STABLE ISOTOPE ECOLOGY OF SOUTH AFRICAN KELP FORESTS

DAVID CLIFFORD DYER

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Supervisors: Prof. John Bolton, A/Prof. Robert Anderson and A/Prof. AJ Smit

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ABSTRACT

Kelp forests are some of the most productive coastal ecosystems in the world and provide numerous ecosystem goods and services. Where they occur, they play a key role in coastal ecology and local fisheries. In South Africa, *Ecklonia maxima* and *Laminaria pallida* form kelp forests which support diverse ecological communities. The species composition of these communities has been shown to be spatially variable along the South African coast, controlled by abiotic processes and species interactions. Despite their importance in the southern Benguela Current Large Marine Ecosystem (BCLME), large-scale research directed towards these habitats has largely waned over the past 30–40 years, prompting a renewed focus on these systems. Stable Isotope Analysis (SIA) is an indispensable tool for investigating food web characteristics, with particular focus on trophic structure and functioning. SIA can be used to understand the basal isotope variability in producers, determine the primary carbon sources of food webs, and investigate the spatial and temporal patterns in consumer isotope values and trophic niches. Unlike in other global kelp ecosystems, this methodology has not yet been applied to the kelp forests in South Africa.

A study among eight geographically separate sites and two seasons highlights the natural variability of stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), at different spatial and temporal scales, within the two dominant kelp species. Additionally, stable isotope variability was investigated within and among different tissues within both kelp species. Within a kelp plant, $\delta^{13}C$ values had a range of 1.65‰ for *E. maxima* and 1.52‰ for *L. pallida*. The $\delta^{15}N$ values had a range of 3.75‰ for *E. maxima* and 4.21‰ for *L. pallida*. There were also consistent variability patterns along the length of a single frond in both species, for both isotopes. Among the localities, *E. maxima* and *L. pallida* were highly variable with ranges in $\delta^{13}C$ (9.37‰ and 11.22‰) and $\delta^{15}N$ (3.44‰ and 4.51‰) for the two species respectively. The $\delta^{13}C$ values of *L. pallida* and *E. maxima* displayed a clear pattern coinciding with depth, particularly for *L. pallida*. Within-site variability was a major contributor to the overall spatial variability for both species. This provides further evidence for the importance of understanding basal variability of stable isotope values when determining the carbon sources of bottom-up controlled ecosystems.

Variability in particulate organic matter (POM) composition is hypothesized to be related to upwelling processes in, and around, a typical west coast kelp forest. Various variables were used to characterise the composition, and determine the dynamics, of the POM along two transects (along-shore and off-shore) originating within a kelp forest. SIA was employed to estimate the contribution of kelp-derived detritus (KDD) to the POM present in the water column, using a unique approach for isolating phytoplankton and kelp end-member values. Under upwelling conditions, stable isotope analyses confirmed the dominance (>70%) of kelp detritus in POM samples, even at distances of 7.5

km off-shore. Under downwelling conditions, however, phytoplankton was dominant (>60%) along both transects. This study therefore highlights the importance of coastal processes such as upwelling for controlling the composition of POM in kelp forests, as well as illustrating how the natural variability in POM composition created by upwelling processes can be used to gather POM end-member isotope values.

Three ecologically distinct kelp forest communities were investigated using a combination of SIA and community-wide niche metrics ('Layman metrics' and Bayesian inferences). Three kelp forests, with differing community composition were selected, including a west coast kelp forest, a False Bay kelp forest and a lobster-invaded kelp forest located east of Cape Hangklip at Betty's Bay. Temporal and spatial variability in stable isotope values was identified in producer and consumer stable isotope values, but was variable among species. Community-wide metrics showed clear seasonal patterns, but despite large differences in community structure, metrics were not vastly different among sites. Seasonal variability was the largest observable trend in metrics at all sites. Community niche areas showed a high degree of overlap (80–95%) further illustrating the similarity among sites and seasons. These findings are largely contrary to expected patterns from community composition data.

Trophic position and isotope niche of the West Coast Rock Lobster (*Jasus lalandii*) was determined at three ecologically different kelp forest habitats, located in Marine Protected Areas in south-western South Africa. Temporal and spatial variability in trophic position and niche size were detected. The stable isotope niche and trophic position of lobsters at Betty's Bay were markedly different from those at Oudekraal and Bordjiesrif, with the summer niche being distinct (0% overlap). Trophic position was lowest at the lobster-invaded Betty's Bay (2.52) and highest at Bordjiesrif (3.16). Similarly, the isotope niche of *Jasus lalandii* was significantly constricted at Betty's Bay compared to the other two study sites. Primarily, these results show that in the region where these lobsters have invaded, the trophic niche is considerably constricted. This likely to be a consequence of the higher densities of lobsters in this area. These findings highlight the influence of the lobster invasion on *Jasus lalandii* itself, adding to the already published ecological effects on the kelp forest ecosystem as a whole. These findings also highlight the differences in trophic niche of this species, despite the overall community niche showing little difference among sites.

The findings of this thesis provide estimates of the variability in stable isotope values of kelp forest seaweeds and consumers, as well as addressing the importance of ocean processes such as upwelling in controlling POM composition in kelp forests. Additionally, the trophic niche of a key kelp forest predator was characterised in ecologically different kelp forests, providing evidence of the effect of community structure on the niche of this species. This is the first concerted research effort into the stable isotope ecology of South African kelp forests, providing an updated look at the ecology of these important ecosystems, and serves as a foundation for future studies of this type.

This thesis is dedicated to my parents

Colin and Stephanie Dyer

PREFACE

The fieldwork described in this study was conducted in the kelp forests along the South African coastline, between Port Nolloth on the west coast near Namibia and Betty's Bay which is east of False Bay. All laboratory processing was conducted at the Department of Biological Sciences, University of Cape Town under the supervision of Prof. John Bolton, A/Prof. Robert Anderson and A/Prof. AJ Smit. Stable isotope analysis was performed at iThemba LABS in Braamfontein, Johannesburg by Mr. Mike Butler.

All animals (particularly lobsters) were collected under the possession of valid permits from the South African National Parks (SANParks) authority, the Department of Forestry and Fisheries (DAFF) and ethical clearance from the University of Cape Town Science Animal Ethics Committee (**2015/V13/JB**).

These studies represent original work by the author and have not otherwise been submitted in any form for any degree to any other tertiary institution. Where the work of others has been used, they have been duly acknowledged in the text.

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PLAGIARISM DECLARATION

I, David Clifford Dyer, declare that

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ii. This dissertation has not been submitted for any degree or examination at any other university.

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August 2018

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John, thank you for all the advice, patience and time you have dedicated to my project. Thank you for sharing your experience and vast knowledge of all things phycology. Through the many field trips to the sea shore, sorting through samples in the laboratory, or through informal discussions, I have gained a new perspective on the importance of seaweeds in the marine environment. Rob, thank you for your continued enthusiasm for field work, and for helping with the collection and identification of various kelp forest organisms. Your keen eye for grammar, punctuation and writing in general is greatly appreciated. AJ, thank you for inspiring the move to Cape Town. Thank you for always pushing me to question my ideas, better my work and find easier and more elegant ways of presenting my findings. This thesis has been fuelled by the many beers you have sponsored at the market, thank you!

Collecting samples for any ecological study is inherently complicated. Co-ordinating divers, boats, research permits and sampling gear to coincide with the correct weather and sea conditions adds several layers of complexity. I would like to thank the Seaweed Research Unit (DAFF)—Chris Boothroyd, Derek Kemp, Mark Rothman—for all their help with the collection of samples from various kelp forests between Port Nolloth and Betty's Bay. Without their logistical support, much of this research would not have been possible. I would like to thank Mark Noffke for helping with sample collections, but especially for taking me out to collect water samples at Kommetjie, often at short notice and when conditions were difficult. I also value all the knowledge and experience you have shared with me to help me get my skippers ticket. Thank you to Grant Pitcher and André Du Randt at the Seapoint Research Aquarium (DAFF), for letting me use your laboratory for the chlorophyll-*a* measurements. To the members of Team Kelp—Robert Williamson, Robert Schlegel and Ross Coppin, thank you for your help and continued interest in my project. Rob S, thank you for all your help with R, especially with maps and figures.

I would like to thank my family for their continued support and interest, not only in my thesis but in my life in general. To my brother Mike, and sister-in-law Cait, thank you for always being interested in my work, and for supporting me throughout my studies.

Thank you to my parents, Colin & Stephanie, for your love and support with everything I do, especially over the course of my university career. I cannot thank you enough for giving me everything I needed to complete my studies. I have always had a big advantage having two acclaimed scientists for parents. Especially as you understand the difficulties and triumphs that are involved with the PhD journey. For this reason, I have dedicated my thesis to you.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. Kelp forests—an ecological overview

True kelps are large brown algae belonging to the order Laminariales, which comprises 147 species of kelp, from 59 genera which are found in 43% of the worlds marine ecoregions (Bolton 2010, Krumhansl et al. 2016). Kelps are found along the coastlines of all continents, with the exception of Antarctica, and contribute ecological goods and services which are valued at billions of dollars annually (Krumhansl et al. 2016). Kelps are vital marine ecosystem engineer species, generating complex 3-dimensional habitats, which support diverse and highly productive rocky reef ecosystems (Jones et al. 1994, Steneck et al. 2002, Steneck and Johnson 2014, Bennett et al. 2016, Teagle et al. 2017). Apart from serving as habitats, canopy-forming kelps influence their environment by changing light levels, water flow, physical disturbance, pH, sedimentation rates as well as food quantity and quality in shallow coastal waters where they are distributed (Reed and Foster 1984, Steneck et al. 2002, Krumhansl and Scheibling 2012, Smale et al. 2013). When kelps form dense beds, they are commonly referred to as kelp forests as they resemble terrestrial forests in their structure (canopy, understory stratification, as well as associated biota) and function (Dayton 1985). The term kelp forest is, however, generally associated with giant kelp (*Macrocystis pyrifera* (Linnaeus) C. Agardh) which has been recorded to reach sizes up to 45 m, and is dominant on the western coastlines of North and South America, the Arctic and sub-Antarctic, Tasmania and New Zealand (Steneck et al. 2002, Graham et al. 2007b, Bolton 2010). However, the term has now been extended to include kelp forests created by other species, such as *Ecklonia* spp., *Laminaria* spp., *Saccharina* spp. and *Nereocystis luetkana* as they provide similar habitats. As kelps are a temperate and sub-polar group, kelp forests are limited to the cooler waters found along the west and southern coastlines of Africa, South America and Australia in the southern hemisphere, as well as temperate and Arctic coastlines in the northern hemisphere and deeper waters in the geographical tropics where conditions are suitable (Mann 1982, Dayton 1985, Graham et al. 2007a, Bolton 2010). Not only do kelps form large three-dimensional habitats, but their holdfast structures and associated epiphytes provide some of the most structurally complex microhabitats in these ecosystems, which are inhabited by a plethora of invertebrate species (Anderson et al. 1997, Christie et al. 2009, Arnold et al. 2016).

Kelp forests are some of the most productive ecosystems in the oceans, with complex food web structuring, and they provide numerous ecosystem goods and services and support myriad associated species (Mann 1973, Duggins et al. 1989, Steneck et al. 2002, Page et al. 2013, Smale et al. 2013). The areal productivity of these systems has been reported to be equivalent to that of rainforests and intensively cultivated agricultural areas (Mann 1973, Leith and Whittaker 1975). Apart from the direct input into the kelp forests themselves, energy generated in these systems, through primary production, is exported to adjacent marine systems, such as the inshore pelagic system, rocky shore, sandy beach and deep sea benthic environments (Griffiths et al. 1983, Bustamante and Branch 1996b, Soares et al. 1997, Vanderklift and Wernberg 2008, Kelly et al. 2012, Krumhansl and Scheibling 2012).

Kelp forests provide numerous goods and services, both indirectly (e.g. nutrient cycling) and directly such as the harvesting of kelp and commercially important fish, crustacean and mollusc species (Steneck et al. 2002, Teagle et al. 2017). Therefore, the existence of kelps, and kelp forests, in coastal ecosystems has major ecological and socio-economic benefits, both on a global and regional scale.

1.2. Kelp forests in southern Africa

The Benguela Current Large Marine Ecosystem (BCLME) is located along the south-western coastline of Africa, between the Angola-Benguela Front in northern Angola and the Cape of Good Hope in South Africa (Shannon 2006). This ecosystem incorporates one of the four major eastern boundary upwelling systems (EBUS) of the world, which provide numerous ecological and socio-economic goods and services (Bakun 1990, Pauly and Christensen 1995, Carr 2001, Carr and Kearns 2003). The major upwelling cell located at Lüderitz in Namibia effectively separates the system into northern and southern sections which have distinct physico-chemical characteristics and biota (Shannon 1985, Blamey et al. 2015).

Along the west coast of southern Africa, *Ecklonia maxima* (Osbeck) Papenfuss and *Laminaria pallida* Greville are the two most common and abundant kelp species, both forming dense and extensive kelp forests between Cape Agulhas (the southernmost point of Africa) and Rocky Point in northern Namibia (Field et al. 1980a, Field and Griffiths 1991, Bolton 2010). Distribution within this area is limited to shallow subtidal (0–25 m) rock surfaces which are needed for attachment (Field et al. 1980a). This area provides the optimal growing environment for kelps as nutrient concentrations are high (due to upwelling), light intensities are high, and there is continuous water movement (Andrews 1974, Field et al. 1980b). In the southern region of the coastline, south of Cape Columbine, *Ecklonia maxima* and *Laminaria pallida* create depth stratified kelp beds, with *L. pallida* occupying the deeper waters below the surface and *E. maxima*, aided by a gas filled float, creating a dense canopy at the surface in shallower (<9 m) areas (Field et al. 1980a). Northward of Cape Columbine (Figure 1.1), *Ecklonia maxima* is progressively replaced in shallow water by *Laminaria pallida*, until the inshore coastal region becomes dominated by the hollow-stiped *L. pallida* (Rothman 2015, Rothman et al. 2017a). Despite the difference in morphology (hollow vs. solid stipe), the *L. pallida* found along the entire west coast is the same species (Rothman et al. 2017b). Subsequently, kelp bed community structure varies along the west coast of South Africa: not only does the composition of kelp species themselves vary but the associated faunal and algal species as well (Field et al. 1980a).

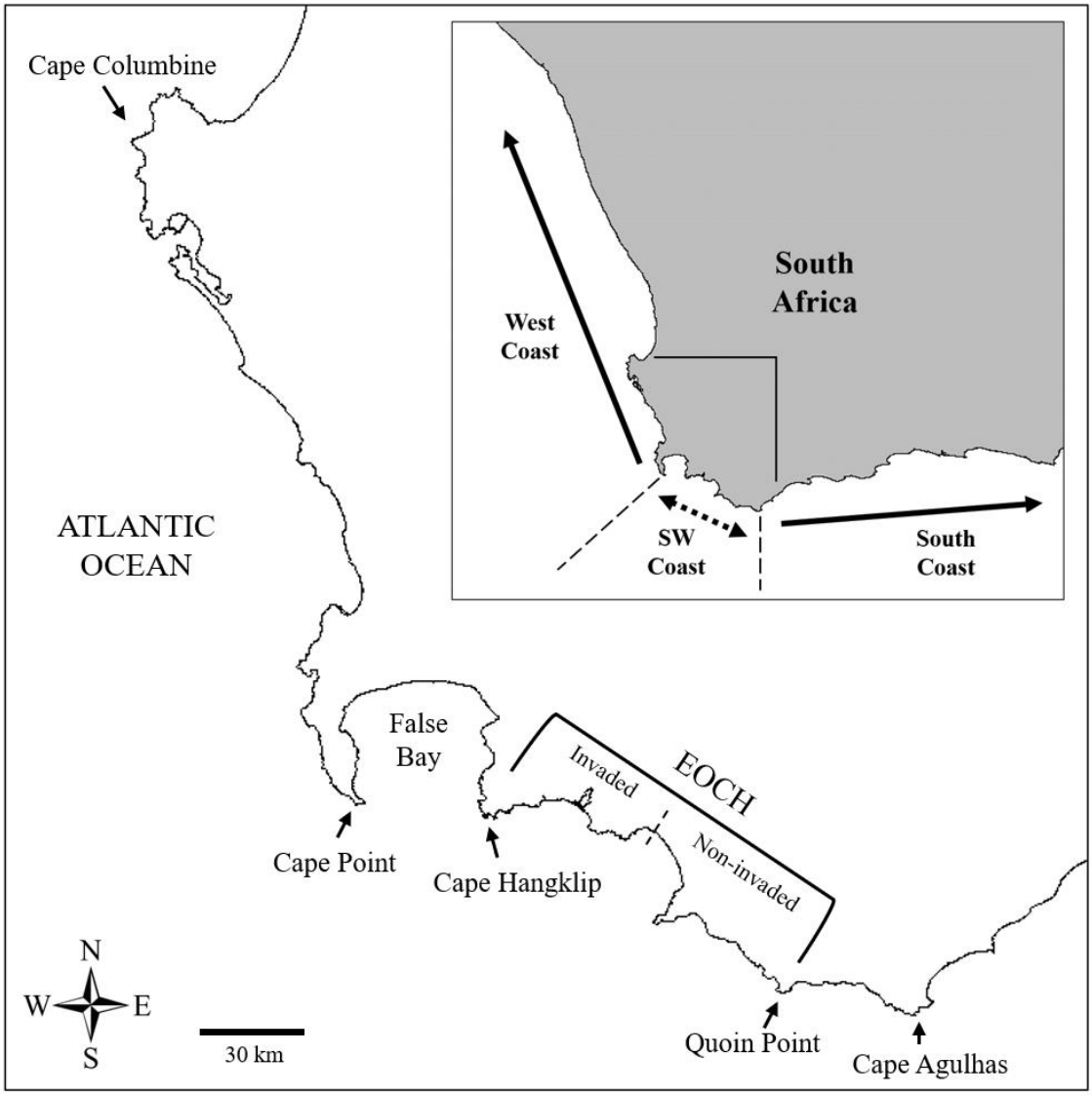

Figure 1.1: The coastline of South Africa between Cape Columbine and Cape Agulhas, showing the location of False Bay and the area east of Cape Hangklip (EOCH). Areas where lobsters have invaded are indicated following Blamey et al. (2010). The major biogeographic regions discussed below are indicated in the inset map.

The coastline between Cape Point and Cape Agulhas (see Figure 1.1), commonly referred to as the south-west coast, represents a transition zone between the west coast and south coast (Bolton 1986, Stegenga et al. 1997). The Cape Peninsula is also known as the break between the cool temperate Benguela Marine Province and the warm temperate Agulhas Marine Province (Spalding et al. 2007). Similarly, Smit et al. (2017) show that the seaweed α-diversity changes at Cape Point, with low α-diversity in the Benguela Marine Province and higher α-diversity in the transition zone (Cape Point to Cape Agulhas). Temperature has been suggested as a major factor resulting in the differences in the seaweed community composition in these regions (Smit et al. 2017). McQuaid and Branch (1984) also show how physical environmental factors, particularly temperature and wave exposure, structure

the inter-tidal communities around the Cape Peninsula in terms of biomass and species composition. Where the shore is exposed to high wave energy, the biomass is dominated by consumers; however, the biomass on sheltered shores is dominated by algae (McQuaid et al. 1985).

Subtidally, the kelp forest communities in these regions also exhibit differences in community structure (Field et al. 1980a). Along the west coast, kelp forests are characterised by a high abundance of the west coast rock lobster (*Jasus lalandii* (H. Milne-Edwards)) and two mussel species (*Choromytilus meridionalis* (Krauss) and *Aulacomya ater* (Molina)) and the seaweed understorey is dominated by Rhodophyta (Field et al. 1980a, Branch and Griffiths 1988, Bustamante and Branch 1996a, Anderson et al. 1997). The south-west coast is, however, very different, with herbivore species such as *Parechinus angulosus* (Leske), *Turbo cidaris* Gmelin, *Turbo sarmaticus* Linnaeus and *Oxystele* spp. becoming more prevalent. Encrusting coralline algae replace the foliar algae and mussels become less dominant in these habitats (Field et al. 1980a, Anderson et al. 1997). Historically, lobster abundances were also significantly lower along the south-west coast when compared to the west coast (Tarr et al. 1996, Cockcroft et al. 2008).

These differences indicate that the kelp forests in the south-west coast region exist in two separate community types, either with or without high abundances of grazing species, particularly sea urchins (Anderson et al. 1997, Leliaert et al. 2000, Blamey et al. 2010). Blamey and Branch (2012) have suggested that these two conditions represent two stable states of kelp ecosystems in the south-western Cape. However, a recent (1990s) invasion of rock lobsters has changed the community structure in some areas (discussed below), creating further differences in the ecological communities within these kelp forest habitats. This then separates the south-west coast into two kelp forest types, which along with the west coast creates three distinct kelp forests in terms of ecological communities. It is likely that the trophic dynamics in these three distinct kelp forest types will be very different, but the scale and magnitude of these differences is not well understood. This thesis will therefore attempt to highlight the differences in trophic dynamics among these ecological communities (see Chapters 4 & 5).

1.3. Kelps of South Africa—overview of biology

Ecklonia maxima and *Laminaria pallida* are both typical aclonal macroalgae (*sensu* Santelices 2004), having fronds which originate from a single stipe that is attached to the substrate via a holdfast (see Figure 1.2). Both species are perennial and have fronds which constantly undergo erosion at the distal ends, matched by continuous growth in the meristematic regions (Dieckmann 1978, 1980, Mann et al. 1979). In South Africa, these kelp species form ecologically and commercially important coastal habitats, kelp forests (Field et al. 1980a, Field and Griffiths 1991).

The erosion of the tips of kelp fronds is suggested to contribute an average of 343 gC m^{-2} yr^{-1} in particulate matter as kelp-derived detritus (KDD), which accounts for 70% of the annual production of both species (see Figure 1.3) (Newell et al. 1982). Conversely, dislodgement only accounts for 6.2% of the production (Newell et al. 1982). Data from N. Jarman (reported in Mazure and Field 1980) suggest the erosion rate of *L. pallida* fronds to be ±15 cm per month in summer, autumn and winter, peaking at 23cm per month in spring. The erosion rate of *E. maxima* fronds is likely to be of a similar magnitude (Mazure and Field 1980). See section 1.4 for further details on kelp productivity.

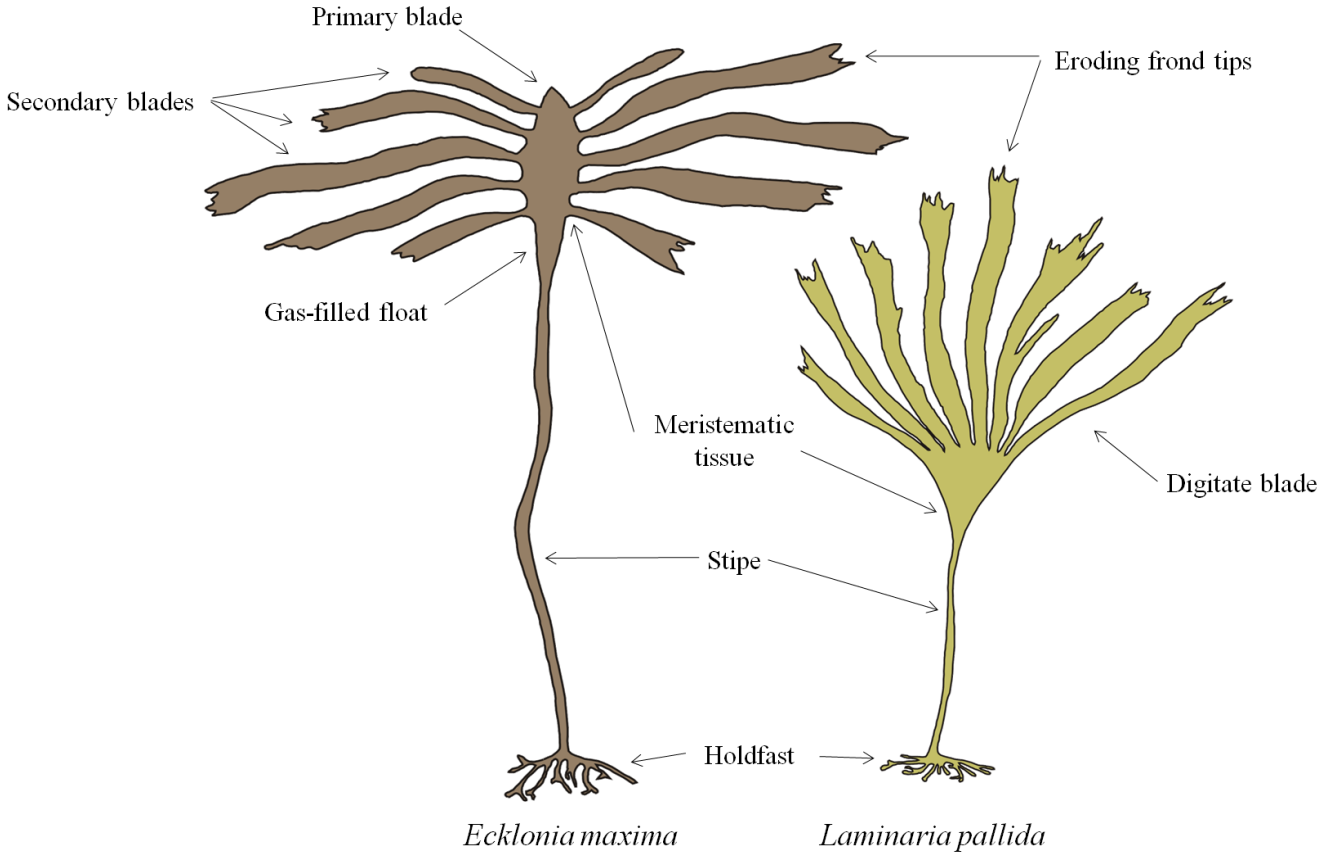

Figure 1.2: Diagram of the two dominant kelp species, *Ecklonia maxima* and *Laminaria pallida*, showing important tissues and parts discussed below.

1.3.1. Ecklonia maxima

Ecklonia maxima has a single primary blade which originates from the hollow stipe, above the gas-filled float. From this primary blade, secondary blades are produced laterally from several meristematic regions along the convoluted margins (Mann et al. 1979, Stegenga et al. 1997) (see Figure 1.2). In adult plants, the production of secondary blades along the primary blade is roughly equal to the erosion rate, with old blades eroded near the apex and new blades formed near the base (Mann et al. 1979). This 'conveyor belt' concept of growth and erosion does however not apply to the

secondary blades, with varying rates of growth and erosion among the different blades (Mann et al. 1979).

The growth patterns of *Ecklonia maxima* are presumed to follow the circannual cycle, with peak production occurring in spring and summer (Jarman and Carter 1981). Spore production of *E. maxima* has been shown to peak in spring and summer, although fertile sori may be present on the secondary blades throughout the year (Joska and Bolton 1987).

Based on the methodology described by Novaczek (1981), the direct measurement of kelp age has been successfully carried out for *Ecklonia radiata* in New Zealand and Australia (Wernberg 2005). This requires the counting of growth rings in the stipe or holdfast to estimate the age of the individual kelps, but the success of the method requires detailed knowledge of the environment from which the kelp was obtained (Novaczek 1981). Contrarily, the age of *Ecklonia maxima* cannot be determined directly (Anderson et al. 2006). However, the abundance of epiphytes could be used as a proxy for age, with the highest abundances found on plants which appear visually older (Anderson et al. 2006). Additionally, clearance experiments have noted that kelps with stipes 1.0–1.5 m in length were recorded after a period of one year (Mann et al. 1979). Therefore, it is assumed that a kelp plant with a stipe length of 3–4 m is roughly 3–4 years old.

Ecklonia maxima has three obligate algal epiphyte species which grow on the stipes (*Gelidium vittatum* (Linnaeus) Kützing, *Polysiphonia virgata* (C. Agardh) Sprengel) and fronds (*Carpoblepharis flaccida* (J.V. Lamouroux) Kützing) (Anderson et al. 2006). These epiphytes are more abundant on older plants as they require some time to become established (Whittick 1983, Christie et al. 1998).

It has also been shown that *Ecklonia maxima* takes up more nitrogen, in the form of NO_3^-, under upwelling conditions (Probyn and McQuaid 1985). However, Smith (2007) showed that on a longer timescale of months, tissue nitrogen and carbon content of *E. maxima* on the West coast did not vary markedly. Thus, it is unlikely that *E. maxima* stores excess carbon and nitrogen to any great extent within its tissues, and thus the concentration of these nutrients is similar throughout the year (Smith 2007).

1.3.2. Laminaria pallida

L*aminaria pallida* is characterised by a single smooth blade which is usually longitudinally divided into regular split sections (digitate) (Dieckmann 1978, Stegenga et al. 1997). This blade originates from a single meristematic region at the junction of the stipe and blade (see Figure 1.2). The stipe, which can attain a length of 3 m, is attached to the hard substrate by a branched and spreading holdfast (Dieckmann 1978). The blade of an adult *L. pallida* plant is comprised of an unsplit basal

section of up to 30 cm in length (with meristematic tissue in the first 10 cm (Dieckmann 1978)) which then splits into roughly equal-width sections up to 2 m in length (see Figure 1.2).

Dieckmann (1980) showed the fronds of *Laminaria pallida* exhibit variable growth rates which could be closely related to the natural seasonal cycle. The peak growth rates of *L. pallida* were found to coincide with spring and summer months, with the lowest growth rates recorded in winter (Dieckmann 1980). It was concluded that the primary mechanism controlling this growth pattern was light intensity and day length, with growth rates increasing as day length and light intensity increase (Dieckmann 1980). Frond biomass turn-over rates are also more rapid in plants growing at 8 m depth (4.7 times), compared to plants growing at 14 m depth (3.5 times) (Dieckmann 1978). Additionally, *L. pallida* plants forming a canopy at 8 m depth are likely to be 4-year-old plants, whereas those forming the canopy at 14 m depth are 8-year-old plants. This is indicative of the influence of light availability on the growth rate of this species (Dieckmann 1978, 1980).

The main algal epiphyte which grows on *L. pallida* is the red alga *Carpoblepharis minima* E.S. Barton, however this species only accounts for a maximum of 1% of the mass of the kelp plant and is more prevalent in shallower (4–8 m) populations (Stegenga et al. 1997). Nevertheless, Stacey (1984) showed that this alga is semi-parasitic and actively extracts photosynthetically produced compounds from *L. pallida*.

The influences of nutrient concentrations and temperature on the growth rate of *L. pallida* are largely unknown and require further investigation. However, carbon and nitrogen content of *L. pallida* tissue was not found to vary with season, thus confirming that this species does not accumulate these nutrients in its tissues for later use in growth (Dieckmann 1978), as is the case in some Northern Hemisphere kelps (e.g. Chapman and Craigie 1977, Chapman and Lindley 1980). *Laminaria pallida* fronds are fertile year-round, with the highest incidence of sori on the blades between December and May (Dieckmann 1980).

1.4. Kelp forests in South Africa—sources of productivity

Productivity of *Ecklonia maxima* on the west coast has been shown to be between 4.1 and 7.8 kg dry mass $m^{-2}yr^{-1}$, depending on the state of succession of the community (Newell et al. 1980). *Laminaria pallida* produces approximately 3.4 kg mass $m^{-2}yr^{-1}$, with seasonal growth rates peaking in early summer due to maximum light availability and water clarity (Dieckmann 1978, 1980). These values of productivity are comparable to those of *Macrocystis pyrifera* in California (2.4 kg $m^{-2}yr^{-1}$) and *Ecklonia radiata* (C .Agardh) J. Agardh in New Zealand (3.0 kg $m^{-2}yr^{-1}$), but much less than *Lessonia* spp. in Chile (23.4 $kg.m^{-2}.yr^{-1}$) and *M. pyrifera* in the Falkland Islands (27.1 kg $m^{-2}yr^{-1}$) (Krumhansl and Scheibling 2012). Kelp is commercially harvested in South Africa and is used for a variety of applications such as alginate production, processed for an agricultural growth stimulant (Kelpak®)

and used fresh as feed on several abalone farms (Anderson et al. 2006, Rothman et al. 2006, Troell et al. 2006). Since 2000, the amount of fresh kelp harvested for abalone feed in South Africa has been around 4,500 tonnes per annum (Blamey and Bolton 2017). Therefore, these organisms provide not only ecological but socio-economic benefits to the region.

Newell et al. (1982) have shown that most of the kelp production enters the detrital food web as particulate material, known as kelp-derived detritus (KDD). For this thesis, KDD will refer only to the small fragments of kelp suspended in the water column and excludes whole fronds or larger fragments. This suspended material is generated from the terminal ends of the distal fronds where the oldest kelp tissue is gradually eroded and fragmented by wave action (Field et al. 1977, Newell et al. 1982, Newell and Field 1983a). Thus, the fronds represent a conveyor belt of production, with the new tissue forming at the meristem and it moves along the length of the frond where it is eventually eroded at the tip. For *Ecklonia maxima,* the meristematic region is located at the base of each secondary frond where it attaches to the primary blade. *Laminaria pallida* has a single frond and thus the meristematic region is located at the base of this frond. The process of frond growth and erosion is however similar in both species. Drift algae, the larger fragments of kelp, is another major export from kelp forests and this can be washed into areas such as sandy beaches where organisms consume and live amongst the kelp (Griffiths and Stenton-Dozey 1981, Koop et al. 1982b, Griffiths et al. 1983).

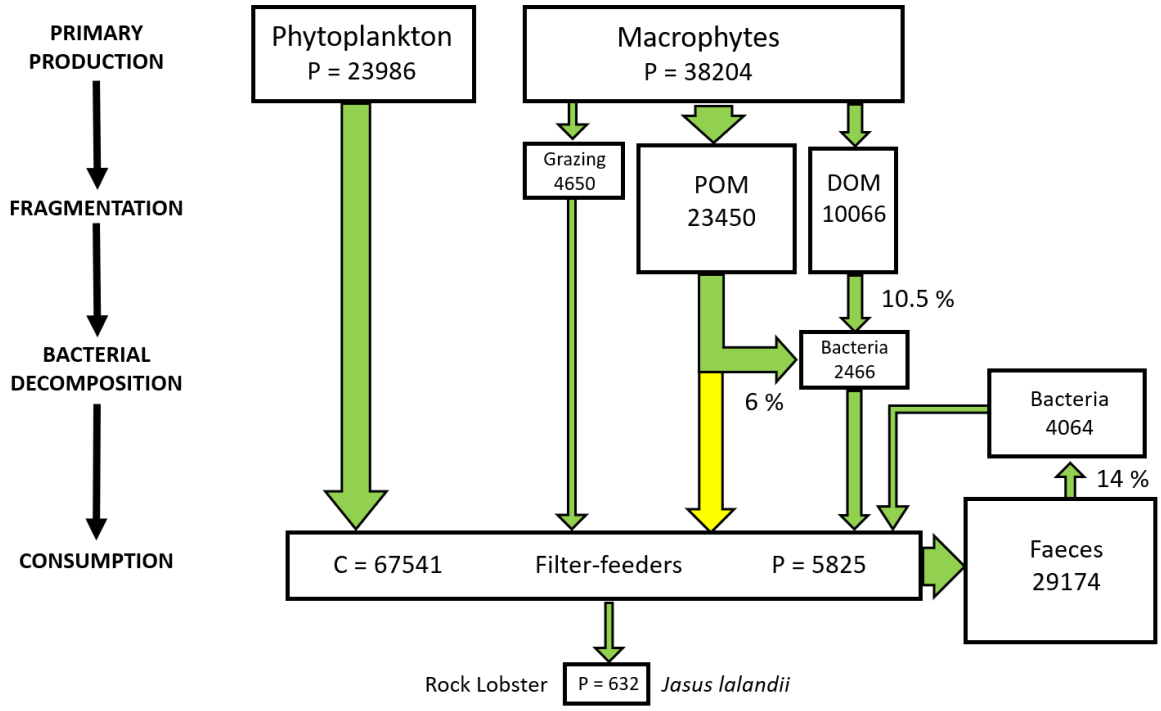

Figure 1.3: Simplified energy flow diagram for a kelp bed on the west coast of Cape Peninsula, South Africa adapted from Mann (1988). Numbers in the boxes represent energy fluxes (in kJ $m^{-2}yr^{-1}$) out of those boxes (after Newell (1984)).

Phytoplankton productivity and KDD contribute similar energy fluxes toward the pool available to filter-feeding herbivores on the west coast of the Cape Peninsula, 23,986 kJ $m^{-2}yr^{-1}$ and 23,450 kJ $m^{-2}yr^{-1}$ respectively (see Figure 1.3, after Newell (1984)). This balance is, however, unique as mismatched production rates of phytoplankton and kelps have been reported in other such systems. Fredriksen (2003) and Kaehler et al. (2000) noted that phytoplankton production is less than a third of the kelp production in kelp forests of Norway and the Prince Edward Islands, respectively. In the Santa Barbara Channel (California), KDD production is only 20% of that measured for phytoplankton (Yorke et al. 2013).

The relative importance of detritus and phytoplankton along the South African coast depends on the frequency of upwelling and on the rate of water movement in the kelp bed (Wulff and Field 1983, Mann 1988). McQuaid and Branch (1985) show that the net import and export of energy from intertidal systems is controlled by wave exposure. Exposed shores generally have higher water turnover rates and thus the availability of food particles is greater (Bustamante et al. 1995a, Bustamante and Branch 1996b). Additionally, where algae dominate (sheltered shores) there is a net export of energy, whereas on wave exposed shores filter-feeders dominate and there is a net import of energy (McQuaid and Branch 1985). Similarly, coastal processes such as upwelling also play a major role in controlling the food availability of kelp forest filter-feeders (Wulff and Field 1983, Mann 1988). Using a simulation model, Wulff and Field (1983) showed that under upwelling conditions, kelp detritus is more prevalent in the water column whereas under downwelling or reduced upwelling intensity, phytoplankton dominates the POM in the water column (Mann 1988).

From an ecosystem perspective, filter-feeding organisms provide a very important link between the benthic and pelagic regions (Miller and Page 2012). Sessile rocky shore organisms on the west coast have also been shown to be highly dependent on detrital material, with most of the carbon and nitrogen in their tissue "probably derived from kelp detritus" (Bustamante and Branch 1996b). Similarly, Newell and Field (1983b) have shown that kelp forest consumers depend on the carbon produced by phytoplankton and KDD, and obtain up to 87.6% of their nitrogen requirements from these two sources. Therefore, it is evident that the kelp community relies heavily on detrital material generated from the erosion of kelp tissues (KDD) as well from phytoplankton production within the system, as both sources generate around 500 gC $m^{-2}yr^{-1}$ (Newell et al. 1982). Understanding the dependence on these two resources will provide pivotal information on the functioning of kelp forest food webs along the South African coastline, especially in light of the suggested recent intensification of upwelling (Rouault et al. 2010, Blamey et al. 2015). The regulation of POM composition within and around kelp forests by coastal processes such as upwelling will be another focus of this study (see Chapter 2).

1.5. Kelp forests in South Africa—trophic interactions

The faunal biomass of South African kelp forests is dominated by filter-feeding organisms, especially along the west coast where upwelling is dominant (Velimirov et al. 1977, Field et al. 1980b, 1980a, Bustamante and Branch 1996b). The organisms rely on phytoplankton and kelp, which are the two primary sources of productivity (Probyn and McQuaid 1985). Grazing organisms, such as abalone, urchins, turban shells and winkles, are less common within west coast kelp beds but form a more dominant part of those systems east of Cape Point (Field et al. 1980a, Jackelman 1996, Anderson et al. 1997, Leliaert et al. 2000). Newell et al. (1982) suggest that grazers only consume around 1% of the kelp production. This is in contrast to kelp ecosystems around the world, where sea urchins graze on adult kelp directly and can even lead to the formation of kelp barrens through over-grazing (see review by Steneck et al. (2002)). However, in South Africa, the presence and absence of grazing organisms affects the structure of the macroalgal communities present (Jackelman 1996, Day 1998, Leliaert et al. 2000). The understory algal communities on either side of the Cape Peninsula, in particular, have been described as very different; foliose red algae (Rhodophyta) are more prevalent on the Atlantic side, whereas green algae (Chlorophyta) and articulated corallines tend to dominate the kelp understory within False Bay (Leliaert et al. 2000). Jackelman (1996) also noted that foliose algae were not prevalent around Cape Hangklip. Some grazer species may form close associations with the kelp itself—an example is the kelp limpet *Cymbula compressa* (ex *Patella compressa*) which lives exclusively on the stipe of *E. maxima* (Field and Griffiths 1991). These grazers consume epiphytic algae which grow on the stipe of *E. maxima*.

The most abundant grazing species in South African kelp forests is the Cape urchin *Parechinus angulosus* (Field et al. 1980a). On the west coast these grazers are often restricted to deeper sections (8–15 m) of the reef. In contrast, Anderson et al. (1997) noted that these urchins are more abundant on the reefs along the south-west coast, regularly extending into shallower areas (2–5 m). *Parechinus angulosus* does not graze on adult kelps, but is known to feed on drift kelp and on kelp sporelings (particularly in shallow water) (Velimirov et al. 1977, Fricke 1979, Anderson et al. 1997, Day and Branch 2002a). Due to the heavy swells and water motion along the coastline where kelps persist, active grazing by urchins on adult kelp fronds is not possible (Fricke 1979, Day and Branch 2002a). This is primarily due to the fact that intense wave energy prevents the urchins from ascending the kelp stipes. This species has therefore been classified as a debris feeder, rather than an active grazer, consuming primarily drift kelp (Velimirov et al. 1977, Day and Branch 2002b). However, exclusion experiments have shown that urchins play a role in regulating the proliferation of foliose algae and promote encrusting corallines (Day 1998).

Perhaps the most well-known grazing species in South African kelp forests, due to its commercial and recreational fishery and lucrative aquaculture industry, is the abalone *Haliotis midae* (Tarr et al. 1996,

Dichmont et al. 2000, Tarr 2000). These molluscs feed primarily on kelp sporelings and red algae as well as trapping drift kelp with their muscular foot. The relationship between *H. midae* and *Parechinus angulosus* is vitally important to the recruitment and subsequent success of these grazing organisms (Tarr et al. 1996, Day and Branch 2000a, 2000b, 2002c, Tarr 2000). Once the planktonic abalone larvae have settled out of the water column, preferentially onto encrusting corallines, the juveniles seek refuge from predators in crevices or, when present, under adult urchins (Day and Branch 2000a, 2000b). Additionally, drift kelp trapped by adult urchins provides a food source for the juvenile abalone, without having to leave the protection of the urchin (Day and Branch 2000a, 2000b). Therefore, not only do urchins regulate the availability of suitable substrate for larval settlement, they also provide shelter and trap food for the juvenile abalone.

Carnivorous organisms are dominated in biomass by the lobster *Jasus lalandii*, polychaetes, and isopods (Field et al. 1980a, Field and Griffiths 1991). The west coast rock lobster, *Jasus lalandii* is a key predator in nearshore, temperate reef ecosystems of the southern African coastline from Walvis Bay to East London (Heydorn 1969, Pollock 1979, Cockcroft and Payne 1999). Within kelp forest ecosystems, *J. lalandii* dominates the carnivore biomass (Field and Griffiths 1991), consuming a variety of kelp forest invertebrates (mussels, urchins, winkles, turban shells, barnacles, sponges), algae, and can be cannibalistic (Pollock 1979, Field et al. 1980a, van Zyl et al. 1998, Mayfield et al. 2000, Haley et al. 2011). Because dietary plasticity allows this species to consume a variety of organisms depending on availability, *J. lalandii* has the ability to markedly impact the benthic community structure as a whole (Pollock 1979, Barkai and Branch 1988a, Barkai et al. 1996). Not only is this species of great ecological importance in the food web, but commercially *Jasus lalandii* was historically one of the top three marine fishery species in South Africa (Melville-Smith and van Sittert 2005). Recently, Johnston and Butterworth (2016) estimated that the exploitable biomass of *Jasus lalandii* is *ca.* 2% of pristine levels. This has resulted in the species being listed as endangered and placed on the WWF SASSI red list in 2016 (Blamey and Bolton 2017).

