm, as shown by significant depletion of nanoplankton at low temperature while at higher temperature, although subjective to treatment, there was an overall decline in microphytoplankton (>20µm). This suggests a significant interaction between temperature and nutrients in influencing copepod feeding regimes based on phytoplankton composition. As such, the exhibition of discriminatory feeding by copepods may be a factor of food quality rather than quantity, meaning copepods can forego larger particles to feed on smaller sized

phytoplankton as suggested by Frost (1972), Gifford and Dagg (1988), Atkinson (1996) and Lee et al. (2012), which as supported by Anderson and Hessen (1995) and Touratier et al. (1999) may be driven by shifts in metabolic carbon demands.

Because my study indicates that copepods can switch between prey items as a result of temperature shifts, it can be speculated that the predicted changes in temperature within the Agulhas Current Large Marine Ecosystem (ACLME), are likely to affect feeding strategies of generalists while among specialist feeders changes in phytoplankton composition may have more detrimental effects such as species diversity loss if their preferred food is depleted by other generalists. It is anticipated that changes in ocean temperature together with pollution from the terrestrial environment and freshwater intrusions from estuaries subsequently alter water chemistry parameters such as pH may impair the uptake of nutrients by phytoplankton directly affecting their abundances and potentially size structure. This occurrence is likely to affect copepod productivity with potential density mediated indirect consequences on other species within the same and /or higher trophic levels.

5.2.2 Bottom-up effects in coastal productivity

There have been conflicting assumptions on the effects of nitrates (N) and phosphates (P) in coastal ecosystem productivity. Although N has been conventionally known as the primary limiting nutrient, there is growing evidence that phosphorus is almost equally important (Sundareshwar et al. 2003) in most communities and is not confined to specific locations as previously assumed. It was observed in this study that, across both temperatures in the presence or absence of grazers, NP enriched treatments had higher phytoplankton densities in comparison to N treatments, while P enriched treatments were also notably higher than control treatments (**Fig 4.4**). In zooplankton communities, there was also a positive increase in biomass, specific growth rates (SGR) and egg ratios in the NP treatments relative to other treatments while the P treatments had notably higher SGR relative to the control treatments. This study together with other studies (e.g. Stolte and Riegman 1995; Treibergs et al. 2014; Poxleitner et al. 2016), acknowledges the significance of N, while at the same time, emphasising the importance of P availability in structuring phytoplankton communities and overall ecosystem function. From basic

plant ecology, P is important for carbon fixation and energy storage and transfer; relating this to the current study, shifts or changes in the dynamics of P can initiate cascading effects on ecosystem sustenance and productivity.

There were notable changes in total phytoplankton biomass before and after the addition of copepods. In the absence of copepods between day 0 and 14, low temperature (17ºC) appeared to have slowed down phytoplankton biomass in comparison to the same time frame at 24°C. On the other hand, after copepod grazing (day 35), an increase in total phytoplankton biomass and copepod biomass were recorded at 17°C while at 24°C, total biomass decreased in both communities despite the initially high phytoplankton biomass recorded at 24°C. Another comparison between the most enriched treatment (i.e. NP) between temperatures indicated higher copepod biomass at 17°C than at 24°C. This highlights the interactive effects of nutrients and temperature had on phytoplankton species composition, potentially promoting the growth of palatable and/ or unpalatable phytoplankton species at each temperature regime with effects on copepod SGR and egg production. It is also evident that an increase in one trophic level does not consequently result in a positive effect on the other.

5.3 Concluding remarks

The results of this study highlighted a clear association between direct and indirect effects of temperature, nutrients and habitat structure and rock pool community structure and species biomass along this south coast intertidal ecosystem. The interaction between temperature and nutrients initiated bottom-up cascading effects on copepod biomass, egg production and growth rates. The presence of copepods had a direct top-down influence on phytoplankton abundances and an indirect impact on phytoplankton community structure. Furthermore, there was a positive shift in water chemistry, including nutrient concentrations, in the presence of copepods. However, there was a general decrease in species abundances with temperature elevation within the sampled coastal communities, with only phytoplankton proliferating at high temperature (24°C) in the absence of grazers. In light of global temperature shifts, this suggests that, although not all communities will diminish in richness with increase in temperature, the effects of

positive shifts are likely to be masked by the overall negative impacts in this case grazing effects by copepods. Furthermore, although overall species richness may not change, there are likely to be significant effects on composition and trophic structure, initiating either positive or negative cascading effects.

This study also recognized the importance and influence of species interactions on community structure in this coastal environment, particularly the presence of grazers (copepods) and predators (fish). The presence of fish and addition of copepods both promoted trophic redundancy potentially minimising functional impairment. However, although it is still debatable in diversity-stability hypotheses, trophic redundancy is important in ecosystem stability as it provides insurance against functional impairment as stated by the redundancy hypothesis (i.e. functionally similar species can take over the role of species that have gone extinct or migrated with minimal disturbance to overall ecosystem functioning).

Based on the evidence provided in this study, although there was a significant interaction between temperature and nutrients on primary productivity, size structure and community composition; temperature and nutrients also indirectly affected animal composition and abundances as observed by the seasonal decline in biomass of copepods, macroinvertebrates and fish. This study showed how direct and indirect trait and/or density- mediated top-down consumer effects could override or interact with physical factors (such as temperature or nutrients) in shaping intertidal community size structure, richness, composition and food-web shape, size and functioning. The change in trophic diversity, composition and community structure in the presence of grazers and other consumers may indicate some of the effects of biotic homogenization in coastal ecosystems. As such, I conclude that although physical factors have a significant effect on community structure, "winner species" contribute to intertidal community size, structure and functioning more than previously recognized.

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APPENDIX 1: Summary of mean pool environmental variables (±SD) recorded in summer and winter.