Since the early 1990s, however, the density of lobsters in some areas East of Cape Hangklip (EOCH) (see Figure 1.1) has increased drastically in what many authors have termed an ‘invasion’ (Tarr et al. 1996, Mayfield and Branch 2000, Cockcroft et al. 2008, Blamey et al. 2010, 2012). This area was not historically part of the lobster fishing grounds and thus this small-scale increase in lobster abundance is not enough to counteract the larger scale population declines recorded elsewhere. However, as a result of the predatory effects of *Jasus lalandii*, the benthic communities in the invaded area have been greatly altered and shifted to an alternative stable state which is maintained by these lobsters (Blamey et al. 2012, 2013). This new state has seen herbivore and particularly urchin abundances decline, resulting in a four-fold increase in macroalgal densities (Blamey et al. 2010, 2012). Therefore, the benthic algal community, with sparse foliose algae, described by Jackelman (1996), has changed considerably. A lack of grazing pressure has seen the proliferation of turf species and

encrusting corallines (Blamey et al. 2010). The decrease in urchin abundance has also had severe knock-on effects on abalone numbers, as urchins are known to facilitate their recruitment (Tarr et al. 1996, Day and Branch 2000a, 2002b). Thus, the impacts have been detected across at least three trophic levels within the community (Blamey et al. 2012). These impacts on the kelp forest communities in invaded areas have persisted for at least 15 years (Blamey et al. 2010, 2012), and are thought to be the result of the overfishing of large fish species that would normally consume lobsters (Blamey et al. 2014). Both abalone and lobsters once sustained highly valuable commercial fisheries, but recently these species have been shifted to the CITES and IUCN red list as endangered species. The invasion of rock lobsters has therefore resulted in several adverse impacts in invaded areas EOCH, both ecologically and economically (Tarr et al. 1996, Cockcroft et al. 2008, Blamey et al. 2010, 2012, 2015, Blamey and Branch 2012, Mead et al. 2013, Blamey and Bolton 2017).

1.6. Ecological impacts of climate change on kelp forests

Global climate change is defined by the Intergovernmental Panel on Climate Change (IPCC) as "a change in the state of the climate that can be identified (e.g. using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer." One of the major impacts of this, with particular pertinence to Eastern Boundary Upwelling Systems (EBUS), is the intensification of regional coastal wind patterns (Bakun 1990, Sydeman et al. 2014, Bakun et al. 2015, García-Reyes et al. 2015, Rykaczewski et al. 2015, Wang et al. 2015).

In South Africa, the changes in wind patterns, which occurred in the early 1980s, have resulted in increased upwelling variability and mean upwelling intensity along the west coast in particular, since the early 1990s (Blamey et al. 2012). This is driven by the shift to stronger south-easterly winds which are the drivers of upwelling in this system (Blamey et al. 2012, Hutchings et al. 2012). Additionally, Rouault et al. (2010) have described a negative trend (0.5°C per decade) in seawater temperature along the west coast which is a suggested result of the intensification of upwelling-favourable wind patterns (Blamey et al. 2015). This is contrary to the global trend of warming ocean temperatures as a result of climate change.

Globally, kelp distribution patterns are changing as a direct result of ocean warming due to global climate change, with distribution ranges shrinking in many places (Connell et al. 2008, Johnson et al. 2011, Harley et al. 2012, Smale et al. 2013, Wernberg et al. 2013). A recent study by Krumhansl et al. (2016) has shown that the extent, abundance or biomass of kelp is declining in 38% of the world's ecoregions. However, this study also shows that the magnitude and direction of kelp forest change is highly variable among regions, not consistently declining everywhere as the global average suggests. Conversely, in South Africa, kelp distribution patterns are changing positively, with ranges expanding (Bolton et al. 2012) and abundances increasing (Mead et al. 2013, Reimers et al. 2014). As the

biogeographical distribution of *Ecklonia maxima* has been hypothesised to be limited by the seawater temperature and not dispersal (Bolton et al. 2012), this expansion is probably due to an increase in wind-driven upwelling intensity along the south and west coastlines which results in a general cooling of the waters in this region (Rouault et al. 2010, Blamey et al. 2015). This could have great impacts on the ecological functioning of these systems and the coastal regions they inhabit.

'Marine heat waves' (*sensu* Hobday et al. (2016)) or periods of ocean warming have also been shown to negatively impact the abundance of kelps (Parnell et al. 2010, Smale and Wernberg 2013, Wernberg et al. 2016) and result in increased rates of blade degradation (Hobday 2000). In a recent study, Schlegel et al. (2017) have shown an increase in the frequency of marine heat wave events for the South African coastline. The impact of these events has not been investigated for South African kelp forests but devastating impacts have been illustrated in some parts of the world (Wernberg et al. (2016), but not in others (Reed et al. 2016).

An additional consequence of climate change is the increased frequency and intensity of storms which can result in the physical removal of kelp habitats, reducing biodiversity and thus simplifying food webs (Byrnes et al. 2011, Teagle et al. 2017). This is likely to have widespread ecological and socio-economic impacts on kelp forests around the world.

Understanding how climate change may influence the kelps, as well as the communities of which they form an integral part, is therefore important for making future projections about these organisms. However, to be able to project how an ecosystem will be impacted, a thorough understanding of its structure and functioning is required as a baseline for comparisons. This study aims to provide further information on the trophic structure and functioning of kelp forest ecosystems in South Africa (Chapters 4 and 5).

1.6. Role of stable isotope analysis in understanding kelp forest ecology

Traditionally, trophic interactions and food webs have been studied and characterised through the use of techniques such as gut content analysis and energy budgets (Hall and Raffaelli 1993, Vander Zanden et al. 1999, Layman et al. 2007a). This has been the case for all the work conducted on South African kelp forests thus far, with benthic surveys (e.g. Field et al. (1980a), Blamey et al. (2010)), energy budgets (e.g. Velimirov et al. (1977), Newell et al. (1982)), predator exclusion experiments (e.g. Barkai and Branch (1988b), Barkai et al. (1996), Day (1998)), and gut content analyses (Barkai and Branch (1988a), Haley et al. (2011)) being commonly applied. For example, part of the Kelp Bed Project which quantified the energy flow through the various components of the kelp forest at Oudekraal relied on the measurement of ash-free dry weights and energy content of different organisms (see Velimirov et al. (1977)). Although traditional methods provide useful insights, stable isotope analysis (SIA) offers several advantages. For the past three decades, stable isotope analysis

has become an increasingly powerful tool in assessing trophic connections and pathways in a variety of ecosystems (West et al. 2006, Layman et al. 2012). Stable isotope analysis, although extremely useful, should, where possible, be combined with traditional methodologies to provide more holistic insights into trophic connections.

All elements occur naturally in various forms known as isotopes, which are different in the number of neutrons in the nucleus, forming either stable or radioactive isotopes (Peterson and Fry 1987, Fry 2006). Each element exists as a proportion of its different isotopes which is controlled by natural processes, such as the carbon cycle for isotopes of carbon. When matter moves between states, one of the isotopes (usually the atomically lighter isotope) is favoured and thus the proportion changes. This is known as isotope fractionation (Peterson and Fry 1987, Fry 2006). The combination of fractionation and mixing produces characteristic isotope distributions within the natural environment (Peterson and Fry 1987, Peterson 1999, Fry 2006). In ecology, the natural abundance of stable isotopes occurring in organic matter (C, N, O, H and S) in various compartments of a system can provide insight into the elemental cycling within that system (Peterson and Fry 1987, Fry 2006).

The use of stable isotope analysis has become increasingly popular for understanding the flow of material through the food web of an ecosystem, (Hobson and Wassenaar 1999, West et al. 2006, Layman et al. 2012). Stable isotope analysis has been transformed from a novel technique to an indispensable tool for many ecologists conducting research in a plethora of ecological fields (Newsome et al. 2012). By measuring and understanding the stable isotope values of organisms within a food web, information on the flow of organic matter can be gathered, as consumer isotope values reflect their diet (DeNiro and Epstein 1976, Wada et al. 1991). In marine ecosystems, consumers are generally enriched in $\delta^{15}N$ relative to their diet by 3–4‰, and thus it is possible to trace diet as well as trophic position within a food web (DeNiro and Epstein 1981, Minagawa and Wada 1984, Peterson and Fry 1987, Cabana and Rasmussen 1994, Post 2002a). The $\delta^{13}C$ values however do not fractionate very much (~1‰) between trophic transfers, and can therefore be used to determine the ultimate source of carbon for a particular organism when there is a mixture of sources available (Peterson and Fry 1987, Fry and Sherr 1989, France and Peters 1997).

Stable isotope analysis has been successfully applied to numerous aspects of kelp forest ecology in other regions of the world (e.g. USA, Canada, Australia, New Zealand, Japan, France and Norway). These studies have focussed on various components of these systems, including, but not limited to, carbon acquisition by macroalgae (e.g. Raven et al. (1995, 2002), Raven and Giordano (2017)), phytoplankton and primary production (reviewed by Miller and Page (2012), Ramshaw et al. (2017)) the variability in macroalgal values (e.g. Stephenson et al. (1984), Simenstad et al. (1993), Dethier et al. (2013), Hyndes et al. (2013), Vanderklift and Bearham (2014), Mackey et al. (2015)), producer-consumer relationships (e.g. Vanderklift and Ponsard (2003), Vanderklift et al. (2006), Vanderklift

and Wernberg (2010), von Biela et al. (2016)), and food web structure and functioning (e.g. Kaehler et al (2000, 2006), Fredriksen (2003), Guest et al. (2010), Nadon and Himmelman (2010)). The kelp forests of South Africa therefore offer numerous research opportunities which are yet to be explored using SIA.

Although stable isotope techniques have improved greatly owing to advances in technology and analysis equipment, there are still areas where an accurate knowledge of the environment and ecosystem are required to interpret results. Natural variability and changes in isotope value of the components in an ecosystem are examples of such knowledge, which is critical for in assessing the dependence of one component on another and accurately measuring isotopic niche space. This thesis examines the ecology of South African kelp forests using SIA and in doing so, it is hoped that the application of new technologies and methodologies will add to the current understanding of the ecology of these important ecosystems.

1.7. Thesis structure and overview

Kelp forests along the west and south-western coastlines of South Africa are changing and are likely to change further as a result of continued global climate change and anthropogenic processes such fishing and pollution. Species distributions and abundances have already changed as a result of these factors, some with severe consequences for kelp forest communities. Further changes to these kelp communities could further impinge on the ecological functioning of the coastal environment and affect the livelihoods of the many people who rely on these systems. Thus, the primary aim of this study was to improve our understanding of the trophic structure and functioning of the kelp forests in South Africa. The main focus of this study is on trophic interactions, and how these interactions vary among ecologically distinct kelp forest communities.

Despite the fact that kelp forests are a major part of nearshore environment of the southern Benguela, research on these habitats has largely waned over the past 30–40 years (Blamey and Bolton 2017). The Kelp Bed Ecology Programme of the 1970s–1980s, which determined productivity estimates, energy flow and various species interactions (see review by Branch (2008)), was the last large-scale research focussing on the kelp forests of South Africa. This recent paucity of research is in stark contrast with the research efforts of other areas where these systems are present, e.g. North America, Europe, Australasia, Japan. Therefore, there is a definite need for new research methodologies and technologies to be applied to these systems to further our understanding of these vitally important habitats.

Against the backdrop of previous studies conducted on kelp forests in South Africa and globally, a series of aims and objectives were developed and examined. The thesis is structured into four research

chapters, each examining a different aspect of the trophic ecology of South African kelp forests. All four studies employed stable isotope analyses and techniques.

Chapter 2: Variability in stable isotope values of *Ecklonia maxima* and *Laminaria pallida*: implications for kelp forest food web studies.

Variability of basal food web components is poorly understood and often neglected, despite being a key assumption of food web models. Variability in stable isotope values has been shown to operate at different spatial and temporal scales, both for basal resources as well as for consumers (Guest et al. 2004, Page et al. 2008, Vanderklift and Wernberg 2010, Hansen et al. 2012, Mackey et al. 2015). The variability observed within marine macrophytes has been shown to be translated up the marine food web (Simenstad et al. 1993, O'Reilly et al. 2002, Vanderklift and Wernberg 2010, Hansen et al. 2012). Stable isotope values of basal resources, such as marine macrophytes, are thus not consistent and can create erroneous conclusions when interpreting the flow of energy through the food web. Kelp forest ecosystems provide an excellent case study for the importance of understanding basal resource variability as these systems exhibit bottom-up controlled food webs. The main aim and research questions of this chapter were:

2. To determine the magnitude of variation in $\delta^{13}C$ and $\delta^{15}N$ values of the two dominant kelp species along the south-western Cape coastline. Specifically, to answer the questions:

    2.1. Do the stable isotope values of different kelp tissues (holdfast, stipe, primary blade and fronds) vary within a single plant?

    2.2. Can frond length, and thus tissue age, be correlated with stable isotope values?

    2.3. Is there any evidence of temporal and spatial (geographical) variation in kelp stable isotope values?

Chapter 3: Characterising kelp forest POM during upwelling and downwelling conditions: using stable isotope analysis to differentiate between detritus and phytoplankton.

The faunal biomass in kelp forests is dominated (>70%) by filter feeding organisms, which consume particulate organic matter (POM) that is suspended in the water column (Miller and Page 2012). Around kelp forests, POM composition is highly variable but is predicted to comprise a high proportion of kelp-derived detritus (KDD). However, phytoplankton has also been shown to be an important carbon source for many benthic filter-feeding organisms within kelp forests (Newell et al. 1982, Stuart et al. 1982, Seiderer and Newell 1988, Cranford and Grant 1990, Levinton et al. 2002). Upwelling processes have been shown to impact the food availability within these systems, as they control the concentration of particulate organic matter (POM) and phytoplankton (Carter 1982, Wulff

and Field 1983, Brown and Hutchings 1987, Hill et al. 2006). Therefore, the main aim and research questions of this chapter were:

3. To characterise the POM in and around a selected kelp forest under upwelling and downwelling conditions, focusing on the proportions of KDD and phytoplankton. Specifically, to answer the questions:

> 3.1. Can the upwelling phase be used to gather 'pure' end-member phytoplankton values for use in stable isotope mixing models?
>
> 3.2. Can stable isotope mixing models be employed to determine the composition of POM collected along long-shore and off-shore transects during upwelling and downwelling conditions?
>
> 3.3. Is POM composition in, and around, a typical west coast kelp forest controlled by upwelling?

Chapter 4: Temporal and spatial variability in stable isotope values of South African kelp forest communities.

The kelp forest communities along the south-western Cape coastline exhibit marked differences in community structure (Field et al. 1980a, Anderson et al. 1997, Leliaert et al. 2000). These differences (discussed above) have resulted in kelp forests that exist in two separate community types (stable states), either with or without high abundances of grazing species, particularly sea urchins (Anderson et al. 1997, Leliaert et al. 2000, Blamey et al. 2010, 2012). The invasion of rock lobsters into areas east of Cape Hangklip has created further differences in the ecological communities within these kelp forest habitats. The natural variability in kelp forest community structure, as well as the impact of the lobster invasion, undoubtedly has impacts on the trophic structure and functioning of these communities. As stable isotope analysis is often used to study food web structure and functioning, these methods were employed to investigate the differences among these ecologically distinct kelp forest communities. The main aim and research questions of this chapter are:

4. To determine the influence of community structuring on the trophic positioning of dominant kelp forest organisms and to use community metrics to determine the magnitude of the differences in trophic structuring among these communities. Specifically, to answer the questions:

> 4.1. What is the magnitude of spatial and temporal variability in stable isotope values of dominant kelp bed producers and consumers?

4.2. Are there differences in the trophic positioning of kelp forest consumers across temporal and spatial scales?

4.3. Do community-wide metrics describing trophic structure vary among sites and seasons?

Chapter 5: Niche size of *Jasus lalandii* (Decapoda, Palinuridae) in South African kelp forests.

Jasus lalandii, the west coast rock lobster, is a key predator within the kelp forests and temperate reef ecosystems of southern Africa (Heydorn 1969, Pollock 1979, Cockcroft and Payne 1999). This species dominates the carnivore biomass and has the ability to markedly impact on the benthic community structure (Pollock 1979, Barkai and Branch 1988b, Field and Griffiths 1991, Barkai et al. 1996). The eastward shift of rock lobsters into the area east of Cape Hangklip has had a marked impact on the ecological and economical functioning of the kelp forests in this area. Stomach content analyses have been used to investigate the dietary shifts of this species following the invasion (Haley et al. 2011), but stable isotope analysis is yet to be applied to understanding the trophic ecology of this important kelp forest species. Stable isotope niche theory proposes the use of stable isotope values to define the scenopoetic (resource use) and bionomic (trophic interactions) dimensions of an organism's ecological niche (Bolnick et al. 2002, 2003, Bearhop et al. 2004, Newsome et al. 2007). Several metrics which analyse different aspects of an organism's niche were proposed by (Layman et al. 2007a) and have been successfully applied in niche ecology (e.g. Layman et al. (2007b), Ercoli et al. (2014) and Fuhrmann et al. (2017)). Subsequently, a more robust Bayesian approach has been developed (Jackson et al. 2011), and together these niche metrics allow for the quantitative comparison of niches among different individuals or among different populations or localities. The main aim and research questions of this chapter are:

5. To determine the stable isotope niche size and trophic position of *Jasus lalandii* among three ecologically distinct kelp forest ecosystems. Specifically, to answer the questions:

5.1. Is the trophic position of *Jasus lalandii* influenced by community structure?

5.2. Are there temporal and spatial differences in the size of the isotope niche of *Jasus lalandii*?

CHAPTER 2

Variability in stable isotope values of *Ecklonia maxima* and *Laminaria pallida*: implications for kelp forest food web studies

2.1 INTRODUCTION

Constructing food webs provides insight into the flow of energy within an ecosystem, particularly the routing of basal resources to higher level consumers (Fry and Sherr 1989, Krumins et al. 2013). The analysis of food webs has been used to study the structure and functioning of aquatic ecosystems globally, by providing an understanding of energy-flow pathways and the role of particular organisms within these habitats (Pimm 1982, Cabana and Rasmussen 1994, 1996, Vander Zanden and Rasmussen 1999). A key aspect of food web ecology is the characterisation of trophic levels within a given food web (Vander Zanden et al. 1999, Post 2002a, 2002b). The trophic level of constituent consumers can be used to assess the influence of natural or anthropogenic factors on the structure of food webs, such as those of coral reefs and kelp forests (Fredriksen 2003, Jack and Wing 2011). Therefore, accurate characterisation of the trophic interactions within an ecosystem is paramount to the understanding of its functioning (Pasquaud et al. 2010, Kadoya et al. 2012).

Traditional studies of marine food webs have relied on methods such as stomach content analysis and energy budgets to reconstruct food web topology (Newell et al. 1982, Hall and Raffaelli 1993, Vander Zanden and Rasmussen 1999), but these methods are limited as they provide a snapshot or temporally biased view of the various links and pathways between compartments (Paine 1988, de la Morinière et al. 2003). Stable isotope analysis, which has become an increasingly versatile tool for studies relating to trophic ecology, provides a more time-integrated depiction of complex interactions overlooked or under-represented by traditional methods (Peterson et al. 1985, Peterson and Fry 1987, Vinagre et al. 2008). Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been used to determine trophic sources and trophic interactions in many different ecosystems due to their reliable and predictable changes during trophic interactions (DeNiro and Epstein 1981, Fry 2006). Carbon isotope values are known to vary among primary producers which utilise different photosynthetic pathways (e.g. C3 vs. C4) and thus different inorganic carbon substrates (Smith and Epstein 1970, Raven et al. 2002, Raven and Giordano 2017). These isotope values are subsequently reflected in the tissue of consumers utilising these resources. Similarly, nitrogen isotope values were shown to be enriched in consumers by 3–4 ‰ relative to their diet (DeNiro and Epstein 1981, Minagawa and Wada 1984). Hence, carbon isotope values provide information on basal resource utilisation and nitrogen isotope values provide estimates of trophic positioning (Minagawa and Wada 1984, Peterson and Fry 1987, Post 2002a, Nadon and Himmelman 2010, Bouillon et al. 2011, Layman et al. 2012, Phillips et al. 2014).

Traditionally, a key assumption of stable isotope studies was the consistency of primary producer stable isotope values over space and time, which allowed traceability through the food web (Simenstad et al. 1993, Boon and Bunn 1994, Woodland et al. 2012, Dethier et al. 2013). For example, an estimate of the trophic position of consumers can be calculated relative to the nitrogen isotope value of the basal resource (i.e. primary producer) within the ecosystem (Post 2002b, 2002a).

Hence, variation of the producer's nitrogen value will result in variation of the calculated trophic position. A poor knowledge of the variability associated with the stable isotope values of primary producers at the base of a food web, can therefore result in erroneous conclusions about the structuring of the food web (Boon and Bunn 1994, Wing and Jack 2012, Dethier et al. 2013, Hyndes et al. 2013). Thus, although potentially informative, stable isotope analysis should be applied with caution when studying food webs. However, variability in stable isotope values has been shown to exist in many organisms and has been successfully used in studies of animal movement and migration (Hobson 1999). Additionally, the field of isoscapes is dependent on the predictable patterns of stable isotope variability across a spatial scale (West et al. 2009).

Variability in stable isotope values has been shown to operate at different spatial and temporal scales, both for basal resources, as well as for consumers (Page et al. 2008, Guest et al. 2010, Hansen et al. 2012, Hyndes et al. 2013). Variability within marine macrophytes has been shown to be translated up the marine food web (Simenstad et al. 1993, O'Reilly et al. 2002, Vanderklift and Wernberg 2010, Hansen et al. 2012). However, the magnitude of the variability decreases toward apex consumers as the longer tissue turnover rates in these organisms counter the short-term variability in lower level organisms (Simenstad et al. 1993, Nordström et al. 2009, Hansen et al. 2012, Hyndes et al. 2013). Stable isotope values of basal resources, such as marine macrophytes and phytoplankton, are thus not consistent and can create erroneous conclusions when interpreting the flow of energy through the food web.

Kelp forest ecosystems provide an excellent case study for the importance of understanding basal resource variability. Kelps are brown macroalgae which form complex three-dimensional habitats in near shore habitats in temperate and Arctic regions of the world (Steneck et al. 2002, Smale et al. 2013). In South Africa, kelp forests are formed by two kelp species, *Ecklonia maxima* and *Laminaria pallida*, which form ecologically and commercially important coastal habitats (Field et al. 1980a, Field and Griffiths 1991). *Ecklonia maxima* is a large, canopy forming species which extends to the surface whereas *Laminaria pallida* is a smaller species, forming a sub-canopy subtidally in the south, but occurring with *E. maxima* in shallow inshore water northwards on the west coast (Stegenga et al. 1997, Rothman et al. 2017a). These habitats support complex food webs, primarily dependent on kelp and phytoplankton as the main sources of carbon (Wulff and Field 1983, Fielding and Davis 1989). Detrital fragments are constantly dislodged and eroded from the distal tips of the kelp fronds and enter the food web via the suspension feeding organisms which inhabit these systems (Mann 1988, Stegenga et al. 1997). Phytoplankton concentrations are however variable, and concentrations within South African kelp forests depend greatly on upwelling cycle (Carter 1982). Therefore, kelp forest systems provide a bottom-up controlled trophic system, where changes in basal isotope values, and the associated variability, have the potential to be reflected in higher level trophic organisms.

This study therefore aims to identify the variability in kelp (*Ecklonia maxima* and *Laminaria pallida*) stable isotope values in order to provide a better understanding of the basal resource variation within these food webs. More specifically, the variability in stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) was evaluated among the different tissues of a kelp plant, and the variability along the length of single kelp frond investigated, and finally the temporal and spatial variability of a representative tissue type across eight sampling localities and two sampling occasions (seasons) was determined. These three steps were repeated for both kelp species, *Ecklonia maxima* and *Laminaria pallida*.

2.2 METHODS

Two aspects of variability in kelp stable isotope values were examined: 1) inter-tissue variability (tissue type and frond position), and 2) spatial and temporal variability.

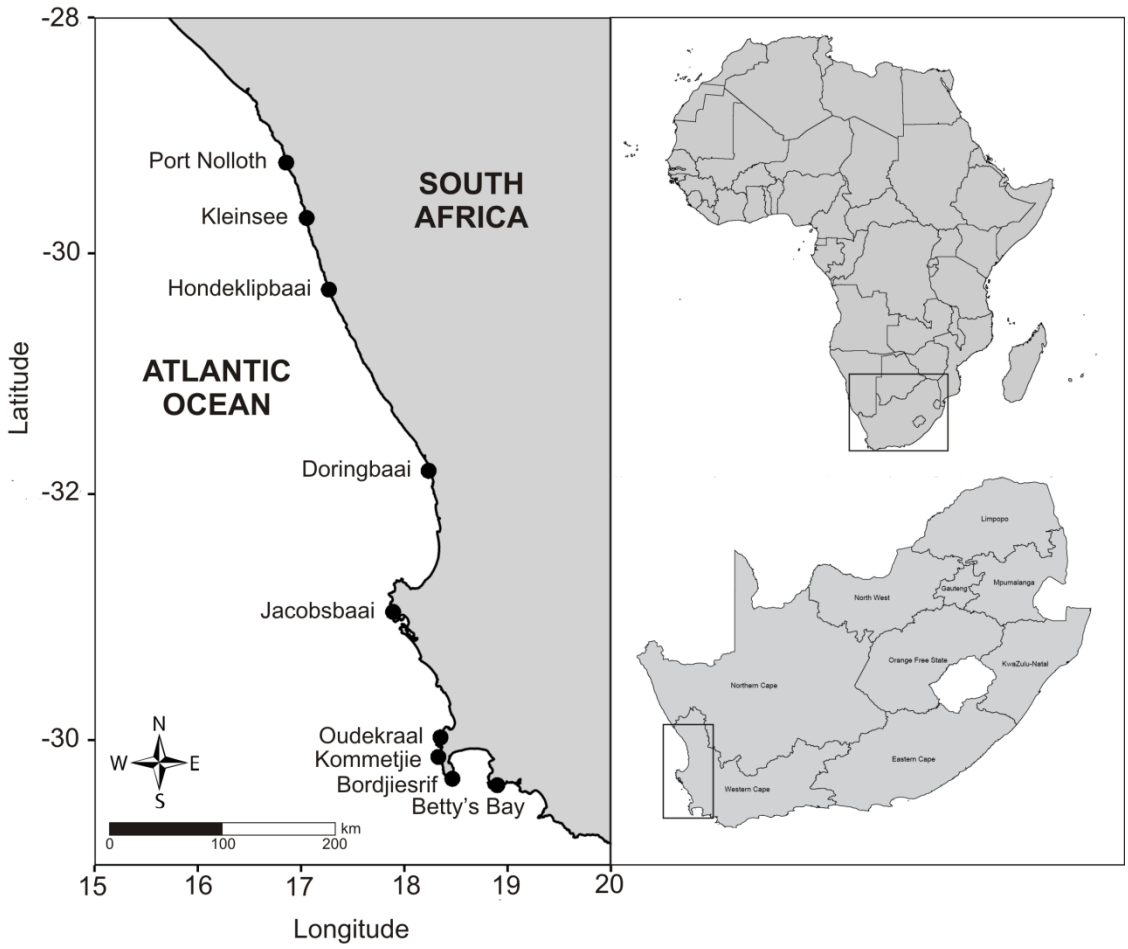

Figure 2.1: Map of the study area in relation to its location within South Africa, and Africa. Sampling localities indicated (•) where *Ecklonia maxima* and *Laminaria pallida* material was collected.

2.1.1. Tissue comparisons

Nine whole kelp plants from each species (*Ecklonia maxima* and *Laminaria pallida*) were collected at Oudekraal, on the west coast of South Africa (Figure 2.1), from a depth of 5m by SCUBA divers. Each plant was split into distinct sections (holdfast, stipe, fronds) before transport back to the laboratory for further processing. Subsamples of the four primary tissue types (holdfast, stipe, primary blade (*Ecklonia*), blade centre (*Laminaria*) and frond) were collected from each plant after thorough washing with distilled water. Tissue samples were collected from the same location on each kelp plant (Figure 2.2). However, as *Laminaria pallida* does not have a primary blade, this sample was collected in the centre of the main blade near the stipe (Figure 2.2).

2.1.2. Frond position

Three whole fronds were collected from each kelp species (*Ecklonia maxima* and *Laminaria pallida*) at Oudekraal from a depth of 5m by SCUBA divers. A single frond was collected from a single plant; thus, each frond represents an individual in the population. Three fronds were used for each species of kelp, representing three individuals. The longest frond on kelp plants of a similar size was collected in order to rule out size-related bias. In *Ecklonia maxima*, this represents the longest secondary blade on the plant whereas for *Laminaria pallida*, this was the longest extension of the split frond. Fronds were kept whole and transported back to the laboratory for further processing. Each frond was thoroughly cleaned with distilled water and the total length was measured. Subsamples were collected at pre-determined positions along the frond, with each position coinciding with 10% intervals of the total length (Figure 2.2). At each position, a strip of frond was excised across the width of the frond. Therefore, frond position refers to these different positions along the frond of both *E. maxima* and *L. pallida* as defined above.

2.1.3. Spatial and temporal sampling

Kelp fronds were collected from both *Ecklonia maxima* and *Laminaria pallida* plants at eight sites from Port Nolloth on the west coast to Betty's Bay, east of False Bay (see Figure 2.1). Samples were collected at Port Nolloth, Kleinsee, Hondeklipbaai, Doringbaai, Jacobsbaai, Kommetjie, Bordjiesrif and Betty's Bay during both the austral summer and winter in 2015/16, however only a single sampling occasion during each season. Because the depth distribution of *L. pallida* changes moving northwards along the coast, it was not possible to keep the sampling depth constant at all sites. Therefore, at some sites (Port Nolloth, Kleinsee, Hondeklipbaai, Doringbaai and Jacobsbaai) both *E. maxima* and *L. pallida* samples were collected from plants at the surface in shallow (2–3 m) water. Whereas at the other sites, *E. maxima* samples were collected in the same position but *L. pallida* samples were collected from deeper (5–8 m) water as they only occur here.

From each kelp frond, a portion of tissue was excised closest to the frond tip (Figure 2.2), and this was frozen prior to laboratory processing. Once back at the laboratory, each sample was thawed and subsequently washed with distilled water.

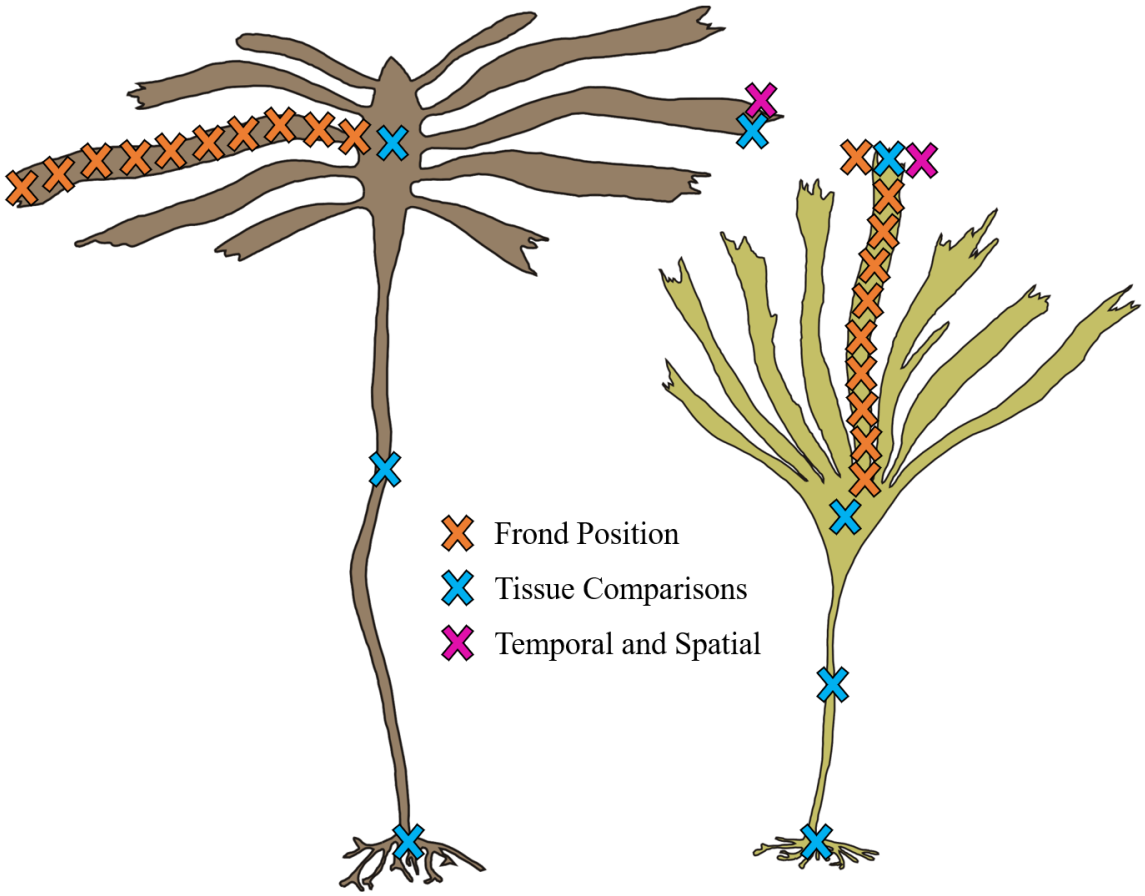

Figure 2.2: Sample collection points on kelps *Ecklonia maxima* (left) and *Laminaria pallida* (right) for frond position (orange), tissue comparisons (blue) and geographic sampling (pink) (See section 1.3 and Figure 1.2 for further details).

2.1.4. Laboratory processing and analysis

All kelp tissue samples were dried in an air-circulated oven (60°C) for a period of 48 hours. Once dried, samples were homogenized into a fine powder using a Retsch MM200 ball-mill. Powdered samples were then individually weighed out into tin capsules. Each capsule contained 1.2 mg of sample material, as specified by the analysis facility.

Stable isotope samples were analysed at iThemba LABS (Johannesburg, South Africa) on a Flash HT Plus elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer using a ConFlo IV interface (all equipment supplied by ThermoFisher, Bremen, Germany).

Isotope values were expressed as the parts per mille deviation from the standard in delta (δ) notation according to:

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

where: X = ^{13}C or ^{15}N & R = corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$

Carbon and nitrogen isotope values were corrected against an in-house standard (Merck Gel). Laboratory standards and blanks were run after every 20 samples.

2.1.5 Statistical analyses

Standard corrected stable isotope values were analysed in the statistical software R (version 3.4.2, (R Core Team 2017). In order to test for differences among different kelp tissue types, a two-way ANOVA was performed for each isotope value ($\delta^{13}C$ and $\delta^{15}N$), with tissue type and species as independent variables.

In order to assess the variability of stable isotope values among and within sites, a two-way analysis of variance (ANOVA) with site and season as random factors was carried out. A series of ANOVAs were used for $\delta^{13}C$, $\delta^{15}N$, C:N ratio, carbon and nitrogen content independently for each species. The assumptions of normality and homoscedascity were tested for all analyses.

Due to interest in the variability of isotope values within and among sites and sampling occasions, the variance explained by each component was calculated, using the magnitude of effects (ω^2), based on the equation below:

$$\omega^2 = \frac{SSQ_{Condition} - (df \times MSE)}{SSQ_{Total} + MSE}$$

Where, $SSQ_{Condition}$ is the sum of squares for the effect variable (site), *df* is the degrees of freedom, *MSE* is the mean square value of the residuals and SSQ_{Total} is the total sum of squares. The residuals are interpreted as the amount of variability within a group, in this case within a site within a season.

2.3 RESULTS

2.3.1. Tissue types

The $\delta^{15}N$ value ($df = 3, F = 59.93, p < 0.001$) as well as the ratio of C:N ($df = 3, F = 32.01, p < 0.001$) among the different tissues of *Ecklonia maxima* differed significantly (Table 2.1). There was however no significant difference in the $\delta^{13}C$ value among the different tissues ($df = 3, F = 2.64, p = 0.06$).

The $\delta^{15}N$ values for the *Laminaria pallida* tissues were significantly different ($df = 3, F = 32.40, p < 0.001$). Similarly, the $\delta^{13}C$ values were also significantly different among *L. pallida* tissues ($df = 3, F = 3.21, p < 0.05$). The ratio of C:N of the different tissues was significantly different ($df = 3, F = 24.82, p < 0.001$).

The $\delta^{13}C$ values of *Ecklonia maxima* and *Laminaria pallida* varied by 1.65‰ and 1.52‰ respectively, among the four different tissues. The $\delta^{15}N$ values were more variable for both species across tissue types, 3.75‰ and 4.21‰ for *E. maxima* and *L. pallida* respectively (Table 2.1).

Table 2.1: Mean stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) and C:N ratio (with standard deviations) of four selected tissue types from *Ecklonia maxima* and *Laminaria pallida*.

Ecklonia maxima

Tissue	**$\delta^{15}N \pm SD$**	**$\delta^{13}C \pm SD$**	**C:N ± SD**
Holdfast	7.29 ± 1.14	-20.74 ± 1.58	22.86 ± 2.74
Stipe	6.17 ± 1.23	-20.88 ± 1.73	29.11 ± 4.00
Primary Blade	5.02 ± 1.24	-21.86 ± 1.28	25.41 ± 1.47
Frond tip	3.54 ± 0.73	-20.21 ± 1.77	20.22 ± 2.71

Laminaria pallida

	$\delta^{15}N \pm SD$	**$\delta^{13}C \pm SD$**	**C:N ± SD**
Holdfast	6.69 ± 1.48	-18.32 ± 1.69	17.71 ± 3.27
Stipe	2.48 ± 0.45	-19.68 ± 0.72	30.53 ± 5.44
Blade Centre	2.94 ± 1.31	-19.60 ± 1.86	21.89 ± 1.22
Frond tip	2.78 ± 0.47	-18.16 ± 0.79	20.46 ± 1.64

2.3.2. Frond position

Consistent patterns emerged between frond position and both stable isotopes, $\delta^{13}C$ and $\delta^{15}N$, as well for the C:N ratio for both *Ecklonia maxima* and *Laminaria pallida* (Figure 2.3). Trends do not conform to linear patterns and thus were not analysed using correlation or regression methods. However, the consistency of the results across three replicate kelps is indicates clear and consistent trends.

The $\delta^{13}C$ values for both species become depleted with distance from the meristematic tissue at the base of the frond until about mid-way along the frond where it begins to become depleted again toward the frond tip. The $\delta^{15}N$ values exhibit a similar trend for *E. maxima* with the frond tip being more depleted than the meristematic region at the base. The trend in *L. pallida* is less clear with more variability in the data. The C:N ratio of both species is very consistent across the three replicates. For *E. maxima*, the C:N ratio drops by almost 15 units along the length of the frond. *Laminaria pallida* however exhibits a different trend with the C:N ratio rising towards the middle of the frond and then

dropping steeply toward the tip, with the meristem and frond tip having similar values. The trends in the C:N ratio of *E. maxima* and *L. pallida* are better interpreted if viewed with the carbon and nitrogen content of each sampling point. Carbon and nitrogen content both increase along the *E. maxima* fronds, whereas an inverse relationship occurs in the *L. pallida* fronds.

The range of $\delta^{13}C$ values within a single frond, from meristem to tip, was 2.56‰ for *E. maxima* and 3.09‰ for *L. pallida*. The $\delta^{15}N$ showed a similar range in both species, 2.88‰ for *E. maxima* and 2.67‰ for *L. pallida*.

2.3.3. Spatial and temporal variability

For the samples collected during summer (Figure 2.4), *Laminaria pallida* was most depleted in $\delta^{13}C$ at Jacobsbaai (-21.63‰) and most enriched in $\delta^{13}C$ at Doringbaai (-10.41‰). However, during winter (Figure 2.5), *L. pallida* was most depleted in $\delta^{13}C$ at Jacobsbaai (-24.03‰) and most enriched in $\delta^{13}C$ at Hondeklipbaai (-11.61‰). *Ecklonia maxima* was most depleted in $\delta^{13}C$ at Port Nolloth (-19.54‰) and most enriched in $\delta^{13}C$ at Kommetjie (-10.17‰) during summer. Similarly, in winter, *Ecklonia maxima* was most depleted in $\delta^{13}C$ at Kleinsee (-22.11‰) and most enriched in $\delta^{13}C$ at Jacobsbaai (-13.59‰).

The summer $\delta^{15}N$ values were most enriched at Jacobsbaai (7.68‰) and Betty's Bay (6.06‰) for *L. pallida* and *E. maxima* respectively, and most depleted at Port Nolloth (3.17‰) and Kleinsee (2.62‰) for *L. pallida* and *E. maxima* respectively. In winter, $\delta^{15}N$ was most enriched at Betty's Bay (7.35‰) for *L. pallida* and Kommetjie (7.61‰) for *E. maxima* respectively. The $\delta^{15}N$ values were most depleted at Doringbaai for both *L. pallida* (0.88‰) and *E. maxima* (0.23‰) respectively.

Across the sampling localities, the range of stable carbon isotope values ($\delta^{13}C$) was found to be higher in *Laminaria pallida* (11.22‰) when compared to *Ecklonia maxima* (9.37‰) during the summer. However, in winter, this pattern was reversed as *Ecklonia maxima* (14.99‰) has a greater range when compared to *Laminaria pallida* (12.42‰). The nitrogen isotope values ($\delta^{15}N$) also displayed the same pattern, with *L. pallida* having a greater range in values (4.51‰) relative to *E. maxima* (3.44‰) in the summer, and *E. maxima* having a greater range in values (6.47‰) relative to *L. pallida* (7.38‰) in the winter.

The most interesting trend in the data, which was evident in both seasons, was the break at Jacobsbaai in the mean $\delta^{13}C$ values of the two species. At this point, *E. maxima* and *L. pallida* mean values begin to diverge from each other with *L. pallida* being more depleted at all subsequent (southward) sites. This is also the point where *E. maxima* and *L. pallida* begin to diverge in terms of depth habitat occupied.

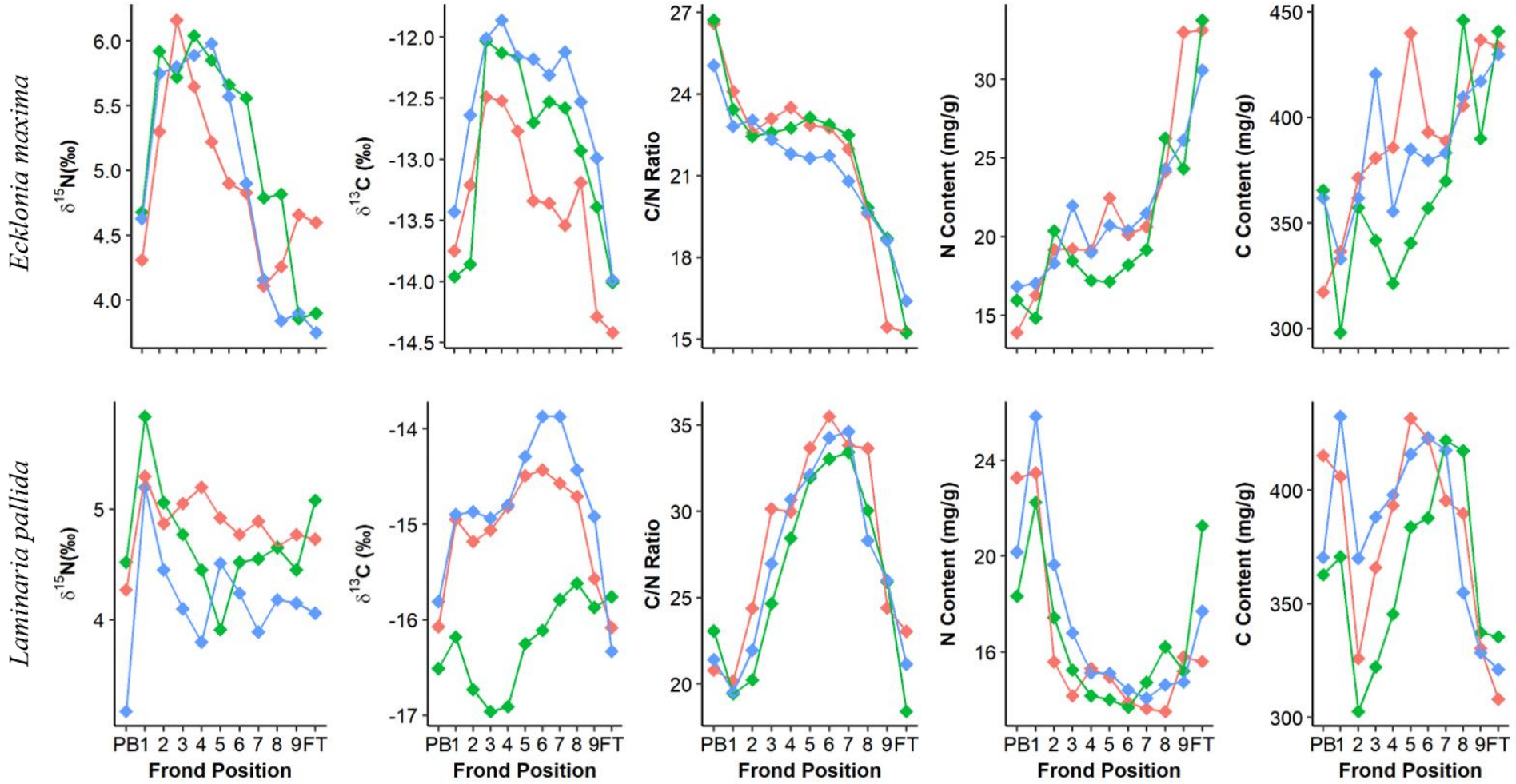

Figure 2.3: Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), C:N ratio, carbon content (mg/g of dried tissue) and nitrogen content (mg/g of dried tissue) of *Ecklonia maxima* and *Laminaria pallida* fronds measured at different frond positions, from primary blade (PB) to frond tip (FT) for three replicate (colours) kelps collected at Oudekraal.