Pools	Depth (cm)	TDS (ppt)	Salinity (ppt)	Conductivity (mS)	ORP (mV)	Temperature (°C)	pH	Area (m^2)	Size class	Substratum	Chl-a (mg/L)
SUMMER											
Pool 1	30.27±14.6	36.7±0.1	35.71±0.1	46.47±0.5	-149.7±1.3	28.9±0.1	8.79±0.4	0.89±0	Small	3	0.25±0.02
Pool 2	33.79±5.03	35.80±0.33	35.51±0.31	45.39±0.28	-137.9±6.5	26.85±3.75	9.31±0.12	1.71±0	Large	1	0.21±0.02
Pool 3	26.10±8.34	36.95±0.41	36.82±0.74	46.640.58	-132.9±4.9	28.85±0.64	9.06±0.01	0.36±0	Small	5	0.32±0.09
Pool 4	23.10±13.15	35.85±0.29	35.96±0.04	45.62±0.02	-102.2±7.9	29.35±0.35	8.74±0.06	0.46±0	Small	2	0.15±0.01
Pool 5	19.77±6.00	35.60±0.09	35.89±0.55	45.09±0.42	-164.3±0.9	29.03±1.55	9.44±0.50	1.47±0	Large	2	1.12±0.15
Pool 6	22.87±18.53	36.51±0.05	35.82±0.43	46.17±0.04	-126.5±1.7	29.17±0.42	8.79±0.21	0.47±0	Small	5	1.87±0.32
Pool 7	13.57±5.29	35.44±0.42	35.06±0.73	45.29±0.17	-103.2±2.3	28.47±0.21	8.71±0.02	0.38±0	Small	1	0.55±0.11
Pool 8	28.17±13.99	35.44±0.42	35.22±0.22	45.16±0.60	-120.9±0.1	27.03±1.45	8.95±0.14	1.87±0	Large	2	0.76±0.33
Pool 9	20.60±4.98	35.73±0.20	35.47±0.12	45.28±0.04	-106.6±0.3	25.60±1.21	8.71±0.09	2.59±0	Large	5	1.31±0.16
Pool 10	24.07±9.11	35.68±0.07	35.26±0.40	45.23±0.32	-117.3±0.7	23.70±0.75	8.92±0.09	2.08±0	Large	2	0.72±0.31
Pool 11	36.90±22.94	35.83±0.19	35.49±0.06	45.44±0.31	-83.33±2.6	25.67±0.40	8.43±0.07	2.47±0	Large	2	0.87±0.04
Pool 12	45.67±10.02	35.92±0.43	35.50±0.03	45.81±0.17	-71.37±0.6	26.80±4.59	8.20±0.95	1.91±0	Large	5	0.46±0.13
WINTER											
Pool 1	30.27±14.63	36.02±0.19	34.56±0.21	45.53±0.27	-146.9±12.1	15.10±0	8.09±0.06	0.89±0	Small	4	0.06±0.05
Pool 2	31.07±5.03	36.17±0.14	35.37±0.6	45.80±0.15	-125.2±15.7	15.80±0.14	7.38±0.01	1.71±0	Large	2	0.10±0.02
Pool 3	23.10±13.15	36.53±0.04	35.95±0.07	46.30±0.07	-126.8±0.07	16.90±0.28	7.36±0	0.36±0	Small	5	0.09±0.01
Pool 4	16.40±3.11	36.84±0.14	36.01±0.14	46.45±0.25	-122.4±8.63	17.50±0.14	7.37±0.01	0.46±0	Small	3	0.08±0.01
Pool 5	29.67±13.18	36.27±0.16	35.69±0.25	45.92±0.34	-118.3±0.47	18.47±0.25	7.38±0.01	1.47±	Large	1	0.06±0.07
Pool 6	13.47±2.60	36.86±0.08	35.88±0.12	46.76±0.52	-120.7±5.61	18.63±0.47	7.38±0.01	0.47±0	Small	5	0.05±0.05
Pool 7	12.35±6.86	36.68±0.03	36.04±0.06	51.10±4.53	-121.8±6.65	18.65±0.07	7.37±0.01	0.38±0	Small	1	0.47±0.06
Pool 8	28.17±13.99	48.69±0.92	35.63±0.87	53.07±2.35	-148.0±5.83	19.69±0.86	9.11±0.02	1.87±0	Large	1	0.04±0.04
Pool 9	20.60±4.98	48.76±2.3	36.35±0.08	54.58±0.43	-162.1±3.21	20.60±0.29	9.26±0.09	2.59±0	Large	5	0.05±0.02
Pool 10	19.10±4.24	48.94±1.17	36.28±0.28	54.69±0.37	-158.8±6.93	18.79±0.3	9.23±0.07	2.08±0	Large	2	0.07±0.06
Pool 11	27.20±6.8	48.27±0.34	36.01±0.35	54.32±0.48	-163.0±3.44	18.87±0.65	9.31±0.06	2.47±0	Large	3	0.02±0
Pool 12	51.93±13.88	46.60±0.2	36.08±0.01	54.44±0	-133.9±0.20	17.56±0.05	8.810.01	1.91±0	Large	5	0.04±0.01

APPENDIX 2: List of rock pool species collected during sampling

FISH
Caffrogobius nudiceps
Clinus agilis
Clinus cottoides
Psammogobius knsynaensis
Caffrogobius caffer
Clinus superciliosus
Epinephelus marginatus

MACROINVERTEBRATES
Diogenes brevirostris
Dardanus arrosor
Turbo sarmaticus
Ischnochiton bergoti
Scutellastra cochlear
Parechinus angulosus
Tedania anhelans
Palaemon peringueyi
Conus tulipa
Siphonaria oculus
Scutellastra spp
Burnupena lagenaria
Actinia equina
Parvulastra exigua
Scutellastra granularis
Patiriella spp
Burnupena cincta
Oxystele tigrina
Oxystele variegate
Cyclograpus punctatus
Acanthochitona garnoti
Siphonaria capensis
Cymbula oculus

MACROALGAE
Ulva fasciata
Codium extricatum
Bartoniella spp
Hypnea tenuis
Gelidium abbottiorum
Chlorodesmis hilderbrandtii
Gelidium pristoides
Lyengaria stellata
Sargassum elegans
Plocamium suhrii
Sargassum incisifolium
Sargassum spp
Hypnea spicifera
Hypnea rosea
Geldium abbottiorum
Polyopes constrictus
Jania verrucosa