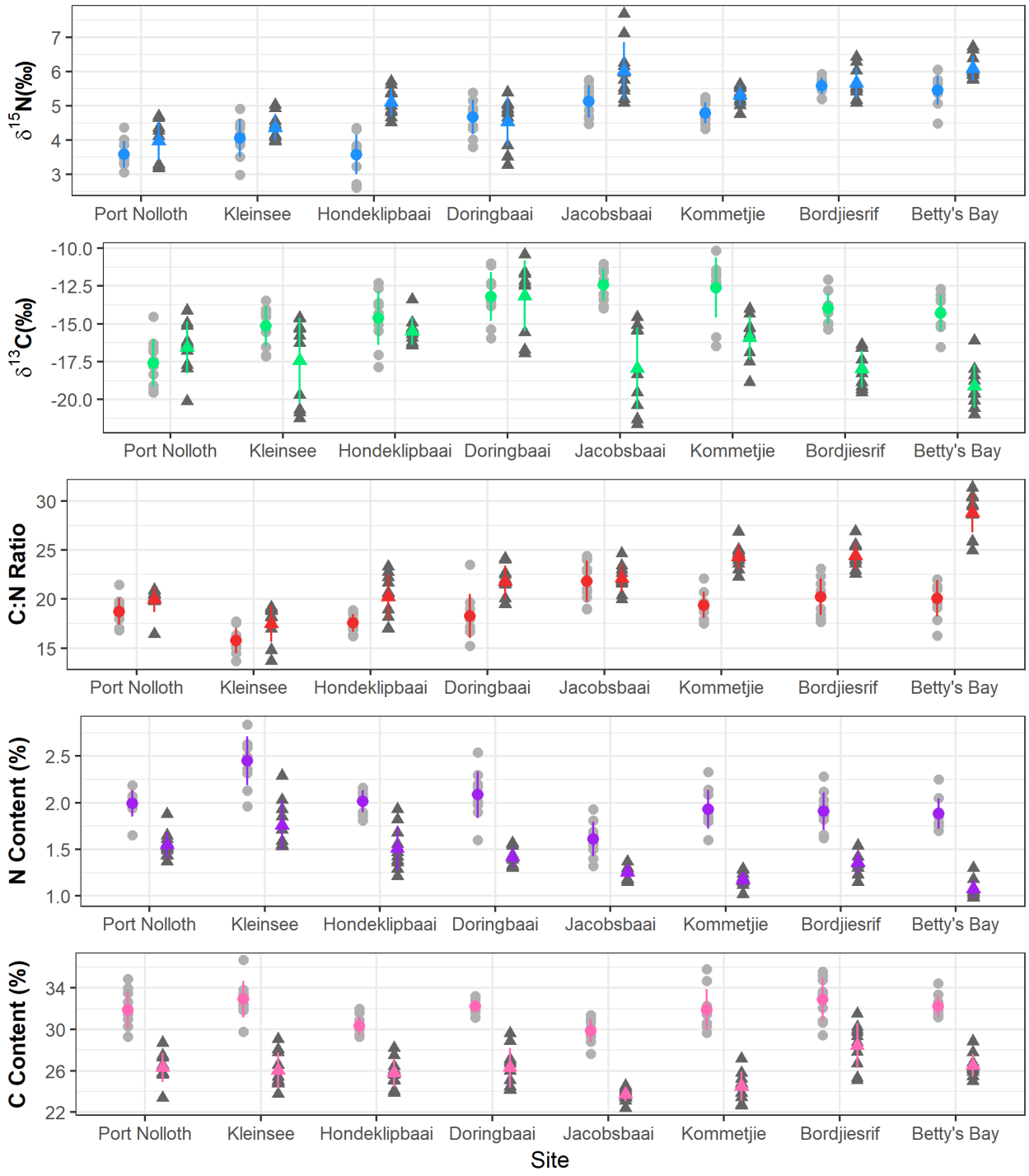

Figure 2.4: Summer stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values, C:N ratio and nitrogen and carbon content (%) for kelps (*Ecklonia maxima* and *Laminaria pallida*) at eight sampling localities. Circles and triangles represent *E. maxima* and *L. pallida* respectively. Coloured points and error bars indicate mean and standard deviation.

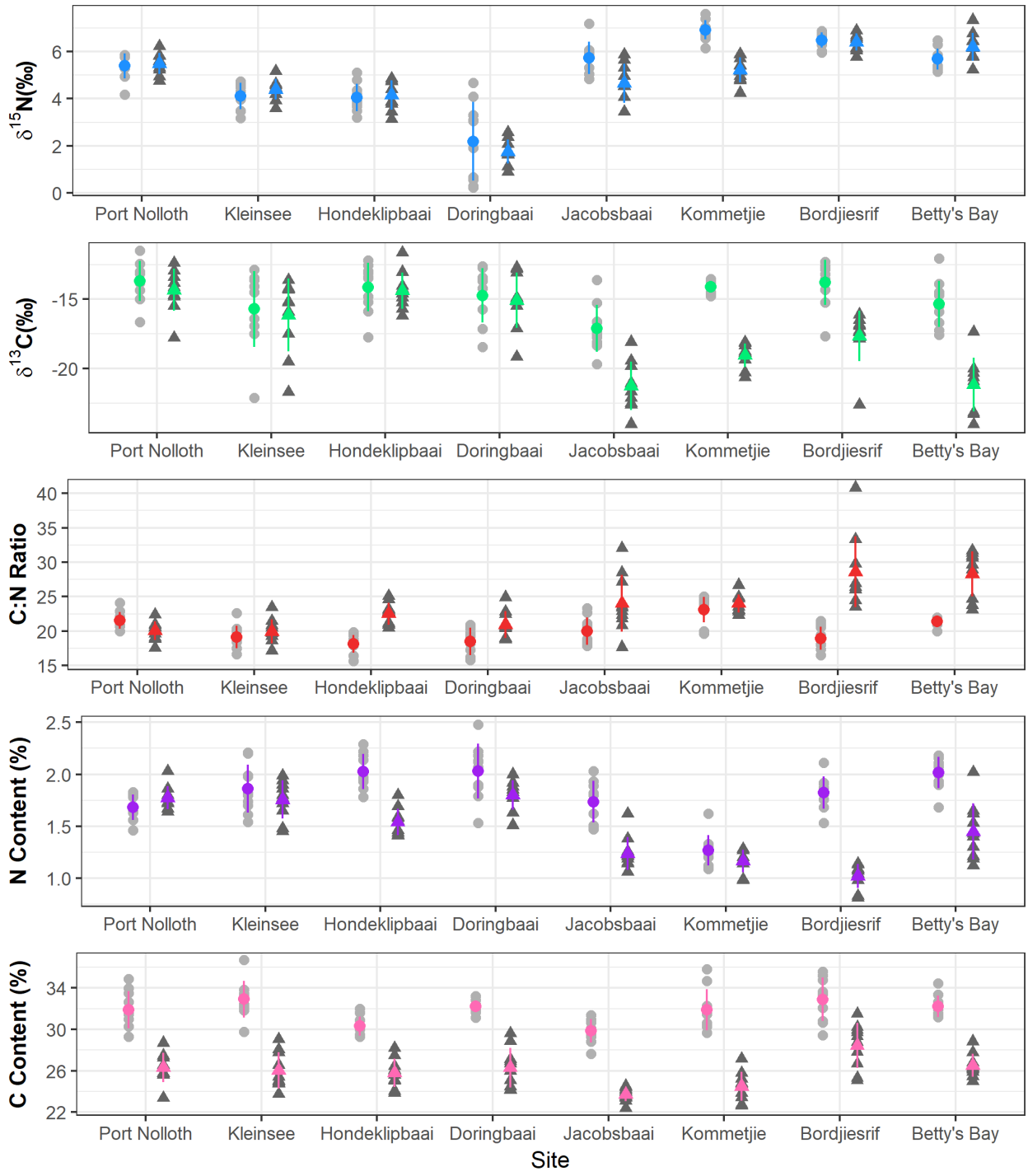

Figure 2.5: Winter stable isotope ($\delta^{13}C$ and $\delta^{15}N$ values, C:N ratio and nitrogen and carbon content (%) for kelps (*Ecklonia maxima* and *Laminaria pallida*) at eight sampling localities. Circles and triangles represent *E. maxima* and *L. pallida* respectively. Coloured points and error bars indicate mean and standard deviation.

Table 2.2: Results of the analyses of variance for *Ecklonia maxima* and *Laminaria pallida* for the two stable isotope values, C:N ratio and carbon and nitrogen content (%), testing for differences among sites and season. Variance explained as indicated by magnitude of effects (ω^2) with the largest value for each marker in bold.

			Ecklonia maxima				***Laminaria pallida***			
Source		***df***	***MS***	***F***	***p***	***ω^2***	***MS***	***F***	***p***	***ω^2***
δ^{15}N	Site	7	141.88	51.56	<0.001	**50.3**	132.56	63.66	<0.001	**53.8**
	Season	1	8.87	22.56	<0.001	3.1	4.58	15.38	<0.001	1.8
	Site x Season	7	68.87	25.03	<0.001	23.9	62.21	29.87	<0.001	24.8
	Residual	144	56.61			22.7	42.84			19.6
δ^{13}C	Site	7	85.95	4.62	<0.001	9.8	652.86	26.62	<0.001	**46.7**
	Season	1	13.52	5.09	<0.05	1.6	18.38	5.25	<0.05	1.1
	Site x Season	7	203.04	10.92	<0.001	26.8	165.54	6.75	<0.001	10.5
	Residual	144	382.55			**61.8**	504.46			41.7
C:N	Site	7	301.46	16.21	<0.001	31.9	1543.58	39.31	<0.001	**59.6**
	Season	1	49.20	18.52	<0.001	5.2	54.67	9.75	<0.01	1.9
	Site x Season	7	152.06	8.18	<0.001	15.0	112.44	2.86	<0.01	2.9
	Residual	144	382.52			**47.9**	807.84			35.6
% C	Site	7	414.58	23.26	<0.001	33.1	753.50	25.45	<0.001	**33.1**
	Season	1	44.1	17.32	<0.001	3.5	291.38	68.89	<0.001	13.1
	Site x Season	7	372.08	20.88	<0.001	29.5	530.59	17.92	<0.001	22.9
	Residual	144	366.6			**33.9**	609.08			30.9
% N	Site	7	5.11	20.09	<0.001	32.3	7.74	44.60	<0.001	**55.6**
	Season	1	1.29	35.48	<0.001	8.3	0.25	10.11	<0.01	1.7
	Site x Season	7	3.36	13.21	<0.001	20.7	2.02	11.63	<0.001	13.6
	Residual	144	5.23			**38.7**	3.57			29.2

The $\delta^{15}N$ values of *Ecklonia maxima* ($F = 51.56$, $df = 7$, $p < 0.001$) and *Laminaria pallida* ($F = 63.66$, $df = 7$, $p < 0.001$) were significantly different among the sampling sites (Table 2.2). The differences among sites accounted for the most variability in $\delta^{15}N$ values of both *E. maxima* (50.3%) and *L. pallida* (53.85). the $\delta^{15}N$ values were significantly different between sampling occasions for both species, however sampling occasion (season) accounted for very little of the variability observed (Table 2.2). The interaction of site and season was significant for both *E. maxima* and *L. pallida* and accounted for approximately 24% of the variability in $\delta^{15}N$ values (Table 2.2). This indicates that the differences among sites were not consistent in the two sampling occasions. Within-population variability (residuals) accounted for 22.7% of the $\delta^{15}N$ variability of *E. maxima* and 19.6% in *L. pallida* (Table 2.2).

The $\delta^{13}C$ values of *E. maxima* ($F = 85.95$, $df = 7$, $p < 0.001$) and *L. pallida* ($F = 652.86$, $df = 7$, $p < 0.001$) were significantly different among sampling sites (Table 2.2). However, the variability explained by site was only 9.8% for *E. maxima* compared to 46.7% for *L. pallida* (Table 2.2). Although differences among sampling occasions (seasons) was significantly different, the variability explained by this factor was less than 2% for both species (Table 2.2). The interaction term (site x season) was statistically significant for both *E. maxima* and *L. pallida*, indicating the differences among sites was dependent on season (Table 2.2). The residuals accounted for a large proportion of the variability explained for both *E. maxima* (61.8%) and for *L. pallida* (41.7%) indicating a large intra-population variability in $\delta^{13}C$ values.

The C:N ratio of *E. maxima* ($F = 301.46$, $df = 7$, $p < 0.001$) and *L. pallida* ($F = 1543.58$, $df = 7$, $p < 0.001$) was significantly different among the sampling sites (Table 2.2). The variability explained by among site differences was however substantially greater in *L. pallida* (59.6%) in comparison to *E. maxima* (31.9%). Sampling occasion (season) was statistically significant for both species, however it only accounted for a small proportion of the variability in C:N ratios (*E. maxima* = 5.2% and *L. pallida* = 1.9%). The interaction term was significant for both *E. maxima* and *L. pallida* and accounted for 29.5% and 22.95 of the variability in C:N ratio respectively (Table 2.2). Intra-population variability, as explained by the residual values, accounted for a large proportion of the variability in C:N ratio of *E. maxima* (33.9%) and *L. pallida* (30.9%).

The tissue carbon content (%) of *E. maxima* ($F = 414.58$, $df = 7$, $p < 0.001$) and *L. pallida* ($F = 753.50$, $df = 7$, $p < 0.001$) was significantly different among sampling sites (Table 2.2). The variability explained by among site differences was the same for both species (33.1%). Sampling occasion (season) was significant for both species, however only accounted for a small fraction of the variability in tissue carbon content (Table 2.2). The interaction of site and season was significant for both species and accounted for a similar proportion of the variability in tissue carbon content of *E. maxima* (29.5%) and *L. pallida* (22.9%). The variability explained by intra-population differences

(among individuals collected at the same time) accounted for 33.9% of the variability in *E. maxima* and 30.9% of the variability in *L. pallida* (Table 2.2).

The nitrogen content (%) of the tissue was significantly different among sites for both *E. maxima* (F = 5.11, df = 7, $p < 0.001$) and *L. pallida* (F = 7.74, df = 7, $p < 0.001$). However, the variability explained by site was substantially higher for *L. pallida* (55.6%) when compared to *E. maxima* (32.2%). Although sampling occasion (season) was significant for both species, the variability explained by season was low for both *E. maxima* (8.3%) and *L. pallida* (1.7%). The interaction term (site x season) was significant for both *E. maxima* and *L. pallida* (Table 2.2), indicating the among site differences were dependent on season. The variability explained by the interaction term was larger for *E. maxima* (20.7%) than *L. pallida* (13.6%). Intra-population variability, as explained by the residual values, accounted for a large proportion of the variability in tissue nitrogen content of *E. maxima* (38.7%) and *L. pallida* (39.2%).

The results in Table 2.2 indicate a similar pattern across all the markers for *E. maxima*, with the exception of $\delta^{15}N$ values. For all other markers ($\delta^{13}C$, C:N ratio, %C and %N) the largest proportion of the variability was explained by intra-population variability. This is the variability among individuals collected at the same place within a single sampling occasion. *Laminaria pallida* however exhibited a different trend, with site explaining the largest proportion of the variability in all five markers used (Table 2.2).

2.4 DISCUSSION

The results of the present study show that stable isotope values of both *Ecklonia maxima* and *Laminaria pallida* vary among different tissues of a single plant (Table 2.1), within a single lamina within each species (Figure 2.3), among seasons, and among sites across a broad spatial scale (Figure 2.4 & 2.5). *Laminaria pallida* has a larger range in both $\delta^{13}C$ and $\delta^{15}N$ when compared with *Ecklonia maxima* across the geographical scale of the sampling sites. Geographical differences in $\delta^{13}C$ values were detected for both species, but accounted for more of the variability in *L. pallida*. Differences between sampling occasion were found in both species for both $\delta^{13}C$ and $\delta^{15}N$ values.

2.4.1. Scales of variability within marine macroalgae

The identification of variability in macrophyte (macroalgae and seagrasses) stable isotope values has become increasingly common in the literature but still remains poorly understood (Dethier et al. 2013). An early study by Stephenson et al. (1984) identified the variability of $\delta^{13}C$ within a single lamina of the kelp *Saccharina latissima* (as *Laminaria longicruris*, see McDevit and Saunders (2010)), and reported significant variation between the meristem and distal portions of the fronds. Similarly, Fredriksen (2003) also found that the distal parts of the fronds of the kelp, *Laminaria hyperborea* (Gunnerus) Foslie, were isotopically lighter, in ^{13}C and ^{15}N, than the basal sections. The results of this study add to this, highlighting the variability of both $\delta^{13}C$ and $\delta^{15}N$ values along the length of a lamina in *Ecklonia maxima* and *Laminaria pallida*. Stephenson et al. (1984) also noted markedly different carbon isotope values between the different *Laminaria* tissues sampled: frond blades, stipe and holdfast. Fronds of both *E. maxima* and *L. pallida* were depleted in $\delta^{15}N$ relative to the other tissues. The $\delta^{13}C$ of the fronds were enriched for both species relative to other tissues. On a finer scale, both species showed considerable but consistent patterns along the length of the frond for the two chosen stable isotope values. This indicates a large degree of variation, even at the small spatial scale of a single lamina or within a single kelp plant. These patterns will be discussed in more detail below.

Spatial variability of marine macrophyte stable isotope values has been shown to operate at different geographical scales, from among sites separated by small distances (10 s of km) (Raven et al. 1995, Dethier et al. 2013) to larger regional distances of 100 s of km (Simenstad et al. 1993, Vanderklift and Wernberg 2010, Mackey et al. 2015, Stepien 2015). Both *Laminaria pallida* and *Ecklonia maxima* showed spatial variability over the scale of the west coast of South Africa, however particularly for $\delta^{13}C$, site explained a greater proportion of the variability in *L. pallida* than for *E. maxima*.

The range in $\delta^{13}C$ values of *E. maxima* (summer: 9.37‰, winter: 14.99‰) and *L. pallida* (summer: 11.22‰, winter: 12.42‰) were similar to those reported by Vanderklift and Bearham (2014) for *Ecklonia radiata* (around 8.9‰ and 9.7‰ for summer and winter respectively); however, the winter

values in this study had a higher range. Similarly, the $\delta^{15}N$ values of *E. maxima* (summer: 3.44‰, winter: 7.38‰) and *L. pallida* (summer: 4.51‰, winter: 6.47‰) had comparable ranges in values to those described for *E. radiata* (4.1‰ and 4.6‰ for summer and winter) by Vanderklift and Bearham (2014). The values in this study also fall within the ranges described by Boon and Bunn (1994), who report variability >10‰ in $\delta^{13}C$ for a variety of aquatic plants.

Temporal variability has also been recorded for marine and aquatic macrophytes in general (Boon and Bunn 1994, Dethier et al. 2013), but also specifically for kelps such as *Ecklonia radiata* (Vanderklift and Bearham 2014, Mackey et al. 2015) and *Laminaria hyperborea* (Fredriksen 2003). Carbon isotope values were more enriched in August (summer) when compared to both November (winter) and March (winter) for *L. hyperborea* (Fredriksen 2003). The results of this study indicate a similar trend as sampling occasion (season) accounted for a large proportion of the variability in stable isotope values of both *E. maxima* and *L. pallida*.

2.4.2. Variability in $\delta^{15}N$ values

The variability of nitrogen stable isotope signatures in marine macroalgae is primarily due to changes in nitrogen source, with algal $\delta^{15}N$ values reflecting that of the source (Dudley et al. 2010). Marine dissolved inorganic nitrogen (DIN) is known to range in $\delta^{15}N$ between 6–8‰ (Miyake and Wada 1967, Liu and Kaplan 1989, Sigman et al. 1997, 2000). As macroalgae $\delta^{15}N$ values reflect those of the nutrient source, many temperate algae have $\delta^{15}N$ values within this range (Monteiro et al. 1997, Cornelisen et al. 2007, Dudley and Shima 2010).

Seasonal differences in $\delta^{15}N$ were detected in both *Ecklonia maxima* and *Laminaria pallida* collected along the coastline. In the northern hemisphere, where growth is often limited by nutrient (C and N) or light availability, kelps have adopted a mechanism to store nitrogen and carbon (see Chapman and Craigie 1977, 1978, Chapman and Lindley 1980). For example, *Saccharina latissima* (as *Laminaria longicruris*) has been shown to accumulate nitrate (NO_3^-) during winter and supply this to meristematic tissue for 6–8 weeks during the growing season in spring (Chapman and Craigie 1977). It has also been shown that *Ecklonia maxima* takes up more nitrogen, in the form of NO_3^-, under upwelling conditions (Probyn and McQuaid 1985). However, the magnitude of seasonal variability in South African systems is much lower than those in the northern hemisphere (e.g. North Atlantic). Therefore, South African kelps, particularly *E. maxima* are not likely to store carbon or nitrogen compounds to the same extent as *S. latissima* (Smith 2007). Nevertheless, short-term changes in tissue nitrogen content can be linked to changes in the nitrogen content of the surrounding water (e.g. upwelling), however, long-term storage of nitrogen has not been recorded for South African kelps. Upwelling intensity is highly seasonal, with increased intensity during summer months and a much reduced frequency and intensity during winter months (Andrews and Hutchings 1980). As upwelling

results in the influx of nitrate into kelp forests, the seasonal trends observed in the $\delta^{15}N$ values, nitrogen content and C:N ratios could therefore be linked to upwelling.

The $\delta^{15}N$ values of both *E. maxima* and *L. pallida* fall within the expected 6–8‰ range, but also show a steady enrichment pattern moving southwards from Port Nolloth, with Betty's Bay having the most enriched values. In winter, the sites located around the Cape Peninsula and Betty's Bay had enriched $\delta^{15}N$ values compared to the other sites further north, however this trend was not statistically significant. Vanderklift and Wernberg (2010) showed how $\delta^{15}N$ of the kelp *Ecklonia radiata* could be influenced by anthropogenic sources of nutrients at certain sites close to cities. (Dudley and Shima 2010)Several authors have shown that macroalgae and consumers located close to sewage outfalls have enriched $\delta^{15}N$ values, allowing the influence of this nutrient source to be successfully traced (McClelland and Valiela 1998, Gartner et al. 2002, Rogers 2003, Costanzo et al. 2005, Dudley and Shima 2010, Connolly et al. 2013, Wang et al. 2016). Similarly, the enrichment of *Ulva lactuca* $\delta^{15}N$ values in Saldanha Bay has been shown to be linked to the nutrient effluent from a pelagic fish processing factory located here (Monteiro et al. 1997).

However, increased nutrient load, in the form of nitrate, has been shown to be taken up rapidly by *Ecklonia maxima* during upwelling conditions (Waldron and Probyn 1992), and is assumed to be true for *Laminaria pallida* as well. This increased nitrogen uptake results in a higher tissue nitrogen content which lowers the C:N ratio (Probyn and McQuaid 1985). This was not evident in the data, instead the nitrogen content of *Laminaria pallida* was significantly reduced in the southern sites, and the C:N ratio of *L. pallida* at Betty's Bay was also the highest of all sites in summer and winter. Nitrogen content of *L. pallida* was also the lowest at Betty's Bay during summer, but not in winter. This therefore implies that nutrient availability is not in fact higher in the southern areas (south of Jacobsbaai), but particularly around Betty's Bay.

2.4.3. Variability in $\delta^{13}C$ values

The most interesting pattern that emerged from the spatial analysis was the deviation in $\delta^{13}C$ values that occurred between the means of *E. maxima* and *L. pallida* once the collection depth changed. When *L. pallida* is restricted to deeper water, the $\delta^{13}C$ value becomes more depleted than *E. maxima*, suggesting a change to the carbon uptake mechanisms, which will be discussed below.

A number of different explanations for the variability in carbon stable isotope values of marine macrophytes were summarised by Stephenson et al (1984). These were classified into five main topics, *viz.* 1) the isotopic composition of source carbon; 2) the proportional utilisation of bicarbonate (HCO_3^-) and carbon dioxide (CO_2); 3) the photosynthetic pathway used (C3 vs. C4); 4) the influence of isotopically distinct epibionts, and 5) the differential storage of biochemical compounds. These

factors will operate at different scales, both spatial and temporal, and therefore create a complex landscape where variability is inevitable.

Light availability has been identified as an important factor which aids in the absorption of HCO_3 from the water column, as this requires more energy via carbon concentrating mechanisms (CCMs) (Simenstad et al. 1993). *Ecklonia radiata* is known to require more energy, gathered from irradiance, to assimilate HCO_3 preferentially over CO_2 (Cornelisen et al. 2007). Additionally, light availability was shown to be the primary cause of variability in $\delta^{13}C$ values of *E. radiata* along the Australian coastline (Vanderklift and Bearham 2014). Raven and Giordano (2017) discuss the ability of certain Phaeophyceae to acquire carbon via C_3 and C_4 metabolism under different light conditions. These authors suggest that algae exposed to greater light at the surface will use C_4 metabolic pathways during photosynthesis. This will result in a more enriched $\delta^{13}C$ value than algae which use C_3 metabolism under lower light availability. However, this has at present only been reported for the Fucales (Raven and Giordano 2017), and thus further investigation is required for South African kelps. In Figure 2.4, it is evident that when *L. pallida* is found at the surface with *E. maxima* (northern sites), the two species have more similar $\delta^{13}C$ values. This suggests that they use the same source of carbon and the same carbon metabolism. However, when the two species are separated by depth (southern sites), with *L. pallida* in deeper water, there is a marked difference in values with *L. pallida* being severely depleted in $\delta^{13}C$. Light availability would certainly correlate with this pattern and therefore it is likely to have resulted in the observed difference in $\delta^{13}C$ values.

Stepien (2015) suggests a simple calculation for determining whether macrophytes depend on a particular dissolved inorganic carbon (DIC) source. There are much more intricate and accurate methods for determining whether macroalgae have CCMs, but this is beyond the scope of the current study. Based on the assumption that the $\delta^{13}C$ value of CO_2 is -10.64‰ and HCO_3 is +0.08‰, any macrophyte tissue which has a $\delta^{13}C$ value between -30‰ and -10‰, is utilising a mixture of these two carbon sources. It is therefore possible to determine that both *Ecklonia maxima* and *Laminaria pallida* depend on a mixture of HCO_3^- and CO_2 as sources of DIC, as both have average values that fall within this range. This has been shown to be true for most marine macrophytes globally (Stepien 2015). Because of the utilisation of multiple carbon sources, variability of the $\delta^{13}C$ values is to be expected (Stepien 2015).

Temperature is another factor which can result in variability of $\delta^{13}C$ in autotrophs (Hemminga and Mateo 1996). Colder water provides a larger pool of CO_2 (isotopically lighter carbon), therefore giving macrophytes more depleted $\delta^{13}C$ values (Mackey et al. 2015). However, Vanderklift and Bearham (2014) showed that the variability in isotope values of *E. radiata* is not linked to temperature but rather light intensity. Our results also show no distinct differences in $\delta^{13}C$ along the coastline, despite the known temperature gradient along the west coast (Smit et al. 2013, 2017).

Variability within the lamina and among the different tissues of the kelps could indicate the differential storage of biochemical compounds among the different tissues, as suggested by Stephenson et al. (1984). Structural components such as the stipe and holdfast, are likely to be comprised of different tissue types when compared with the fronds which are responsible for photosynthesis. Meristematic tissue can be considered as sinks of carbohydrates as these tissues require these compounds in order to facilitate the formation of new tissue (Chapman 1979). The compounds produced photosynthetic are also known to be translocated to different areas within kelps (Chapman 1979).

Another source of variation in isotope values is the age of the kelp plants. In the study of Fredriksen (2003), younger *L. hyperborea* plants were isotopically lighter in $\delta^{13}C$ than mature plants. Page et al. (2008) also noted differences between actively growing and senescent fronds of the giant kelp *Macrosystis pyrifera* for both $\delta^{13}C$ and $\delta^{15}N$ values. The age of the tissue becomes important when looking at the samples collected along the length of the frond. The frond tip represents the oldest tissue on the frond, and the opposite end, where the meristematic tissue is located, will be the youngest tissue. There are definite trends along the length of the frond for C:N ratios and the carbon and nitrogen content within these tissues. However, differences in stable isotope values are not as apparent when looking only at the frond tip and meristematic tissue. There are, however, substantial changes between these points which will also coincide with the healthiest and photosynthetically active tissue on the frond. Because the same representative tissue was collected when conducting spatial sampling, it is unlikely that differences among the sites can be attributed to kelp age.

Other environmental variables such as upwelling, pH, salinity and wave action are known to influence the availability of carbon within coastal environments (Stepien 2015). However, Mackey et al. (2015) found that stable isotope value of *Ecklonia radiata* were not correlated with the environmental variables measured and could thus not be used for predictive isoscape modelling. Nevertheless, the processes resulting in the variability of $\delta^{13}C$ and $\delta^{15}N$ values are complex and often inter-related. Dedicated studies are required to determine the factors responsible for the variability in the stable isotope values of *Ecklonia maxima* and *Laminaria pallida*.

2.4.4. Implications for food web studies

Historically, one of the primary assumptions of stable isotope analysis when studying food webs was the consistency of primary producer values, allowing them to be traced through the food web (Fry 2006). Although poorly understood, variability, such as that which has been identified in this study, must be taken into account in order to gather accurate information about the food web (Nordström et al. 2009, Dethier et al. 2013, Hyndes et al. 2013). This is especially pertinent when determining the ultimate carbon sources of the food web in systems which potentially rely on several plant or algal components (Boon and Bunn 1994). Hadwen et al. (2010) illustrated how temporal variability of algal

$\delta^{13}C$ values can lead to differences in source contributions of up to 11% when determining the diet of stream consumers.

Although variability at the base of the food web is not likely to be observed at the same magnitude in higher trophic organisms, there is evidence to suggest that $\delta^{13}C$ variability is translated to these organisms and can be localised to sites (Simenstad et al. 1993, O'Reilly et al. 2002). This is particularly evident in sessile or territorial organisms which utilise local primary production sources (Simenstad et al. 1993). As the majority, in terms of faunal biomass, of South African kelp forest fauna is sessile filter-feeders, such as mussels, sponges and ascidians (Field and Griffiths 1991), there is a strong possibility this will impact studies of kelp bed food webs. Any variability in algal stable isotope values will be translated through the food web to consumers, creating differences at each site. However, the magnitude and scale of this variability needs to be determined through the application of stable isotope mixing models. In order to do this, the dependence on kelp-derived carbon needs to be ascertained for various organisms across spatial and temporal scales. A study by Leclerc et al. (2013b) shows how the utilisation of kelp can be determined through examining the variability in kelps and consumers concurrently.

Stephenson et al. (1984) acknowledged that the variability of the carbon isotope values of *Saccharina latissima* (as *Laminaria longicruris*) meant that there was significant overlap in the carbon isotope values of the producers present in the kelp bed. This, however, meant that kelp would not provide an isotopically unique value, which could be traced through the food web (Stephenson et al. 1984). Similarly, if algal variability results in values beyond the range of the consumer, it is not possible to generate valid solutions from dietary mixing models (Hadwen et al. 2010). This poses a difficult problem for studying systems which rely on overlapping carbon sources as it becomes very difficult to distinguish which source is driving the food web.

Variability in $\delta^{15}N$ becomes problematic when this variance is greater than 3–4‰, which is the typical enrichment of consumers relative to their diet (DeNiro and Epstein 1981, Minagawa and Wada 1984, Peterson and Fry 1987, Cabana and Rasmussen 1994, Post 2002a). If basal resources vary by more than this, identifying the trophic level of consumers depending on these resources is problematic (Boon and Bunn 1994). The variability in $\delta^{15}N$ values of *Ecklonia maxima* and *Laminaria pallida* was found to exceed the trophic level difference across the study region. Similarly, the $\delta^{15}N$ variability of *Ecklonia radiata* is of a similar magnitude (Vanderklift and Bearham 2014). The influence of temporal and spatial variability can be mitigated through careful site and time specific sample collection. However, intra-population variability poses more of a problem and thus needs further attention when designing ecological studies.

One important aspect which needs to be considered when modeling South African kelp forest food webs with stable isotope values then, is the overlap of species' isotopic values. Therefore, if

E. maxima and *L. pallida* consistently have statistically identical isotope values, they will have to be grouped into a single "kelp" source for these models. The results, however, suggest that this is highly dependent on the location of the study site. Where *E. maxima* and *L. pallida* grow at different depths, their values are significantly different. However, north of Cape Columbine the mean isotope values of both species are statistically similar. In these areas, the role of the respective species will not be distinguishable in the food web. If the stable isotope values of the kelp overlap with those of other macroalgae, it will also become difficult to distinguish which algae are the primary carbon sources of the ecosystem.

To understand the impact of this variability on the food web the way in which kelp is used by higher level consumers must be considered. Due to most of the kelp production entering the food web as detrital material, there is a further source of variability to which the kelp particles will be exposed. Kelp values are likely to change due to the degradation process as well as due to the bacterial action which acts on these particles. Hill and McQuaid (2009a) have demonstrated how the isotope values of intertidal red algae change as a result of degradation and bacterial action. These authors showed that the $\delta^{13}C$ values became depleted in both species of algae studied, whereas the $\delta^{15}N$ values became depleted in only one species. Dethier et al. (2014) also demonstrated how bacterial action can alter the food quality of algal tissues, resulting in preference by consumers of certain species over others. Whether the isotope values of *Laminaria pallida* and *Ecklonia maxima* change due to degradation and bacterial colonisation is unknown, but this should be considered for future studies.

2.5 CONCLUSION

The stable isotope values of South African kelp species are highly variable across various scales of space and time. Stable isotope values were variable on the scale of centimetres within the lamina of a single plant to hundreds of kilometres across geographical sites. Temporal and spatial factors were identified as primary explanation of variability in $\delta^{15}N$ and $\delta^{13}C$ values; however, intra-site variability accounted for a large proportion of the observed variability across the three markers, particularly for *E. maxima*.

Several authors have shown that using a single point sample to assign a stable isotope value to a source of production is fundamentally flawed, as it does not take into account the variability which has been demonstrated to operate at different spatial and temporal scales (Fenton and Ritz 1989, Fry and Sherr 1989, Boon and Bunn 1994, Dethier et al. 2013). The findings of the present study are in strong agreement with these studies and demonstrate the variability within South African kelps is similar to places elsewhere. *Ecklonia maxima* and *Laminaria pallida* values are variable at the scale of centimetres along the length of the frond as well as at the scale of hundreds of kilometres among sampling sites.

Variability in stable isotope values needs to be accounted for when analysing trophic interactions in marine food webs. It is therefore recommended that a sound understanding of the scale and magnitude of variability in basal resources be considered when designing ecological studies. Using values from one site, one sampling occasion or literature values and applying this for studies across temporal and/or spatial scales, is strongly discouraged. This will ensure that site and time specific variability will be better represented in mixing models.

CHAPTER 3

Characterising kelp forest POM during upwelling and downwelling conditions: using stable isotope analysis to differentiate between detritus and phytoplankton

3.1 INTRODUCTION

Kelp forests are highly productive ecosystems found on nearshore temperate rocky reefs (Dayton 1985, Mann 1988, Field and Griffiths 1991, Steneck et al. 2002). The faunal biomass in these systems is often dominated (>70%) by filter feeding organisms which consume particulate organic matter (POM) that is suspended in the water column (Miller and Page 2012). These organisms therefore create the primary link between the benthic and pelagic communities in these ecosystems.

Around kelp forests, the POM is thought to comprise mainly (but not entirely) kelp-derived detritus (KDD) due to the high biomass of these algae. Most of the kelp productivity is not directly consumed (by grazing), but instead enters the food web through detrital pathways, either in dissolved or particulate form, as well as larger fragments (blades, fronds and wholes plants) termed drift kelp (Newell et al. 1982, Mann 1988, Duggins et al. 1989, Bustamante and Branch 1996b). Phytoplankton has been shown to be an important carbon source for many benthic filter-feeding organisms within kelp forests, including bivalves, sponges and ascidians (Stuart et al. 1982, Seiderer and Newell 1988, Cranford and Grant 1990, Levinton et al. 2002). Therefore, filter-feeding organisms are exposed to a mixture of phytoplankton and KDD, with the proportion of its constituents changing constantly (Carter 1982, Wulff and Field 1983, Probyn and McQuaid 1985). Is it therefore possible to determine which of these carbon sources is more important for these food webs?

Stable isotope analysis has become a powerful tool for studying marine food webs and its application to distinguishing carbon sources in marine systems is not new (Michener and Kaufman 2007). Subsequently, several studies using stable isotope analysis have supported the understanding that kelp-derived detrital material is an important source of carbon to the filter-feeding organisms in kelp forests (Dunton and Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, 2006, Hill and McQuaid 2009b). Conversely, other studies have shown that phytoplankton is more important in the diet of filter-feeding consumers (Bode et al. 2006). However, stable isotope analysis has also provided contrasting evidence for the dependence of temperate reef fish on KDD, with fish in northeast Pacific highly dependent on KDD (von Biela et al. 2016), and fish in Chilean systems more dependent on phytoplankton (Docmac et al. 2017). Additionally, this methodology isn't without its own set of caveats and problems, and therefore the findings of these studies need to be critically examined. Two key problem areas have been identified from the literature: 1) isolating kelp and phytoplankton values, 2) changes to kelp stable isotope values following bacterial decay.

Firstly, the success of stable isotope analysis relies on accurately determining the contribution of multiple sources to a mixture (e.g. diet or POM). To do this, suitable estimates of the mixture constituents are required. In this case suitable estimates of KDD and phytoplankton are required to determine the composition of a coastal POM sample. Generally, marine phytoplankton is more depleted in $\delta^{13}C$ when compared to kelp (Dunton and Schell 1987, Duggins et al. 1989). However,

isolating a pure phytoplankton sample from the nearshore environment is nearly impossible as there is inevitably some contamination by KDD and micro-organisms (Koop et al. 1982b, Kaehler et al. 2006, Miller and Page 2012). One proposed solution to this problem has been to use off-shore phytoplankton values as a proxy for the phytoplankton which is found closer to shore (Miller and Page 2012). With minimal contribution from kelp detritus, these values are more representative of pure phytoplankton and are often used as a substitute for coastal phytoplankton (Ramshaw et al. 2017). However, oceanic phytoplankton that is collected further off-shore (>5 km), is commonly more depleted than nearshore phytoplankton (Hill et al. 2006, Miller et al. 2013).

Secondly, fresh kelp is likely to have more depleted stable isotope values than decaying kelp, which forms the kelp detritus (Kaehler et al. 2000, 2006, Kaehler and Pakhomov 2001). Hill and McQuaid (2009a) have documented the changes in stable isotope values of intertidal red algae as a result of microbial action and decay. Yorke et al. (2013) found that the C:N ratio of kelp detritus particles (*Macrocystis pyrifera*) was very low (7.5) when compared to the known values for kelp blades. This was attributed to the presence of bacteria, which are rich in nitrogen, on the detrital particles (Yorke et al. 2013). This study revealed that $\delta^{15}N$ values became depleted as a result of degradation; however, changes to $\delta^{13}C$ values were species specific. Similarly, Dethier et al. (2014) showed that bacterial colonisation of kelps increased the food quality of aged kelp tissues for suspension feeders by increasing the nitrogen content and thus decreasing the C:N ratio. Additionally, the quality of KDD as a food source is highly dependent on bacterial degradation, which decreases the C:N ratio of these particles (Hill and McQuaid 2009b).

Therefore, using fresh kelp and oceanic phytoplankton stable isotope values can potentially lead to uncertainty when determining their contribution to coastal POM and to the diet of kelp forest organisms. As a result, the contribution of either source (KDD vs. phytoplankton) can be easily overestimated (Miller and Page 2012, Ramshaw et al. 2017). Consequently, determining the primary carbon sources of kelp forest food webs is still considered difficult (Miller and Page 2012). Understanding the dynamics of the POM in and around kelp forests is therefore critical to elucidate the functioning of the food webs within these ecosystems.

Coastal upwelling is the offshore movement of surface water, through wind-driven processes that results in the influx of cold, nutrient-rich bottom water into the coastal zone. In the southern Benguela region on the west coast of South Africa, this process is driven by south-easterly winds which prevail in the summer months (Andrews and Hutchings 1980). The entire water volume within a kelp forest may be replaced 3–7 times a day under these conditions (Field et al. 1980b). This equates to a large nutrient influx, and a substantial change in both the physical environment and the biological conditions within these systems. A reversal of the prevailing wind direction, to northerly, results in downwelling conditions in the coastal environment (Andrews and Hutchings 1980). Under these

conditions, warm offshore surface water is driven inshore along with phytoplankton and particulate matter which have accumulated in the offshore region following the last upwelling event (Carter 1982). This alternation of upwelling and downwelling conditions creates a complex physical environment, which ultimately influences the biological processes of the nearshore environment.

From a biological perspective, the process of upwelling is responsible for shaping the communities present in nearshore coastal habitats. The reliable influx of nutrients means that large habitat-forming algae such as *Ecklonia maxima* and *Laminaria pallida* are able to form extensive forests along the coastal margin (Field et al. 1980a). The phytoplankton and kelp within these systems is highly dependent on the influx of nutrients with upwelling, particularly nitrate (NO_3^-), as this is major factor controlling productivity (Probyn and McQuaid 1985). However, as these nutrients are depleted quickly, and the Benguela system is considered to be nitrate limited (Brown and Hutchings 1987). The natural growth and senescence of these algae result in the suspension of detrital particles within the water column which are then filtered out by filter-feeding organisms (Kaehler et al. 2000, 2006). Upwelling processes have been shown to impact the food availability within these systems, as they control the concentration of particulate organic matter (POM) and phytoplankton (Carter 1982, Wulff and Field 1983, Brown and Hutchings 1987, Hill et al. 2006). As the faunal biomass within kelp forests is often dominated by filter-feeding organisms, this has major repercussions for the flow of energy in these food webs (Wulff and Field 1983, Field and Griffiths 1991). Under upwelling conditions, POM and phytoplankton concentrations are at their lowest within kelp forests as these particles are constantly driven offshore with the water currents (Field et al. 1980b, Fielding and Davis 1989). Wickens and Field (1986) have shown, through modelling the nitrogen flow of a typical kelp forest, that these conditions are not optimal for filter feeding organisms as most of the potential food available in the water column is washed out of the system.

When downwelling occurs, food availability is at its peak as offshore water is driven into kelp forests, often potentially containing the remnants of a phytoplankton bloom (Field et al. 1980b, Wulff and Field 1983). Under these conditions, phytoplankton contributes a large proportion of the nitrogen content in kelp forest POM and thus the food of filter feeding organisms (Wickens and Field 1986). During calmer periods, any POM in the water column settles out onto the sea bed (Field et al. 1980b). Therefore, upwelling processes are vital controlling mechanisms of the food quantity available to filter feeders within kelp forests.