APPENDIX 3: Consumer trophic position, species code, carbon and nitrogen mean and ranges. Abbreviations: *n* – number of species sampled, *pool* – pool number from which sample was collected, TP – trophic position and C/N is the carbon to nitrogen ratio

MACROINVERBRATE SPECIES

WINTER					δ15N (‰)		δ13C (‰)		C/N	
Taxa	**Species code**	***N***	**Pool**	**TP**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Oxystele tigrina	C6	3	a	3.8	8.64-9.1	12.42±0.3	-11.49-(-9.04)	-10.25±1.2	3.91-4.09	3.99±0.1
Burnupena cincta	C9	3	a	2.4	12.03-13	8.25±0.6	-12.73-(-11.56)	-12.15±0.6	4.25-4.6	4.45±0.2
Scutellastra granularis	C5	4	a	2.6	7.12-9.1	8.95±0.9	-9.57-(-4.57)	-7.77±2.1	4.35-6.6	5.33±0.9
Ischnochitona bergoti	C8	3	a	2.7	8.41-9.1	9.2±0.5	-10.63-(-5.67)	-8.85±2.8	4.12-12.7	7.02±4.9
Burnupena cincta	C9	3	c	3.7	12.54-12.8	12.67±0.1	-13.23-(-12.13)	-12.62±0.6	4.05-4.7	4.33±0.4
Actinia equina	C2	3	c	3.1	10.48-10.5	10.54±0.1	-18.08-(-17.35)	-17.65±0.4	4.61-4.9	4.75±0.1
Patiriella spp	C7	3	c	2.8	8.95-10	9.33±0.6	-8.12-(-7.28)	-7.68±0.4	6.98-9.8	5.55±1.6
Diogenes brevirostris	C4	2	c	2.6	8.73-9.1	8.94±0.3	-10.13-(-8.53)	-9.33±1.1	5.55-5.7	5.63±0.1
Oxystele tigrina	C6	3	c	3.9	8.68-9.2	12.67±0.2	-13.35-(-9.17)	-12.62±2.1	3.95-4.2	4.33±0.1
Patiriella spp	C7	4	e	2.6	8.96-10.1	8.93±0.5	-7.22-(-6.42)	-11±0.4	8.2-9.8	4.1±0.8
Scutellastra granularis	C5	3	e	2.6	8.22-10.3	8.94±1.2	-13.28-(-10.78)	-12.33±1.4	4.07-4.58	4.27±0.1
Burnupena spp	C22	3	g	2.7	8.63-9.6	9.37±0.6	-12.6-(-11.85)	-12.12±0.4	3.91-4.12	4.04±0.1
Actinia equina	C2	4	g	3.1	10.36-10.8	10.78±0.3	-17.62-(-17.14)	-17.41±0.2	4.72-5	4.8±0.1
Patiriella spp	C7	3	g	3	9.66-10.6	9.978±0.5	-9.27-(-7.19)	-7.99±1.1	7.99-10.03	8.94±1
Oxystele tigrina	C6	3	g	2.6	9.06-9.4	8.95±0.2	-12.43-(-11.02)	-12.33±0.8	3.86-4.03	3.97±0.1
Burnupena cincta	C9	3	i	3.5	11.21-12.6	12.08±0.7	-14.65-(-11.81)	-13.41±1.5	3.67-4.3	4.07±0.3
Actinia equina	C2	2	i	3.2	10.31-10.6	10.5±0.2	-18.26-(-18.15)	-18.2±0.1	4.99-5	5.01±0.0
Parvulastra exigua	C3	3	i	2.8	9.32-9.7	9.48±0.2	-7.59-(-7.06)	-7.4±0.3	6.91-9.8	8.23±1.5
Burnupena cincta	C9	3	k	3.6	11.27-12.2	11.85±0.5	-13.49-(-12.01)	-12.89±0.8	3.82-4.1	3.91±0.1
Oxystele tigrina	C6	3	k	2.5	8.46-8.9	8.64±0.2	-12.85-(-11.85)	-12.39±0.5	3.71-4.1	3.96±0.2