The primary aim of this study is to characterise the POM in and around the chosen kelp forest at Kommetjie under upwelling and downwelling conditions, focusing on the proportions of KDD and phytoplankton. To achieve this, several indices and metrics, which were available in the literature, were used to characterise the POM samples collected, deciding whether they were phytoplankton or KDD dominated (see methods for further details). Based on the characterisation of the POM, stable

isotope values were used to determine the proportion of KDD and phytoplankton in the different samples.

It is predicted that under upwelling conditions, the POM will be dominated by kelp-derived detrital material and thus the stable isotope value of the POM will be closer to kelp. Under downwelling conditions, phytoplankton will dominate the POM and could provide a more representative stable isotope value of nearshore phytoplankton.

In addressing these aims, I hope to further the understanding of how KDD and phytoplankton contribute to the nearshore POM and more specifically to kelp forest food webs. Additionally, the use of coastal upwelling to provide representative stable isotope values of phytoplankton and KDD is a unique approach to understanding POM dynamics within kelp forest systems.

3.2 METHODS

3.2.1. Sample collection

The kelp forest at Kommetjie (Figure 3.1) was selected as representative of a typical west coast kelp forest on the Cape Peninsula, South Africa. The kelp bed is exposed to seasonal upwelling, which is driven by south easterly winds (see below). This kelp bed was also chosen as it is fairly extensive with a high standing biomass (21.3 ± 4.26 kg wet wt.m^{-2} total kelp)(Field et al. 1980a, Rand 2006, Rothman 2006, Anderson et al. 2007). Therefore, it is assumed that there will be a significant contribution of kelp detritus from the kelps (*Ecklonia maxima* and *Laminaria pallida*) in this area to the nearshore environment.

Two transects, originating in the kelp bed at Kommetjie (Figure 3.1), were used to gather information about the POM dynamics around this kelp bed. A point in the centre of the kelp bed was chosen to be the origin of both transects. Transect A followed a trajectory close in-shore in a northerly direction for 3 km, away from the main kelp bed, with sample collection points every 0.5 km (the 'along-shore transect' from here on). Although not strictly parallel to the shore, this transect provides information on the conditions close to shore moving away from kelp and towards a sandy beach environment.

Transect B moved directly off-shore from the main kelp bed for a distance of 7.5 km, with sampling points every 1.25 km (the 'off-shore transect' from here onwards). This was to be more representative of the change in the ocean characteristics between the in-shore and off-shore zones (Figure 3.1).

In both transects, at each sampling point a single 10 L water sample was collected at the surface with a bucket and transported back to the laboratory for processing. As the main goal of the study was to determine the influence of upwelling condition on the POM dynamics around the kelp forest, only one replicate was collected at each station on each sampling day. Triplicate transects were, however, performed in each upwelling condition. A small inflatable ski-boat was used to collect the samples as

it is able to easily access the shallow water in and around the kelp forest. This, however, meant that poor sea conditions often prevented sampling, despite the upwelling index (see below) being appropriate.

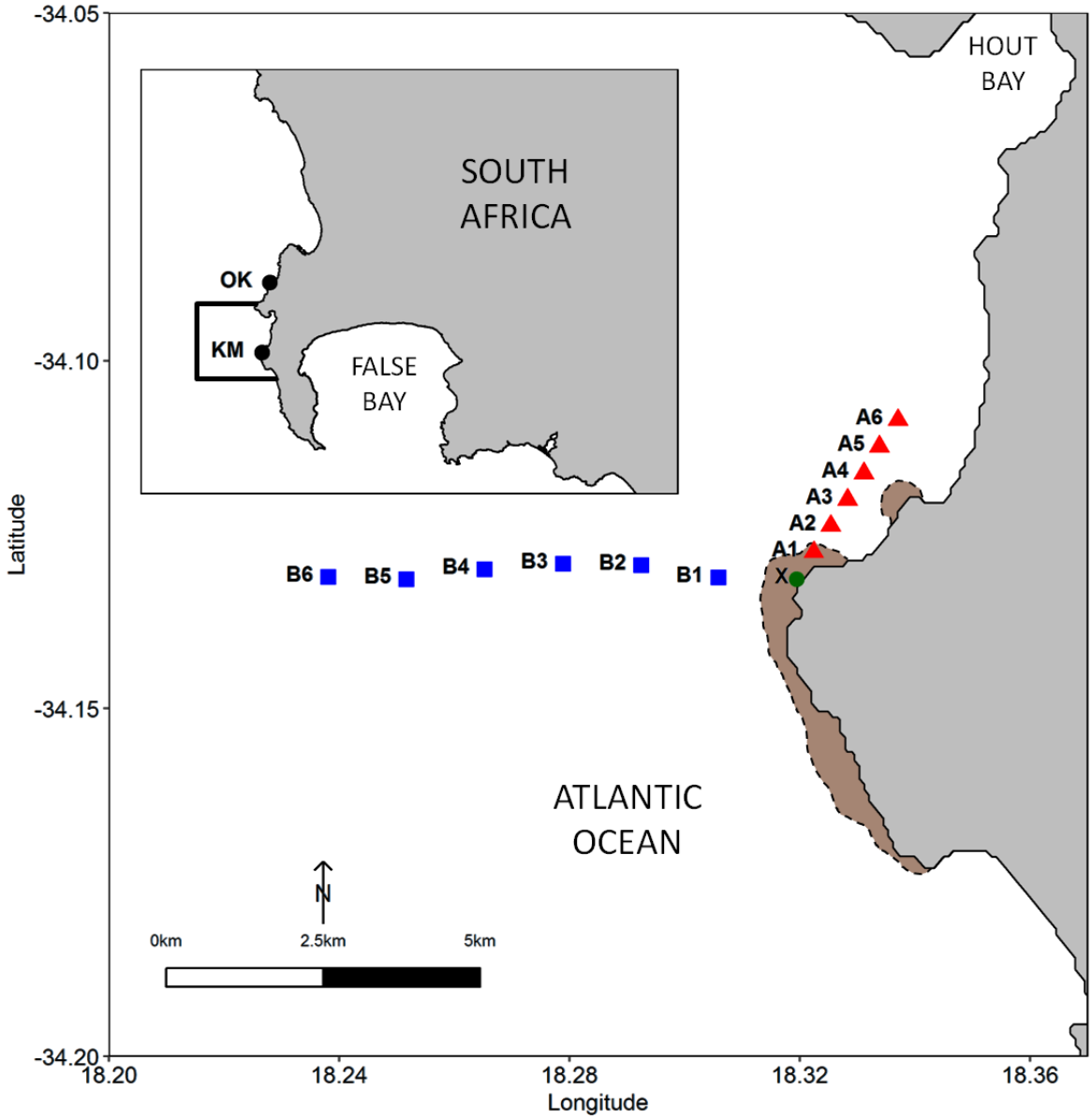

Figure 3.1: Map showing the two transects conducted with transect A denoted by red triangles and transect B denoted by blue squares. The common origin of both transects in the main kelp forest, is indicated by a green circle. The extent of the kelp forest was estimated following Rand (2006), and is indicated by the brown shaded area. The location of the study site in South Africa is denoted by the black box on the inset map, along with the position of Kommetjie (KM) in relation to Oudekraal (OK).

3.2.2. Upwelling Index

To determine the upwelling condition, an upwelling index was calculated following the formula presented in Fielding and Davis (1989), which was developed for Oudekraal, roughly 18 km north of the chosen sampling locality (see Figure 3.1).

The upwelling index gives an indication of the intensity of the upwelling currently taking place and is calculated with the following equation:

$$Upwelling\ Index = \mu(Cos\ \theta - 160)$$

Here, μ is the wind speed (m/s) and θ is the wind direction in degrees. The 160 refers to the angle of the coastline. It was decided to keep this consistent with that used for the Oudekraal calculations as the angle of the coastline at Kommetjie is very similar.

The index therefore relies on the wind speed and direction data to calculate the intensity of upwelling likely to be present. Wind data were gathered daily from the Windguru website (www.windguru.cz) for Kommetjie, and from this the upwelling index was determined and used as a predictive tool to plan sampling occasions.

As the upwelling index was highly variable (see Figure 3.2), it was not logistically possible to collect samples under the same upwelling/downwelling conditions (equal index strength) each time. Samples were collected under the correct predicted conditions (upwelling and downwelling) only when conditions were suitable to guarantee the collection of all 13 samples along both transects. Additionally, the predicted upwelling condition did not always match the actual *in situ* ocean conditions. For the final two days, Days 5 and 6, the upwelling index and actual ocean conditions were reversed (discussed in more detail below). For example, on Day 5, the index predicted upwelling conditions but the ocean conditions were more similar to days 1 and 2 which were downwelling days. For this reason, the predicted index was not used for these two days and the actual conditions were used to characterise the state of the conditions (i.e. upwelling vs. downwelling).

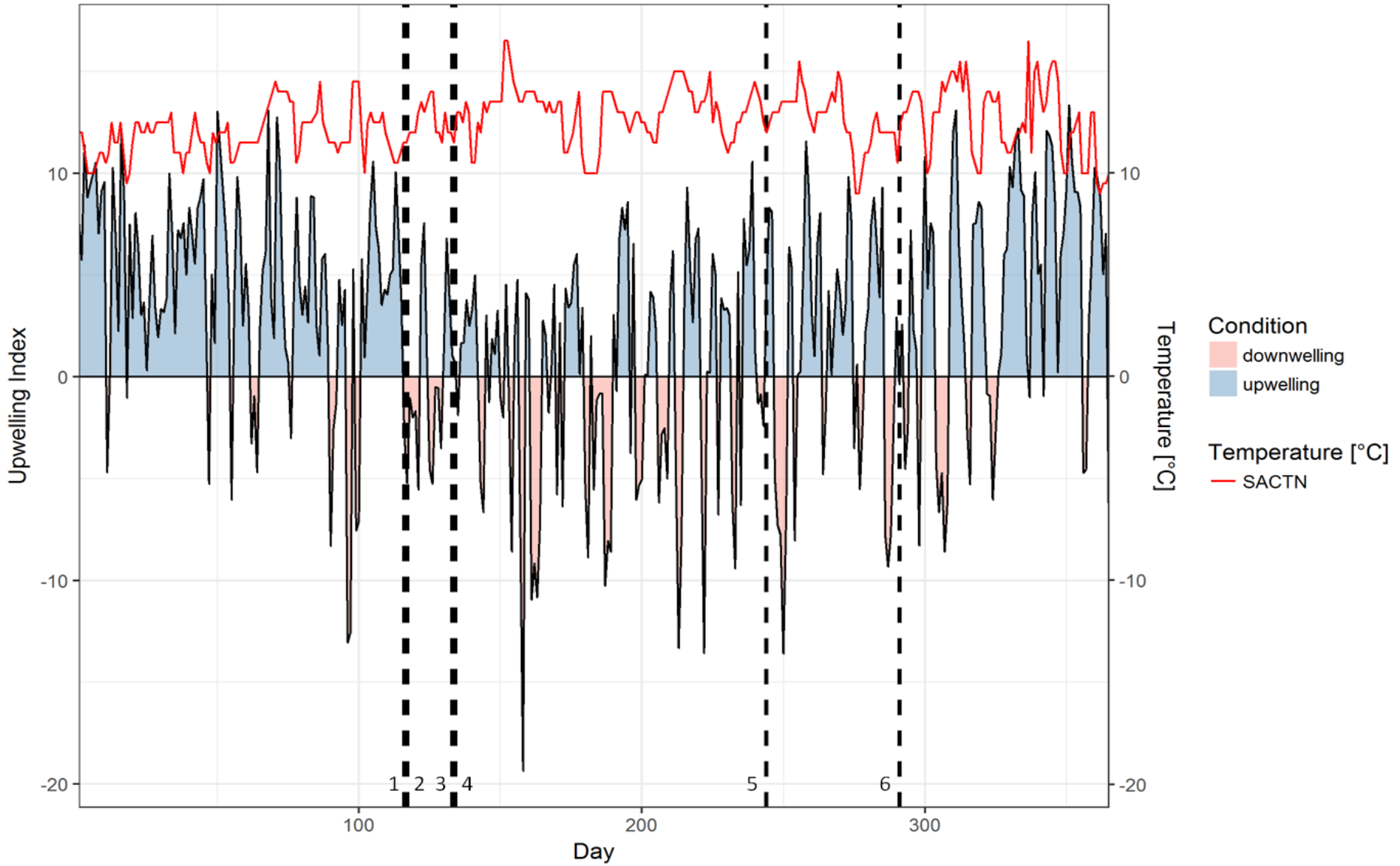

Figure 3.2: Upwelling index at Kommetjie plotted for each day in 2017 along with daily *in-situ* temperatures (red line) sourced from the South African Coastal Temperature Network (SACTN). Sampling days are marked by vertical dashed lines and numbered.

3.2.3. Laboratory processing

Immediately after the collection of the samples, each 10 L water sample was partitioned into two separate fractions which were used for the different parameters, viz. total suspended solids (TSS), stable isotope analysis and chlorophyll-*a*. The filters used for TSS determination were re-used for stable isotope analysis (see below).

Chlorophyll-*a* concentration was determined via standard acetone extraction and fluorescence procedures (Arar and Collins 1997). A 3 L fraction of the collected water sample was filtered through a pre-combusted (450°C for 6 hrs) Whatman GF/F filter. Each filter, on which the particulate matter was retained, was placed into a foil envelope and placed on ice while all the samples were filtered for a specific day. The entire batch of filters was then transferred to a -80°C freezer for storage prior to the chlorophyll-*a* extractions. Pigment extractions were performed at the Department of Agriculture, Forestry and Fisheries (DAFF) research aquarium in Cape Town. Each filter was placed into a 10 ml polypropylene test tube with 9 ml of 90% acetone, and macerated with a sterile glass rod to facilitate the extraction procedure. All extraction vials were then placed into a dark freezer (-10°C) for 24 hours before fluorescence readings were taken. Once the extraction process was complete, samples were centrifuged at 3,000 rpm for 10 min in a Rotofix 32A (Hettich) centrifuge. Due to the high concentration of pigments in some samples, dilution of the supernatant was required (Arar and Collins 1997). A dilution of 1 ml of supernatant and 6 ml of 90% acetone was prepared for each sample (dilution factor of 7). Fluorescence readings were taken on a Turner Designs 10-AU fluorometer. Readings were taken before and after the addition of 150 µL of 10% HCl solution.

A second 3 L fraction of the sample was filtered through a pre-combusted (450°C for 6 hrs) and pre-weighed Whatman GF/F filter for TSS (total suspended solids) analysis. Each filter was inspected and all zooplankton and unwanted items (e.g. microplastics) were removed. The filters were placed onto a foil-lined tray and oven dried (60°C for 24 hrs) prior to re-weighing. Once the oven-dried mass was determined, each filter was placed into a foil envelope and stored in a desiccator. In order to calculate the amount of suspended material in the water column, the TSS (mg/L) was determined by calculating the difference in filter mass before and after filtration of a known volume of sample. This was determined for each filter and the quantity is expressed as the amount of material per litre of sample. The filters used for TSS were then prepared for stable isotope analysis.

Each dried filter was halved and treated with 10% HCl to remove biogenic carbonates. The material from one half of the filter was scraped off and packaged into a 5 × 9 mm tin capsule for stable isotope analysis. All samples were sent to iThemba LABS in Johannesburg for analysis. Here, analyses were performed on a Flash HT Plus elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer by means of a ConfloIV interface (all equipment supplied by ThermoFisher, Bremen, Germany).

Stable isotope values were expressed in delta (δ) notation:

$$\delta X = \left[R_{sample} \div R_{standard}\right] \times 1000$$

where: X = ^{13}C or ^{15}N

R = corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$

Carbon and nitrogen isotope values were corrected against in-house standards (Merck Gel and Urea) which were run every 24 samples. Precision for the analyses were 0.06 and 0.10 ‰ respectively. This analysis also provided estimates of particulate organic carbon (%) and the C:N ratio of the material retained on each filter.

3.2.4. Characterising nearshore POM

The ratio of POC:chlorophyll-*a* has been used by several authors to characterise POM in nearshore or open ocean systems (Cifuentes et al. 1988, Richard et al. 1997, Bentaleb et al. 1998, Savoye et al. 2003). Some variability exists in the limits, or 'cut-off values', associated with phytoplankton and detritus (Montagnes et al. 1994, Head et al. 1996); however, Cifuentes et al. (1988) suggest that a POC:chl-*a* ratio of lower than 200 indicates newly produced phytoplankton and values higher than 200 indicate degraded material or detritus.

Characterising POM is also possible when the C:N ratio is examined (Savoye et al. 2003). Detrital material is characterised by having a C:N ratio of 15 to 20, whereas phytoplankton is around 6 and bacteria at 3 (Brzezinski 1985, Seiderer and Newell 1985). However, some caution should be exercised when using the C:N ratio to characterise POM as differential rates in the decay of carbon and nitrogen, as well as bacterial activity, can alter these ratios (Smith et al. 1982, Thornton and McManus 1994). Stable isotope values and chlorophyll-*a* can also be used to distinguish between phytoplankton and kelp-derived material, however, these can be highly variable among coastal regions (Miller and Page 2012, Ramshaw et al. 2017).

Based on the literature values, which describe phytoplankton dominance in coastal POM, samples were selected that were likely to be dominated by phytoplankton. This approach was successfully applied by Ramshaw et al. (2017) for a study of the nearshore POM on the coast of Nova Scotia. A C:N ratio of between 6-10 (Brzezinski 1985, Montagnes et al. 1994), and a POC:chlorophyll-*a* ratio less than 200 (Cifuentes et al. 1988, Richard et al. 1997, Bentaleb et al. 1998) were chosen to represent a phytoplankton dominated sample. Importantly, the samples were also preferentially selected from the along-shore transect as this restricts the discrimination between coastal and off-shore phytoplankton values.

From the samples that matched all the criteria, mean $\delta^{13}C$ and $\delta^{15}N$ values were calculated to represent those of a coastal phytoplankton end member. Kelp stable isotope values for *Ecklonia maxima* and

Laminaria pallida were selected from data presented in Table 3.1, from samples collected at Kommetjie in an earlier study (Chapter 2). Fresh kelp stable isotope values were used as there is currently no information available as to the likely changes in signature for either *E. maxima* or *L. pallida* when their tissues degrade. Mean stable isotope values were calculated from samples collected in summer and winter as transects were conducted during different seasons. The proportion of kelp-derived detritus was pooled for both species (*E. maxima* and *L. pallida*) to give an estimate of total kelp contribution.

Table 3.1: Mean (± SD) stable isotope values and C:N ratio of *Ecklonia maxima* and *Laminaria pallida* collected at Kommetjie during summer and winter (data from Chapter 2) and estimated phytoplankton values. Bold values used for MixSIAR analyses.

Species	Season	n	$\delta^{13}C \pm SD$ (‰)	$\delta^{15}N \pm SD$ (‰)	C:N ± SD
Ecklonia maxima	Summer	10	-12.61 ± 1.88	4.79 ± 0.29	19.39 ± 1.25
	Winter	10	-14.09 ± 0.40	6.93 ± 0.39	23.10 ± 1.75
	Overall	**20**	**-13.35 ± 1.95**	**5.86 ± 1.13**	**21.24 ± 2.40**
Laminaria pallida	Summer	10	-15.92 ± 1.38	5.30 ± 0.27	24.31 ± 1.19
	Winter	10	-19.05 ± 0.81	5.23 ± 0.51	24.02 ± 1.24
	Overall	**20**	**-17.48 ± 1.55**	**5.27 ± 0.41**	**24.17 ± 1.22**
Phytoplankton	**Overall**	**19**	**-20.10 ± 1.23**	**4.73 ± 0.76**	**7.39 ± 0.58**

3.2.5. Mixing models

The stable isotope mixing model MixSIAR (version 3.1, Stock and Semmens, (2016)) was used to estimate the contribution of kelp-derived detritus to each POM sample along the two transects. These models are based on Bayesian stable isotope mixing models as discussed in Parnell et al. (2013) and Moore and Semmens (2008). Concentration dependence (C:N) data were incorporated into the model for the three sources. The fractionation/trophic enrichment factors were set to 0 for both $\delta^{13}C$ and $\delta^{15}N$ and no informative priors were used for the analysis. It was assumed that values would not deviate significantly between sources (kelp and phytoplankton) and mixture (POM) as studies on the change in stable isotope values due to microbial activity have not been carried out for these kelp species. Process-only error structure was selected as each data point was analysed individually. Analyses were performed with a chain length of 1 million and a burn-in value of 500,000. Mean values for the contribution of each constituent, as a percentage, were retained and added to the statistical analyses. All analyses were performed in R (version 3.4.3, R Core Team (2017)).

3.2.6. Statistical analysis

Since graphical displays showed the relationship of the measured POM and phytoplankton variables related in a non-linear way with distance away from the source (kelp bed), a generalised additive model (GAM; Wood (2017)) was used to capture the relationship statistically. Included in the model is the smooth coefficient, station (which relates to the distance from the source), and two parametric terms, condition and direction. Day was not considered as an additional factor as the measurements from the different days were used as replicates for the upwelling and downwelling conditions. These semi-parametric models, which are estimated from the data using penalised regression splines using restricted maximum likelihood (REML), are visually represented as smooth trends in the resultant plots. The additive model is presented as follows:

$$y_i = \beta_0 + f_1(direction_i) + f_2(\text{condition}_i) + \varepsilon_i, \varepsilon = N(0, \sigma^2)$$

where y_i is the measured variable relating to POM and phytoplankton, β_0 is the intercept term, f_x are the smooth functions of direction and condition, ε_i are the model residuals that are assumed to Gaussian random variables with a mean of 0 and variance of σ^2. The dimension of the basis representing the smooth term was set to k = 6. At the start, the full model included both parametric terms, and these were sequentially dropped until only a smooth term was retained in the model. The various outcomes were compared using Akaike's information criterion (AIC) and the model with the smallest AIC retained. The mgcv package (Wood 2017) was used under R v.3.4.3. (R Core Team 2017).

This same methodology was applied to the calculated mean proportions of POM constituents obtained from the MixSIAR analysis. A mean value for each constituent was used for each sampling station on each day and the GAM was applied to each constituent as with the POM and phytoplankton variables.

Models were run on a reduced data set (Day 1-4) to test whether the final two sampling days had a major impact on the results. These figures are presented in the supplementary material (Figure S3 and S4). As the trends were similar, it was subsequently decided to run the models on all six sampling days, with the mis-matched index days correctly classified according to the actual ocean conditions (see conclusion and section 6.3.2 for further details and discussion).

3.3 RESULTS

3.3.1. TSS concentrations

The concentration of TSS was significantly different under upwelling and downwelling conditions (t = -3.465, $p < 0.01$), with higher concentrations under downwelling conditions (Figure 3.3). There was a significant trend (R^2 = 0.319) with distance from the kelp bed (F = 6.205, $p < 0.01$) with concentrations decreasing markedly from the kelp bed to the third sampling station and then evening out (Figure 3.3A).

3.3.2. Chlorophyll-a concentrations

The chlorophyll-*a* concentrations were significantly different under upwelling and downwelling conditions (t = -7.173, $p < 0.001$), with significantly higher concentrations during downwelling conditions (Figure 3.2B). There was, however, no difference with distance from the kelp bed (F = 2.881, p = 0.096, R^2 = 0.195) with concentrations remaining constant along the length of the transects.

3.3.3. Stable isotope values

The $\delta^{13}C$ values were significantly different between upwelling and downwelling conditions (t = 2.257, $p < 0.05$) with significantly more enriched values under upwelling conditions (Figure 3.2C). There was no significant difference between the along-shore and off-shore transects (t = -1.582, p = 0.120). The trend in $\delta^{13}C$ values however shows a significant decrease with distance from the kelp bed (F = 23.39, $p < 0.001$, R^2 = 0.625) with a steady depletion in values with increased distance from the kelp bed (see Figure 3.2C).

Under downwelling conditions, the mean $\delta^{13}C$ values for the along-shore transect ranged from -15.31‰ (±0.57‰) in the kelp forest to -20.45‰ (±0.52‰) at the furthest station (3 km from the kelp). This is a depletion of almost 5‰ over a fairly short distance. Similarly, under upwelling conditions the mean $\delta^{13}C$ values showed a depletion of 4‰, changing from -15.18‰ (±1.01‰) in the kelp forest to -19.18‰ (±2.93‰). The trends were almost identical for the off-shore transect with the only exception being that the changes happened over a distance of 7.5 km.

In contrast, the $\delta^{15}N$ values were more consistent (Figure 3.2D). The $\delta^{15}N$ values were however significantly different between upwelling and downwelling conditions (t = 6.822, $p < 0.001$), but again, no significant difference between the direction of the transects. There was no significant trend in $\delta^{15}N$ with distance from the kelp bed (F = 0.944, p = 0.396, R^2 = 0.458).

Unlike $\delta^{13}C$, the $\delta^{15}N$ values remained fairly consistent along the length of both the along-shore and off-shore transects under both upwelling and downwelling conditions. In the along-shore direction, the mean $\delta^{15}N$ values ranged from 5.30‰ (±0.11‰) in the kelp forest to 4.36‰ (±0.59‰) at the furthest station 3 km away under downwelling conditions. This is only a difference of 0.94‰ across

the transect. Similarly, under upwelling conditions, the mean $\delta^{15}N$ values ranged from 5.60‰ (±0.06‰) within the kelp to 5.89‰ (±0.93‰) 3 km away, with a difference of 0.29‰. The off-shore transect was again very similar in terms of the range in $\delta^{15}N$ values, except over a longer distance of 7.5 km. Under downwelling conditions, the mean $\delta^{15}N$ values differed by 0.98‰ between the kelp forest and the furthest station (7.5 km off-shore). Under upwelling conditions, the difference between these stations was 0.49‰ with values becoming more enriched further off-shore.

3.3.4. POC:chlorophyll-a ratio

The ratio of particulate organic carbon (POC) to chlorophyll-*a* was significantly different between upwelling and downwelling conditions ($t = 3.711$, $p < 0.001$) but not significantly different between the along-shore and off-shore transects ($t = -0.869$, $p = 0.389$). The trend with distance from the kelp bed was also not significant ($F = 0.841$, $p = 0.306$, $R^2 = 0.226$) indicating that POC:chl-*a* ratios remained similar along the length of both transects (Figure 3.2E).

3.3.5. C:N ratio

The C:N ratio (Figure 3.2F) was significantly different between upwelling and downwelling conditions ($t = 5.445$, $p < 0.001$) but not significantly different between the along-shore and off-shore transects. There was however a significant decrease in C:N ratio with a distance from the kelp bed ($F = 7.99$, $p < 0.001$, $R^2 = 0.469$) (Figure 3.2F).

Table 3.2: Model statistics for generalised additive models (GAM) fitted to the variables associated with POM composition in two *directions* away from kelp beds (offshore and alongshore) and during two ocean *conditions* (upwelling and downwelling). edf – estimated degrees of freedom; Ref. df. – residual degrees of freedom; R^2-adj. – adjusted R^2; Dev. expl. – deviance explained.

	Parametric coefficient			**Smooth term**				**Model fit**		
		t	*P*	edf	Ref. df.	*F*	*P*	R^2-adj.	Dev. expl.	*n*
TSS	condition	-3.465	<0.01	2.47	2.796	6.205	<0.01	0.319	36.20%	56
Chl-*a*	condition	-7.173	<0.001	1.000	1.000	2.881	0.096	0.488	50.60%	56
POC:Chl-*a*	direction condition	-0.869 3.711	0.389 <0.001	1.457	1.757	0.841	0.306	0.226	27.40%	56
$\delta^{13}C$	direction condition	-1.582 2.257	0.120 <0.05	2.786	2.963	23.39	<0.001	0.625	65.80%	56
$\delta^{15}N$	condition	6.822	<0.001	1.684	2.001	0.944	0.396	0.458	48.40%	56
C:N	condition	5.445	<0.001	2.363	2.714	7.99	<0.001	0.469	50.10%	56

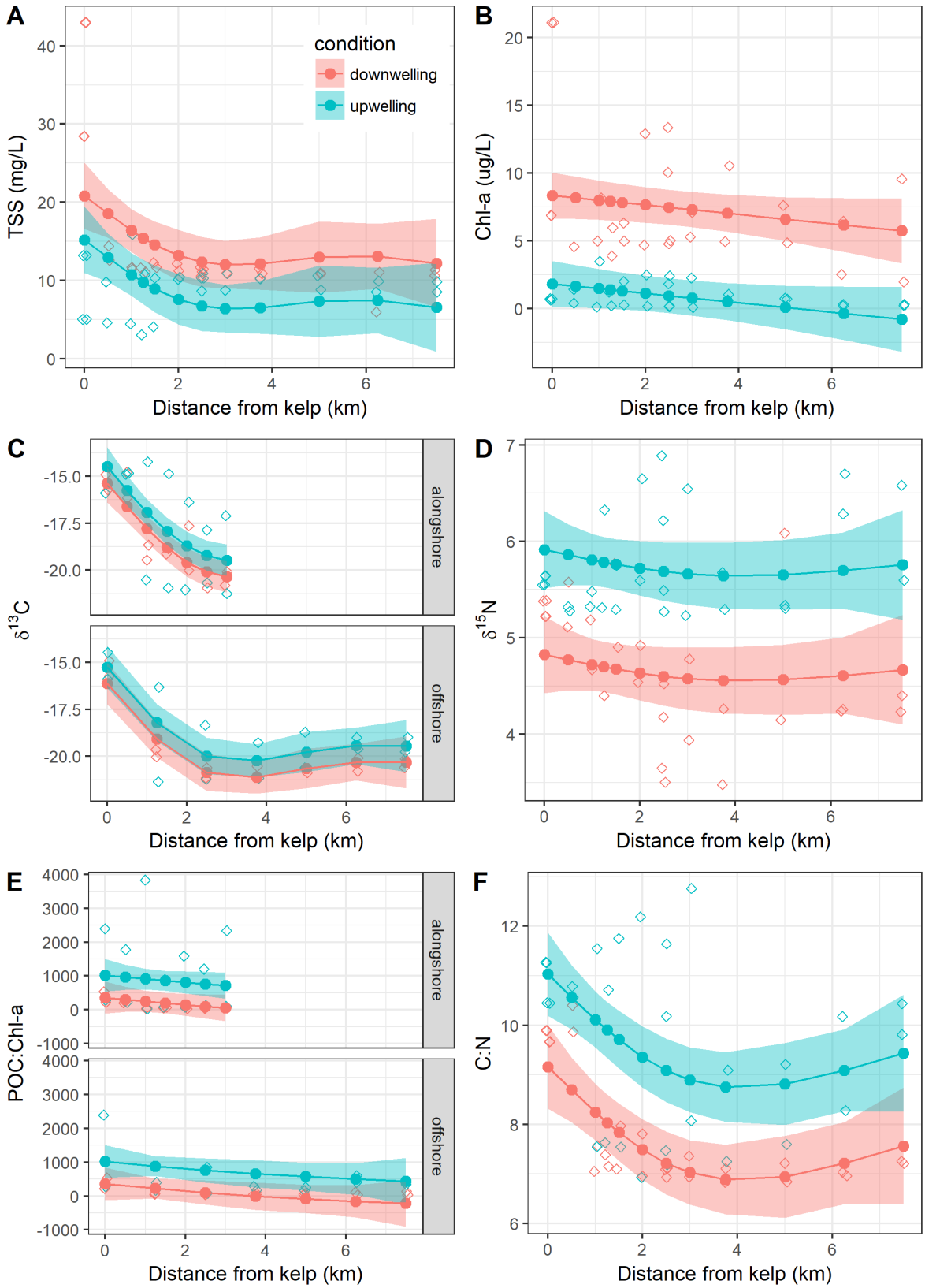

Figure 3.3: Graphical representation of the generalised additive models (GAM) fitted to the variables associated with POM composition in two *directions* away from kelp beds (off-shore and along-shore) during two ocean *conditions* (upwelling and downwelling). Only condition was significant for A, B, D and F, whereas direction and condition were significant for C and E (see Table 3.2).

3.3.6. Proportion of KDD and phytoplankton

The mean proportional contribution of phytoplankton to the POM was significantly different between upwelling and downwelling conditions (t = -23.95, $p < 0.001$), but was however not significantly different between the along-shore and off-shore transects. There was a significant increase in the proportion of phytoplankton with distance from the kelp bed (F = 6.965, $p < 0.005$, R^2 = 0.914), however, this was most apparent between the kelp and the first sampling station (Figure 3.4A).

Similarly, the mean proportion of kelp (total kelp) was significantly different between upwelling and downwelling conditions (t = 23.908, $p < 0.001$). There was a significant decrease in the proportion of kelp with distance from the kelp (F = 6.972, $p < 0.005$, R^2 = 0.914) with the most marked change between the kelp forest and the first sampling station (Figure 3.4B. Kelp-derived detritus (KDD) accounted for >75% of the POM under upwelling conditions but less than 25% of the POM under downwelling conditions (Figure 3.4B).

Looking at the kelp species independently, the proportion of both *Ecklonia maxima* (t = 4.238, p <0.001) and *Laminaria pallida* (t = 8.848, p <0.001) was significantly different under upwelling and downwelling conditions (Table 3.3). There was however no significant decrease in the proportion of *E. maxima* with distance from the kelp bed (F = 1.675, $p < 0.001$, R^2 = 0.267). Similarly, the proportion of *L. pallida* was not significantly related to the distance from the kelp bed (F = 0.257, p = 0.614, R^2 = 0.6) (Figure 3.4D).

Table 3.3: Model statistics for generalised additive models (GAM) fitted to the mean calculated MixSIAR proportion of POM constituents in two *directions* away from kelp beds (offshore and alongshore) and during two ocean *conditions* (upwelling and downwelling). edf – estimated degrees of freedom; Ref. df. – residual degrees of freedom; R^2-adj. – adjusted R^2; Dev. expl. – deviance explained.

	Parametric coefficient			**Smooth term**				**Model fit**		
		t	*P*	edf	Ref. df.	*F*	*P*	R^2-adj.	Dev. expl.	*n*
E. maxima	condition	4.238	<0.001	1.467	1.772	1.675	0.136	0.267	30.00%	56
L. pallida	condition	8.848	<0.001	1	1	0.257	0.614	0.582	59.70%	56
Kelp	condition	23.908	<0.001	2.076	2.456	6.972	<0.005	0.914	91.90%	56
Phytoplankton	condition	-23.95	<0.001	2.077	2.457	6.965	<0.005	0.914	91.90%	56

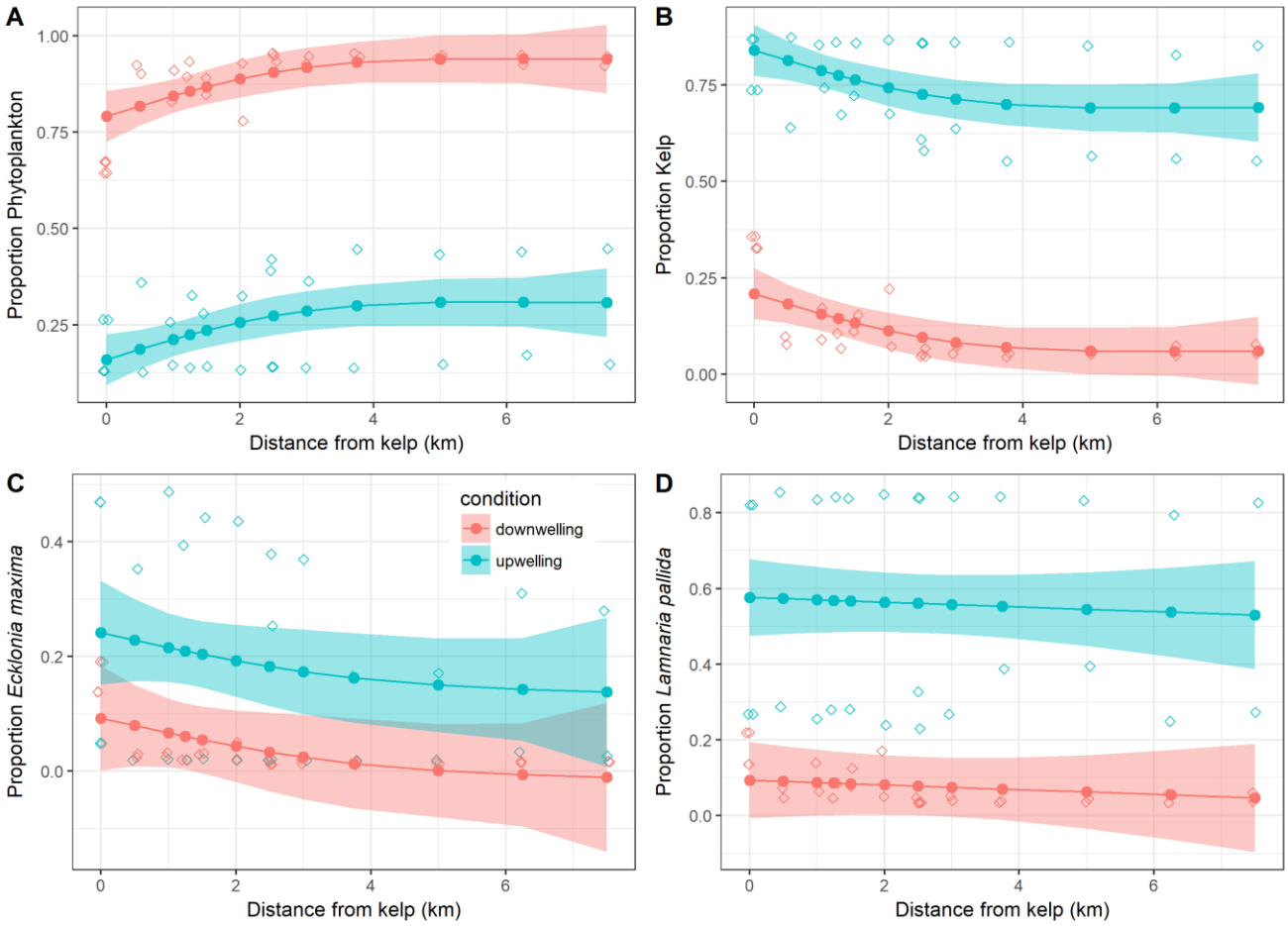

Figure 3.4: Graphical representation of the generalised additive models (GAM) of the mean calculated MixSIAR proportion of POM constituents in two *directions* away from kelp beds (off-shore and along-shore) during two ocean *conditions* (upwelling and downwelling).

3.4 DISCUSSION

The results indicate the strong influence of upwelling and downwelling in controlling the characteristics of the water column, and the composition of suspended POM in the coastal zone surrounding South African kelp forests. The TSS concentration and chlorophyll-*a*, were significantly higher under downwelling conditions, which was corroborated by the higher contribution of phytoplankton present under these conditions. The ratios of POC:chlorophyll-*a* and C:N were significantly higher under upwelling conditions which matched the higher proportion of KDD in the POM. Similarly, the $\delta^{13}C$ and $\delta^{15}N$ values of the POM were significantly more enriched under upwelling conditions. The composition of the POM was highly dependent on the upwelling condition with clear differences between upwelling and downwelling. Additionally, the proportion of KDD accounted for by *Ecklonia maxima* and *Laminaria pallida* were shown to be variable, with the contribution of *E. maxima* decreasing within a short distance from the kelp bed. Interestingly, the contribution of *Laminaria pallida* was much higher than expected.

3.4.1. TSS concentrations

Downwelling conditions are characterised by the shoreward movement of surface water facilitated by the onshore (NW) wind (Andrews and Hutchings 1980). This movement of water carries any suspended particulate with it towards the shore (Wulff and Field 1983). The results showed that this pattern was evident with higher TSS concentrations under downwelling conditions, as well as higher TSS conditions closer to shore. However, the presence of kelp seemed to exacerbate this, with TSS concentrations highest within the kelp forest when compared to the other stations close to shore. Kelp forests attenuate wave action and can retard the flow of water, and thus the flux of suspended POM, larvae and nutrients within these systems (Jackson and Winant 1983, Eckman et al. 1989, Hurd 2000). Therefore, it is possible that the kelp forest retains a higher TSS load in the water column than in the areas directly adjacent.

Under upwelling conditions, the trend is expected to be reversed, with the highest concentrations of TSS found off-shore (Wulff and Field 1983). This is as a result of the off-shore SE winds moving surface waters away from shore, thus resulting in the upwelling of cooler, nutrient-rich water along the shore. Similar to the downwelling trend, TSS concentrations were highest within the kelp forest and decreased with distance from the kelp. This suggests that the export of KDD particles is not as pronounced as has been reported elsewhere (Wulff and Field 1983). It is, however, possible that the material is not accumulated in surface waters, where the samples were collected, and instead sinks out of the water column, or that it is exported even further away from the kelp forest.

3.4.2. Chlorophyll-a concentration

The highest chlorophyll-*a* concentrations were recorded under downwelling conditions with a significant decrease under upwelling conditions. This is in agreement with Carter (1982) who showed that during the upwelling relaxation phase (downwelling) phytoplankton concentration increased rapidly, along with water temperature. Similarly, Brown (1980, 1984) showed that phytoplankton concentration was much lower during upwelling conditions when compared to downwelling periods. There was however no trend in the chlorophyll-*a* concentrations with distance from the kelp. The gradient of phytoplankton production, with higher biomass recorded offshore under upwelling conditions (Brown 1980), was not detected in this study. The findings of this study highlight the variability in phytoplankton biomass present driven by coastal processes such as upwelling.

3.4.5. Stable isotope values

Upwelling conditions had a marked impact of the stable isotope values of the POM. The $\delta^{13}C$ and $\delta^{15}N$ values were significantly enriched under upwelling conditions. Fry and Wainright (1991) show that phytoplankton have depleted $\delta^{13}C$ between -21‰ and -25‰. However, there is natural stable isotope variability (6–10‰) among different phytoplankton groups co-occurring in the same area (Pel et al. 2003). It is also widely accepted that kelp and phytoplankton isotope stable isotope values, particularly $\delta^{13}C$, are distinct (Dunton and Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, Fredriksen 2003, Miller and Page 2012). The results of this study indicate that not only are $\delta^{13}C$ values more enriched under upwelling conditions, but there is also a distinct trend with distance from the kelp bed with values becoming more depleted with distance from the kelp. This gradient was most evident closer to the kelp suggesting the importance of proximity to the kelp forest in influencing POM composition From Chapter 2, the $\delta^{13}C$ values of the kelp collected at Kommetjie were very similar to that of the POM collected in the kelp bed, thus corroborating the mixing model results (discussed below). The results were also in agreement with those of Hill et al. (2006, 2008), which highlighted the depletion of $\delta^{13}C$ values when moving from the nearshore further off-shore. Both studies related the enriched coastal $\delta^{13}C$ values to the increased proportion of macrophyte detritus in the suspended POM. However, the Hill et al. (2008) study was conducted at Kenton-on-sea along the south coast of South Africa where upwelling is small-scale and sporadic.

There are no universal values or cut-off limits for $\delta^{15}N$ values which can be used to discriminate the constituents of POM, and these values are characteristically highly variable among different systems (Middelburg and Herman 2007). Hill et al. (2006, 2008) also documented highly variable $\delta^{15}N$ values for coastal POM; however, there were no clear patterns or trends that could be identified from either study. Similarly, the results of this study indicate that although $\delta^{15}N$ values were markedly enriched under upwelling conditions, there were no gradients with distance from shore. The increased nutrient

content water (Andrews and Hutchings 1980), and influx of ^{15}N-enriched nitrate of upwelled would explain the enriched $\delta^{15}N$ values (Liu and Kaplan 1989).

3.4.4. POC:chlorophyll-a ratio

The values obtained from the ratio of POC:chlorophyll-*a* were largely in agreement with the results of the mixing model used to determine the proportion of KDD (discussed below). Nutrients and light have been shown to influence the POC:chlorophyll-*a* ratio dramatically, with the highest values recorded under low nutrient conditions in natural plankton communities (Jakobsen and Markager 2016). Similarly, values over 200 were recorded within the kelp bed, and thus indicate detrital material (Cifuentes et al. 1988). Values far below 200 were recorded off-shore and along-shore under downwelling conditions, and thus corroborated the influence of phytoplankton under these conditions. This characterisation of the composition of POM therefore provided useful information as to the nature of the POM samples collected.

3.4.5. C:N ratio

It is evident from the results that the C:N ratio within the kelp bed is the highest along the length of both transects and close to kelp itself (as seen in Chapter 2). Away from the kelp forest, the C:N ratio of the POM drops and matches more closely with that reported for phytoplankton in the literature. Upwelling resulted in higher C:N ratios along the length of both transects in comparison to downwelling conditions. These patterns are very similar to those of the $\delta^{13}C$ values and thus further corroborate the mixing model results.

3.4.6. Proportion of KDD

Under upwelling conditions, it was expected that KDD would dominate the POM and under downwelling conditions, phytoplankton would be dominant as these patterns have been suggested in the literature (Brown 1980, 1984, Wulff and Field 1983, Brown and Hutchings 1987). The results strongly confirm the dominance of phytoplankton under downwelling conditions and the switch to KDD dominance under upwelling conditions. Additionally, the KDD of was highest within the kelp bed under both conditions and dropped markedly to the first sampling station. After this point the trend is more consistent. This suggest that the influence of KDD is higher within the kelp bed itself in comparison to the areas beyond the edge of the kelp forest. The main influence on the variability in the proportion of KDD appears to be *Ecklonia maxima*, as this species displayed the gradient in contribution with distance from the kelp bed under both upwelling and downwelling conditions. Interestingly, however, *Laminaria pallida* contributed 50% of the total KDD under upwelling conditions. This is most likely explained by the fact that *L. pallida* grows in deeper water than *E. maxima* and forming extensive beds which are not always visible from the surface. Hence, detrital material generated here would be carried shore-wards and toward the surface under upwelling

conditions. However, the biomass of each species has not been quantified at this fine scale. Knowing the exact proportion of *E. maxima* and *L. pallida* within the kelp bed at Kommetjie would allow for greater accuracy in the mixing models.

Although in agreement with other studies from the kelp forests of South Africa (Field et al. 1980b, Koop et al. 1982a, Bustamante and Branch 1996b) and some around the world (Dunton and Schell 1987, Duggins et al. 1989, Kaehler et al. 2000), the results are contradictory to those from other areas. The *Macrocystis pyrifera* kelp forests of California have been well documented, with several studies into the dynamics and importance of particulate organic matter in this system (Page et al. 2008, Miller et al. 2011, 2013, Yorke et al. 2013). Yorke et al. (2013) found that the particle size of the majority of suspended kelp detritus within *Macrocystis* forests was ≤250 μm, which is the same size spectrum as phytoplankton and bacterioplankton. However, their study suggests that kelp-derived carbon accounts for less than 1% of the total POM pool available to filter feeders. This corroborates the main findings of Miller et al. (2011, 2013) for the Santa Barbara Channel (California) kelp forests, stating that phytoplankton and not kelp derived detritus is the main constituent of the POM.

The reason for this stark contrast in the importance of KDD in these systems is most likely due to the differences in kelp and phytoplankton productivity. Phytoplankton productivity and KDD have been shown to contribute similar energy fluxes toward the pool available to filter-feeding herbivores in a kelp bed on the west coast of the Cape Peninsula, 23,986 $kJ.m^{-2}.yr^{-1}$ and 23,450 $kJ.m^{-2}.yr^{-1}$ respectively (Newell 1984) (see Figure 1.2); however, this balance is unique as mismatched production rates of phytoplankton and kelps have been reported in other kelp forest ecosystems. Fredriksen (2003) and Kaehler et al. (2000) noted that phytoplankton production is less than a third of the kelp production in kelp forests of Norway and the Prince Edward Islands, respectively. In the Santa Barbara Channel, KDD production is only 20% of that measured for phytoplankton (Yorke et al. 2013). However, these figures must be considered carefully, as the area available to phytoplankton production is much larger than that available for kelp. Nevertheless, it is likely that KDD would comprise a larger proportion of the POM in the kelp forests along the South African coastline when compared to these other systems based on the data available.

Needless to say, the results of this study have further demonstrated the large variability in the composition of coastal POM which is available to filter feeders, both within kelp forests and those in the nearshore pelagic environment (Bustamante et al. 1995a, Bustamante and Branch 1996b). This study highlights the importance of KDD in the suspended POM within South African kelp forests, as well as documenting the importance of coastal processes, such as upwelling, in controlling POM composition and thus food availability within the nearshore environment. These findings add to the existing studies which highlight the importance of the exchange of detrital material among coastal habitats, specifically around kelp forests (Krumhansl and Scheibling 2012).

3.4.7. Food web implications

Several authors have suggested the importance of kelp-derived material to the diet of sessile filter feeding organisms, such as bivalves, sponges, ascidians and bryozoans within kelp forests, based largely on stable isotope analysis (Seiderer and Newell 1985, Dunton and Schell 1987, Duggins et al. 1989, Kaehler et al. 2000, Fredriksen 2003, Tallis 2009, Leclerc et al. 2013a). These studies suggest that kelp forest suspension feeders have a $\delta^{13}C$ which lies between that of kelp and offshore phytoplankton, very similar to bulk POM signatures. In this way, these authors inferred that kelp derived carbon accounts for a large proportion of the POM, and between 20–80% of the diet of the suspension feeding organisms inhabiting the reefs. However, variability of stable isotope values, both of producers and consumers, could lead to overestimates of the dependence on this source (Nadon and Himmelman 2006, Miller and Page 2012). The most pertinent problem is the choice of stable isotope values used for the mixing models, which calculate the dependence of organisms on a particular source. Page et al. (2008) provide an extensive review on the use of different end member stable isotope values for kelp forest food web studies. The largest problem is the identification of pure detrital and pure coastal phytoplankton stable isotope values, as these always occur in a mixture in coastal waters (Page et al. 2008).

The methods used in this study, similar to those employed by Ramshaw et al. (2017) along the coast of Nova Scotia, provide a unique way of tackling the problem of 'pure' phytoplankton and KDD values for stable isotope analysis. Although not perfect, this does provide a more suitable alternative to using off-shore phytoplankton values. There is however a definite need for further studies on the change in $\delta^{13}C$ and $\delta^{15}N$ *Ecklonia maxima* and *Laminaria pallida* following a gradient of decay. Having this information will greatly improve the accuracy of stable isotope mixing models for studying POM compositions and kelp forest ecology in general. Studies have documented the changes in macroalgal stable isotope values as a result of bacterial decay (Hill and McQuaid 2009a, Dethier et al. 2014). The $\delta^{15}N$ and $\delta^{13}C$ intertidal algae became depleted following bacterial decay (Hill and McQuaid 2009a), and it is therefore plausible that *E. maxima* and *L. pallida* values will also undergo changes as a result of microbial degradation. Similarly, phytoplankton values may change following after a bloom event. Thus, degraded phytoplankton and kelp-derived detrital material colonised by bacteria could in effect have similar C:N ratios (Lancelot and Billen 1985). It is however impossible to predict the magnitude of these changes without experimental studies to ascertain this. Additionally, variability in coastal phytoplankton stable isotope values needs to be investigated. By understanding the variability in both components of POM, we can better determine the dynamics of this important food source.

Another important consideration is the preferential or selective feeding of filter feeders, regardless of the composition of the POM. Studies have highlighted that although kelp particles may be abundant in

the water column, they may not be actively filtered out as a food source. For example, Siederer and Newell (1988) showed that despite the ascidian *Pyura stolonifera* (Heller) ingesting kelp particles, these were not retained and phytoplankton was the primary dietary item for these filter feeders. This may require a simultaneous investigation into the particles present in the water column and those ingested by filter-feeding organisms. It is known that the nutritional quality of kelp increases as a result of degradation through microbial activity, by increasing the %N and thus decreasing the C:N ratio (Newell et al. 1982, Mann 1988, Duggins and Eckman 1997, Krumhansl and Scheibling 2012). Several studies have shown that filter feeding organisms show a preference for aged kelp detritus rather than fresh or man-made kelp particles (Stuart et al. 1982, Duggins and Eckman 1994, 1997, Norderhaug et al. 2003). Similarly, although phytoplankton may be dominant under downwelling conditions, the composition may not favour the dietary requirements of the filter feeders. For example, Barlow et al. (2005) reported that diatoms are the dominant phytoplankton in inshore regions of the southern Benguela. However, Mitchell-Innes and Winter (1987) showed that coccolithophores can be a major component of the phytoplankton in upwelled water. Nevertheless, the results of the present study are in agreement with Seiderer and Newell (1985) who suggest that the mixing created by upwelling conditions, is important for carbon and nitrogen balance within kelp systems as it results in the variability of POM composition.

3.5 CONCLUSION

This study has shown that kelp-derived detritus from both *Ecklonia maxima* and *Laminaria pallida* is an important component of the particulate organic matter suspended in the water column within the kelp forest at Kommetjie, and likely the majority of west coast kelp beds in southern Africa. This material can account for up to 89% of the POM in these systems and is therefore likely to be an important source of carbon for benthic and pelagic filter-feeding organisms. Oceanographic processes such as upwelling having a drastic influence on the composition of this suspended material. Through stable isotope analysis I have corroborated the findings which suggest the export of KDD away from the source and to systems both off-shore and along-shore. What now needs to be determined is whether this material is being consumed by benthic filter-feeders or if phytoplankton is preferentially selected when it is available. Understanding which source, KDD or phytoplankton, is the prominent carbon source of kelp forest food webs is critical to our understanding of the energy transfer in these systems. Additionally, the sampling design of this study limits the conclusions and inferences to the surface waters as samples were only collected here. Further investigation into the dynamics and composition of POM throughout the water column need to be performed.

A major limitation of the current methodology is the dependence on suitable sea and weather conditions for the collection of boat-based samples. Additionally, the timing of sampling can be greatly impacted by relying on a wind-based index, as sea conditions and atmospheric conditions are

unlikely to be synchronised. Wind patterns are likely to change faster than sea conditions, introducing a lag phase between the calculated index and the actual upwelling conditions. From Figure 3.2 it is evident that there is some lag between the upwelling index and the *in-situ* water temperature measured at Kommetjie. If samples are collected before conditions have changed, i.e. during the lag phase, the data may not reflect what the index is forecasting. This proved to be the case with sampling Days 5 and 6 as these samples were collected very early in the upwelling cycle when wind conditions had only changed for a few hours. Therefore, sea conditions may still have been representative of the opposite upwelling condition. To combat this, the use of *in-situ* data loggers to measure real-time changes in the parameters associated with upwelling conditions (temperature, turbidity, chlorophyll-*a*) could provide a far superior estimate of the influence of these coastal processes on the kelp forest ecosystem.

CHAPTER 4

Temporal and spatial variability in stable isotope values of ecologically different South African kelp forest communities

4.1 INTRODUCTION

Kelp forests, and the communities they support, are highly influenced by physical and biological processes which shape their distribution, composition and community structure (Lüning 1979, Dayton 1985, Kendrick et al. 2004, Tuya et al. 2012, Wernberg et al. 2016, Smale and Moore 2017, Teagle et al. 2017). Additionally, anthropogenic factors such as overfishing have further impacted community structure by removing top-predator species (Tegner and Dayton 2000, Jackson et al. 2001, Estes et al. 2011, Blamey et al. 2014, Hamilton et al. 2014). Changes in community composition among different areas is likely to result in variability in trophic structure and ultimately ecosystem functioning.

4.1.1. Kelp forests in South Africa—physical environment

The southwestern coast of South Africa (Figure 1.1, Chapter 1) is located at the intersection of the Benguela and Agulhas Marine Provinces which meet at Cape Point (Spalding et al. 2007). However, the section between Cape Point and Cape Agulhas (*ca*. 200 km), the south-west coast, has been referred to as a transition zone (Bolton 1986, Stegenga et al. 1997, Leliaert et al. 2000, Smit et al. 2013). The most prominent physical effect of this break, and transition zone, is the marked effect it has on the seawater temperature regime—with an increase in temperature east of Cape Point (Smit et al. 2013). A further difference between the west coast and south-west coast is the frequency and intensity of wind-driven upwelling (see Chapter 2). Along the west coast, upwelling is seasonal with frequency and intensity peaking in the summer months as a result of south-easterly winds (Andrews and Hutchings 1980). Upwelling along the south-west coast is less intense than on the west coast and is often more sporadic in frequency (Cram 1970, Bustamante et al. 1995b, Stegenga et al. 1997), and False Bay in particular is largely protected from coastal upwelling processes (Smit et al. 2013). However, upwelling does occur in False Bay but it is not on the same scale or intensity as that which is observed on the west coast. As a consequence of upwelling, nutrient concentrations are therefore expected to be higher along the west coast where upwelling is more prevalent (Waldron and Probyn 1992).

These differences in the physical environment have resulted in marked changes in the community structure and composition of the biota among the west coast, south coast and transition zone (Stegenga et al. 1997). The biogeographical break between marine provinces is evidenced in the biogeography of several groups of marine organisms including fish (Turpie et al. 2000), invertebrates (Emanuel et al. 1992, Procheş and Marshall 2002), and seaweeds (Bolton 1986, Bolton and Anderson 1987, Leliaert et al. 2000). However, many species of seaweeds and shore animals whose distribution is centred in the Benguela Marine Province have an eastern limit to their distribution at Cape Agulhas, whereas the Cape Peninsula is the western limit for species from the Agulhas marine province (Emanuel et al. 1992, Stegenga et al. 1997). Therefore, the seaweed communities in the transition region, between these two points, comprise a high diversity, with the interdigitation of species from

both adjacent marine provinces (Jackelman et al. 1991, Stegenga et al. 1997). On a biogeographical scale (>50 km), seaweed community structure is thus largely controlled by seawater temperature and consequently there are distinct differences in the community composition along the temperature gradient of the transition zone (Bolton and Anderson 1990). However, at a local scale, wave action is arguably more important for structuring community composition (McQuaid and Branch 1984, 1985).

Kelp forests, formed by *Ecklonia maxima* and *Laminaria pallida*, occur along the southern African coastline between Rocky Point in northern Namibia and De Hoop Nature Reserve, 70 km east of Cape Agulhas (Field et al. 1977, Field and Griffiths 1991, Bolton 2010, Bolton et al. 2012, Rothman et al. 2017a). *Ecklonia maxima* is a large species (generally not exceeding 10 m but can reach 17 m in total length) and forms a dense canopy at the surface, aided by a gas-filled float near the apex of the primary blade (Field and Griffiths 1991, Stegenga et al. 1997). *Laminaria pallida* is a smaller species and south of Cape Columbine it creates a sub-canopy roughly two meters above the substrate and dominates in deeper water (Field and Griffiths 1991, Rothman et al. 2017a). The community structure of both the faunal and floral communities of the kelp forests along the south-western coastline is highly variable (Velimirov et al. 1977, Field et al. 1980a, Leliaert et al. 2000). This variability is driven by abiotic variables such as light, temperature, wave exposure and depth gradients, as well as by biological interactions and species assemblages (Field et al. 1980a, Anderson et al. 1997, Leliaert et al. 2000, Blamey et al. 2010).

4.1.2. Kelp forests in South Africa—community structure

The understorey algal communities on either side of the Cape Peninsula in particular have been described as very different, with foliose red algae (Rhodophyta) more prevalent on the Atlantic side, whereas green algae (Chlorophyta) and articulated corallines tend to dominate the kelp understory of False Bay (Leliaert et al. 2000). At Cape Hangklip, the biomass of foliose algal taxa was low in historical studies (Field et al. 1980a, Jackelman 1996).

Along the west coast, the faunal biomass of these kelp habitats is dominated by filter-feeding animals such as mussels (*Aulacomya ater* and *Choromytilus meridionalis*), ascidians (*Pyura stolonifera*) and sponges (Field et al. 1980a). These filter-feeding organisms are thought to rely largely on the kelp-derived detritus which is suspended in the water column along with phytoplankton and other particulate organic matter (POM) (Newell et al. 1982, Stuart et al. 1982, Bustamante and Branch 1996b). East of Cape Point however, particularly along the south-west coast, filter feeding organisms become scarcer and the faunal biomass is dominated by grazers such as urchins (*Parechinus angulosus*), turban shells (*Turbo cidaris*) and limpets (*Cymbula compressa* (Linnaeus)), (Field and Griffiths 1991, Anderson et al. 1997).

Along the west coast, carnivore biomass was once dominated by the rock lobster *Jasus lalandii*, which is known to consume, mussels (*C. meridionalis* and *A. ater*), urchins, and turban shells (Pollock 1979, van Zyl et al. 1998). Historically, lobster biomass and the commercial fishery it sustained was concentrated along the west coast (Cockcroft et al. 2008). However, the south-eastward shift of lobsters into the area East of Cape Hangklip (EOCH, see Figure 4.1) in the 1990s resulted in a fourfold increase in lobster abundance in this area in what has been termed a lobster invasion (Tarr et al. 1996, Mayfield and Branch 2000, Cockcroft et al. 2008). This has resulted in large-scale changes to the benthic communities in this region since the mid-1990s (Blamey et al. 2010). Lobster predation on the invertebrates in these habitats has drastically reduced the biomass of numerous species, in particular the sea urchin *Parechinus angulosus* (Blamey et al. 2010). The close association of this species with the abalone *Haliotis midae* (Day and Branch 2000a, 2000b, 2002a, 2002b, 2002c), has subsequently had negative effects for the recruitment of this commercially harvested species (Tarr et al. 1996, Tarr 2000). The removal of the dominant grazing species has also resulted in the increase of foliose and turf algae, which now dominate the understory seaweed communities (Blamey et al. 2010).

It has subsequently been suggested that the kelp forests in the south-west coast exist in two alternative stable states: either with or without high abundances of sea urchin grazers (Blamey et al. 2010, 2013, Blamey and Branch 2012). These differences, therefore, create three ecologically distinct communities within a short stretch of coastline: the typical west coast kelp forests on the Atlantic coast of the Cape Peninsula; the traditional south west coast kelp forests on the eastern side of the Cape Peninsula (False Bay); and the lobster-invaded kelp forests EOCH (see Figure 1.1, Chapter 1).

4.1.3. Stable isotope ecology

Stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) has become a powerful tool for studying the trophic ecology of marine ecosystems (Layman et al. 2007a, 2012). By measuring the stable isotope values of organisms within a food web, information on the flow of organic matter can be gathered, as consumer isotope values reflect their diet (DeNiro and Epstein 1976, Wada et al. 1991, Layman et al. 2012). Most of the early stable isotope studies conducted used bi-plots of $\delta^{13}C$ - $\delta^{15}N$ to view all the organisms in a food web in isospace and determine qualitative relationships among organisms (Newsome et al. 2007). Subsequently, Layman et al. (2007a) proposed a set of quantitative metrics to study the trophic structure of food webs among communities by measuring of the extent and spacing of the means of the isotope values ($\delta^{13}C$ and $\delta^{15}N$) in isospace (Layman et al. 2007a, Newsome et al. 2007, Hoeinghaus and Zeug 2008, Layman and Post 2008). These ‘Layman metrics’ coupled with Bayesian analyses of niche area have been successfully used to study trophic niche dynamics in single species (Layman et al. 2007b, Olsson et al. 2009, Jackson et al. 2011, Layman and

Allgeier 2012, Syväranta et al. 2013, Ercoli et al. 2014), as well as the trophic structure of whole communities (Layman et al. 2007a).

The aim of this study was therefore to examine the influence of kelp forest community composition on the trophic structure, using stable isotope analysis. More specifically, it is predicted that the large differences in community composition among the kelp forests of the west coast, False Bay and EOCH will create very different trophic structuring among these communities. By investigating the temporal and spatial variability in stable isotope values, trophic positioning and community metrics the influence of community composition was determined for three selected kelp forest ecosystems.

4.2 METHODS

4.2.1. Study Sites

Three study sites with contrasting ecological communities were selected for this study (Figure 4.1). Oudekraal, on the western side of the Cape Peninsula was the selected site in the Atlantic Ocean, representing a West Coast kelp forest. Bordjiesrif, near Cape Point was selected to represent a False Bay kelp forest community. Betty's Bay, situated east of Cape Hangklip, and represents a recently changed ecosystem following the lobster invasion in this area (see Figure 1.1). All three sites are located within marine protected areas (MPAs).

4.2.2. Sample Collection

Based on recent benthic surveys conducted by Coppin (2017) at the three selected sampling sites (Oudekraal, Bordjiesrif and Betty's Bay) along with published literature, commonly occurring species from different trophic guilds were selected. However, due to natural variability in the community composition, not all algae and animals were present at all sites in both seasons. Nevertheless, at each site, the dominant organisms were collected. Species included commonly occurring understorey algae as well as benthic invertebrates which are resident in kelp bed systems (see Table 4.1). At each site, five individuals from each of the chosen species were collected by SCUBA divers during winter and five during summer. Where possible, larger organisms of similar size were collected for each species at all sites to avoid potential bias resulting from size differences. Sampling was carried out late in the respective seasons to allow for the incorporation of dietary isotope values into the animal tissues. Summer samples were collected in April and winter samples were collected in October. All collected organisms were placed on ice for transport back to the laboratory with the exception of the west coast rock lobster (*Jasus lalandii*).

Thirty *Jasus lalandii* individuals were collected at each sampling site, both in summer and winter. Thirty individuals were collected as to provide enough replicates for a parallel stomach content study, as well as for the isotopic niche study described in Chapter 5. Due to animal ethics considerations,

lobsters were euthanized on site by immersion in a saturated salt (NaCl) solution for five minutes before being placed on ice. All samples were subsequently transported back to the laboratory where they were frozen (-15°C) prior to further processing.

To collect suspended particulate organic matter (POM), triplicate 5 L water samples were collected at the surface in the kelp forest on each sampling occasion and transported back to the laboratory for processing.

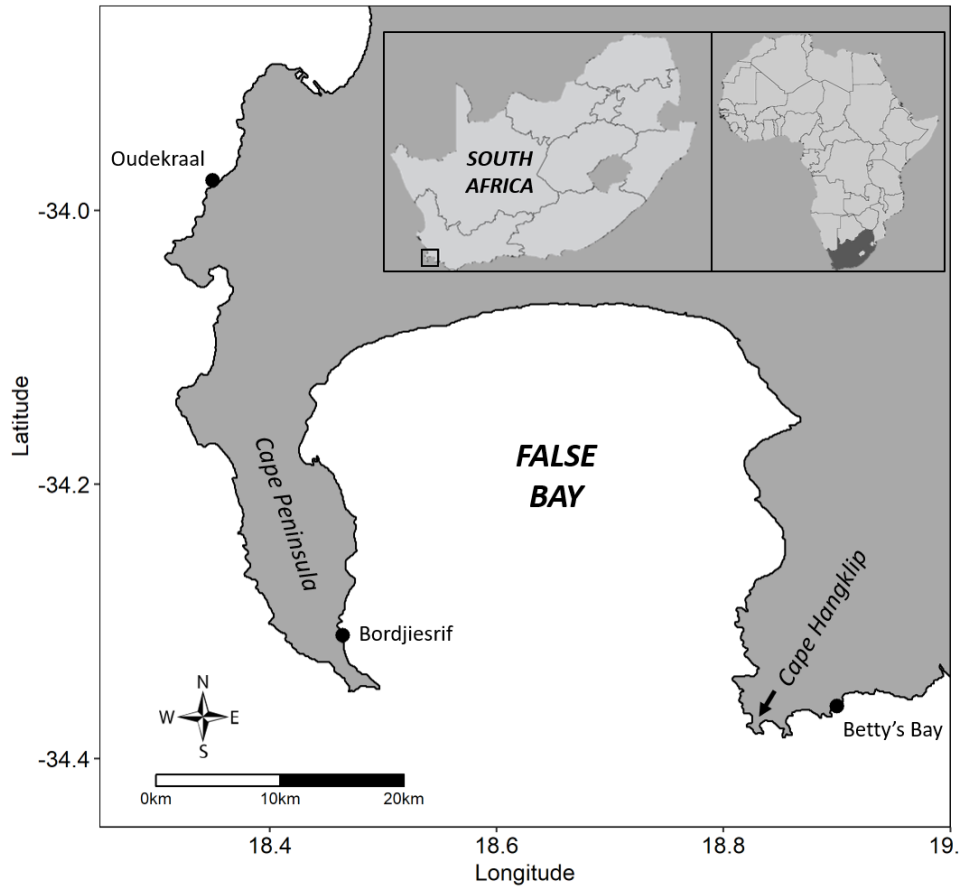

Figure 4.1: Geographic location of the three sampling localities (Oudekraal, Bordjiesrif and Betty's Bay) in relation to the Cape Peninsula, False Bay and Cape Hangklip. Inset map indicating the location of study area within South Africa.

4.2.3. Laboratory Processing

Once thawed, algal samples were thoroughly rinsed with distilled water to remove any contaminants and then dried in an air-circulated oven (at 60°C) for 48 hours. Muscle tissue was excised from the invertebrates collected at each site. For each species, the most appropriate muscle tissue was chosen based on commonly used tissues in the literature (Table 4.1). Muscle tissue was chosen as it provides

a time-incorporated stable isotope value of the diet. Tissue samples were oven dried in an air-circulated oven (60°C for 48 hrs).

Each water sample was vacuum-filtered through a pre-combusted (450°C for 6 hrs) Whatman GF/F filter. The filters were placed onto a foil-lined tray, inspected for unwanted contaminants (e.g. zooplankton or microplastics), and oven dried (60°C for 24 hrs). Each dried filter was then treated with 10% HCl to remove biogenic carbonates. The POM retained on the filter was scraped off and packaged into a 5 × 9 mm tin capsule for stable isotope analysis.

Once dried, algal and animal tissue samples were homogenized into a fine powder using a Retsch MM200 ball-mill, before being individually weighed out into 5x9 mm tin capsules. For the algal samples, each capsule contained 1.2 mg of sample material.

Before weighing out the animal samples into tin capsules, each sample was split into two equal portions. One portion was weighed out for analysis immediately, with each capsule containing 0.5 mg of sample material. However, lipids present in the tissue can alter the $\delta^{13}C$ isotope values as they are more depleted relative to other biochemical compounds such as carbohydrates and proteins (Post et al. 2007, Logan et al. 2008). Thus, samples required lipid treatment in order to remove this bias which can cause considerable variation in isotope values. The lipid treatment process can however affect the $\delta^{15}N$ values (Post et al. 2007, Logan et al. 2008). Half the sample is therefore left untreated to preserve the $\delta^{15}N$ values. Using the $\delta^{13}C$ values from the treated samples and the $\delta^{15}N$ values from the untreated samples gives the most accurate representation of the organism in isotope space (Logan et al. 2008). Algal samples were not lipid treated as lipid contents were assumed to be low.

Lipids were extracted from the second half of the sample using a modified version of the Bligh and Dyer (1959) method, used by Logan et al. (2008). Once treated, samples were dried in an air-circulated oven (60°C for 24 hrs) before being weighed out into tin capsules.

All samples were analysed at iThemba LABS (Johannesburg, South Africa) using a Flash HT Plus elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer, with a ConFlo IV interface (all equipment supplied by ThermoFisher, Bremen, Germany). Carbon and nitrogen isotope values were corrected against an in-house standard (Merck Gel). Laboratory standards and blanks were run after every 20 unknown samples.

Table 4.1: List of organisms collected as well as tissue type used for stable isotope analysis from each organism. Species codes and sample sizes (n) for each site per season. Collection at each site (BB = Betty's Bay, BR = Bordjiesrif, OK =-Oudekraal) indicated by S for summer and W for winter for each species.). Algal phyla are denoted by R (Rhodophyta), B (Phaeophyta) and G (Chlorophyta). Lipid extraction was only performed on animals.

Species	Species code	n	Tissue used	Lipid corrected	BB	BR	OK
Macroalgae							
Botryocarpa prolifera (R)	BP	5	Thallus	No	S+W	-	S+W
Codium fragile (G)	CF	5	Thallus	No	W	-	S+W
Codium stephensiae (G)	CS	5	Thallus	No	S+W	S+W	S+W
Ecklonia maxima (B)	EM	5	Frond tip	No	S+W	S+W	S+W
Gelidium vittatum (R)	GV	5	Thallus	No	-	-	S+W
Laminaria pallida(B)	LP	5	Frond tip	No	S+W	S+W	S+W
Plocamium beckeri (R)	PB	5	Thallus	No	-	S+W	-
Pachymenia cornea (R)	PC	5	Thallus	No	S+W	S+W	S+W
Pachymenia orbitosa (R)	PO	5	Thallus	No	S	-	-
Ulva capensis (G)	UC	5	Thallus	No	S+W	S+W	S+W
POM							
Particulate Organic Matter	POM	5	Filtrate	No	S+W	S+W	S+W
Filter-feeders							
Aulacomya ater	AA	5	Adductor muscle	Yes	-	-	S+W
Choromytilus meridionalis	CM	5	Adductor muscle	Yes	-	S+W	S+W
Pyura stolonifera	PS	5	Siphon muscle	Yes	S+W	S+W	S+W
Grazers							
Cymbula compressa	CC	5	Foot muscle	Yes	S+W	S+W	S+W
Parechinus angulosus	PA	5	Aristotle's lantern	Yes	S+W	S+W	S+W
Turbo cidaris	TC	5	Foot muscle	Yes	S+W	S+W	S+W
Predators							
Jasus lalandii	JL	10	Pleon (tail)	Yes	S+W	S+W	S+W
Marthasterias glacialis	MG	5	Tube feet	Yes	-	S+W	W

4.2.4. Trophic positioning

Following Post (2002a), the trophic position of animal food-web members at each site was calculated based on the following formula:

$$Trophic\ position = \frac{(N_{consumer} - N_{basal\ resource})}{\Delta N} + Z$$

where $N_{consumer}$ refers to the $\delta^{15}N$ of the consumer organism, $N_{basal\ resource}$ is the $\delta^{15}N$ of the lowest trophic level in the ecosystem and ΔN is the trophic enrichment factor (TEF) or change in $\delta^{15}N$ with each step in the trophic position, Z is the trophic position of the basal resource.

In order to mitigate any bias caused by macroalgal variability in the calculation of trophic positioning, a longer-lived consumer, which is likely to incorporate variability in primary producers, was selected (Post 2002a, 2002b). The smooth turban shell, *Turbo cidaris*, was selected as the trophic base at all sites and all other trophic positions were determined from this accordingly. As *T. cidaris* is a large grazing snail, it was assumed that it would have a trophic position of 2 (therefore, $Z = 2$). Although direct evidence of the diet of *T. cidaris* is not available, it does occur in areas which have varied macroalgal communities (see Anderson and Velimirov 1982, Leliaert et al. 2000). Therefore, it is assumed that this species is a generalist grazer, consuming a variety of macroalgal species. The TEF values were kept constant across all sites and seasons at 3.4 as this is the standard fractionation of $\delta^{15}N$ (Post 2002a).

4.2.5. Trophic structure using SIBER

Layman et al. (2007a) document six community-wide metrics which can be used to understand important aspects of trophic structure within food webs. The $\delta^{15}N$ range (NR) is the total range of all $\delta^{15}N$ and gives a measure of the vertical structure of the food web. The $\delta^{13}C$ range (CR) is the total range of all $\delta^{13}C$ values and provides information on the diversity of carbon sources used. The total area (TA) give an estimate of the total niche area occupied and thus provides an extent of the trophic diversity of the food web. The mean distance to centroid (CD) provides a measure of the average degree of trophic diversity of the species in the food web. Mean nearest neighbour distance (NND) estimates the overall species packing in the web. The standard deviation of the NND (SDNND) provides a measure of the evenness in species packing in isotope biplot space. See Layman et al. (2007a) for further details on each of the metrics.

The Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011), was used to determine the trophic structure at each of the three sites. Community niche widths were calculated across sites and seasons by estimating Bayesian standard ellipse area (SEA_B) using $\delta^{13}C$ and $\delta^{15}N$ values. As sample sizes were small ($n = 5–30$), a small-sample-size-corrected standard ellipse area (SEA_C) was also estimated (Jackson et al. 2011, Syväranta et al. 2013). This analyses pairwise comparisons of the niche size and determines the probability that one niche is larger or smaller than another. The amount of overlap among different niches was determined using the nicheROVER package in R (Lysy et al. 2014). For these analyses, the complete suite of species, algae and consumers, was used instead of the reduced set as for the statistical analyses. All analyses were performed in R v3.4.2 (R Core Team 2017).

4.2.6. Statistical analyses

In order to compare among sites and between seasons, organisms from each site were selected that present in both seasons and at all three sites. This left 5 animal species and 5 algal species along with POM for the comparisons (see Tables 4.3 & 4.4 for list of organisms).

Two-way analysis of variance (ANOVA) was performed on each species of each of the three markers ($\delta^{13}C$, $\delta^{15}N$ and C:N ratio). Trophic position of all animals (excluding *T. cidaris*) was also tested for temporal and spatial variability using a two-way analysis of variance (ANOVA). Tukey *post-hoc* comparisons were performed where there were differences among sites and between seasons. To determine the variance components of stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), C:N ratio as well as trophic position, a magnitude of effects term (ω^2) was calculated for each of the ANOVA analyses. This determines the proportion of variance explained by each variable in the analysis based on mean sum of squares (see section 2.1.5 for equation). All analyses were performed in R v3.4.2 (R Core Team 2017).

4.3 RESULTS

4.3.1. Temporal and spatial variability—macroalgae

There were clear visual differences between the different groups of algae collected when their values are plotted in isospace ($\delta^{15}N$ vs $\delta^{13}C$: Figures 4.2–4.4). The Rhodophyta were in general much more depleted in $\delta^{13}C$, particularly for *Botryocarpa prolifera* and *Plocamium beckeri*. The green algae, particularly the *Codium* species and *Ulva capensis*, were the most enriched in $\delta^{13}C$ at all sites. Both kelp species, *Ecklonia maxima* and *Laminaria pallida*, had $\delta^{13}C$ values which were generally between those of the Rhodophyta and Chlorophyta (Figures 4.2–4.4).

Among the three sites, the macroalgae had comparable $\delta^{15}N$ values, generally between 6 and 8‰ (Figures 4.2–4.4). There were however some exceptions to this trend. *Pachymenia cornea* was evidently more depleted at Bordjiesrif in winter (Figure 4.3). At Betty's Bay in winter, the Chlorophyta were highly enriched in their $\delta^{15}N$ values, well above even the top predator values. This was particularly evident with *Ulva capensis* which was enriched by more than 4‰ in winter compared to summer sampling occasions.

From Table 4.3, it is evident that there is a large degree of temporal and spatial variability among all the species of macroalgae which were analysed. The $\delta^{15}N$ and C:N ratios of all five species and POM were significantly different among the three sites ($p < 0.05$; Table 4.3). There was a similar trend for the $\delta^{13}C$ values, with significant differences among the sites for all species except *Ecklonia maxima* ($F = 1.60$, $df = 2$, $p = 0.22$).

Sampling occasion (season) was significant for the $\delta^{13}C$ values of all algal species and POM ($p < 0.001$; Table 4.3). Similarly, season was statistically significant for all algal species and POM with the exception of *Codium stephensiae* ($F = 0.00$, $df = 1$, $p = 0.98$). The C:N ratios were significantly different between seasons for all species except *Laminaria pallida* ($F = 0.23$, $df = 1$, $p = 0.88$) and *Pachymenia cornea* ($F = 0.00$, $df = 1$, $p = 0.98$).

The proportion of variability explained by site and season was highly variable among the different algal species and the two stable isotopes (Table 4.3). Season accounted for a large proportion of the variability in $\delta^{15}N$ of *Ecklonia maxima* (60%), *Laminaria pallida* (62%), and particulate organic matter (40%). However, differences in $\delta^{15}N$ among sites accounted for a large proportion of variability in *Codium stephensiae* (45%), *Pachymenia cornea* (58%), and *Ulva capensis* (53%). The variability in $\delta^{13}C$ of *C. stephensiae*, *L. pallida* and *P. cornea* were largely determined by differences between seasons, 45%, 58% and 53% respectively. Variability in $\delta^{13}C$ of POM and *U. capensis*, both 55% (Table 4.3) were attributed to differences among sites. However, the interaction of site and season was often significant for the different species and further explained the variability (Table 4.3).

From the *post-hoc* analyses, differences in $\delta^{13}C$ were not consistently explained for the different species. For example, *Codium stephensiae* values were similar among sites in summer, but completely different among sites in winter. *Laminaria pallida* values were similar among sites in each season, but different between seasons. Differences were also not consistent, *Pachymenia cornea* values were similar at Oudekraal in summer and winter, but at the other two sites they were completely different seasonally. *Ulva capensis* was similar at Oudekraal and Betty's Bay but different at Bordjiesrif in both seasons. POM was similar at Oudekraal and Betty's Bay in both seasons, with Bordjiesrif being different in both seasons.

Similarly, differences in $\delta^{15}N$ among sites and seasons were not consistent among species. *Codium stephensiae* values were similar in summer among sites, but in winter Betty's Bay was distinct. *Laminaria pallida* values were similar among sites in summer, but in winter Oudekraal had a distinct signal. *Pachymenia cornea* values were distinct at Oudekraal in the summer and Bordjiesrif in the winter, with all other sampling occasions being similar. *Ulva capensis* was different among sites in winter, but similar among sites in summer. POM values were highly variable both spatially and temporally.

4.3.2. Temporal and spatial variability—consumers

Similar to the macroalgae, the animals collected at the three study sites displayed a large degree of temporal and spatial variability in the stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values, C:N ratios as well as their trophic positioning (Tables 4.2 and 4.4; Figures 4.2–4.4).

The $\delta^{15}N$ of the five selected animal species were significantly different among the sampling sites for all species (Table 4.4). Season was however only statistically significant for *Jasus lalandii* ($F = 10.28$, $df = 1$, $p < 0.001$), *Pyura stolonifera* ($F = 11.04$, $df = 1$, $p < 0.05$) and *Turbo cidaris* ($F = 8.85$, $df = 1$, $p < 0.05$).

The $\delta^{13}C$ values were significantly different among sites for all the selected animal species (Table 4.4). Season was also statistically significant for the $\delta^{13}C$ of all animals except *Pyura stolonifera* ($F = 0.05$, $df = 1$, $p = 0.82$).

The C:N ratios of the selected animals were significantly different among sites for all species except for *Cymbula compressa* ($F = 1.84$, $df = 1$, $p = 0.18$). Season was only significant for *C. compressa* ($F = 7.10$, $df = 1$, $p < 0.05$) and for *Jasus lalandii* ($F = 31.60$, $df = 1$, $p < 0.001$).

For all three markers ($\delta^{15}N$, $\delta^{13}C$ and C:N ratio) the interaction of site and season was statistically significant in several cases (Table 4.4). This indicates that the differences observed among sites were not consistent between the sampling occasions (seasons). Furthermore, the interaction term explained up to 345 of the variability in some cases (Table 4.4).

As expected, *Jasus lalandii* had the most enriched $\delta^{15}N$ at all study sites, with the exception of Bordjiesrif in the summer where the starfish *Marthasterias glacialis* had a more enriched value. *Turbo cidaris* had the most depleted $\delta^{15}N$ value of the animals collected at all three sites.

From the stable isotope biplots for all three sites, it is evident that the variability in macroalgal values is larger than for the consumer organisms, as evidenced by the size of the associated error bars (Figures 4.2–4.4). However, grazing organisms such as *Turbo cidaris* and *Parechinus angulosus* tended to go against this trend in certain instances, displaying variability in both $\delta^{13}C$ and $\delta^{15}N$ values. Filter feeders and predators however displayed low variability in stable isotope values across all sites and seasons.

The proportion of variability explained by site accounted for the majority of the variability for several species, both in $\delta^{13}C$ and $\delta^{15}N$ (Table 4.4). The variability of $\delta^{13}C$ values of all the animal species was controlled by site, accounting for between 45% and 80% of the total variability. Site was also highly influential in the variability of $\delta^{15}N$ values, accounting for 69% of the variability in *Parechinus angulosus* and 52% of the variability in *Pyura stolonifera* values. However, intra-species variability also accounted for some of the variability in the $\delta^{15}N$ values of *Cymbula compressa* (80 %), *Jasus lalandii* (61 %) and *Turbo cidaris* (45 %). Season did not account for a significant amount of the variability in either isotope for any of the animal species.

Post-hoc analyses of $\delta^{13}C$ values revealed similar inconsistent patterns among sites and seasons. *Cymbula compressa* values were similar between seasons within sites, but Betty's Bay was distinct from Oudekraal and Bordjiesrif in both seasons. In contrast, *Jasus lalandii* values were distinct at

Oudekraal in both seasons from Bordjiesrif and Betty's Bay, which were similar. The $\delta^{13}C$ of *Parechinus angulosus* were distinct among sites in winter but similar among sites in summer. *Pyura stolonifera* values were similar at each site between seasons but different among sites. *Turbo cidaris* values were distinct at Betty's Bay in winter but similar among sites in summer.

With the exception of *Parechinus angulosus*, *Pyura stolonifera* and *Turbo cidaris*, the $\delta^{15}N$ among sites and seasons did not reveal clear patterns. These species however showed clear differences among sites, with Betty's Bay being distinct from the other two sites for all three species.

4.3.3. Trophic positioning

Mean trophic position ranged from 2.00 which was set for *Turbo cidaris* at all sites, to 3.22 ± 0.08 for *Jasus lalandii* at Bordjiesrif in winter (Table 4.2). There were, however, statistically significant differences in trophic position among sites and between seasons for all animal species selected (Table 4.4). The trophic position of *Jasus lalandii* and *Cymbula compressa* was significantly reduced at Betty's Bay, particularly when compared to the other two sites (Table 4.2). These differences were most evident in winter at Betty's Bay, e.g. *C. compressa* trophic position was ~2.10 at Bordjiesrif and Oudekraal, 1.99 at Betty's Bay in summer and 1.69 at Betty's Bay in winter (Table 4.2.). The calculated positions of *Parechinus angulosus* and *Pyura stolonifera* were more similar among sites. Statistically, all species except *P. stolonifera* exhibited site and seasonal variability in trophic positioning (Table 4.4). The interaction of site and season was significant for *C. compressa, J. lalandii* and *P. stolonifera* indicating that the differences observed among sites was different between sampling occasions (seasons) (Table 4.4).

Anomalous results were obtained for *Parechinus angulosus* at Betty's Bay in the summer and winter sampling occasions as the trophic position for this species was higher than *Jasus lalandii* in summer and only 0.07 less than this species in winter.

Variability in trophic position was largely determined by differences among individuals collected in the same season at the different sites (Table 4.4). This was true for all species collected with the exception of *Jasus lalandii* for which differences among sites accounted for the largest proportion of variability (52%). The interaction term accounted for less than 10% of the variability in trophic position of *C. compressa* and *J. lalandii,* however for *P. stolonifera* the interaction of site and season accounted for 33% of the variability.

Post-hoc comparisons revealed distinct patterns in trophic positioning for *Cymbula compressa*, *Pyura stolonifera* and *Jasus lalandii*. In winter, the trophic position of these species was similar among sites but in summer, Betty's Bay was distinctly different from the other two sites.

4.3.4. Community metrics—trophic structure

The $\delta^{15}N$ range (NR) of the entire community was largest at Bordjiesrif (8.49‰ (S) and 7.81‰ (W) when compared to the other two sites which had more similar ranges (Table 4.5). The $\delta^{15}N$ range was higher in winter at both Oudekraal (5.97‰) and Betty's Bay (6.38‰), whereas Bordjiesrif had a greater $\delta^{15}N$ range in summer (8.49‰) versus winter (7.81‰).

The $\delta^{13}C$ range had a contrary pattern with the smallest ranges found at Bordjiesrif (18.76‰ (S) and 19.42‰ (W)) when compared to Oudekraal and Betty's Bay which had greater and more similar values (see Table 4.5). The largest $\delta^{13}C$ range was found at Betty's Bay from the winter sampling (22.39‰).

Total Area (TA) was largest at Bordjiesrif during both seasons in comparison to the other two sites (Table 4.5). The TA at Oudekraal was larger than Betty's Bay in both seasons. The CD values were larger in winter at all sites in comparison to the summer values. The smallest values were recorded at Oudekraal whereas the largest values were recorded at Betty's Bay, particularly in the winter. The nearest neighbour metrics (MNND and SDNND) were very similar among the sites and seasons. However, winter had larger mean values at Oudekraal and Betty's Bay but the summer value was larger at Bordjiesrif (Table 4.5).