APPENDIX 3

WINTER					δ15N (‰)		δ13C (‰)		C/N	
Taxa	**Species code**	***N***	**Pool**	**TP**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Oxystele variegata	C10	4	m	2.8	9.57-9.8	9.5±0.4	-12.4-(-10.05)	-10.92±1.1	4.01-4.2	4.12±0.1
Burnupena cincta	C9	4	m	3.7	11.5-12.5	12.08±0.5	-13.41-(-11.18)	-12.03±0.7	3.4-4.3	4.05±0.5
Burnupena cincta	C9	4	o	3.8	12.01-12.5	12.25±0.2	-12.6-(-9.18)	-12.66±1	3.85-3.9	3.93±0.1
Oxystele tigrina	C6	3	o	2.6	7.98-9.1	8.68±0.6	-14.99-(-12.48)	-10.36±1.9	3.86-4.1	3.95±0.1
Oxystele tigrina	C6	4	o	2.5	7.79-8.8	8.41±0.4	-12.48-(-14.99)	-13.7±1	3.66-4.9	4.07±0.6
Cymbula oculus	C11	3	o	2.2	6.18-9	7.69±1.4	-9.54-(-8.93)	-9.17±0.3	4.03-5.3	4.55±0.6
Actinia equina	C2	3	o	3.1	10.29-10.7	10.43±0.2	-17.14-(-16.68)	-16.97±0.3	4.32-4.78	4.54±0.2
Parvulastra exigua	C3	3	o	2.8	9.26-9.68	9.53±0.2	-8.33-(-7.04)	-7.74±0.7	7.37-8.78	8.01±0.7
Scutellastra granularis	C5	3	o	2.2	7.55-8.4	7.9±0.5	-13.61-(-12.45)	-13.06±0.6	5.1-5.66	5.35±0.3
Burnupena cincta	C9	3	q	3.9	12.4-13	12.69±0.3	-13.84-(-12.84)	-13.17±0.6	3.8-4.63	4.21±0.4
Diogenes brevirostris	C4	4	q	2.6	8.34-9.51	8.89±0.53	-8.52-(-6.82)	-7.86±0.7	4.65-5.51	5.09±0.4
Parvulastra exigua	C3	2	q	2.8	9.48-9.55	9.51±0.05	-8.09-(-7.78)	-7.94±0.2	6.6-6.82	6.71±0.2
Parechinus angulosus	C12	4	q	3	7.87-11.08	9.86±1.5	-4.24-(-2.7)	-3.51±0.8	16.48-39.4	25.78±10.2
Burnupena cincta	C9	3	s	3.7	11.91-12.6	12.19±0.4	-13.21-(-12.38)	-12.67±0.5	3.86-4.06	3.98±0.1
Oxystele variegata	C10	2	s	2.6	8.4-9.09	8.75±0.5	-4.24-(-11.3-12.13)	-11.71±0.6	4.23-4.47	4.35±0.2
Scutellastra cochlear	C13	3	s	2.5	7.1-9.64	8.64±1.4	-12.39-(-6.91)	-10.47±3.1	4.99-5.35	5.18±0.2
Tedania anhelans	C14	3	s	2.1	7.39-7.53	7.44±0.1	-14.88-(-14.24)	-14.56±0.3	5.07-5.95	5.59±0.5
Turbo sarmaticus	C15	2	u	1.6	2.27-9.41	5.84±5.1	-3.46-(-0.74)	-2.1±1.9	28-43.58	35.79±11
Ischnochitona bergoti	C8	3	u	2.7	8.65-9.38	9.09±0.4	-9.75-(-9.04)	-9.44±0.4	4.2-4.64	4.46±0.2
Parechinus exigua	C3	3	u	2.9	9.17-10.65	9.7±0.8	-9.17-(-6.99)	-8.06±1.1	7.55-9.86	8.46±1.2
Scutellastra cochlear	C13	3	u	1.7	5.14-6.85	6.18±0.9	-5.11-(-3.42)	-4.44±0.9	4.3-6.08	5.32±0.9
Parechinus angulosus	C12	4	u	2.2	6.7-8.9	7.89±0.1	-6.45-(-5.05)	-13.06±0.6	13.41-18.6	5.59±2.4
Tedania anhelans	C14	3	u	2	6.39-7.4	7.01±0.9	-14.03-(-13.31)	-13.06±0.5	4.53-5.25	5.59±0.4
Palaemon peringueyi	C16	5	u	3.2	10.11-11.3	10.61±0.5	-11.52-(-10.66)	-13.06±0.4	3.91-4.38	5.59±0.2
Chiton tulipa	C17	3	u	2.5	7.94-8.51	8.41±0.5	-13.07-(-10.55)	-11.45±1.4	3.99-4.86	4.41±0.4
Burnupena lagenaria	C1	4	w	3.8	11.53-12.9	12.48±0.7	-13.91-(-13.38)	-13.17±0.9	3.68-4.1	3.88±0.2
Parvulastra exigua	C3	5	w	2.8	9.05-9.77	9.36±0.3	-7.36-(-6.33)	-6.92±0.4	7.64-8.51	8.13±0.4

Sculletastra spp	C18	3	w	2.4	7.97-8.88	8.31±0.5	-10.07-(-9.3)	-9.66±0.4	5.29-6.82	6.07±0.8
SUMMER					**δ15N (‰)**		**δ13C (‰)**		**C/N**	
Taxa	**Species code**	***N***	**Pool**	**TP**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Burnupena cincta	C9	3	b	3.1	12.06-12.5	12.32±0.2	-12.54-(-10.59)	-11.74±1.0	3.67-3.89	3.77±0.1
Pavulastra exigua	C3	4	b	2.4	9.83-10.37	10.15±0.3	-8.14-(-7.05)	-7.45±0.5	9.6-13.22	10.65±1.7
Palaemon peringueyi	C16	3	b	2.8	10.25-12.5	11.35±1.1	-15.99-(-10.59)	-12.53±3	4.45-4.83	4.64±0.2
Tedania anhelans	C14	3	b	2	9.1-9.36	9.2±0.1	-5.36-(-5.03)	-5.17±0.2	14.08-15.45	14.72±0.7
Actinia equina	C2	3	d	2.6	10.45-11.01	10.74±0.3	-17.3-(-17.09)	-17.17±0.1	4.08-4.87	4.59±0.4
Burnupena cincta	C9	4	d	3.7	11.83-12.36	12.16±0.2	-13.77-(-12.29)	-13.05±0.8	3.77-3.98	3.77±0.1
Oxystele tigrina	C6	3	d	1.8	7.87-8.79	8.35±0.5	-15.53-(-12.83)	-13.05±0.8	3.91-4.14	4.03±0.1
Pavulastra exigua	C3	3	d	2.6	10.73-11.13	10.9±0.2	-8.54-(-7.4)	-7.92±0.6	8.93-9.87	9.32±0.5
Parechinus angulosus	C12	2	d	2.4	9.65-10.8	10.22±0.8	-5.46-(-5.42)	-5.44±0.0	17.79-18.47	18.13±0.5
Tedania anhelans	C14	4	d	2	8.83-8.97	8.91±0.1	-15.17-(-14.09)	-4.74±0.5	5.21-6.02	5.48±0.4
Oxystele variegata	C10	2	f	1.9	8.58-8.63	8.61±0.0	-15.84-(-15.84)	-15.84±0	3.97-4.04	4.01±0.1
Oxystele tigrina	C6	3	h	1.4	8.19-8.77	8.48±0.3	-14.44-(-13.84)	-14.13±0.3	4.12-4.14	4.13±0.01
Pavulastra exigua	C3	4	h	1.8	9.36-10.51	9.84±0.5	-7.39-(-6.78)	-14.13±0.3	8.95-9.99	9.34±0.5
Actinia equina	C2	4	j	2.5	10.13-11.04	10.6±0.4	-17.67-(-17.29)	-17.42±0.2	4.75-4.96	4.8±0.1
Burnupena cincta	C9	3	l	3.7	11.53-12.81	12.14±0.6	-13.04-(-11.97)	-12.57±0.6	3.95-4.08	3.99±0.1
Oxystele tigrina	C6	3	l	2.5	10.47-10.75	10.58±0.2	-7.9-(-6.99)	-7.39±0.5	9.84-11.98	10.65±1.2
Burnupena cincta	C9	3	n	3	11.86-12.14	11.96±0.2	-13.17-(-12.2)	-12.78±0.1	3.9-4.04	3.99±0.1
Cyclograpus punctatus	C42	4	n	1.8	8.04-9.2	8.48±0.6	-12.48-(-8.85)	-10.17±2	6.21-6.35	6.27±0.1
Oxystele tigrina	C6	3	n	2	8.86-9.25	9.12±0.2	-12.01-(-9.99)	-10.83±1.1	3.93-4.18	4.03±0.1
Parechinus angulosus	C12	4	n	2.5	10.11-10.99	10.5±0.4	-7.59-(-7.24)	-7.41±0.1	11.41-13.31	12.52±0.9
Actinia equina	C2	3	p	2.5	10.13-11.07	10.53±0.5	-17-(-16.27)	-16.66±0.4	4.6-4.68	4.65±0.0
Acanthochitona garnoti	C19	3	p	2	8.43-9.56	9.12±0.6	-9.23-(-7.24)	-8.53±1.1	5.23-5.53	5.4±0.2
Cymbula oculus	C11	4	p	1.8	8.18-8.84	8.5±0.3	-11.09-(-8.19)	-9.34±1.4	4.04-4.43	4.22±0.2
Oxystele tigrina	C6	3	p	2	8.63-10.16	9.2±0.8	-15.4-(-14.09)	-14.67±0.7	4.12-4.24	4.17±0.1
Pavulastra exigua	C3	4	p	2.4	9.92-10.64	10.18±0.3	-9.07-(-7.72)	-8.45±0.6	8.36-11.21	9.39±1.3