Summer SEA_C values were lower at all three sites compared to winter values at the respective sites (Figure 4.5). Oudekraal had the lowest value (20.66‰^{2}) during summer and Bordjiesrif had the highest SEA_C value (29.74‰^{2}) during winter (Table 4.5). Oudekraal also had the largest difference in SEA_C values between seasons (6.57‰^{2}); followed by Betty's Bay (4.03‰^{2}) and Bordjiesrif had the smallest difference between seasons (2.88‰^{2}). Summer SEA_C values were distinctly different among the three sites. However, in winter, the SEA_C values were more similar among sites, with the three sites only different by 2.14‰^{2}.

The pairwise comparisons of niche overlap among the sites (Figure 4.6) show that there is a high degree of overlap among all the sites (>80% overlap). The community niche at Betty's Bay in summer overlapped with the niche at Oudekraal by almost 95%.

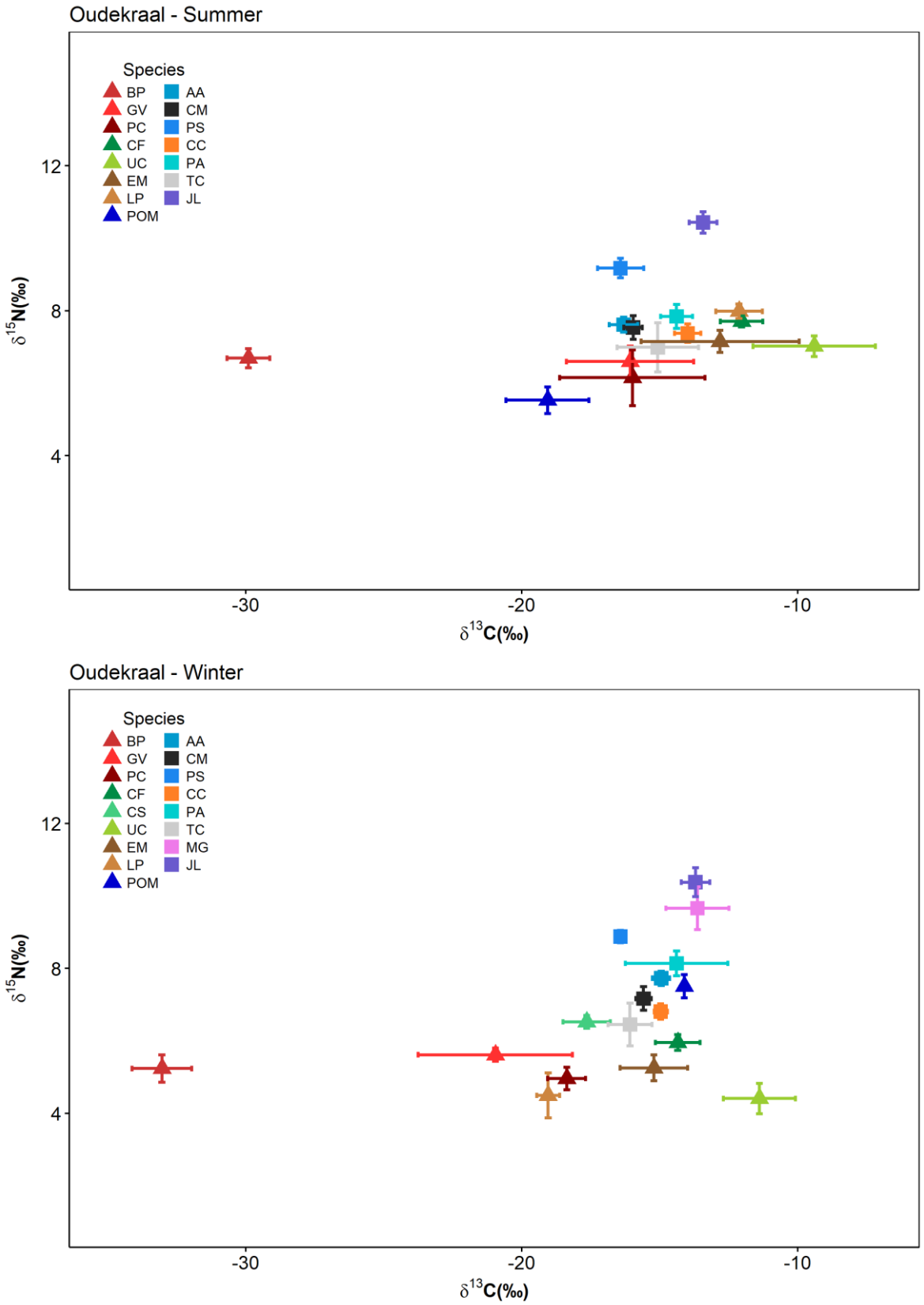

Figure 4.2: Mean $\delta^{13}C$ and $\delta^{15}N$ (± SD) for food web members from Oudekraal during summer (top) and winter (bottom). Algae and POM are denoted by triangles while consumers are denoted by squares. See Table 4.1 for species codes.

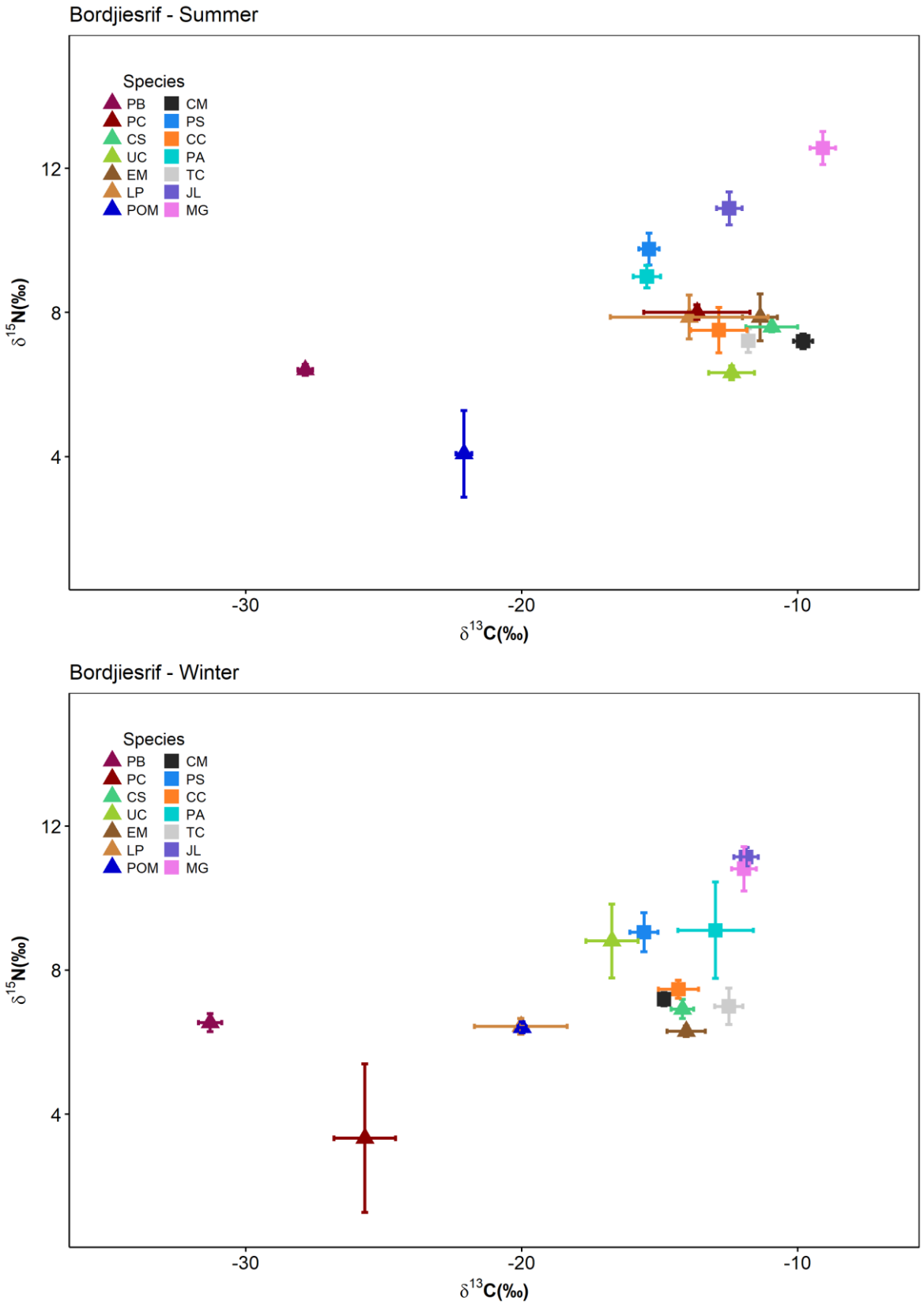

Figure 4.3: Mean $\delta^{13}C$ and $\delta^{15}N$ (± SD) for food web members from Bordjiesrif during summer (top) and winter (bottom). Algae and POM are denoted by triangles while consumers are denoted by squares. See Table 4.1 for species codes.

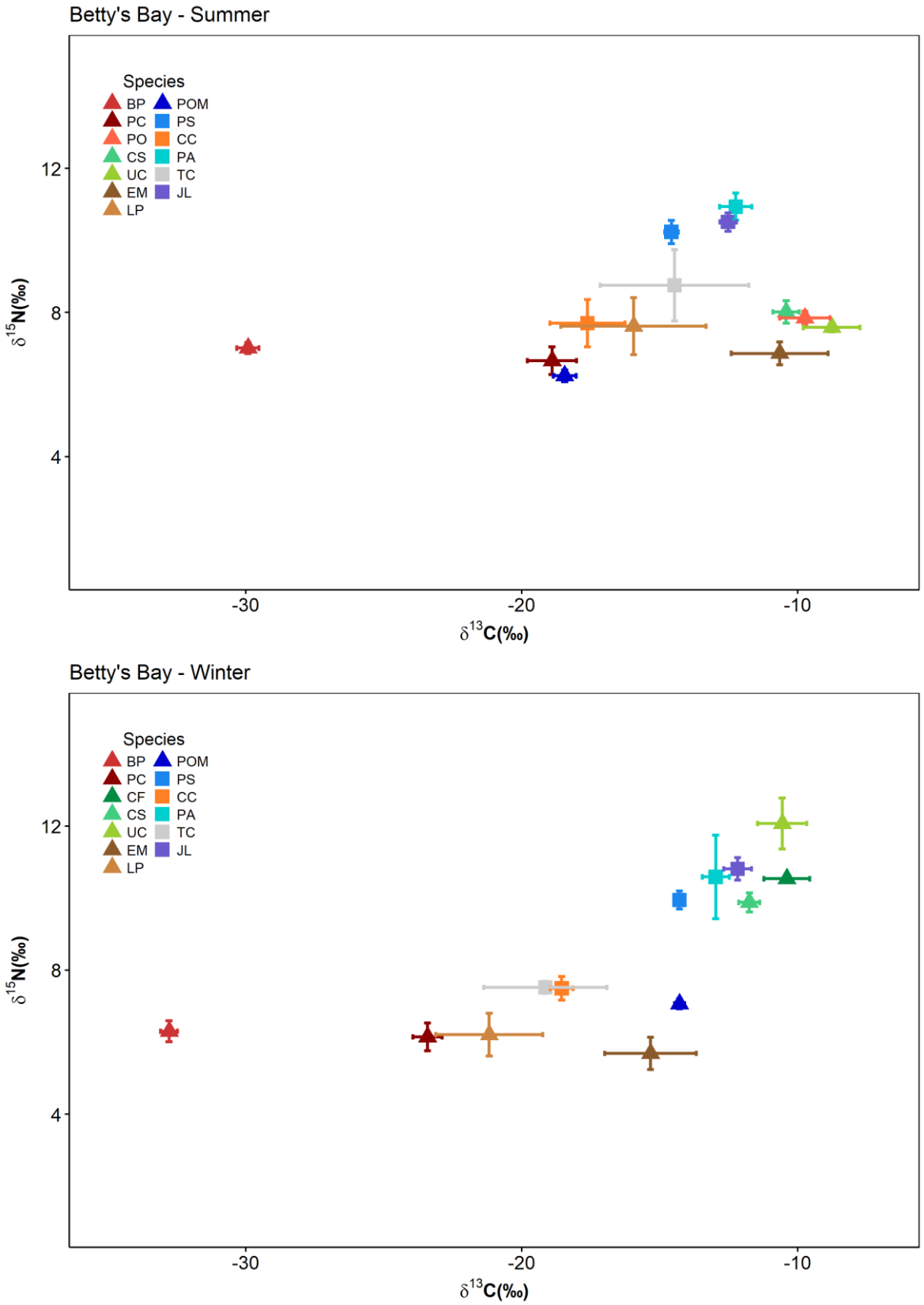

Figure 4.4: Mean $\delta^{13}C$ and $\delta^{15}N$ (± SD) for food web members from Betty's Bay during summer (top) and winter (bottom). Algae and POM are denoted by triangles while consumers are denoted by squares. See Table 4.1 for species codes.

Table 4.2: Mean trophic position (TP) of animal food web members for each site and season, corrected against *Turbo cidaris* values.

		Oudekraal				Bordjiesrif				Betty's Bay			
		Summer		Winter		Summer		Winter		Summer		Winter	
ID	Species	TP	SD	TP	SD	TP	SD	TP	SD	TP	SD	TP	SD
CC	*Cymbula compressa*	2.11	0.07	2.1	0.06	2.09	0.17	2.14	0.07	1.69	0.17	1.99	0.09
JL	*Jasus lalandii*	3.01	0.08	3.16	0.12	3.08	0.13	3.22	0.08	2.52	0.07	2.97	0.09
PA	*Parechinus angulosus*	2.25	0.09	2.5	0.09	2.52	0.08	2.62	0.35	2.64	0.1	2.9	0.3
PS	*Pyura stolonifera*	2.64	0.07	2.71	0.04	2.75	0.12	2.61	0.14	2.44	0.09	2.71	0.07
TC	*Turbo cidaris*	2	0.18	2	0.15	2	0.09	2	0.13	2	0.26	2	0.04

Table 4.3: Results of the two-way ANOVA for macroalgae and POM for stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) and C:N ratio. Statistically significant results in bold font. Variability proportions indicated by ω^2 with largest value in bold.

Source		*d.f.*	*MS*	*F*	*p*	ω^2	*MS*	*F*	*p*	ω^2	*MS*	*F*	*p*	ω^2
			***Codium stephensiae* (CS)**				***Ecklonia maxima* (EM)**				***Laminaria pallida* (LP)**			
$\delta^{15}N$	Sites	2	20.81	202.52	**<0.001**	**0.58**	4.70	13.99	**<0.001**	0.20	5.05	8.09	**<0.05**	0.06
	Season	1	0.00	0.00	0.98	0.00	19.00	113.16	**<0.001**	**0.60**	34.83	111.57	**<0.001**	**0.62**
	Interaction	2	13.32	129.58	**<0.001**	0.37	0.75	2.24	0.12	0.01	7.46	11.96	**<0.001**	0.12
	Residual	24	1.23			0.05	4.87			0.19	9.05			0.20
$\delta^{13}C$	Sites	2	71.57	78.44	**<0.001**	0.37	8.79	1.60	0.22	0.02	48.30	6.42	**<0.05**	0.17
	Season	1	86.46	189.52	**<0.001**	**0.45**	95.90	35.02	**<0.001**	0.47	299.74	79.66	**<0.001**	**0.58**
	Interaction	2	22.97	25.17	**<0.001**	0.11	9.26	1.69	0.20	0.02	4.10	0.55	0.59	0.01
	Residual	24	10.95			0.07	79.41			**0.49**	109.12			0.24
C:N	Sites	2	10.94	17.56	**<0.001**	**0.40**	275.38	27.52	**<0.001**	**0.30**	187.53	12.93	**<0.001**	0.43
	Season	1	2.10	6.73	**<0.05**	0.07	169.88	33.96	**<0.001**	0.19	3.59	0.49	0.49	0.01
	Interaction	2	5.06	8.12	**<0.05**	0.17	253.84	25.37	**<0.001**	0.29	7.15	0.49	0.61	0.02
	Residual	24	7.48			0.36	145.09			0.22	210.32			**0.54**
			***Pachymenia cornea* (PC)**				**Particulate Organic Matter (POM)**				***Ulva capensis* (UC)**			
$\delta^{15}N$	Sites	2	14.67	36.79	**<0.001**	**0.49**	10.84	11.35	**<0.001**	0.31	84.86	136.65	**<0.001**	**0.48**
	Season	1	8.44	42.31	**<0.001**	0.28	17.18	35.92	**<0.001**	**0.40**	15.83	50.97	**<0.001**	0.09
	Interaction	2	1.23	3.08	0.06	0.03	2.07	2.16	0.15	0.03	66.97	107.83	**<0.001**	0.38
	Residual	24	4.79			0.20	8.12			0.26	7.45			0.05
$\delta^{13}C$	Sites	2	80.83	18.05	**<0.001**	0.14	96.05	82.48	**<0.001**	**0.55**	139.64	41.68	**<0.001**	**0.55**
	Season	1	298.43	133.25	**<0.001**	**0.53**	72.57	124.65	**<0.001**	0.35	54.97	32.82	**<0.001**	0.22
	Interaction	2	128.62	28.72	**<0.001**	0.22	8.32	7.15	**<0.05**	0.03	10.02	2.99	0.07	0.03
	Residual	24	53.75			0.11	9.90			0.07	40.20			0.20
C:N	Sites	2	216.76	46.13	**<0.001**	**0.76**	28.54	51.55	**<0.001**	0.39	97.58	24.24	**<0.001**	0.11
	Season	1	0.05	0.23	0.88	0.01	4.50	16.27	**<0.001**	0.06	296.48	147.31	**<0.001**	0.36
	Interaction	2	4.30	0.91	0.41	0.00	31.95	57.72	**<0.001**	**0.46**	379.13	94.19	**<0.001**	**0.46**
	Residual	24	56.39			0.23	4.71			0.09	48.30			0.07

Table 4.4: Results of the two-way ANOVA for animals for stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values, C:N ratio and calculated trophic position. Statistically significant results in bold font. Variability proportions indicated by ω^2 with largest value in bold.

Source		*d.f.*	*MS*	*F*	*p*	ω^2	*MS*	*F*	*p*	ω^2	*MS*	*F*	*p*	ω^2	*MS*	*F*	*p*	ω^2	*MS*	*F*	*p*	ω^2
			***Cymbula compressa* (CC)**				***Jasus lalandii* (JL)**				***Parechinus angulosus* (PA)**				***Pyura stolonifera* (PS)**				***Turbo cidaris* (TC)**			
$\delta^{15}N$	Sites	2	1.42	3.83	**<0.05**	0.15	11.25	49.02	**<0.001**	0.33	39.18	32.60	**<0.001**	**0.69**	5.83	22.94	**<0.001**	**0.52**	10.42	14.34	**<0.001**	0.40
	Season	1	0.56	3.00	0.10	0.05	1.18	10.28	**<0.05**	0.03	0.00	0.00	0.95	0.01	1.40	11.04	**<0.05**	0.12	3.21	8.85	**<0.05**	0.12
	Interaction	2	0.37	0.99	0.39	0.00	1.11	4.85	**<0.05**	0.03	0.55	0.46	0.64	0.01	0.29	1.13	0.34	0.00	1.33	1.82	0.18	0.03
	Residual	24	4.46			**0.80**	19.97			**0.61**	14.42			0.29	3.05			0.36	8.36			**0.45**
$\delta^{13}C$	Sites	2	113.44	87.26	**<0.001**	**0.80**	68.90	162.87	**<0.001**	**0.60**	34.86	33.54	**<0.001**	**0.45**	19.78	49.00	**<0.001**	**0.77**	116.90	22.11	**<0.001**	**0.46**
	Season	1	9.46	14.56	**<0.001**	0.06	2.30	10.89	**<0.05**	0.02	8.41	16.18	**<0.001**	0.10	0.01	0.05	0.82	0.01	34.13	12.91	**<0.05**	0.13
	Interaction	2	0.44	0.34	0.71	0.01	6.24	14.75	**<0.001**	0.05	19.43	18.70	**<0.001**	0.24	0.28	0.70	0.51	0.00	24.12	4.56	**<0.05**	0.08
	Residual	24	15.60			0.13	36.80			0.33	12.47			0.21	4.84			0.22	60.80			0.33
C:N	Sites	2	0.06	1.84	0.18	0.04	0.40	22.85	**<0.001**	0.17	0.04	4.75	**<0.05**	0.13	0.43	5.68	**<0.05**	0.21	0.03	4.23	**<0.05**	0.18
	Season	1	0.12	7.10	**<0.05**	0.13	0.28	31.60	**<0.001**	0.12	0.01	3.20	0.09	0.04	0.17	4.42	0.05	0.08	0.00	1.16	0.29	0.00
	Interaction	2	0.19	5.76	**<0.05**	0.20	0.02	1.32	0.27	0.00	0.09	11.06	**<0.001**	0.34	0.13	1.72	0.20	0.03	0.00	0.56	0.58	0.03
	Residual	24	0.40			**0.63**	1.53			**0.71**	0.10			**0.49**	0.90			**0.68**	0.09			**0.79**
TP	Sites	2	0.48	15.03	**<0.001**	0.40	5.76	292.55	**<0.001**	**0.52**	0.80	7.78	**<0.05**	0.29	0.07	3.27	0.06	0.08	0.00	0.00	0.99	0.08
	Season	1	0.99	6.14	**<0.05**	0.07	2.66	270.04	**<0.001**	0.24	0.30	5.80	**<0.05**	0.10	0.33	3.05	0.09	0.04	0.00	0.00	0.98	0.04
	Interaction	2	0.13	4.15	**<0.05**	0.09	0.97	49.05	**<0.001**	0.09	0.04	0.38	0.69	0.03	0.22	10.10	**<0.001**	0.33	0.00	0.00	0.99	0.08
	Residual	24	0.39			**0.44**	1.71			0.15	1.24			**0.58**	0.26			**0.55**	0.72			**0.80**

Table 4.5: Six community metrics and two Bayesian community metrics (SEA_B & SEA_C) calculated using SIBER for each of the study sites during summer and winter (see methods section for description of metrics).

Metric	Oudekraal		Bordjiesrif		Betty's Bay	
	Summer	Winter	Summer	Winter	Summer	Winter
$\delta^{15}N$ range	4.91	5.97	8.49	7.81	4.7	6.38
$\delta^{13}C$ range	20.5	21.65	18.76	19.42	21.16	22.39
TA	78.53	103.01	100.01	117.61	65.55	94.88
CD	3.12	3.53	3.89	4.65	4.43	5.39
MNND	1.77	1.81	1.89	1.58	1.78	1.97
SDNND	2.71	2.75	2.09	2.14	2.81	2.29
SEA_B	20.45	27.82	25.58	29.41	23.3	27.31
SEA_C	20.66	28.08	26.86	29.74	23.57	27.6

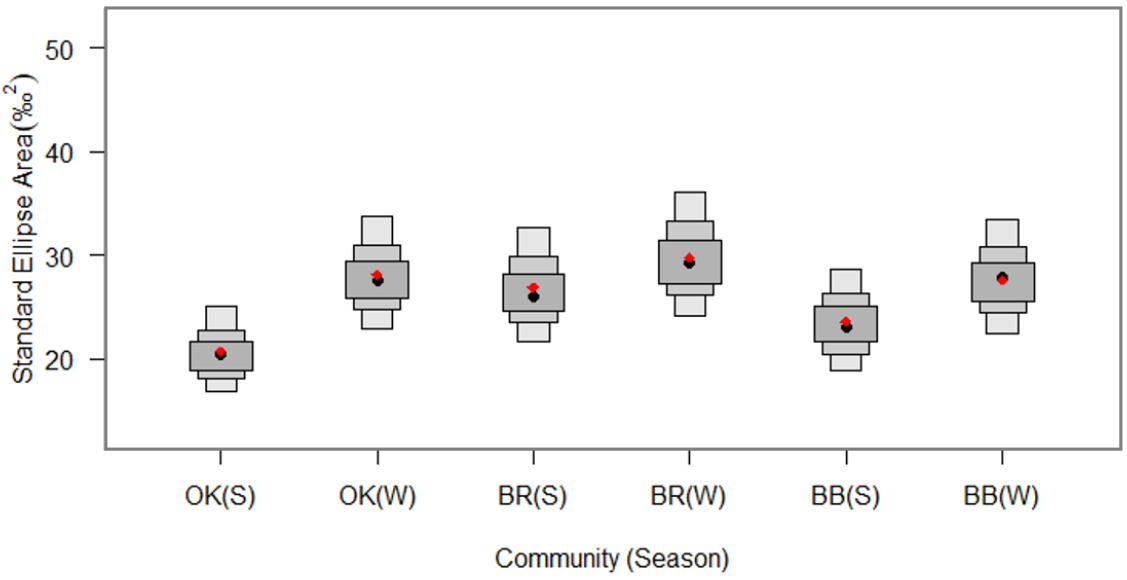

Figure 4.5: Community niche areas for each sampling occasion (OK = Oudekraal, BR = Bordjiesrif, BB = Betty's Bay; (S) = Summer, (W) = Winter). The black dot in each box corresponds to the mean standard ellipse area (SEA_B) and the red diamond indicates the small-sample-size-corrected values (SEA_C) for each sampling occasion. Box areas represent the 95 % (light grey), 75 % (grey) and 50 % (dark grey) Bayesian credibility intervals.

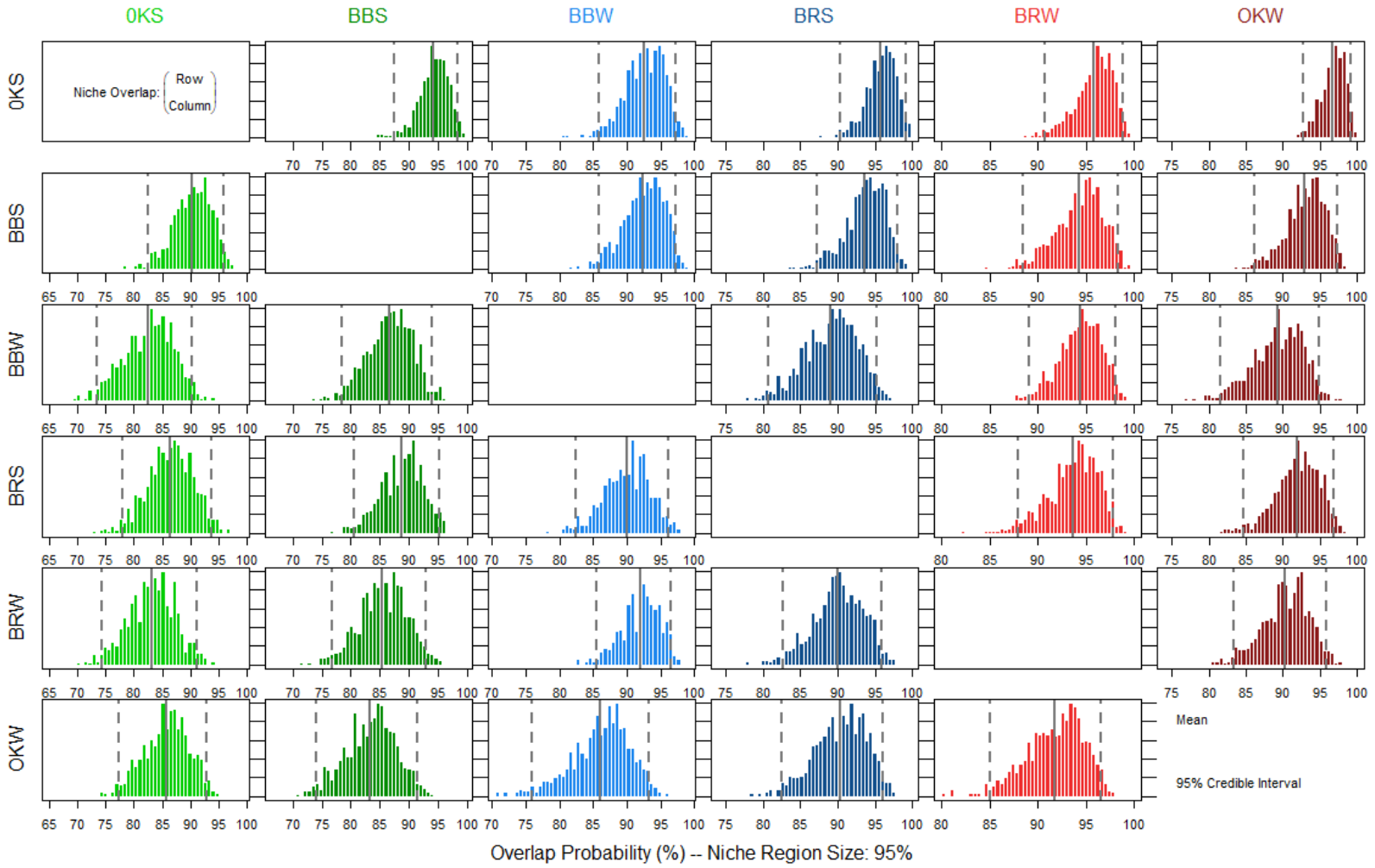

Figure 4.6: Pairwise comparisons (row vs. column) of community niche overlap at three selected sites (BB = Betty's Bay, BR = Bordjiesrif, OK = Oudekraal) for each season (S= summer, W = winter). Mean (solid) and 95% credible intervals (dashed) indicated by grey lines on each plot.

4.4 DISCUSSION

The results of this study show that there is large degree of variability in stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values of both the kelp forest macroalgal community as well as the common consumers found in these systems. Variability in stable isotope values is not consistent among groups, with species-specific patterns among sites and seasons. However, site x seasonal differences were also detected for some species of algae and consumers. Although to a lesser extent, the variability in the macroalgal species is mirrored in higher level consumers within these habitats, particularly grazing species. The present study shows both temporal (seasonal) and spatial variability among sites in $\delta^{13}C$, $\delta^{15}N$, C:N ratio as well as the community metrics and trophic positioning of these kelp forest organisms. Community metrics revealed differences among sites and clear seasonal patterns, particularly in SEA_C values. However, differences were not as marked as predicted based on community composition (kelp forest community types).

4.4.1. Stable isotope variability in algae

Several studies have investigated the variability in $\delta^{13}C$ values of marine algae, especially those found in association with kelp forests (Stephenson et al. 1984, Simenstad et al. 1993, Raven et al. 1995, Fredriksen 2003, Guest et al. 2010, Vanderklift and Bearham 2014, Mackey et al. 2015). From these studies, several different factors responsible for $\delta^{13}C$ variability in macroalgae have emerged including, but not limited to, light availability, photosynthetic pathway used, nutrient availability and tissue specific storage of isotopically distinct compounds. The effects of these factors are however highly dependent on the taxonomic group (Stephenson et al. 1984, Raven et al. 2002, Hyndes et al. 2013). Similarly, variability in $\delta^{15}N$ values among the algal species is highly influenced by the form of nitrogen which is assimilated (nitrate vs. ammonium), by differences in nitrogen fractionation among species, as well as through nitrogen limitation (Pennock et al. 1996, Ostrom et al. 1997, Needoba et al. 2003, Hansen et al. 2012). The variability of nitrogen stable isotope values is also dependent on changes in nitrogen source, with algal $\delta^{15}N$ reflecting that of the source (Dudley et al. 2010). Therefore, $\delta^{15}N$ values are likely to be highly variable in space and time as a result of the dynamic nature of the marine environment (Cabana and Rasmussen 1994, 1996, Post 2002a, 2002b).

The results suggest that the differences among sites are more important in driving $\delta^{13}C$ variability in several of the algae collected. Additionally, differences between sampling occasions accounted for most of the variability in $\delta^{15}N$ values. Temperature is the most obvious difference among the three study sites, with Oudekraal distinctly cooler than Bordjiesrif and Betty's Bay (see Figures S1 and S2 in supplementary material). Upwelling frequency and intensity are driving these temperature differences among the three sites, with Oudekraal being a typical west coast kelp forest that receives seasonal upwelling. Despite these differences, POM $\delta^{13}C$ values were similar at Oudekraal and Betty's Bay but distinct at Bordjiesrif. This suggests that upwelling may still influence the sites

EOCH, but not False Bay to the same extent. A consequence of upwelling is higher water clarity within kelp beds and thus enhanced light availability (Anderson and Bolton 1985, Stegenga et al. 1997). Kelp stable isotope values in particular are known to be to highly influenced by light availability (Vanderklift and Bearham 2014). Hyndes et al. (2013) found similar patterns in $\delta^{15}N$ values of macroalgae, but variability patterns were more similar among different taxonomic groups. The differences in nutrient concentration and light availability among the three sites could therefore be responsible for the differences in stable isotope values, but species-specific studies are required to test this.

Allochthonous nutrient inputs, such as those from sewage outfalls or fish processing factories, can result in enriched carbon and nitrogen values, particularly in macroalgae (McClelland et al. 1997, Monteiro et al. 1997, McClelland and Valiela 1998, Gartner et al. 2002, Rogers 2003, Costanzo et al. 2005, Connolly et al. 2013, Wang et al. 2016). Distinct enrichment was evident at Betty's Bay in the winter season with the green algae *Ulva capensis*, *Codium stephensiae* and *Codium fragile* all exhibiting highly enriched $\delta^{15}N$ in comparison to summer (see Figure 4.4). Values were well above the expected 6–8‰ range for temperate macroalgae (see Chapter 2). Similarly, Monteiro et al. (1997) showed that waste from a fish processing plant resulted in enriched (+1.9‰) *Ulva lactuca* $\delta^{15}N$ in comparison to a control site. The results are therefore indicative of a highly enriched nutrient source in the area around Betty's Bay. Winter months are associated with increased rainfall in the south-western Cape and thus freshwater run-off from the surrounding landscape. Additionally, the presence of the African Penguin colony near the study site could also have supplied an influx of $\delta^{15}N$ enriched material (uric acid) into the water at this site. Nutrient input such as the guano generated by these birds, which is high in nitrogen, will drive $\delta^{15}N$ values to become more enriched. The impact of nitrogen export from penguin rookeries on Marion Island has been documented to increase terrestrial plant growth (Lindeboom 1984), and could therefore have similar consequences for sub- and intertidal marine algae. Interestingly, only the Chlorophyta exhibited the clear signs of $\delta^{15}N$ enrichment and no other algal species. Authors have however used *Ulva* spp. is indicator species for tracing nutrient pollution (Cornelisen et al. 2007). This enrichment was also not evident further up the food web with winter values of *Turbo cidaris* and *Parechinus angulosus*, both known grazing species, not exhibiting signs of enrichment. *Parechinus angulosus* values did however display higher variability in $\delta^{15}N$ in winter which could indicate the consumption of isotopically variable food sources. However, the direct effect of the $\delta^{15}N$ enrichment of the macroalgae on the rest of the food web was not evident and requires further investigation.

As the turnover rate at the base of the food web is high (O'Reilly et al. 2002, Post 2002a, 2002b), variability in the environment (e.g. nutrient availability) is quickly reflected in these species. Cabana and Rasmussen (1996) also suggest that autotrophs at the base of the food web will display greater

variability in their stable isotope values when compared to higher trophic levels, as a result of the higher rates of tissue turnover.

4.4.2. Stable isotope variability in consumers

The stable isotope values of consumers are controlled largely by their diet, with their values a reflection of the average values of their dietary constituents (Fry 2006, Layman et al. 2012). Generalist predators are however very unlikely to be in perfect equilibrium with their diet in terms of stable isotope composition with several factors resulting in discrepancies in their values (Nordström et al. 2009). Additional factors such as size, sex, age and individual physiology can also add to the variability in stable isotope values within species (Bearhop et al. 2004, Matthews and Mazumder 2005). Consumers which have a stable diet, with a low diversity of organisms, or those which consume a variety of organisms with similar isotope values will have a more constant stable isotope value themselves. However, when the diet of a consumer is varied, with diverse constituents all with different stable isotope values, it is likely that the stable isotope value of the consumer is likely to fluctuate depending on the proportion of the different dietary constituents (Bearhop et al. 2004). Hyndes et al. (2013) identified among-replicate variability as the greatest source of variation in $\delta^{15}N$ of marine consumers. The results are largely in agreement with this as *Cymbula compressa*, *Jasus lalandii* and *Turbo cidaris* were highly variable among replicates. Vanderklift and Wernberg (2010) noted that variability in stable isotope value of grazing sea urchins was correlated to among-site variability in their dietary macroalgae. Similarly, the results show that among-site differences accounted for most of the variability in $\delta^{13}C$ and $\delta^{15}N$ of the urchin *Parechinus angulosus* and ascidian *Pyura stolonifera*. In particular, Oudekraal was distinct from the other sites when looking at the $\delta^{13}C$ of *P. stolonifera*, *P. angulosus* and *J. lalandii*, suggesting that the diet (composition and/or prey values) of these organisms at Oudekraal is very different from those at Bordjiesrif and Betty's Bay. *Pyura stolonifera* derives its carbon from both phytoplankton and kelp-derived detritus (Klumpp 1984), and would therefore show differences among sites where upwelling patterns are different. Indeed, spatial differences accounted for a large proportion of the variability in POM and *P. stolonifera* $\delta^{13}C$ values, thus suggesting the importance of POM to the diet of these ascidians.

In contrast, Betty's Bay values were distinct for two grazing species, *C. compressa* and *T. cidaris*, particularly in summer. This matches up with the high variability in macroalgae which was measured here. *Parechinus angulosus* was however highly variable, with values often more enriched than most algae and even some predators. This sea urchin species is known to feed preferentially on certain understory algae (Anderson and Velimirov 1982), but the results could indicate further dietary plasticity and even omnivory. Sea urchins have been documented to display omnivory, consuming any available food when their preferred dietary constituents are not available (Vanderklift et al. 2006, Lawrence et al. 2013).

Although the large variability in basal resource values is transferred through the food web, it becomes less evident in species occupying higher trophic levels (Hansen et al. 2012). The results of this study show that stable isotope variability of the consumers was controlled by differences among the three study sites, particularly for the $\delta^{13}C$ values, with very little influence of season overall (<15% of variability). Smaller species, with shorter tissue turnover times are more likely to display temporal fluctuations in their stable isotope values (Hesslein et al. 1993, Post 2002a). Conversely, larger, long-lived species generally have slower tissue turnover rates (months to a year) and thus show little evidence of variation in their $\delta^{13}C$ and $\delta^{15}N$ values (Hesslein et al. 1993, Post 2002a). The consumers in this study did not show the seasonal variability in isotope values which was evident in the macroalgae. This is most likely as a result of the slower tissue turnover in these organisms.

Jasus lalandii was the most enriched ($\delta^{15}N$) member of the food web in most instances, which supports the fact that this species is the dominant benthic carnivore (Field et al. 1980a, Griffiths and Seiderer 1980). The starfish, *Marthasterias glacialis* had $\delta^{15}N$ values very similar to those of *Jasus lalandii*, which corroborates the predatory nature of this species (Penney and Griffiths 1984).

4.4.3. Community metrics and trophic positioning

The community metrics suggest a larger degree of trophic diversity at Bordjiesrif in comparison to the other sites, with similar values in both summer and winter. Interestingly, the TA metric indicates that Oudekraal and Betty's Bay have similar trophic diversity. Despite the documented changes in the benthic community as a result of the lobster invasion at Betty's Bay (Blamey et al. 2010), the overall community is now more similar to that at Oudekraal. A caveat of using the TA metric is that is highly influenced by community members with extreme isotope values (Jackson et al. 2011), which can make the use of this metric unreliable. For this reason, TA values are often disregarded and instead SEA_C provides a better estimate of niche size (Jackson et al. 2011). This being said, the SEA_C values from the analyses in this study show similar trends to those calculated for TA.

Despite the large differences among the sites in terms of community structure and physical environment, the community niches (SEA_C) were very similar among sites, only differing by 6.2‰^{2} in summer and 2.1‰^{2} in winter. This indicates that differences among the sites is variable between seasons, which fits appropriately with seasonal patterns such as upwelling. However, looking at the degree of niche overlap among sites and between seasons, with a high degree of overlap recorded for all comparisons (>80%), indicates that these differences may be less important when comparing spatial patterns.

The results show an increase in SEA_C in the winter at all three sites, which translates to a larger community niche size during winter in comparison to summer. Larger community niche, which occupies a larger area in isospace, is often driven by species which exhibit large fluctuations in their

stable isotope values. This increase in community niche is largely driven by the variability in the red algal isotope values at all three of the study sites, particularly *Botryocarpa prolifera* and *Pachymenia cornea* which were more depleted in $\delta^{13}C$ in the winter, thus expanding the niche area.

The $\delta^{13}C$ range, which provides an indication of the diversity of basal resources available to the food web, was heavily influenced by the inclusion of Rhodophyta. This was particularly due to the influence of *Botryocarpa prolifera* at Oudekraal and Betty's Bay and by *Plocamium beckeri* at Bordjiesrif. The $\delta^{13}C$ of red algae are known to be highly depleted as a result of use of different photosynthetic pathways (Raven et al. 1995). Using this as an indication of resource diversity can be misleading as these algal species are not preferentially consumed by grazers such as *Parechinus angulosus* due to the presence of unpalatable secondary metabolites (Anderson and Velimirov 1982). However, *P. angulosus* is known to consume a large variety of algae and thus it may therefore consume these species when food availability is low or when its preferred food is unavailable.

The MNND and SDNND metrics were very similar among sites and seasons and no clear differences of patterns were evident. These metrics both provide information on the trophic redundancy within the food webs (Layman et al. 2007a). This also suggests that the diversity of the trophic niches among the three sites is very similar.

Interestingly, the trophic position of the consumers collected in this study also followed the same pattern as SEA_C, with higher trophic positions in winter when compared to summer. Seasonal enrichment of $\delta^{15}N$ values throughout the food web would result in higher trophic levels of all the consumers.

4.5 CONCLUSION

Temporal and spatial differences in stable isotope values of producers and consumers are often recorded in kelp forests and temperate reef ecosystems (Fredriksen 2003, Nordström et al. 2009, Vanderklift and Wernberg 2010, Hansen et al. 2012, Hyndes et al. 2013, Vanderklift and Bearham 2014, Mackey et al. 2015). Although natural variability of stable isotope values exists among all species, it is often over-looked when constructing stable isotope mixing models and can result in erroneous conclusions about trophic relationships (Dethier et al. 2013, Hyndes et al. 2013). Understanding the patterns and processes which shape natural communities may aid in the interpretation of stable isotope patterns and community-wide measures of trophic structure.

The results indicate a strong seasonal trend in the variability of macroalgae which was not evident among the consumers which are thought to rely on these species. Spatial patterns were instead more important in shaping the stable isotope values of consumers among sites. These findings are largely in agreement with studies which show that variability in basal food web components is more detectable as a result of faster tissue turnover rates (Hesslein et al. 1993, Hansen et al. 2012).

Most interestingly, the distinct patterns in community composition and physical differences among sites was not mirrored in the community niche to a large extent. Therefore, the trophic structure and functioning of these kelp forests, as evidenced by stable isotope data, seem to be quite similar, which is contrary to what was expected.

CHAPTER 5

Niche size of *Jasus lalandii* (Decapoda, Palinuridae) in South African kelp forests

5.1 INTRODUCTION

Niche theory is one of the central paradigms in ecosystem ecology for understanding the role of individuals, populations and species in an ecosystem. Elton (1927) suggested that the niche of an organism was the sum of all the interactions that link it to those around it, especially trophic interactions. Thereafter, Hutchinson conceptualised an organism's niche as an *n*-dimensional hypervolume, and later refined this by distinguishing the roles of scenopoetic (resources used) and bionomic (trophic interactions) niche axes in defining the niche of an organism (Hutchinson 1978). At a population or species level, niche variability is a product of individual variability in a population (Van Valen 1965). Since then the application of niche theory has waned, largely as a result of it being difficult to quantify – until recently. Niche theory has emerged again among ecologists through the advancement in technology and analytical methods such as stable isotope analysis (SIA) (Layman et al. 2007a, Newsome et al. 2007).

Stable isotope analysis (SIA) provides a time-integrated insight into the use of resources by a particular organism, which is a major advantage of this method over more traditional ways to study resource use (Dalerum and Angerbjörn 2005). Stable isotope studies generally rely on a comparison of carbon and nitrogen stable isotope values as an indicator of carbon sources and trophic structuring within ecosystems repsectively (Fry 2006, Layman et al. 2007a). The stable isotope value of a consumer's tissue is derived from all the trophic pathways which lead to it, and therefore SIA provides a powerful way to study the flow of carbon and nitrogen through an ecosystem (Layman et al. 2007a, 2012).

Trophic positions of top consumers can provide information about the trophic structure and functioning of ecological communities. The use of stable nitrogen isotope values ($\delta^{15}N$) to analyse food web structure has provided insight into the structuring of aquatic ecosystems (Cabana and Rasmussen 1996, Fry 2006). This relies on the steady and predictable enrichment of $\delta^{15}N$ isotope values with each step in the food web (Pinnegar and Polunin 1999). The enrichment of 3.4‰ (±1‰) in nitrogen isotope values between prey and its consumer (Post 2002a) has been widely applied in stable isotope studies of food web ecology. Food chain length can, however, be less informative in very complex ecosystems where numerous trophic interactions occur or where there is a high degree of omnivory in the ecosystem.

More recently, the isotopic niche of an organism has been defined by its position in isotope space (e.g. $\delta^{13}C$ versus $\delta^{15}N$), and reflects the scenopoetic and bionomic dimensions of its ecological niche (Bolnick et al. 2002, 2003, Bearhop et al. 2004, Newsome et al. 2007). Although the stable isotope niche is not directly equivalent to the trophic niche of an organism, it is considered to be closely linked (Jackson et al., 2011). Variability of the position of individuals in isotope space can provide insight into dietary variability and thus niche width (Bearhop et al. 2004).

Layman et al. (2007a) proposed several niche metrics which allowed the quantification of isotope niche size among individuals as well as for entire communities. Despite their successful application in ecological studies (Layman and Allgeier 2012), these metrics have been shown to be highly sensitive to small sample sizes ($n < 50$), which are typical of most ecological studies (Jackson et al. 2011, Syväranta et al. 2013). A more robust approach based on Bayesian statistics has been proposed by Jackson et al. (2011), which provides more reliable results despite small sample sizes (Syväranta et al. 2013). The use of these niche metrics allows for the quantitative comparison of niches among different individuals or among different populations or localities.

The niche variation hypothesis, proposed by Van Valen (1965), suggests that more variable populations, those using a larger variety of sources and feeding methods, will have larger niches. Bolnick et al. (2007) have shown that higher niche variation is consistent with more generalised (ecologically variable) populations. Similarly, Layman et al. (2007b) illustrated that variation in resource use leads to larger intra-population variability in isotope values and thus results in larger niche widths. Contractions in niche width have been shown to be linked to the decrease in prey diversity, particularly in fragmented habitats (Layman et al. 2007b).

Variability in stable isotope niches has been effectively used to show differences in trophic niche size and niche overlap in systems invaded by alien species (Olsson et al. 2009, Ercoli et al. 2014, Fuhrmann et al. 2017), and to illustrate the recovery of species following overfishing (Hamilton et al. 2014). Therefore, niche width variability can elucidate differences in resource and/or habitat use of a single species, different species, or a population, over time and in different areas.

The west coast rock lobster, *Jasus lalandii* is a key predator in nearshore, temperate reef ecosystems of the southern African coastline from Walvis Bay in central Namibia to East London on the southeast coast of South Africa (Heydorn 1969, Pollock 1979, Cockcroft and Payne 1999). Within kelp forest ecosystems, *J. lalandii* dominates the carnivore biomass (Field and Griffiths 1991), and has the ability to markedly impact the benthic community structure as a whole (Pollock 1979, Barkai and Branch 1988b, Barkai et al. 1996). Not only is this species of great ecological importance in the food web, but commercially *Jasus lalandii* was historically one of the top three marine fishery species in South Africa (Melville-Smith and van Sittert 2005). Recently, Johnston and Butterworth (2016) estimated that the exploitable biomass of *Jasus lalandii* is *ca.* 2% of pristine levels. This has resulted in the species being listed as endangered and placed on the WWF SASSI red list in 2016 (Blamey and Bolton 2017).

The density of lobsters east of Cape Hangklip (EOCH) (see Figure 1.1 in Chapter 1) has however increased drastically since the 1990s in what has been termed an ‘invasion’ (Tarr et al. 1996, Mayfield and Branch 2000, Cockcroft et al. 2008, Blamey et al. 2010, 2012). The EOCH region between Cape Hangklip and Quion Piont can be further separated into invaded and non-invaded areas, with those

closer to Cape Hangklip being invaded (see Figure 1.1, Chapter 1). Blamey et al. (2010) review the change in abundance of *Jasus lalandii* EOCH and the subsequent impact on the ecology of the ecosystem. These authors also show that lobsters were absent from the area before 1980, but abundances have had increased by 1996 with lobster densities of 0.4–0.8 m^{-2} at Cape Hangklip and Betty's Bay. The increase in lobster abundances EOCH was also evident in the lobster fisheries, both recreational and commercial. Cockcroft et al. (2008) discuss the overall shift in the lobster resource along the coastline over the last 20 years, with a major increase in the contribution of the lobster landings from the southern coastline (18% to 60%), and a decrease in the contribution of west coast landings (60% to <10%) over this period.

As a result of the predatory effects of *Jasus lalandii*, the benthic communities in the invaded area have been greatly altered and have shifted to an alternative stable state which is maintained by these lobsters (Blamey et al. 2012, 2013). This new state has seen herbivore and urchin abundances decline, resulting in a four-fold increase in macroalgal densities (Blamey et al. 2010, 2012). Stomach content analyses of the lobsters in the EOCH region showed marked differences between invaded and non-invaded sites (Haley et al. 2011). The authors show that at invaded sites, *J. lalandii* switched its diet to smaller low-energy prey items including sponges, barnacles and foliose algae. This was in direct contrast to non-invaded sites where lobsters consumed high-energy mobile prey items such as urchins and winkles (Haley et al. 2011). Dietary selectivity indices also revealed marked changes in dietary preferences between invaded and non-invaded sites (Haley et al. 2011).

The aim of the present study was to compare the trophic positioning and size of the isotopic niche of the west coast rock lobster *Jasus lalandii* among three ecologically distinct kelp forests. Although some work has been done on the diets of lobsters in the invaded areas EOCH (Haley et al. 2011) and in South African kelp forests in general (Griffiths and Seiderer 1980, Barkai et al. 1996, van Zyl et al. 1998, Mayfield et al. 2000), stable isotope analysis in general has not yet been employed to study the diet of these organisms. In particular, the use of stable isotope niches has yet to be applied to investigate differences among kelp forest lobster populations. Therefore, this study represents a novel approach to studying the trophic ecology of this key kelp forest predator in South Africa. Specifically, I aimed to determine whether lobsters at Betty's Bay would have smaller trophic niches and lower overall trophic positioning when compared to Bordjiesrif or Oudekraal; this prediction stems from the assertion that there is a decreased food diversity and availability EOCH (Blamey et al. 2010, 2012). I also tested whether lobsters have varying niches and/or trophic positions between sampling occasions (seasons).

5.2 METHODS

5.2.1. Study sites

Three kelp forests (sites) along the south-west coast of South Africa were selected for this study (Figure 5.1). These study sites represent three 'types' of kelp forests, which have been identified in the region based on their community assemblages (see Chapters 1 and 4). Oudekraal on the western side of the Cape Peninsula was selected to represent a typical west coast kelp forest. Bordjiesrif in False Bay and Betty's Bay are more typical of the kelp forests on the south-west coast (east of Cape Point), however the kelp forests at Betty's Bay have been recently (1990s) invaded by lobsters. This invasion has created a community structure more similar to the west coast (see Chapter 4). The results of Chapter 4 do however indicate that the community structure in these three kelp forest types is quite similar, from a stable isotope perspective.

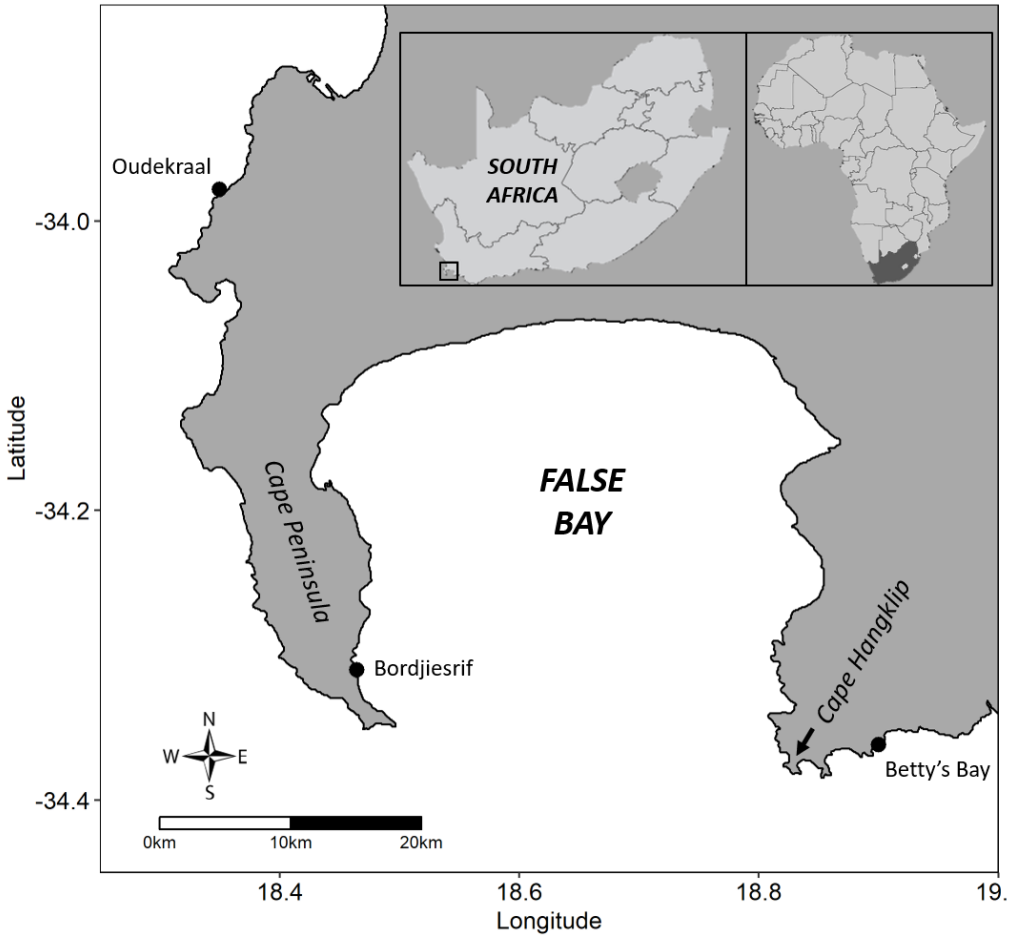

Figure 5.1: Geographic location of the three sampling localities (Oudekraal, Bordjiesrif and Betty's Bay) in relation to the Cape Peninsula, False Bay and Cape Hangklip. Inset map indicating the location of study area within South Africa. See Figure 1.1(Chapter 1) for further details.

5.2.2. Sample collection

Thirty *Jasus lalandii* individuals were collected haphazardly at each sampling site by SCUBA divers, both in summer and winter (a total of 60 lobsters from each site during the study). Despite efforts to collect similar-sized lobsters at each site, lobsters within the kelp forest at Oudekraal were naturally smaller than the other two sites (see Figure 5.2). Sampling was carried out late in the respective seasons to allow for the incorporation of dietary isotope values into the animal tissues. Tissue turnover rate for lobsters of 147 days (Suring and Wing 2009), will mean that only organisms consumed over a sustained period will be evidenced in the stable isotope values of the lobsters. Therefore, winter samples were collected in October 2015 and summer samples were collected in April 2016. Thus, only a single sampling occasion for each season. Following animal ethics considerations, lobsters were euthanized on site by immersion in a saturated salt (NaCl) solution for five minutes. Once all movement had ceased, lobsters were removed from the salt solution and placed onto ice for transport back to the laboratory at the University of Cape Town. Here, all samples were frozen (-15°C) prior to further processing.

5.2.3. Laboratory processing

For each lobster, the carapace length (CL) was measured to the nearest mm with a Vernier calliper and recorded along with the sex. The sex was determined visually by looking for the presence of a genital aperture at the base of the third pereiopod (walking leg), which is only present in females.

Once thawed, abdominal muscle tissue was excised from the pleon (tail) of each lobster. Muscle tissue was chosen as it provides a time-integrated stable isotope value of the diet. Tissue samples were oven dried in an air-circulated oven (60°C for 48 hrs).

Once dried, the tissue samples were homogenized into a fine powder using a Retsch MM200 ball-mill. Before weighing out the lobster samples into tin capsules, each sample was split into two equal portions. One portion was weighed out for analysis immediately, with each capsule containing 0.5 mg of sample material. However, lipids present in the tissue can alter the $\delta^{13}C$ isotope values as they are more depleted relative to other biochemical compounds such as carbohydrates and proteins (Post et al. 2007, Logan et al. 2008). Thus, samples required lipid treatment in order to remove this potential bias, which can cause considerable variation in isotope values. The lipid treatment process can however affect the $\delta^{15}N$ (Post et al. 2007, Logan et al. 2008). Half the sample was therefore left untreated to preserve the $\delta^{15}N$ values. Using the $\delta^{13}C$ from the treated samples and the $\delta^{15}N$ from the untreated samples gives the most accurate representation of the organism in isotope space (Logan et al. 2008).

Lipids were extracted from the second half of the sample using a modified version of the Bligh and Dyer (1959) method, used by Logan et al. (2008). Once treated, samples were dried in an air-circulated oven (60°C for 24 hrs) before being weighed out into 5x9 mm tin capsules.

All processed and weighed out samples were analysed at the Environmental Isotope Laboratory at iThemba LABS (Johannesburg, South Africa) using a Flash HT Plus elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer, with a ConFlo IV interface (all equipment supplied by ThermoFisher, Bremen, Germany). Carbon and nitrogen isotope values were corrected against an in-house standard (Merck Gel) and a Urea Working Standard (IVA Analysentechnik e.K., Meerbusch, Germany). Laboratory standards and blanks were run after every 20–24 unknown samples. Precisions of 0.05‰ and 0.20‰ were measured for Merck Gel and Urea respectively during the analysis of the samples.

Stable isotope values were expressed as parts per thousand (‰) deviation from the standard (atmospheric nitrogen for nitrogen and Vienna Pee Dee Belemnite for carbon) in delta (δ) notation according to:

$$\delta X = \left[R_{sample} \div R_{standard}\right] \times 1000$$

where X = ^{13}C or ^{15}N and R = corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

5.2.4. Trophic positioning

Following Post (2002a), the trophic position of each lobster was calculated based on the following formula:

$$Trophic\ position = \frac{(N_{lobster} - N_{basal\ resource})}{\Delta N} + 2$$

where $N_{lobster}$ refers to the $\delta^{15}N$ of the consumer organism, $N_{basal\ resource}$ is the $\delta^{15}N$ of the lowest trophic level in the ecosystem and ΔN is the trophic enrichment factor (TEF) or change in $\delta^{15}N$ with each step in the trophic position. In order to mitigate the influence of macroalgal variability on the calculation of trophic positioning, a longer-lived consumer was selected which is likely to incorporate variability in primary producers (Post 2002a). For this study, the smooth turban shell, *Turbo cidaris*, was selected as the trophic base at all sites (see Chapter 4 for details on collection and processing). As this is a grazing snail, it was assumed that it would have a trophic position of 2. This organism is also known to be a preferential dietary item for *Jasus lalandii* in kelp forest habitats (van Zyl et al. 1998). The TEF values were kept constant across all sites and seasons at 3.4 as this is the standard fractionation of $\delta^{15}N$ (Post 2002a).

5.2.5. Niche area

A major consideration when comparing among-site variability in niches is the natural variability of primary producers at each site. Because of this, a carbon correction was applied to the $\delta^{13}C$ values of *Jasus lalandii* at each site. Again, the values of the grazing smooth turban shell (*Turbo cidaris*) were used as a baseline. Long-lived consumers such as snails provide reduced spatio-temporal variability in

isotope values when compared to producers (Cabana and Rasmussen 1996, Vander Zanden et al. 1999, Post 2002a, 2002b). The carbon corrections were calculated according to the following formula (Olsson et al. 2009, Ercoli et al. 2014):

$$\delta^{13}Cc_{lobster} = (\delta^{13}C_{lobster} - \delta^{13}C_{basal\ resource})/C_{Rbase}$$

where $\delta^{13}Cc_{lobster}$ is the baseline-corrected carbon isotope value of the lobster, $\delta^{13}C_{lobster}$ is the measured isotope value of the lobster, $\delta^{13}C_{basal\ resource}$ is the mean carbon isotope value of *Turbo cidaris* collected in each season at each site and C_{Rbase} is the range ($\delta^{13}C_{max}$ - $\delta^{13}C_{min}$) in the respective carbon values of *T. cidaris* in each instance.

The Stable Isotope Bayesian Ellipses in R (SIBER) package was used to determine the niche area for *Jasus lalandii* at each of the three sites. Niche area, based on stable isotope values of carbon and nitrogen, provides insight into the resource use of a particular organism or community (Layman et al. 2007a, Jackson et al. 2011). SIBER calculates niche area in two ways, by determining convex hull area (TA) and standard ellipse areas (SEA_B). The SEA approach was selected over the more traditional convex hull area that was proposed by Layman et al. (2007a), as it has been shown to be more robust when dealing with smaller sample sizes (Jackson et al. 2011, Syväranta et al. 2013). To facilitate comparisons among sites and seasons, corrected carbon (C_c) and nitrogen (T_p) were used to calculate niche areas. The SEA was also supplemented with the correction for small sample sizes (SEA_C) as although the groups did not vary in size; the sample size was only 30 for each season. The $\delta^{13}C$ range (CR) was the difference between maximum and minimum corrected $\delta^{13}C$ values. Similarly, the $\delta^{15}N$ range (NR) was the difference in maximum and minimum trophic positioning (corrected $\delta^{15}N$). Both CR and NR were determined using SIBER. Variation in niche width was determined using the built-in likelihood test in the SIBER package (Jackson et al. 2011). This analyses pairwise comparisons of the niche size and determines the probability that one niche is larger or smaller than another. The amount of overlap among different niches was determined using the nicheROVER package in R (Lysy et al. 2014). All analyses were performed in R v3.4.2 (R Core Team 2017).

5.2.6. Statistical analyses

The size of lobsters was compared among sampling localities, seasons and sexes with an analysis of variance (ANOVA). Post-hoc comparisons were performed using a Tukey HSD test. A linear regression was used to test whether trophic position was controlled by the size (CL) of the lobsters. The effect of sex and sampling occasion (season) was also tested against the trophic position using an analysis of variance (ANOVA). All assumptions of these tests were met.

5.3 RESULTS

5.3.1. Lobster size and sex

Overall, the lobsters collected were largest at Betty's Bay (Figure 5.2), with a mean size of 70 ± 12.8 mm (mean ± SD). The mean size of lobsters collected at Bordjiesrif was 68.3 ± 13.5 mm. Oudekraal had the smallest lobsters, with a mean carapace length of 60.0 ± 17.2 mm. Size was found to be significantly different among the sites ($F = 10.23$, $p < 0.05$, $n = 180$) and seasons ($F = 43.14$, $p < 0.05$, $n = 120$), however, *post-hoc* comparisons revealed that the smaller lobsters at Oudekraal were responsible for this difference and lobsters at Betty's Bay and Bordjiesrif were not statistically different in size. Sex was also found to be significant in the analysis of size ($F = 8.22$, $p < 0.05$, $n = 180$) with male lobsters being larger on average at all sites except Oudekraal. The sex ratios were skewed at all sites in favour of male lobsters (Bordjiesrif 60%, Oudekraal 58.3%); however, this was most pronounced at Betty's Bay where 39 of the 60 lobsters were male (65%).

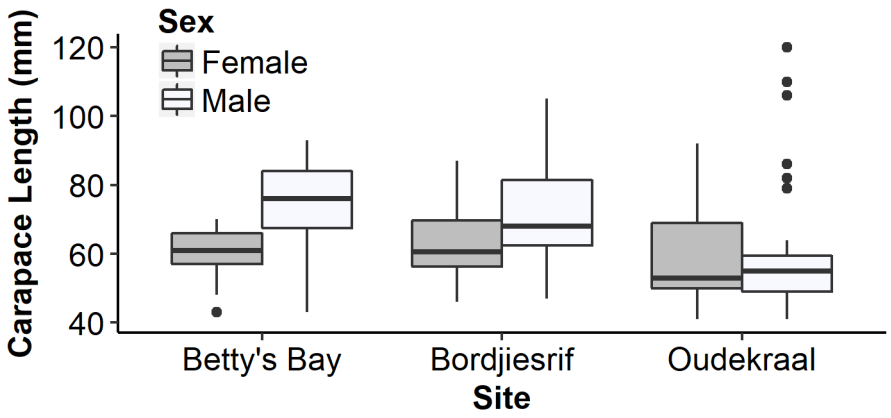

Figure 5.2: Carapace length (mm) of *Jasus lalandii* at the three study sites, with female (grey) and male (male) data shown separately for each site.

5.3.2. Trophic position

Trophic position was not related to the size (CL) of the lobsters ($F = 1.73$, $p = 0.19$, $n = 180$, $R^2 = 0.01$). The results of the ANOVA indicated that trophic position was indeed different among the three study sites ($F = 304.48$, $p < 0.001$, $n = 180$), as well as significantly different for the different sampling occasions (seasons) ($F = 279.20$, $p < 0.001$, $n = 180$). Sex was not found to be statistically significant for trophic position ($F = 3.60$, $p > 0.05$, $n = 180$). The interaction of site and season was, however, also found to be significant ($F = 53.69$, $p < 0.001$, $n = 180$).

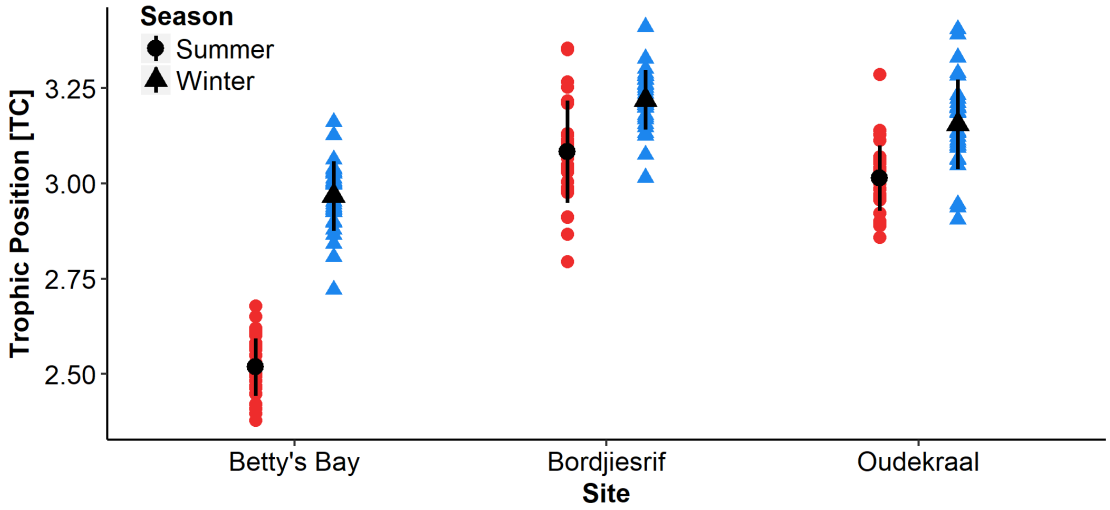

Figure 5.3: Trophic position of *Jasus lalandii* at each selected kelp forest calculated relative to the grazer *Turbo cidaris*. Mean and standard deviation indicated for each season with black dots (summer) and black triangles (winter).

The mean trophic position of *Jasus lalandii* (Figure 5.3) during summer was lowest at Betty's Bay (2.52 ± 0.08) compared to Bordjiesrif where it was the highest (3.08 ± 0.13). During winter, the trophic position was again lowest at Betty's Bay (2.98 ± 0.09) and highest at Bordjiesrif (3.22 ± 0.78). Oudekraal was more similar to Bordjiesrif in summer (3.01 ± 0.09) and winter (3.16 ± 0.12) than Betty's Bay in both seasons.

5.3.3. Niche area

Niche width was found to follow the same trend as trophic position, with the smallest niche recorded for the lobsters at Betty's Bay in both summer (SEA_C: 0.0113‰^{2}) and winter (SEA_C: 0.0272‰^{2}). However, winter niche area was substantially larger than summer at this site. The largest niche area was calculated for the lobsters at Bordjiesrif in both seasons. The Oudekraal lobsters had a niche area much more similar to those at Bordjiesrif in both seasons (Table 1). All three calculated niche size metrics provided the same trend in niche area across the three sampling localities (Table 5.1).

The $\delta^{13}C$ dispersion (CR) was greatest at Bordjiesrif in summer (4.8778‰) and winter (1.4330‰) and smallest at Betty's Bay for both seasons (Table 5.1). The $\delta^{15}N$ dispersion (NR) was greatest at Bordjiesrif in summer (0.5596‰), but interestingly Oudekraal had the greatest dispersion in winter (0.4992‰), and Bordjiesrif the smallest range in this season (Table 5.1).

Table 5.1: Niche metrics of *Jasus lalandii* at each site and for each season. Convex hull area (TA), $\delta^{13}C$ range (CR) and $\delta^{15}N$ Range (NR) presented along with standard ellipse area (SEA_B) and size corrected standard ellipse area (SEA_C) for each instance. The largest value for each niche metric is presented in bold font for each occasion. All values determined from baseline corrected data.

	Site	TA	SEA_B	SEA_C	CR	NR
Summer	Betty's Bay	0.04	0.0109	0.0113	0.2254	0.3007
	Bordjiesrif	**1.4481**	**0.4178**	**0.4327**	**4.8778**	**0.5596**
	Oudekraal	0.1328	0.0326	0.0338	0.6053	0.4278
Winter	Betty's Bay	0.1006	0.0262	0.0272	0.3578	0.44
	Bordjiesrif	**0.3969**	**0.0942**	**0.0976**	**1.433**	0.3995
	Oudekraal	0.2442	0.0737	0.0764	0.7925	**0.4992**

The niche areas, represented by the ellipses in Figure 5.4, display a large degree of overlap; however, there is clear separation of seasonal niches at all sites except Bordjiesrif. The size of the ellipses, however, is evidently different, with Betty's Bay having the smallest ellipses of the three sites during both sampling occasions. The niche size of the lobsters collected at Bordjiesrif during summer is by far the largest niche, spanning a wide range of $\delta^{13}Cc$ values.

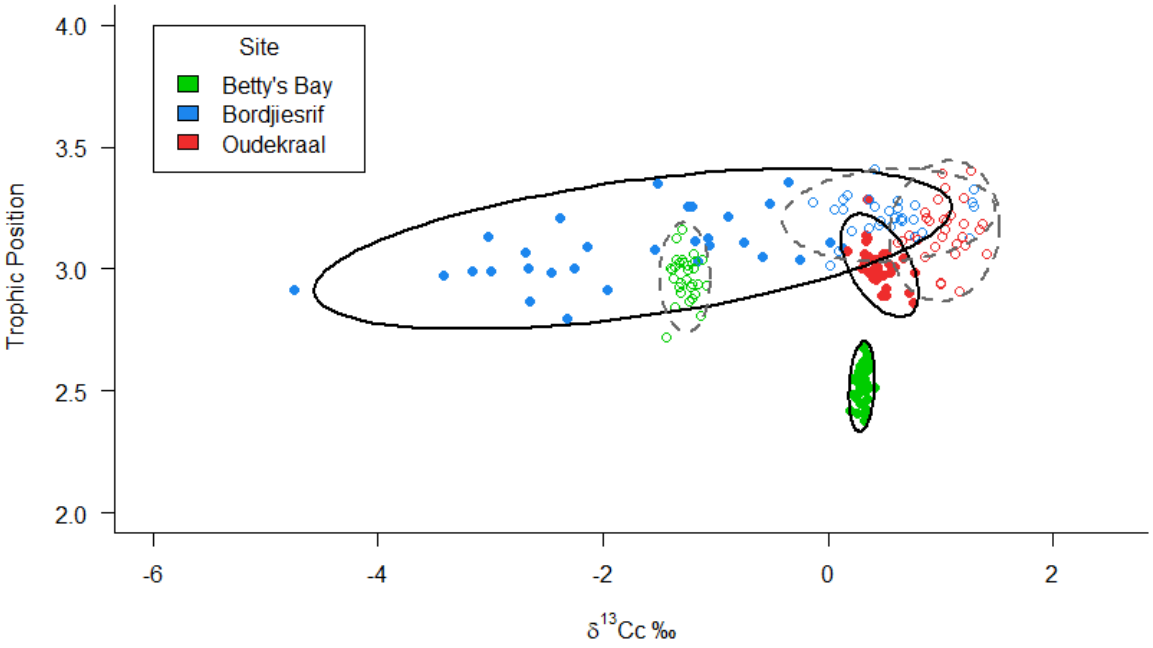

Figure 5.4: Standard ellipse area (SEA_B) of *Jasus lalandii* calculated for each season at each site based on baseline corrected data (^{13}Cc) and trophic position. Solid dots and solid black lines represent summer data and ellipses respectively. Hollow dots and dashed grey lines represent winter data and ellipses respectively.

Figure 5.5 provides confirmation of the size of the niches depicted in Table 5.1 and Figure 5.4. It is immediately evident that the niche size at Bordjiesrif in the summer is the largest. Betty's Bay has the smallest niche for each season and Oudekraal lies between the two. From this figure it is also evident that Betty's Bay and Oudekraal have larger niches in the winter when compared to summer. This trend is however reversed for Bordjiesrif.

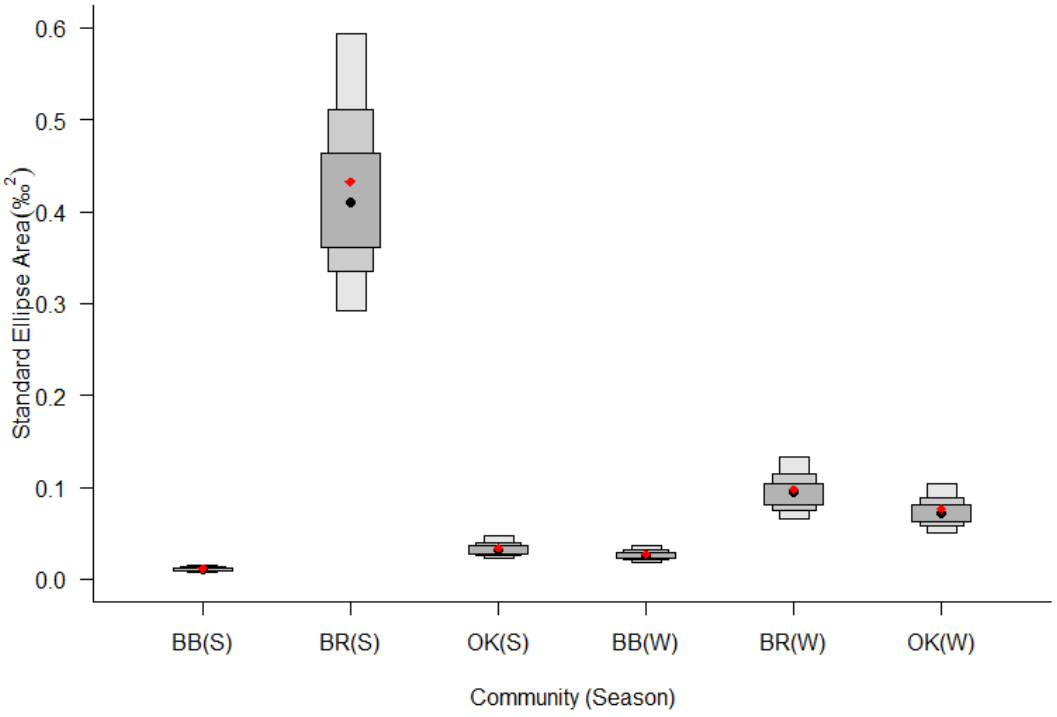

Figure 5.5: Niche areas of *Jasus lalandii* for each season (S = Summer, W = winter) at each sampling location (BB = Betty's Bay, BR = Bordjiesrif, OK = Oudekraal). The black and red dots represent the mean standard ellipse area (SEA_B) and size corrected standard ellipse area (SEA_C) respectively. Boxes represent 95% (light grey), 75% (medium grey) and 50% (dark grey) Bayesian credibility intervals.

Pairwise comparisons of the posterior distributions indicated that the niche area at Betty's Bay was smaller in summer than in winter (p = 0.995). The niche area at Bordjiesrif in summer was larger than in winter (p = 1.000). Oudekraal had a larger niche in winter than in summer (p = 0.999). The summer niche at Oudekraal was larger than Betty's Bay (p = 1.000). The winter niche at Oudekraal was larger than Betty's Bay (p = 1.000).

Therefore, visually (Figures 5.4 & 5.5), and statistically (Table 5.1 & above), Bordjiesrif had the largest niche in both seasons, Oudekraal had the next largest niche and Betty's Bay had the smallest niche in both seasons.

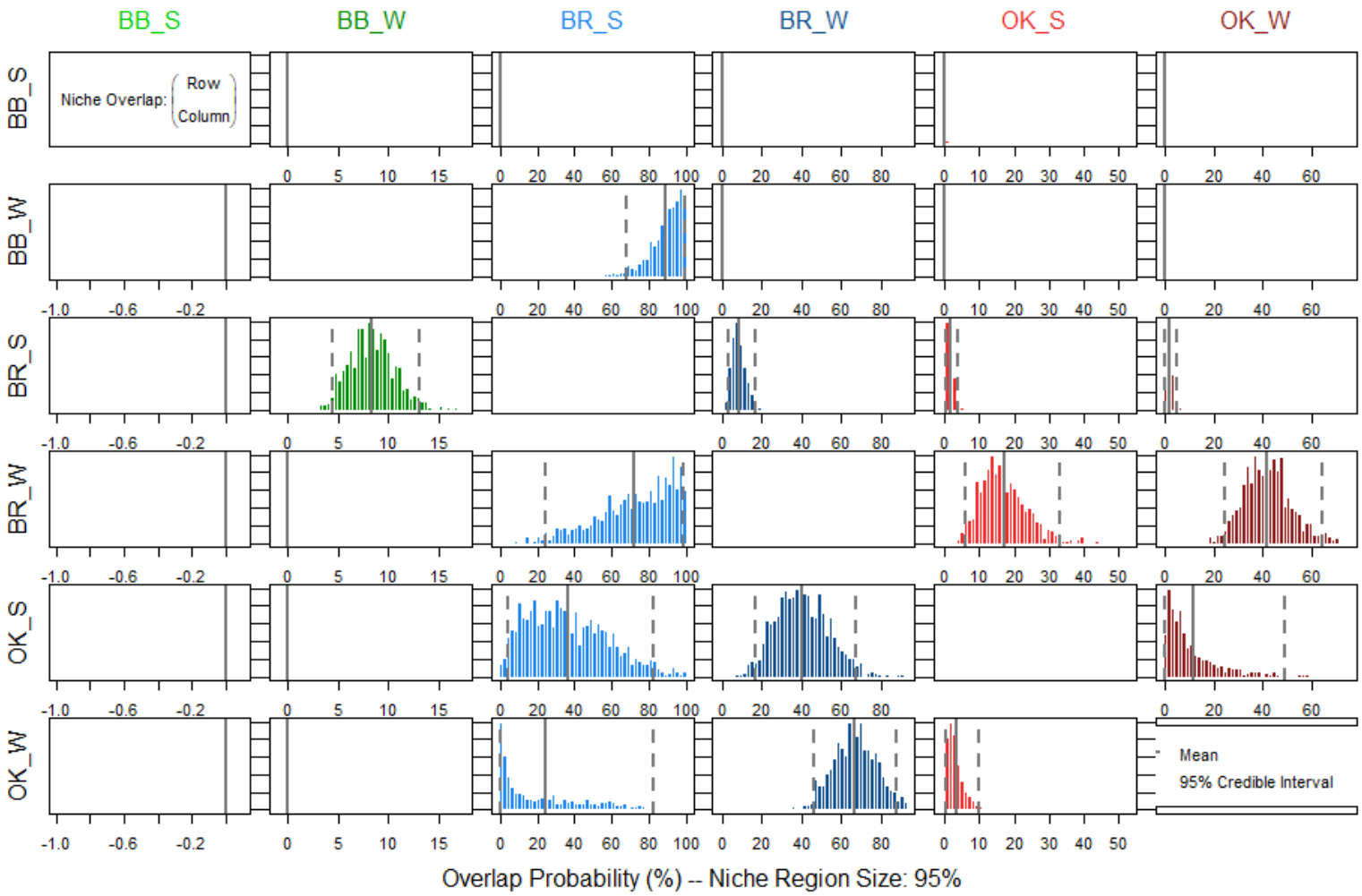

Figure 5.6: Pairwise comparisons (row vs. column) of seasonal niche overlap of *Jasus lalandii* at three selected sites. Mean (solid) and 95% credible intervals (dashed) indicated by grey lines on each plot.

The seasonal analysis of niche overlap indicated that overlap between seasons was highly variable among sites (Figure 5.6). The niches for Betty's Bay showed no overlap with any sites or with each other, except the winter niche which overlapped with Bordjiesrif summer niche by less than 10%. The Betty's Bay summer niche was drastically different from all others, showing no overlap with any site. The large niche at Bordjiesrif in the summer overlapped with the winter niche (70%) and with the Oudekraal niches by less than 40% (Figure 5.6). Oudekraal seasonal niches were different, with very little overlap between seasons (<20%).

5.4 DISCUSSION

The results show that the west coast rock lobster, *Jasus lalandii*, has a smaller isotopic niche and lower trophic position at Betty's Bay in comparison to Bordjiesrif and Oudekraal in both summer and winter. However, Bordjiesrif was by far the largest isotope niche of the three sites, particularly during summer. Trophic position was variable across seasons with summer trophic positions consistently lower than in winter across all sites. The lobsters at Bordjiesrif had the highest trophic position of the three sites for both sampling occasions. Niche sizes were also variable across the seasons with the largest niches recorded at Bordjiesrif in the summer and winter. Despite the smaller overall size of the lobsters collected at Oudekraal, their calculated trophic position and isotopic niche size was still larger than for the lobsters collected at Betty's Bay. The lobsters at Betty's Bay had the smallest niche size in both seasons from the three sites, with an isotopically distinct niche recorded in summer.

Post-hoc analyses of the raw stable isotope values of *Jasus lalandii* at the three sites revealed that Betty's Bay and Bordjiesrif were more similar to each other in terms of $\delta^{15}N$ and $\delta^{13}C$ values in both seasons. Oudekraal was distinct from the other two sites during summer and winter (Chapter 4). This is likely to be an artefact of lobster size differences among the sites. Despite this however, the trophic positioning showed a different trend. Oudekraal and Bordjiesrif were similar in both seasons with Betty's Bay having a distinctly smaller trophic position in both seasons. One caveat that must be taken into consideration with this analysis, is that it is based on baseline corrected values. Therefore, if the *Turbo cidaris* values at Betty's Bay are highly variable, then this will also impact the calculated trophic position of *Jasus lalandii*. Therefore, trophic position data should be interpreted with caution when looked at in isolation.

The findings of the present study are congruent with expectations of niche width under conditions where lobsters have invaded the region east of Cape Hangklip. The smaller niche size and lower trophic position of the lobsters at Betty's Bay is likely to indicate the impact these organisms have had on the ecosystem in this area. Jack and Wing (2011) have illustrated how the trophic level of *Jasus edwardsii* (Hutton) is lower at sites where the abundance of these lobsters is highest. Additionally, where lobsters are found in high densities they may be forced to forage in a smaller area, potentially resulting in a lower food intake and thus causing a density-dependent reduction of their growth rate

(Mayfield et al. 2000). This was however not the case when considering the size of the lobsters at Betty's Bay, where lobsters were biggest despite the smaller niche size. One potential explanation for this could be that lobsters might be consuming each other. Cannibalism has been discussed for *Jasus lalandii* by Pollock (1986), who found that mortality of juvenile lobsters through cannibalism is most likely in overcrowded situations. This is a plausible explanation for the larger average size of lobsters at Betty's Bay in comparison to the other two sites. However, the isotope analysis of the adults did not reveal elevated $\delta^{15}N$ values at Betty's Bay in comparison to the other sites, which would have expected.

The diet of *Jasus lalandii* has been shown to vary among invaded sites and non-invaded sites east of Cape Hangklip, with unusual organisms forming part of the diet at sites where lobsters had invaded (Haley et al. 2011). Brown algae and barnacles were positively selected for at invaded sites whereas at sites considered non-invaded these sources were negatively selected for as prey items by the lobsters (Haley et al. 2011). This is linked to the dietary flexibility displayed by this species when it's preferred prey items are not readily available (Barkai and Branch 1988a). At Betty's Bay, lobster densities are extremely high, and this has led to the depletion of dietary sources which the lobsters usually consume (e.g. mussels & sea urchins) (Blamey et al. 2012). Apart from the documented impacts on the community structure in this area, I now provide evidence that the lobsters are reducing their own foraging niche.

In their study of freshwater crayfish, Olsson et al. (2009) showed that introduced crayfish had a greater niche width, which reflects a broader use of habitat and/or prey species, when compared to native species. Similarly, Semmens et al. (2009) have shown that individual dietary variability drives the expansion of niche width among consumers. The lobsters at Bordjiesrif and Oudekraal had larger isotopic niches than at Betty's Bay, but it may be misleading to assume that this means that the lobsters here have larger total niche widths. The high dispersion of points along the $\delta^{13}C$ axis of the lobsters at Bordjiesrif indicates that this population is either using a resource which varies widely in its $\delta^{13}C$ values or, more plausibly, that it uses a wide range of resources with different $\delta^{13}C$ values (Matthews and Mazumder 2004, Newsome et al. 2007). Layman et al. (2007a) relate the range of carbon isotope values to extent of niche diversification at the base of the food web which could result from multiple basal sources being used. Additionally, Newsome et al. (2012) note that dispersion in the isotope values of a consumer is highly influenced by the variability of the isotope values of food resources. The niches of lobsters from Oudekraal, and especially Bordjiesrif, which showed a high dispersion, could also be a result of greater dietary diversity. In contrast, the lobsters from Betty's Bay had very contracted niches along the $\delta^{13}C$ axis, thus implying a very limited trophic diversity. Lobsters at Oudekraal also had different seasonal niches, with very little overlap, with the main difference occurring along the $\delta^{13}C$ axis. This could therefore also indicate seasonal differences in trophic niches, with different dietary sources in summer and winter, or large seasonal differences in

dietary source values. *Jasus lalandii* has been documented to migrate seasonally towards and away from shore (Newman and Pollock 1971, Pollock 1982, Goosen and Cockcroft 1995) and it is therefore possible that these lobsters, or part of the population, are using different sources at different times of the year.

Similarly, dispersion of values along the $\delta^{15}N$ axis, or total $\delta^{15}N$ range, can be related to the vertical structure of the food web; with greater dispersion aligning with more trophic levels (Layman et al. 2007a). Bordjiesrif and Oudekraal again showed larger dispersion along the $\delta^{15}N$ axis which could indicate that these lobsters are consuming organisms from a variety of trophic levels. The lower dispersion along the $\delta^{15}N$ axis for lobsters at Betty's could again imply a narrower range of dietary sources from more similar trophic levels. Interestingly, the NR of lobsters at Oudekraal was the largest during the winter sampling period, whereas NR for the entire Oudekraal community in winter was the smallest of the three sites (Chapter 4). This could imply that lobsters are not feeding within the kelp forests during this period. The kelp forests on the west of the Cape Peninsula have been characterised as having fewer urchins when compared to sites within False Bay (Anderson et al. 1997). Lobsters feeding on a larger variety of organisms on the west coast, will lead to a greater dispersion of $\delta^{15}N$ values. From the dispersion values (NR and CR) alone, it is evident that the niche of lobsters at Betty's Bay is highly contracted along both axes, which is likely to be indicative of the limited dietary breadth at this site.