Burnupena cincta	C9	3	r	2.7	9.24-12.42	11.24±1.7	-12.67-(-9.86)	-11.58±1.5	4.05-4.19	4.12±0.1
Diogenes brevirostris	C4	3	r	2	9.11-9.2	9.15±0.1	-10.76-(-8.49)	-9.33±1.2	5.05-5.43	5.18±0.2
SUMMER					**δ15N (‰)**		**δ13C (‰)**		**C/N**	
Taxa	**Species code**	***N***	**Pool**	**TP**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Pavulastra exigua	C3	3	r	1.8	6.86-10.68	8.38±1.9	-16.21-(-6.92)	-12.36±4.6	8.86-20.65	14.41±4.9
Burnupena cincta	C9	3	t	2.9	11.24-12.1	11.67±0.6	-11.12-(-10.71)	-10.92±0.3	3.88-3.9	3.89±0.0
Oxystele variegata	C10	3	t	2	8.81-9.37	8.96±0.4	-11.64-(-7.91)	-9.79±1.9	4.15-4.29	4.21±0.1
Diogenes brevirostris	C4	3	t	1.7	8.17-8.33	8.25±0.1	-8.3-(-8.09)	-8.19±0.1	5.18-5.62	5.4±0.2
Pavulastra exigua	C3	4	t	2.4	9.87-10.69	10.19±0.4	-7.44-(-6.23)	-6.61±0.6	9.27-12.31	10.17±1.4
Siphonaria capensis	C20	3	t	2.1	9.06-9.3	9.19±0.1	-6.97-(-6.19)	-6.65±0.4	5.67-6.23	5.91±0.3
Tedania anhelans	C14	3	t	1.8	8.14-8.81	8.49±0.3	-13.17-(-12.28)	-12.81±0.5	7.4-7.97	7.71±0.3
Oxystele tigrina	C6	4	v	1.9	8.55-9.16	8.85±0.3	-13.01-(-9.75)	-11.67±1.6	4.16-4.26	4.22±0.1
Parechinus angulosus	C12	3	v	2.9	10.18-14.23	11.69±2.2	-14.41-(-6.43)	-10.19±4.0	10.05-24.58	16.86±7.3
Pavulastra exigua	C3	4	v	2.5	10.03-11.08	10.52±0.4	-8.43-(-7.6)	-8.11±0.4	8.8-10.92	9.6±0.9
Palaemon peringueyi	C16	3	v	2.5	9.78-11.84	10.47±1.2	-13.26-(-11.09)	-12.44±1.2	4.69-4.96	4.86±0.2
Tedania anhelans	C14	3	v	2	8.81-9.25	9.02±0.2	-14.38-(-13.87)	-14.11±0.3	5.14-5.46	5.31±0.2
Burnupena cincta	C9	3	x	2.9	10.91-12.28	11.79±0.8	-14.09-(-12.05)	-12.99±1.0	3.88-4.23	4.04±0.2
Oxystele tigrina	C6	4	x	1.9	8.36-9.01	8.75±0.3	-14.18-(-9.26)	-12.24±2.4	3.93-4.18	4.03±0.1
Parechinus angulosus	C12	3	x	1.9	8.1-9.37	8.72±0.6	-10.57-(-5.52)	-8.17±2.5	11.65-17.45	15.19±3.1
Siphonaria anneae	C21	3	x	1.5	7.35-7.81	7.56±0.2	-6.08-(-4.2)	-4.93±1.0	4.4-4.52	4.47±0.1

MACROALGAL SPECIES

SUMMER				$\delta^{15}N$ (‰)		δ^{13C} (‰)		C/N	
Taxa	**Species code**	***N***	**Pool**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Jania verrucosa	A3	3	b	7.09-8.68	7.8±0.81	-5.69-(-5.16)	-5.45±0.27	31.89-34.08	33.3±1.23
Ulva fasciata	A4	3	b	6.71-6.97	6.83±0.13	-4.99-(-4.47)	-4.67±0.3	9.08-10.25	9.84±0.66
Codium extricatum	A6	4	d	6.16-6.72	6.45±0.28	-10.03-(-9.63)	-9.88±0.18	12.51-13.15	12.76±0.29
Jania verrucosa	A3	3	d	4.83-5.2	5±0.15	-10.37-(-8.95)	-9.76±0.73	17.5-21.04	19.13±1.79
Bartoniella sp	A5	4	d	6.9-7.75	7.43±0.38	-22.39-(-21.24)	-21.82±0.49	9.2-10.27	9.6±0.5
Ulva fasciata	A4	3	d	6.4-6.83	6.58±0.22	-10.55-(-10.1)	-10.38±0.24	10.33-11.83	11.28±0.83
Hypnea tenuis	A7	4	f	5.4-5.84	5.61±0.23	-26.22-(-24.57)	-25.28±0.81	8.49-9.07	8.8±0.27
Jania verrucosa	A3	3	f	6.03-7.29	6.59±0.64	-10.74-(-8.43)	-9.45±1.18	20.15-24.29	22.37±2.09
Sargassum elegans	A8	3	f	7.01-7.68	7.34±0.34	-15.21-(-12.48)	-13.73±1.38	11.77-20.16	16.19±4.21
Ulva fasciata	A4	3	f	6.41-7.29	6.9±0.45	-10.45-(-7.39)	-8.66±1.6	11.26-11.84	11.47±0.32
Gelidium abbottiorum	A9	3	h	6.42-6.82	6.62±0.28	-21.35-(-21.25)	-21.3±0.07	10.58-11.02	10.8±0.31
Jania verrucosa	A3	3	h	6.68-8.26	7.45±0.79	-6.88-(-6.31)	-6.56±0.29	24.67-26.25	25.22±0.89
Ulva fasciata	A4	3	h	6.6-6.76	6.7±0.09	-5.48-(-4.94)	-5.25±0.28	14.47-17.01	15.69±1.27
Codium extricatum	A6	3	j	6.31-6.61	6.47±0.15	-12.74-(-12.37)	-12.6±0.2	12.16-12.45	12.3±0.15
Chlorodesmis hilderbrandtii	A12	3	j	5.6-6.6	6.06±0.5	-10.29-(-8.57)	-9.46±0.86	15.76-17.47	16.61±0.86
Gelidium pristoides	A11	3	j	5.68-5.92	5.81±0.12	-15.13-(-12.38)	-13.99±1.43	17.02-21.11	18.74±2.12
Lyengaria stellata	A10	4	j	4.57-5.38	4.98±0.57	-7.73-(-7.6)	-7.67±0.09	13.39-14	13.7±0.43
Sargassum elegans	A8	3	j	6.19-6.22	6.21±0.02	-12.74-(-12.35)	-12.55±0.28	16.36-19.56	17.96±2.26
Ulva fasciata	A4	4	j	6.48-6.91	6.68±0.19	-7.17-(-6.16)	-6.56±0.47	11.15-12.59	11.86C0.79
Lyengaria stellata	A10	3	l	6.06-7.27	6.83±0.56	-7.16-(-6.41)	-6.89±0.33	17.52-19.11	18.11±0.75
Sargassum elegans	A8	3	l	7.04-7.63	7.35±0.3	-13.45-(-11.94)	-12.6±0.77	14.55-18.72	16.19±2.22
Sargassum incissifolium	A13	3	l	6.23-6.63	6.38±0.22	-11.71-(-11.41)	-11.57±0.15	18.98-20.14	19.63±0.59
Ulva fasciata	A4	4	l	6.69-7.09	6.82±0.19	-7.52-(-5.8)	-6.32±0.81	11.06.12.48	11.8±0.72
Ulva fasciata	A4	3	n	6.37-7.09	6.73±0.36	-6.16-(-4.58)	-5.29±0.8	10.71-13.61	12.4±1.51