Despite the similarity in community structuring among the three sampling sites which was revealed in Chapter 4, the niche overlap among sites was different. The high degree of niche overlap and similarity of trophic position between lobsters collected at Oudekraal and Bordjiesrif is likely to be a result of the similar community structuring, and therefore resource availability at these sites. In contrast, Betty's Bay lobsters had markedly lower trophic positions as well as visibly separate niches. Niche overlap is often associated with competition for resources within a particular habitat (Olsson et al. 2009); however, when comparing the same organism among different habitats it can provide insight into differences in resource use among habitats. Therefore, it is likely that lobsters at Betty's Bay are consuming different resources from those at Oudekraal and Bordjiesrif, which are more similar to each other. This largely corroborates the dietary analyses which have been performed on the lobsters in invaded and non-invaded areas (Haley et al. 2011).

5.5 CONCLUSION

This study provides additional evidence to illustrate the impacts of the lobster invasion east of Cape Hangklip, highlighting the influence on the trophic niche of the invading species *Jasus lalandii*. Previous studies showed that the dietary composition of this species has been altered in invaded sites, but this study provides the first stable isotope evidence to corroborate this. Not only has dietary composition changed, but I have shown that the trophic niche of the lobsters in this area is

significantly reduced when compared to sites around the Cape Peninsula. A question that arises is how these populations are able to maintain such high densities despite the constricted trophic niche and altered diets? One possibility could be cannibalism; however, the trophic positioning of the lobsters at Betty's Bay would then be expected to be higher than at other sites.

Despite similarities in the community structure of the kelp forests at the three sites, from stable isotope evidence (Chapter 4), differences among *Jasus lalandii* populations were clear. This indicates that although the community structure may be similar from a stable isotope perspective, there are distinct differences in the trophic ecology of single species within these systems.

Quantifying the stable isotope niche width of species in different habitats provides an additional measure of resource use and trophic diversity among habitats. When used in conjunction with measures such as trophic position it can provide powerful insights into ecosystem functioning. However, careful consideration of baseline variability must be accounted for as this can provide erroneous results, particularly where baselines vary greatly among and within sites. Baseline corrected niche determination was able to expose the differences in niches among sites and thus provided a superior understanding of the spatial and temporal niche variability in this species.

CHAPTER 6

GENERAL DISCUSSION

6.1 Synthesis

Food webs, and in particular the processes which control their structuring, are one of the most studied subjects in ecology. The application of stable isotope analysis has become an indispensable way to study the flow of energy through food webs, with particular focus on structure and functioning (Fry 2006, Newsome et al. 2007, Layman et al. 2012). The major advantage that this has over more traditional methods is that it provides a time-integrated approach to study the various interactions between food web compartments (Layman et al. 2012). Several different techniques can be employed, depending on the question being investigated and thus stable isotope ecology is extremely versatile. Most recently, the use of quantitative metrics and Bayesian statistics have greatly improved the ability to compare ecosystems across space and time (Newsome et al. 2007). However, in order to apply these methods to answering ecological questions about food web structure and functioning, researchers need to have a clear understanding of natural variability of stable isotope values, predator-prey interactions, and factors which could structure the communities being studied.

Although natural variability of stable isotope values exists within all species, it is often over-looked when constructing stable isotope mixing models, and can result in erroneous conclusions about trophic relationships (Dethier et al. 2013, Hyndes et al. 2013). Basal food web compartments exhibit the largest variability as the organisms which comprise the lower trophic levels often have the most rapid tissue turnover rates (Dethier et al. 2013). Several studies have investigated the variability in $\delta^{13}C$ values of marine algae, especially those found in association with kelp forests (Stephenson et al. 1984, Fenton and Ritz 1989, Simenstad et al. 1993, Raven et al. 2002, Fredriksen 2003, Guest et al. 2010, Vanderklift and Bearham 2014, Mackey et al. 2015). These studies show that variability of marine macrophyte isotope values occurs across different temporal and spatial scales, but despite a growing body of research the scale, magnitude and factors responsible remain poorly understood. In Chapter 2 of this thesis, the stable isotope values of two South African kelp species were shown to be highly variable across various scales of space and time. Stable isotope values were variable on the scale of centimetres within the lamina of a single plant to hundreds of kilometres across geographical sites. Temporal and spatial factors were identified as primary factors resulting in $\delta^{15}N$ and $\delta^{13}C$ variability, however, intra-site variability accounted for a large proportion of the observed variability across the three markers. This means that several factors, which operate at different scales, are likely to be causing the variability in these values. Some members of the Phaeophyceae (Fucales) are known to exhibit C3, C4 and potentially CAM photosynthetic pathways which are controlled by light availability and depth (Raven and Giordano 2017). However, additional processes are likely to be acting on the stable isotope values of the kelps along the coastline and these may be adding to the measured variability in stable isotope values.

Baseline variability in stable isotope values poses two major problems when studying food webs, 1) overlap in $\delta^{13}C$ can make it extremely difficult to distinguish carbon sources and determine ecosystem drivers (France 1995, Fry 2006), 2) variable $\delta^{15}N$ values create confounding trophic levels, particularly when values vary by more than 3.4‰ (the generic jump between trophic levels). Algal stable isotope values are known to change rapidly (in less than 2h) as a result of changes in the environmental conditions which control them (e.g. light availability, pH, temperature) (Lajtha and Michener 1994, Hadwen and Bunn 2005). Large within-species variability in stable isotope values (>2‰) are known to occur on different spatial and temporal scales (Fry and Sherr 1989, Hemminga and Mateo 1996, Jennings et al. 1997). Understanding this variability and the changes, particularly in $\delta^{13}C$ values, are vital to determining the contribution of sources to a consumer and ecosystem (Boon and Bunn 1994, Vander Zanden and Rasmussen 2001).

The food web implications of baseline variability have been mitigated through the use of longer-lived organisms, particularly for $\delta^{15}N$ baselines, as these do not exhibit the high variability of their diet (Post 2002a, 2002b). These organisms, which include grazers and filter-feeders, integrate stable isotope values over a longer period than macroalgae and phytoplankton and therefore provide a more consistent baseline value (Post 2002a). Using the values of these primary consumers as the basal component of the food web, thus eliminates the potential for error when using highly variable primary producers. For the chapters which examined food web structure and isotope niche sizes, I decided to use these correction methods in order to facilitate unbiased comparisons among sites. I have however, not yet attempted dietary analyses for the consumer species among sites which will definitely require careful consideration of the variability in $\delta^{13}C$ values of the producers.

One of the areas of kelp forest ecology which has received particular research attention, and where stable isotope analysis has been widely applied, is the determination of ecosystem drivers or primary carbon sources (Miller and Page 2012). More specifically, whether kelp-derived detritus or phytoplankton is more important for the filter-feeding organisms in these ecosystems. Several studies have shown that kelp-derived detrital material is an important source of carbon to the filter-feeding organisms in kelp forests (Dunton and Schell 1987, Eckman et al. 1989, Kaehler et al. 2000, 2006, Hill et al. 2006). However, others have shown that phytoplankton is likely to be more prevalent (Miller et al. 2013, Yorke et al. 2013). The application of this method isn't without its own set of caveats and problems and therefore the findings of these studies need to be critically examined. The largest problem facing researchers is acquiring pure end-member stable isotope values for phytoplankton and kelp-derived detritus (KDD).

In Chapter 3, I tested the prediction that under upwelling conditions, the particulate organic matter (POM) suspended in the water column would be dominated by kelp-derived detrital material and under downwelling conditions, that phytoplankton will dominate the POM. The use of coastal

upwelling provided a unique approach to isolating representative stable isotope values of phytoplankton and KDD, something which has been difficult to do in past studies. The methods applied, similar to that employed by Ramshaw et al. (2017) along the coast of Nova Scotia, therefore provided a different way of tackling the problem of 'pure' phytoplankton and KDD values for stable isotope analysis. Although not perfect, this does provide a more suitable alternative to using off-shore phytoplankton values. The results of Chapter 3 showed that kelp-derived detritus is an important component of the particulate organic matter suspended in the water column within the kelp forest at Kommetjie and this can likely be applied to the majority of west coast kelp beds in southern Africa. This material accounted for up to 89% of the POM in these systems under upwelling conditions, but contributions were significantly reduced during the downwelling phase. These findings show that in South African kelp forest systems, KDD is far more important to POM than in other parts of the world (e.g. Canada (Nova Scotia) and California (Santa Barbara)) where KDD comprises a very small fraction of POM. This is most likely due to the differences in kelp and phytoplankton productivity in these areas, whereas in South Africa the production from these two sources is comparable. However, the results from this study need to be taken as preliminary and further evidence from other kelp forests along the coastline is required. Additionally, the availability of KDD in the system does however not directly translate to its consumption and therefore requires further research (see Section 6.2 below).

Chapter 4 focussed on the influence of community composition on the trophic structure of the kelp forest community at three sites, using stable isotope analysis. The differences in kelp forest community composition create three ecologically distinct communities within a short stretch of coastline: the typical west coast kelp forests on the Atlantic coast of the Cape Peninsula; the traditional south west coast kelp forests on the eastern side of the Cape Peninsula (False Bay); and the lobster-invaded kelp forests in an area east of Cape Hangklip.

The results showed a large degree of variability in stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values of both the kelp forest macroalgae as well as the common consumers found in these systems. The strong seasonal trend in the variability of macroalgae was not evident among the consumers, for which spatial patterns were more important in shaping their stable isotope values among sites. The community metrics revealed differences among sites and clear seasonal patterns, particularly in SEA_C values. Most interestingly, however, despite the large differences among the sites in terms of community structure and physical environment, the community niches (SEA_C) were very similar among sites, only differing by 6.2‰^{2} in summer and 2.1‰^{2} in winter. Additionally, there was a high degree of overlap among sites and seasons (80–95%) which corroborates the similarity in SEA_C values. Seasonal variability in trophic positioning of consumers coupled with the seasonal variability in community niches is indicates the influence of upwelling which leads to $\delta^{15}N$ enrichment. Despite this, the trophic structure and functioning of these kelp forests seems to be quite similar, which is contrary to what was expected. The differences in community composition among the three different types of kelp forest

were not mirrored in the community metrics or niche comparisons. This suggests that although these systems may appear different, their similar trophic structures result in common trophic functioning among sites.

In Chapter 5, the trophic positioning and size of the isotopic niche of the west coast rock lobster *Jasus lalandii* was compared among the three ecologically distinct kelp forests selected for Chapter 4. Not only is this species of great ecological importance in the food web, but commercially *Jasus lalandii* was historically one of the top three marine fishery species in South Africa (Melville-Smith and van Sittert 2005). *Jasus lalandii* has the ability to markedly impact the benthic community structure as a whole, especially where it exists in high abundance (Pollock 1979, Barkai and Branch 1988b, Barkai et al. 1996). A study conducted by Haley et al. (2011), based on stomach content analysis, showed that the diet of these predators has changed significantly in the area east of Cape Hangklip, where it had recently invaded. As stable isotope analysis had not been applied to study this species in South African kelp forests, this provided an excellent opportunity to test the isotope niche methodology. Variability in stable isotope niches has been effectively used to show differences in trophic niche size and niche overlap in systems invaded by alien species (e.g. Olsson et al. (2009), Ercoli et al. (2014), Fuhrmann et al. (2017)) and to illustrate the recovery of species following overfishing (Hamilton et al. 2014). Therefore, using this approach, I tested to see whether there was any variability in the isotope niche of *Jasus lalandii* among the different kelp forest communities.

The results showed distinct differences in trophic positioning and isotope niche size among the three study sites. Betty's Bay, the invaded site, had the smallest niche size and lowest trophic positioning of all sites. Niche overlap also suggested a distinct trophic niche at Betty's Bay, particularly in the summer as the niche showed no overlap with other sites. However, the niches at Bordjiesrif and Oudekraal overlapped by as much as 70%. Apart from the documented impacts on the community structure in this area, evidence that the lobsters are reducing their own foraging niche is now provided. The findings of this chapter were quite different to those of Chapter 4, which showed that the community niche as a whole was very similar among the three study sites. It is likely that the influence of community composition may manifest differently in single species as opposed to the entire community. If this is the case, *Jasus lalandii*, may therefore provide an indication of differences among other areas.

In summary, the findings of this thesis highlight the following important aspects of the ecology of South African kelp forests, particularly from a stable isotope perspective:

- There is a high degree of variability in stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values of *Ecklonia maxima* and *Laminaria pallida* across spatial, geographical and temporal scales. The processes which are thought to drive this variability are discussed, with a major difference in *Laminaria* values though to be driven by depth and thus light availability.

- POM composition in the kelp forest, and nearshore, is largely controlled by upwelling and downwelling conditions, with distinct differences between these. Kelp-derived detritus is a major constituent of POM under upwelling conditions, but is less dominant under downwelling conditions. These results support the results of previous research which has been done on kelp POM dynamics. However, the use of a unique approach to isolating 'pure' phytoplankton and KDD end member values, begins to solve the inherent problems of using stable isotope analysis to study POM composition.

- The ecological differences in kelp forests along the south-western Cape coastline were not as evident when analysed using stable isotope-based community metrics. The trophic functioning of these systems appears to be more similar than expected, which challenges the current understanding of community composition and its impact on trophic ecology. However, seasonal differences were still evident in trophic positioning and community-wide metrics, thus illustrating the influence of seasonal processes such as upwelling.

- The effect of the lobster invasion has been well documented, with marked impact on the benthic community structure. I expected that the trophic niche of the lobsters in invaded sites such as Betty's Bay would be negatively impacted by this, which is what the results showed. Trophic niche and trophic position of lobsters was markedly smaller at Betty's Bay when compared to Oudekraal and Bordjiesrif. This is the first study to show how the lobster invasion is impacting the invading species itself.

6.2 A note on the limitations of stable isotope ecology

Prior to the widespread use of stable isotope analysis for studying ecological systems, several traditional methodologies were applied for food web analyses (Lajtha and Michener 1994). The most common of these are the direct analysis of stomach contents to determine dietary compositions (Hesslein et al. 1993) and the use of energetics (e.g. Newell et al. 1982). Despite the successful application of these methods, and others, for studying food webs each method has its own set of limitations (Michener and Kaufman 1994). When considering stomach content analyses for example, considerable time is required to collect, dissect and determine the content of stomach contents and subsequently piece together the diet (Hesslein et al. 1993, Michener and Kaufman 2007). Additionally, some dietary items are digested rapidly or not at all and thus stomach contents can potentially provide a biased snap-shot of the organism's diet (Hesslein et al. 1993). Therefore, this approach only provides a short-term indication of what the organism ate rather than a time-incorporated image of its diet (Michener and Kaufman 2007). Similarly, using behavioural studies of

predator-prey relationships, exclusion experiments and even camera footage to study food web interactions has its limitations.

Stable isotope analysis has however become a powerful tool for studying food webs, proving to be an alternate, complementary and even replacement analytical method (Michener and Kaufman 2007). Since the first implementation of stable isotope analysis in ecology in the 1980s, considerable advances have been made and this technique has been used to answer a plethora of ecological questions in numerous fields of biology. Analytical and technological advances in sample analysis procedures have provided time and cost-effective way of surveying organisms in various types of ecosystems (Michener and Kaufman 2007, Layman et al. 2012). But, as with any analytical tool, there will always be advantages and limitations in its application to answer ecological questions. The successful application of stable isotope analysis is however highly dependent on information about the system being studied. This is particularly relevant when looking at trophic relationships as information on tissue turnover rates, dietary composition, fractionation and trophic enrichment factors. The misapplication of these methods can lead to erroneous and thus biased conclusions about the ecological processes being studied.

The metrics proposed Layman et al. (2007a) were adopted from other fields specifically for use with stable isotope data (see Layman et al. 2007a, 2012, Jackson et al. 2011). These methods have been successfully applied in several studies (see Layman et al. 2007b, Schmidt et al. 2007, Turner et al. 2010, Ercoli et al. 2014, Hill et al. 2015, Muller and Strydom 2017, Raw et al. 2017) and thus can provide robust inferences about the systems being studied. However, more recently, Bayesian methodology has become preferred for studying niche stable isotope data (Jackson et al. 2011, Syväranta et al. 2013). This is particularly effective when sample sizes are small ($n < 50$). Although some studies have abandoned the use of the Layman metrics, opting instead for the Bayesian techniques, several authors still apply both mythologies. This integrative approach, combining the Layman metrics with the Bayesian analyses, provides the most robust analytical approach for studying isotope niches.

Whichever methodology is applied, gathering additional information from other sources will provide a more robust view of the ecological processes. For example, using stomach content data to accompany stable isotope mixing models provides a more definitive picture of the organism's diet when compared to either method applied in isolation. Similarly, using Layman metrics and Bayesian analyses to study ecological communities should be applied with caution without a detailed knowledge of the system being studied.

6.3 Recommendations for further research

Although the work in this thesis covers a broad range of topics, there is still substantial work which is required to fully understand the trophic ecology of the kelp forests in South Africa. As with many scientific fields, a greater knowledge of a subject often raises further questions which need answering. A number of further questions or knowledge/data gaps were identified throughout the course of these studies. Some of these ideas were posed throughout the preceding chapters but, to provide a synthesis they may be repeated here. I have arranged these into sections which follow the same order as the chapters in the thesis. These questions need to be addressed in future research projects to further the understanding of some of the patterns revealed in this thesis.

6.3.1. Variability in isotope values following bacterial degradation

Chapters 2 specifically looked at the variability of stable isotope values at across different spatial and temporal scales and found that both species of kelp were highly variable in their $\delta^{15}N$ and $\delta^{13}C$ values across these scales. Hill and McQuaid (2009a) have demonstrated how the isotope values of intertidal red algae change as a result of degradation and bacterial action. These authors showed that the $\delta^{13}C$ values became depleted in both species of algae studied, whereas the $\delta^{15}N$ values became depleted in only one species. Dethier et al. (2014) also demonstrated how bacterial action can alter the food quality of algal tissues, resulting in preference by consumers of certain species over others. Similarly, bacterial action on kelp-derived detrital (KDD) particles would probably result in changes to the stable isotope values as fresh kelp is likely to have more depleted stable isotope value than decaying kelp, which forms the kelp detritus (Kaehler et al. 2000, 2006, Kaehler and Pakhomov 2001, Yorke et al. 2013). However, the magnitude of the variability in stable isotope values following bacterial degradation has yet to be determined for either species of kelp found in South Africa. To determine this variability, an elegant experiment incorporating frond position, repeated sampling and the correct length of time will need to be devised in order to separate the natural variability in kelp tissue from that which is caused by microbial action. This is probably most feasibly conducted in a laboratory environment; however, this has its own set of assumptions and limitations.

Similarly, using fresh kelp and oceanic phytoplankton stable isotope values can potentially lead to uncertainty when determining their contribution to coastal POM and to the diet of kelp forest organisms (Chapter 3). Organisms are consuming degraded kelp particles and thus a signature is needed for this. Similarly, the use of off-shore phytoplankton signatures has resulted in much debate in the literature (see Miller and Page 2012). As a result, the contribution of either source (KDD vs. phytoplankton) can be easily overestimated (Miller and Page 2012, Ramshaw et al. 2017). Consequently, determining the primary carbon sources of kelp forest food webs is still considered difficult (Miller and Page 2012).

Answering this question will therefore not only provide a better understanding of the factors responsible for and scale of variability in kelps but will also provide better stable isotope values for use in food web models. This is particularly relevant to understanding the effect of climate change on kelp forests. Studies have shown that marine heat waves are negatively impacting kelp abundances and also increasing the rates of blade degradation (Hobday 2000, Smale and Wernberg 2013, Wernberg et al. 2016). Schlegel et al. (2017) have shown an increase in the frequency of marine heat wave events for the South African coastline. The impact of these events has not been investigated for South African kelp forests but devastating impacts have been illustrated in other parts of the world (Wernberg et al. 2016).

6.3.2. Real-time monitoring of upwelling conditions

The study in Chapter 3, on the dynamics of POM in and around the kelp forest at Kommetjie proved to be extremely challenging. The main difficulty was aligning the wind-derived upwelling index to the actual ocean conditions. The solution that I applied was to wait for a few days of the same conditions and thus hopefully get the right sampling conditions. This was not always possible, as evidenced in the final two days of sample collection.

Sea conditions and atmospheric conditions are unlikely to be completely synchronised. Wind patterns change faster than sea conditions, which introduces a lag phase between the calculated upwelling index and the actual upwelling conditions. The length of this lag phase also seems to be quite variable, with more drastic changes expected with higher wind speeds. To combat this, I propose two possible solutions: 1) the use of *in-situ* data loggers to measure real-time changes in upwelling conditions, 2) using filter feeder gut contents to provide a snap-shot of what is currently suspended in the water column.

The use of *in-situ* data loggers, which measure real-time changes in the parameters associated with upwelling conditions (temperature, turbidity, chlorophyll-*a*), could provide a far superior image of the conditions within a kelp forest during upwelling or downwelling. The use of these data could then better inform the timing of sample collection and could therefore provide more accurate measures of the impact of upwelling on kelp forest POM.

By analysing the stomach content of filter-feeding organisms such as mussels and ascidians, a snap-shot of the particles available in the water column at the time of collection can be obtained. The stable isotope value of the filter-feeders is not likely to change at the same temporal scale as the particulates they are consuming, and therefore direct analysis of the stomach content material will be required. This, however, still relies on the accuracy of determining the upwelling conditions. Nevertheless, this will also provide details on what particles are being consumed and could provide further details as to the primary carbon source of South African kelp forest food webs.

6.2.3. Dietary analysis of Jasus lalandii

The results of Chapter 5 indicate that the foraging niche of this species is different among the three sites used for this study. Further analysis of the dietary composition, using stable isotope analysis and stomach content analysis is required to determine the major differences among the sites which could be driving the variability in niches.

Preliminary evidence from gut content analyses suggest that there are differences in dietary composition between invaded and non-invaded sites EOCH (Haley et al. 2011). This was however focused on the area EOCH and thus the study could be expanded to incorporate several sites in each of the kelp forest types. Additionally, this study would benefit greatly from the implementation of stable isotope mixing models to support the findings. Stable isotope analysis has many advantages over gut content analysis, mainly as it provides a time-integrated approach instead of the 'snap-shot' view from stomach contents alone. However, using both stable isotope mixing models and stomach content data to complement stable isotopic niche measurements would allow for the most robust scenario.

SUPPLEMENTARY MATERIAL

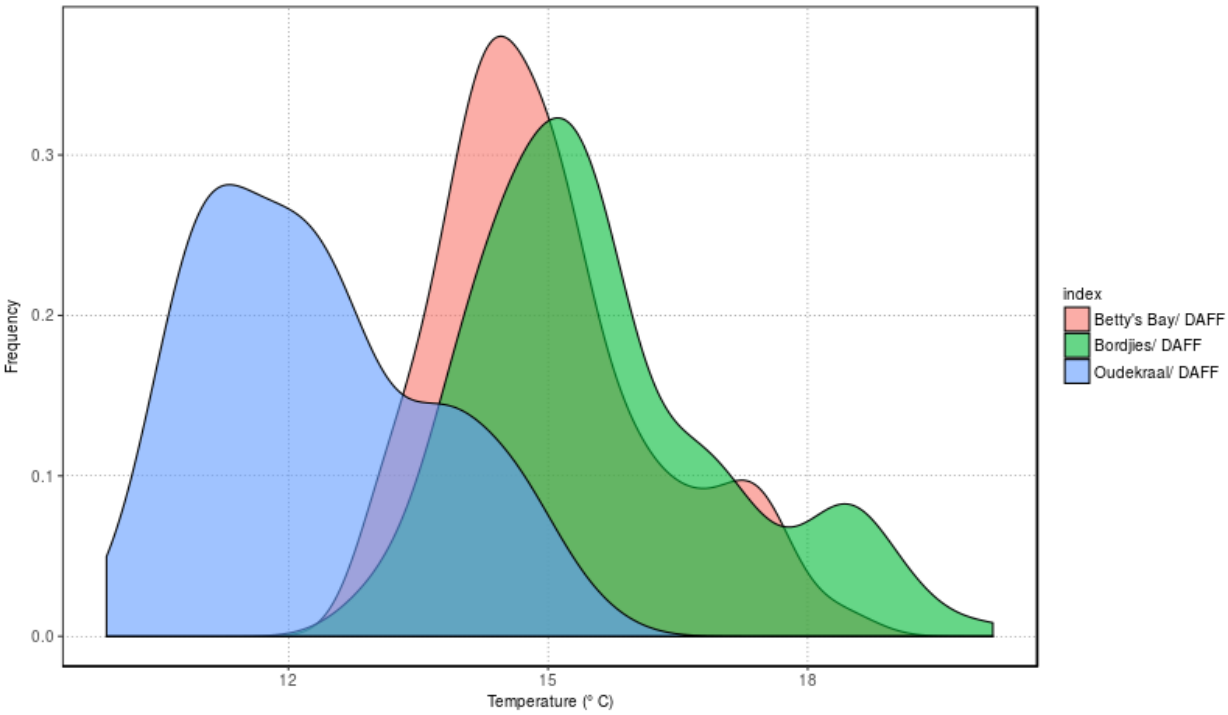

Figure S1: Frequency plot of *in-situ* temperatures at Oudekraal (blue), Bordjiesrif (green) and Betty's Bay (salmon), figure sourced from the South African Coastal Temperature Network (SACTN).

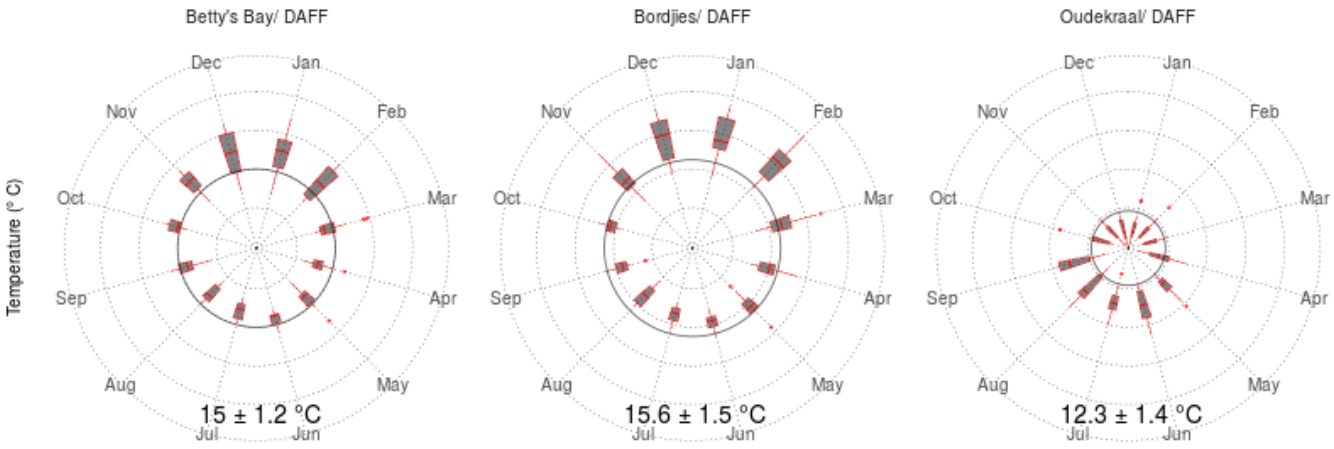

Figure S2: Polar plot of monthly in-situ temperatures at Oudekraal, Bordjiesrif and Betty's Bay with each month displayed as a box-plot within the polar plot. Data and figure sourced from the South African Coastal Temperature Network (SACTN).

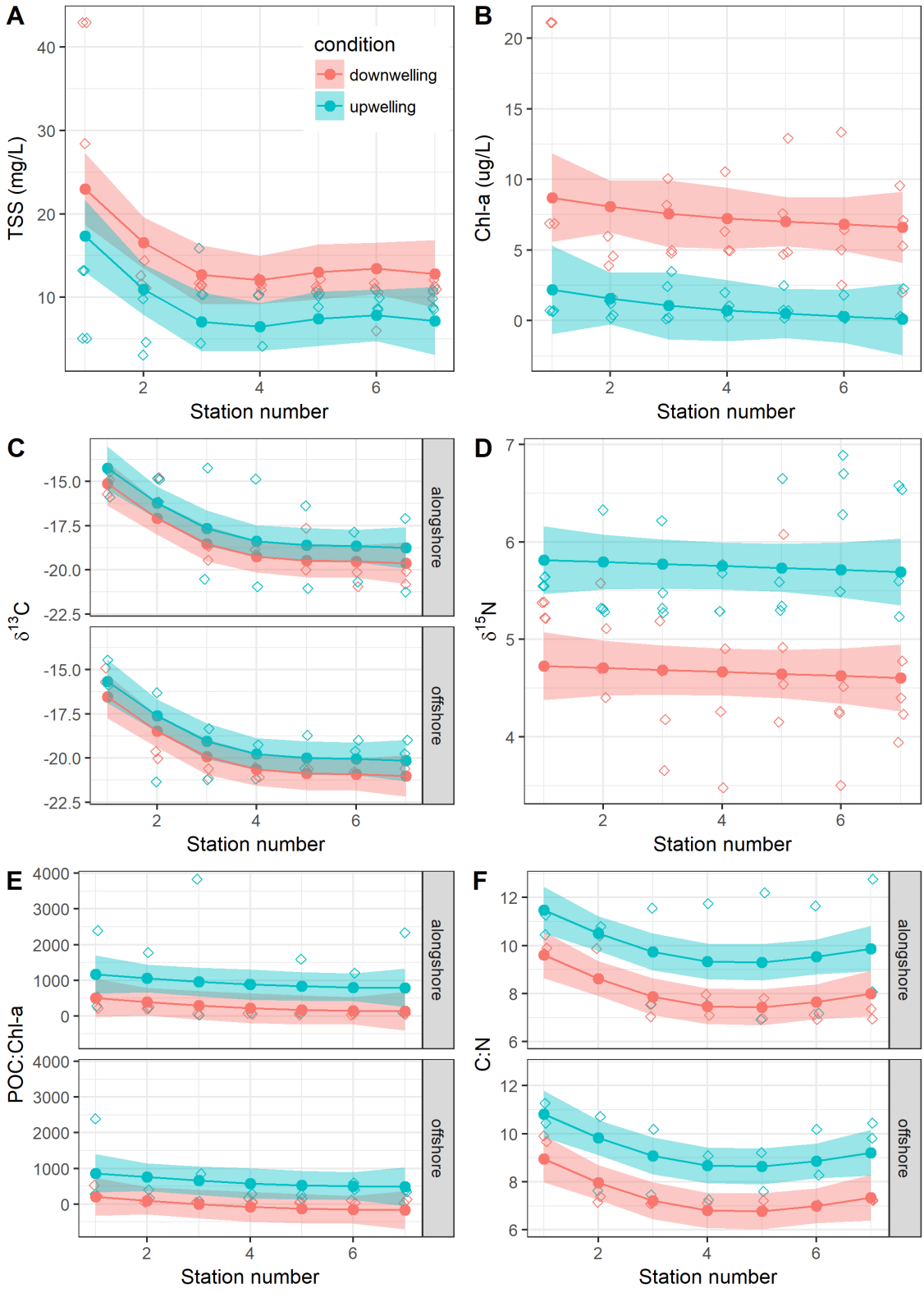

Figure S3: Graphical representation of the generalised additive models (GAM) fitted to the variables associated with POM composition in two *directions* away from kelp beds (off-shore and along-shore) during two ocean *conditions* (upwelling and downwelling). A reduced data set of four days was used for the analysis (Day 1–4).

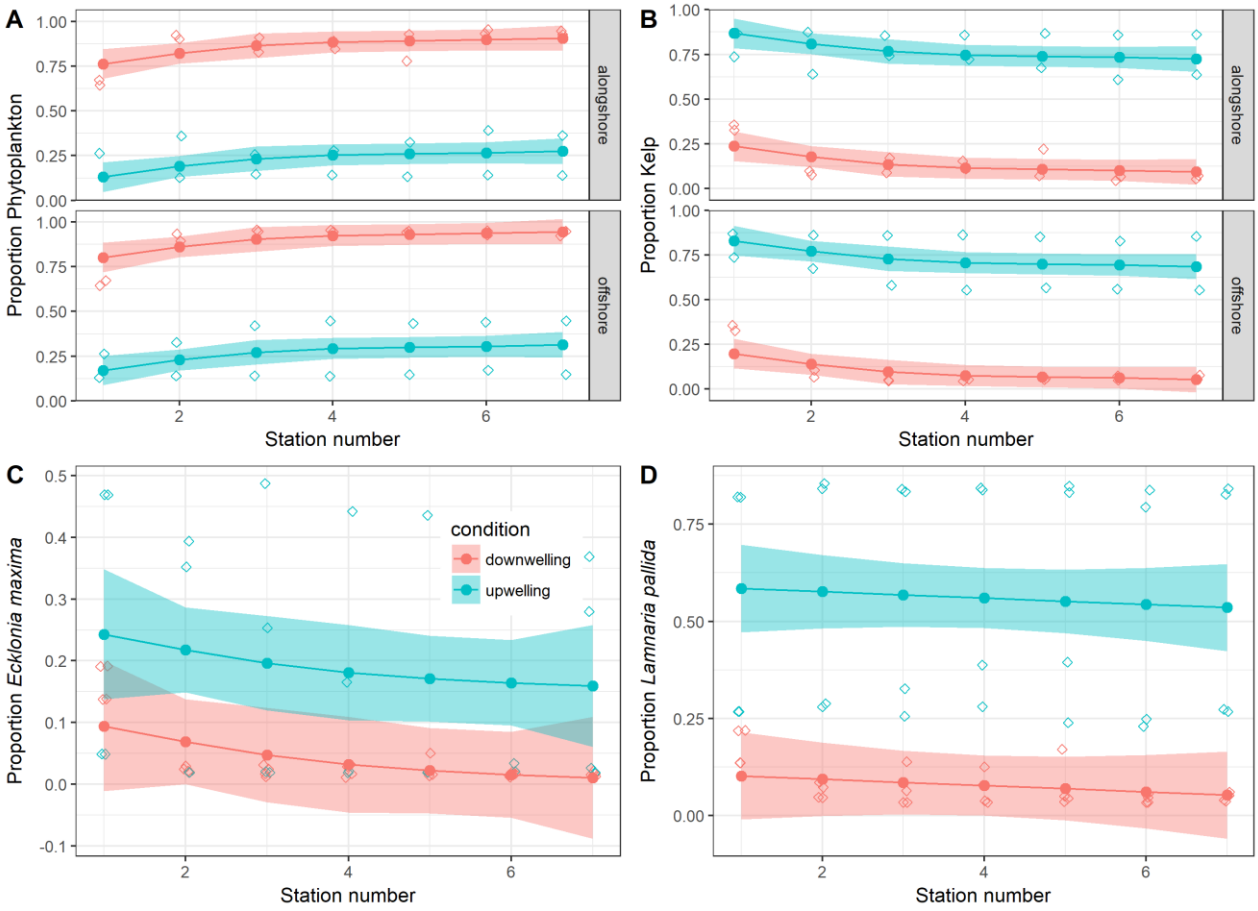

Figure S4: Graphical representation of the generalised additive models (GAM) to the mean calculated MixSIAR proportion of POM constituents in two *directions* away from kelp beds (off-shore and along-shore) during two ocean *conditions* (upwelling and downwelling). A reduced data set of four days was used for the analysis (Day 1–4).

Table S1: Data summary for Betty's Bay showing mean and SD values for each variable for summer and winter sampling occasions.

Summer							
ID	**Species**	**$\delta^{15}N$**	**SD**	**$\delta^{13}C$**	**SD**	**TP**	**SD**
BP	*Botryocarpa prolifera*	7.01	0.13	-29.92	0.36		
CS	*Codium stephensiae*	8.01	0.28	-10.42	0.42		
EM	*Ecklonia maxima*	6.87	0.28	-10.66	1.57		
LP	*Laminaria pallida*	7.62	0.71	-15.95	2.35		
PC	*Pachymenia cornea*	6.66	0.34	-18.90	0.80		
PO	*Pachymenia orbitosa*	7.85	0.17	-9.75	0.82		
POM	Particulate Organic Matter	6.24	0.13	-18.45	0.34		
UC	*Ulva capensis*	7.58	0.12	-8.77	1.02		
CC	*Cymbula compressa*	7.70	0.59	-17.63	1.22	1.69	0.17
JL	*Jasus lalandii*	10.51	0.25	-12.52	0.30	2.52	0.07
PA	*Parechinus angulosus*	10.94	0.34	-12.25	0.52	2.64	0.10
PS	*Pyura stolonifera*	10.24	0.29	-14.58	0.22	2.44	0.09
TC	*Turbo cidaris*	8.75	0.89	-14.46	2.41	2.00	0.26
Winter							
ID	**Species**	**$\delta^{15}N$**	**SD**	**$\delta^{13}C$**	**SD**	**TP**	**SD**
BP	*Botryocarpa prolifera*	6.30	0.29	-32.78	0.30		
CF	*Codium fragile*	10.54	0.09	-10.40	0.74		
CS	*Codium stephensiae*	9.88	0.23	-11.75	0.34		
EM	*Ecklonia maxima*	5.68	0.42	-15.34	1.58		
LP	*Laminaria pallida*	6.21	0.56	-21.18	1.84		
PC	*Pachymenia cornea*	6.14	0.34	-23.42	0.48		
POM	Particulate Organic Matter	7.06	0.11	-14.29	0.15		
UC	*Ulva capensis*	12.07	0.63	-10.57	0.80		
CC	*Cymbula compressa*	7.49	0.29	-18.55	0.37	1.99	0.09
JL	*Jasus lalandii*	10.81	0.31	-12.18	0.49	2.97	0.09
PA	*Parechinus angulosus*	10.59	1.04	-12.97	0.44	2.90	0.30
PS	*Pyura stolonifera*	9.94	0.22	-14.29	0.17	2.71	0.07
TC	*Turbo cidaris*	7.52	0.15	-19.14	2.00	2.00	0.04

Table S2: Data summary for Bordjiesrif showing mean and SD values for each variable for summer and winter sampling occasions.

Summer							
ID	**Species**	**$\delta^{15}N$**	**SD**	**$\delta^{13}C$**	**SD**	**TP**	**SD**
CM	*Choromytilus meridionalis*	7.20	0.18	-15.47	0.44		
CS	*Codium stephensiae*	7.59	0.12	-10.94	0.84		
EM	*Ecklonia maxima*	7.87	0.58	-11.37	0.57		
LP	*Laminaria pallida*	7.87	0.55	-13.93	2.56		
PB	*Plocamium beckeri*	6.40	0.14	-27.85	0.24		
PC	*Pachymenia cornea*	8.01	0.18	-13.65	1.72		
POM	Particulate Organic Matter	4.08	1.10	-22.10	0.26		
UC	*Ulva capensis*	6.32	0.17	-12.40	0.74		
CC	*Cymbula compressa*	7.51	0.57	-12.86	0.91	2.11	0.07
JL	*Jasus lalandii*	10.89	0.45	-12.48	0.46	3.01	0.08
MG	*Marthasterias glacialis*	12.57	0.41	-9.09	0.41	3.58	0.12
PA	*Parechinus angulosus*	9.00	0.28	-9.80	0.31	2.25	0.09
PS	*Pyura stolonifera*	9.76	0.40	-15.39	0.33	2.64	0.07
TC	*Turbo cidaris*	7.21	0.29	-11.79	0.14	2.00	0.18
Winter							
ID	**Species**	**$\delta^{15}N$**	**SD**	**$\delta^{13}C$**	**SD**	**TP**	**SD**
CM	*Choromytilus meridionalis*	7.19	0.16	-14.84	0.13		
CS	*Codium stephensiae*	6.92	0.24	-14.18	0.37		
EM	*Ecklonia maxima*	6.30	0.13	-14.04	0.62		
LG	*Laurencia glomerata*	7.14	0.06	-14.31	0.51		
LP	*Laminaria pallida*	6.44	0.20	-20.04	1.50		
PB	*Plocamium beckeri*	6.54	0.22	-31.30	0.38		
PC	*Pachymenia cornea*	6.53	0.37	-25.69	1.00		
PL	*Plocamium sp.*	6.19	0.51	-21.64	0.59		
POM	Particulate Organic Matter	6.41	0.12	-19.99	0.12		
UC	*Ulva capensis*	8.81	0.92	-16.73	0.84		
CC	*Cymbula compressa*	7.47	0.23	-14.33	0.65	2.10	0.06
JL	*Jasus lalandii*	11.14	0.26	-11.87	0.43	3.16	0.12
MG	*Marthasterias glacialis*	10.81	0.55	-11.95	0.40	2.94	0.16
PA	*Parechinus angulosus*	9.10	1.20	-12.98	1.22	2.50	0.09
PS	*Pyura stolonifera*	9.05	0.49	-15.57	0.45	2.71	0.04
TC	*Turbo cidaris*	6.99	0.45	-12.49	0.46	2.00	0.15

Table S3: Data summary for Oudekraal showing mean and SD values for each variable for summer and winter sampling occasions.

Summer							
ID	**Species**	**$\delta^{15}N$**	**SD**	**$\delta^{13}C$**	**SD**	**TP**	**SD**
BP	*Botryocarpa prolifera*	6.69	0.24	-29.91	0.69		
CF	*Codium fragile*	7.70	0.13	-12.03	0.69		
EM	*Ecklonia maxima*	7.15	0.28	-12.82	2.56		
GV	*Gelidium vittatum*	6.60	0.39	-16.07	2.06		
LP	*Laminaria pallida*	7.98	0.18	-12.13	0.75		
PC	*Pachymenia cornea*	6.15	0.69	-15.99	2.36		
POM	Particulate Organic Matter	5.53	0.33	-19.07	1.35		
UC	*Ulva capensis*	7.02	0.25	-9.40	1.98		
AA	*Aulacomya ater*	7.61	0.19	-16.31	0.46	1.61	0.05
CC	*Cymbula compressa*	7.38	0.23	-13.99	0.43	2.10	0.07
CM	*Choromytilus meridionalis*	7.54	0.29	-15.97	0.30	1.59	0.09
JL	*Jasus lalandii*	10.44	0.29	-13.43	0.49	2.44	0.08
PA	*Parechinus angulosus*	7.84	0.29	-14.39	0.52	1.68	0.09
PS	*Pyura stolonifera*	9.18	0.24	-16.42	0.75	2.07	0.07
TC	*Turbo cidaris*	6.99	0.61	-15.07	1.32	1.43	0.18
Winter							
ID	**Species**	**$\delta^{15}N$**	**SD**	**$\delta^{13}C$**	**SD**	**TP**	**SD**
BP	*Botryocarpa prolifera*	5.24	0.34	-33.04	0.97		
CF	*Codium fragile*	5.96	0.19	-14.35	0.73		
CS	*Codium stephensiae*	6.18	0.63	-17.63	0.74		
EM	*Ecklonia maxima*	5.26	0.32	-15.22	1.10		
GV	*Gelidium vittatum*	5.62	0.16	-20.96	2.50		
LP	*Laminaria pallida*	4.49	0.55	-19.05	0.37		
PC	*Pachymenia cornea*	4.96	0.28	-18.37	0.61		
POM	Particulate Organic Matter	7.51	0.26	-14.12	0.05		
UC	*Ulva capensis*	4.41	0.37	-11.39	1.17		
AA	*Aulacomya ater*	7.73	0.17	-15.01	0.27	1.52	0.91
CC	*Cymbula compressa*	6.80	0.19	-14.97	0.21	2.11	0.06
CM	*Choromytilus meridionalis*	7.16	0.29	-15.64	0.19	1.81	0.09
JL	*Jasus lalandii*	10.38	0.39	-13.71	0.51	2.76	0.12
MG	*Marthasterias glacialis*	9.66	0.53	-13.18	0.42	2.54	0.16
PA	*Parechinus angulosus*	8.14	0.31	-13.67	0.42	2.10	0.09
PS	*Pyura stolonifera*	8.88	0.15	-16.42	0.13	2.31	0.04
TC	*Turbo cidaris*	6.45	0.51	-16.39	0.87	1.22	0.77

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