Chlorodesmis hilderbrandtii	A12	3	p	4.81-7.47	5.98±1.36	-10.12-(-6.07)	-7.86±2.06	10.18-17.12	13.81±3.48
Jania verrucosa	A3	4	p	6.15-6.93	6.54±0.36	-6.84-(-6.08)	-6.6±0.35	29.86-35.54	33.01±2.47
Sargassum incissifolium	A13	3	p	6.81-7.76	7.2±0.5	-14.17-(-13.2)	-13.62±0.5	23.16-24.83	24.06±0.84
Ulva fasciata	A4	3	p	6.21-7.07	6.56±0.45	-8.57-(-7.65)	-8.22±0.5	9.88-11.43	10.61±0.78
Chlorodesmis hilderbrandtii	A12	3	r	5.6-7.23	6.67±0.92	-9.1-(-8.84)	-8.95±0.13	15.78-17.92	16.61±1.15
Sargassum incissifolium	A13	3	r	6.32-6.5	6.44±0.1	-13.74-(-13.61)	-13.67±0.07	16.7-18.33	17.4±0.84
Ulva fasciata	A4	4	r	6.03-7.5	6.54±0.69	-8.23-(-7.69)	-7.89±0.23	11.38-11.74	11.57±0.15
Codium extricatum	A6	3	t	6.38-7.02	6.62±0.35	-11.22-(-10.71)	-10.94±0.26	11.87-12.04	11.97±0.09
Gelidium abbottiorum	A9	4	t	6.67-7.78	7.19±0.52	-10.68-(-8.83)	-9.51±0.81	12.14-18.05	14.61±2.56
Jania verrucosa	A3	4	t	5.97-8.47	7.26±1.18	-4.98-(-4.16)	-4.65±0.37	31.2-35.68	34.06±1.97
Ulva fasciata	A4	3	t	6.25-6.49	6.38±0.12	-8.48-(-6.07)	-7.16±1.22	11.21-12.99	12.24±0.92
Chlorodesmis hilderbrandtii	A12	3	v	4.47-4	4.52±0.05	-15.2-(-14.92)	-15.05±0.14	7.11-7.37	7.22±0.14
Lyengaria stellata	A10	4	v	5.75-7.37	6.69±0.7	-6.72-(-6.17)	-6.46±0.25	16.74-18.34	17.56±0.7
Sargassum elegans	A8	3	v	5.58-6.48	6±0.45	-12.33-(-10.8)	-11.56±0.77	25.72-29.3	26.94±2.04
Chlorodesmis hilderbrandtii	A12	3	x	3-3.34	3.17±0.24	-13.72-(-13.7)	-13.71±0.01	7.01-7.1	7.06±0.06
Polyopes constrictus	A14	3	x	5.53-6.73	5.99±0.65	-13.5-(-13.16)	-13.31±0.17	20.99-25.17	22.47±2.34
Sargassum incissifolium	A13	3	x	5.75-6.14	5.89±0.22	-11.86-(-11.7)	-11.8±0.09	20.98-23.76	22.04±1.5
WINTER				**δ^{15}N (‰)**		**δ^{13C} (‰)**		**C/N**	
Taxa	**Species code**	***N***	**Pool**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
Ulva fasciata	A4	3	a	6.59-7.45	7.01±0.43	-6.59-(-5.03)	-5.91 ± 0.8	10.29-12.8	11.6± 1.28
Codium extricatum	A6	3	a	7.5-9.16	8.08±0.94	-10.7-(-10.7)	-10.73± 0.04	12.2-16.44	13.97±2.21
Jania verrucosa	A3	3	a	6.04-8.74	7±1.52	-7.89-(-7.4)	-7.57±0.27	22.98-27	24.98±2.01
Jania verrucosa	A3	4	c	5.38-6.4	6.01±0.45	-10.28-(-8.7)	-9.34±0.7	17.37-20.9	19.01±1.45
Codium extricatum	A6	5	c	6.69-8.02	7.39±0.65	-12.8 -(-10.2)	-11.77±1.02	13.66-18.6	15.23±2.17
Ulva fasciata	A4	3	c	7.03-7.67	7.37± 0.3	-7.58-(-7.22)	-7.36±0.19	10.13-12.2	11.03±1.07
Sargassum elegans	A8	4	c	7.21-9.36	8.37± 1.1	-13.6-(-12.2)	-11.95 ± 0.71	18.43-28.2	17.86 ± 5.3
Sargassum elegans	A8	3	e	7.48-7.83	7.66±0.25	-12.2-(-11.9)	-12.11 ±0.22	17.03-17.8	17.44 ±0.5
Ulva fasciata	A4	3	e	6.8-8.17	7.57±0.7	-7.07-(-5.69)	-6.32 ±0.69	10.73-11.5	11.17±0.4

Jania verrucosa	A3	3	g	5.65-6.74	6.14± 0.6	-7.46-(-6.53)	-6.88± 0.51	15.84-19.4	18.05 ± 1.9
Ulva fasciata	A4	3	g	6.42 -7.05	6.66± 0.3	-10.88-(-9.8)	-10.22±0.58	8.74-9.89	9.32±0.57
Ulva fasciata	A4	3	i	6.83-6.95	6.87±0.07	-5.7-(-5.64)	-5.69±0.04	10.74-11.6	11.55±1.04
Sargassum elegans	A8	1	i	0	8.74±0	0	-11.85±0	0	17.33±0
Gelidium pristoides	A11	4	i	7.14-7.43	7.3±0.12	-15.32-(14.2)	-14.73 ±0.47	11.88-13.06	12.6 ±0.53
Codium extricatum	A6	3	i	7.22-8.49	8.01±0.69	-13.8- (-12.8)	-13.29 ± 0.52	12.06-12.7	12.29±0.4
Ulva fasciata	A4	3	k	7.21-8.09	7.67±0.44	-5.73 -(-5.52)	-5.99 ± 0.65	9.95 -11.8	10.79± 0.9
Lyengeria stellata	A10	3	k	5.43-8.22	6.73 ±1.4	-7.9 -(-6.28)	-7.05 ± 0.81	16.98 - 19.	17.96±1.02
Plocamium suhrii	A15	3	k	6.3-9.38	7.52 ±1.6	-13.1 -(-10.6)	-11.57 ± 1.63	12.1 - 14.5	13.56±1.26
Ulva fasciata	A4	3	m	6.76-7.13	6.95 ±0.2	-6.6 -(-6.33)	-6.41 ± 0.17	10.86 - 11.26	11.1±0.21
Gelidium pristoides	A11	3	o	6.64-7.91	7.09±0.71	-11.64 -(-11)	-11.04 ± 0.31	10.99- 16.81	13.42±3.03
Sargassum elegans	A8	3	o	7.5-8.15	7.8±0.33	-16.68 -(-13.3	-14.53 ± 1.87	16.9 - 23.72	19.53±3.36
Ulva fasciata	A4	5	o	6.42 – 7	6.67±0.25	-15.1 -(-8.46)	-10.7 ± 4.04	9.6 - 10.12	10.68±1.92
Jania verrucosa	A3	3	o	5.7 - 6.61	6.05±0.5	-7.44 -(-6.61)	-7.12 ± 0.45	18.44-27.6	22.92±4.59
Hypnea spicifera	A17	3	o	6.63 - 8.3	7.23±0.91	-14.3 -(-10.2)	-12.56 ± 2.11	10.3 - 19.1	13.96±4.56
Lyengeria stellata	A10	3	q	3.75 -7.86	5.8±2.06	-7.46 -(-3.8)	-5.82 ± 1.86	12.06 - 31.04	21.65±9.49
Ulva fasciata	A4	4	q	7.04-7.32	7.16±0.13	-5.03 -(-4.15)	-4.71 ± 0.41	11.7-12.44	12.71±1.01
Codium extricatum	A6	3	q	6.64-8.03	7.18±0.75	-12.4 -(-11.4)	-12.09 ± 0.57	12.94-13.7	13.35±0.41
Jania verrucosa	A3	5	s	6.38-7.92	7.42±0.9	-7.23 -(-6.76)	-7 ± 0.18	21.8-23.63	225±0.96
Ulva fasciata	A4	3	s	6.69-7.38	7.01±0.35	-5.53 -(-4.56)	-5.13 ± 0.51	11.28-14.9	12.66±1.97
Sargassum elegans	A8	3	s	6.28-8.17	7.02±1.01	-13.2 -(-12.5)	-12.53 ± 0.58	17.8-21.89	19.81±2.01
Hypnea rosea	A18	3	u	5.24-8.44	6.56±1.67	-12.6 -(-6.25)	-9.17 ± 3.24	9.7-23.37	15.74±6.98
Sargassum elegans	A8	3	u	7.09-8.01	7.4±0.53	-13.8 -(-12.1)	-12.74 ± 0.98	18.3-21.52	20.06±1.63
Sargassum spp	A19	4	u	6.79-6.94	7.05±0.34	-14.5 -(-13.5)	-13.95 ± 0.43	16.3-18.38	17.38±0.93
Sargassum elegans	A8	3	w	6.94-8.61	7.82±0.84	-14.9 -(-12.9)	-13.66 ± 1.1	22.77-25.3	24.19±1.28

FISH SPECIES

WINTER					SUMMER				
Species	**Code**	***n***	**Pool**	**TP**	**Species**	**Code**	***n***	**Pool**	**TP**
Caffrogobius nudiceps	C36	1	a	4.1	*Clinus cottoides*	C35	1	d	3
Clinus agilis	C37	1	m	4.1	*Caffrogobius nudiceps*	C36	1	j	3.2
Clinus agilis	C37	1	m	3.7	*Caffrogobius nudiceps*	C36	1	j	3.2
Caffrogobius nudiceps	C36	1	o	3.8	*Caffrogobius nudiceps*	C36	1	r	3.3
Caffrogobius nudiceps	C36	1	o	3.9	*Caffrogobius nudiceps*	C36	1	r	3
Caffrogobius nudiceps	C36	1	o	3.8	*Caffrogobius nudiceps*	C36	1	r	3
Psammogobius knsynaensis	C39	1	o	3.8	*Caffrogobius nudiceps*	C36	1	r	3.4
WINTER					**SUMMER**				
Species	**Code**	***n***	**Pool**	**TP**	**Species**	**Code**	***n***	**Pool**	**TP**
Caffrogobius caffer	C38	1	u	4	*Caffrogobius nudiceps*	C36	1	r	3.1
Caffrogobius nudiceps	C36	1	u	4	*Caffrogobius caffer*	C38	1	t	3.2
Clinus superciliosus	C40	1	u	3.9	*Caffrogobius caffer*	C38	1	t	3.2
Epinephelus marginatus	C41	1	u	4.4					
Caffrogobius caffer	C38	1	w	3.9					
Caffrogobius caffer	C38	1	w	3.9					

APPENDIX 4: Mean (±SE) water chemistry parameters recorded in laboratory microcosms

Temperature	Time	Treatment	Salinity (ppt)	Conductivity (mS)	pH	TDS (ppt)	Temperature (°C)	Resistivity (Ω)	ORP (mV)	P (µM)	N (µM)
17	Day 14	NP	27.95±0.33	109.68±0.54	6.04±0.01	36.09±0.17	17.9±0.02	10.03±0.04	-55.4 ± 0.89	3.26±0.29	0.14±0.03
		N	27.98±0.35	109.9±0.98	6.04±0.01	35.63±0.82	17.88±0.04	10.18±0.25	-55.15±0.88	1.16±0.13	14.55±1.17
		P	28.13±0.35	111.67±0.72	6.04±0.01	36.51±0.28	17.9±0.04	9.91±0.07	-55.4± 0.9	2.79±0.23	0.26±0.03
		C	28.35±0.34	110.88±0.62	6.04±0.01	36.45±0.21	17.85±0.02	9.92±0.05	-55.4±0.91	0.84±0.21	0.18±0.02
17	Day 35	NP	30.45±0.19	106.43±2.81	8.42±0.05	35.55±0.24	17.78±0.06	10.195±0.06	-82.47±2.71	7.34±1.35	2.14±0.01
		N	30.55±0.32	108.57±0.91	8.29±0.03	35.15±0.96	17.7±0.09	10.34±0.29	-76.06±2.29	4.87±3.9	24.5±6.71
		P	30.81±0.54	110.22±1.58	8.32±0.07	36.3±0.53	17.68±0.04	9.98±0.13	-76.15±1.82	6.96±0.24	0.18±0.03
		C	31.05±0.43	111.13±1.65	8.28±0.04	36.35±0.46	17.7±0.04	9.96±0.12	-78.26±3.31	0.81±0.21	0.14±0.03
24	Day 14	NP	30.13±0.26	106.63±0.55	8.42±0.01	35.15±0.19	23.75±0.07	10.29±0.05	-84.68±0.82	2.23±0.13	0.21±0.03
		N	30.28±0.26	106.28±0.28	8.48±0.04	34.77±0.16	23.85±0.05	10.39±0.05	-88.1±2.63	1.71±0.36	1.3±0.18
		P	30.65±0.32	107±0.54	8.42±0.01	35.12±.02	23.75±0.04	10.31±0.05	-85.78±1.52	2.42±0.29	0.17±0.03
		C	30.37±0.23	107.05±0.53	8.41±0.01	35.08±0.08	23.87±0.02	10.32±0.03	-83.97±0.39	1.68±0.44	0.17±0.05
24	Day 35	NP	30.28±0.14	101.68±0.49	8.59±0.01	33.49±0.14	23.7±0.06	10.81±0.04	-94.32±0.99	4.37±0.25	2.26±0.03
		N	29.95±0.26	100.56±0.48	8.59±0.02	33.16±0.14	23.6±0.03	10.93±0.05	-94.4±1.62	1.83±0.27	2.25±0.11
		P	30.07±0.35	102.28±0.54	8.48±0.02	33.64±0.18	23.62±0.04	10.77±0.06	-87.38±1.13	5.23±0.23	0.21±0.03
		C	30.42±0.1	101.73±0.33	8.48±0.01	33.57±0.09	23.63±0.07	10.79±0.03	-87.72±1.02	1.86±0.24	0.21±0.4