2018

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Recommended Citation

Rae, C. (2018). *The distribution and trophic ecology of Golden ghost crabs (Ocypode convexa)*. Edith Cowan University. Retrieved from https://ro.ecu.edu.au/theses/2058

The distribution and trophic ecology of Golden ghost crabs (*Ocypode convexa*)

This thesis is presented in partial fulfilment of the degree
of **Master of Science (Biological Sciences)**

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Schlacher & Dr Michael Payne

Edith Cowan University

School of Science

2018

Declaration

I certify that this thesis does not, to the best of my knowledge and belief:

i. incorporate without acknowledgment any material previously submitted for a degree or diploma in any institution of higher education;
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Caitlin Rae

Abstract

Sandy beaches make up approximately three-quarters of the world's shorelines. They are important ecosystems, hosting abundant invertebrate macrofaunal communities that provide food resource for vertebrate predators such as shorebirds, seabirds, marine mammals and fish. Although possessing a terrestrial appearance, food input on sandy beaches is derived predominantly from the sea. Such food input includes detrital matter, mostly in the form of wrack, and has the potential to support a great diversity of species, as well as stabilising energy fluxes and dynamics of consumer populations. The movement of detritus, along with other vectors such as organisms and nutrients, across ecosystem boundaries can alter productivity and change consumers' distribution, abundance, and growth rates at multiple trophic levels in recipient systems. Ultimately, the input of nutrients and detritus can increase primary and secondary production and alter food web structures and community dynamics in recipient ecosystems, a process termed "spatial subsidy".

Ghost crabs (*Ocypode* spp.) form an important component within beach communities in several places around the world and are part of this trophic complexity. However, little is known of their densities, trophic structure and the role they play as vectors for spatial subsidies through movement of marine derived nutrients inland. The aim of this study was to determine the trophic ecology of the Golden ghost crab (*Ocypode convexa*) and understand what its role is in terms of marine connectivity along the Mid-West coastline of Western Australia. Using ghost crab burrows as a proxy for relative abundance, this study illustrated that *Ocypode* spp. are abundant and reside along beaches with minimal foot- and off-road vehicle traffic and exist in the upper intertidal zone in comparison to zones within the dune environment. In addition, from stomach content (percentage frequency (%F) and percentage volume (%V)) and stable isotope analyses (δ^{13}C and δ^{15}N), as well as laboratory assays, it was found that the Golden ghost crab is an omnivore that consumes a wide variety of plant and animal material. A larger proportion of its diet comprises material derived from the marine environment, compared to material derived from the terrestrial environment. These results support the importance of marine detritus as a spatial subsidy on beaches, and the important role ghost crabs are likely to play as consumers within sandy beach ecosystems, and as vectors for the transfer of marine material through the beach-dune food web.

Acknowledgements

I am grateful to WA Landskills Inc., the School of Science, Edith Cowan University, the Centre for Marine Ecosystems Research and the Hillarys Rotary Marine Club for their support and funding towards this research in terms of equipment purchases, sample analyses, conference attendance and additional field costs associated with this project.

I would like to send out a huge thank you to my talented research supervisors, Professor Glenn Hyndes, Professor Thomas Schlacher and Dr Michael Payne, for their assistance and dedication through every step of this journey. Glenn, thank you for your patience, guidance and sharing your infinite amount of knowledge throughout all aspects of this project, from the field and experimental techniques to the innumerable edits and ‘suggestions’ writing this thesis. It would have not have been possible without you. Thomas, thank you for your wealth of knowledge regarding the topics on sandy beach ecology and ghost crabs, as well as your much-needed feedback whilst writing – you made me a better scientist for it, so thank you. I would also like to express my gratitude towards Michael Payne for his practical advice on ghost crab locations within the Mid-West region, his feedback whilst drafting this thesis and for his approachable demeanour which made meetings a breeze.

I would like to sincerely thank the Meares family in Dongara, Western Australia – Meredith, Mal and Jacquie, as well as Skeeta and Grub (the faithful crab-hunting and cheerful canine companions). Without their permission and immense generosity, I would not have been able to access this unique and important study site. Thank you very much for allowing this research in part to take place on your property.

I would also like to say a special thanks to the Laboratory technicians, OHS and administrative staff within the School of Science. Thank you to Clay Millar, Janine Bruemmer, Jody Harris-Walker and Simon Collins for all your efforts helping prepare for field trips, loaning field equipment (knowing full well you may never see it again once it went into the abyss that is the marine lab!) and for the pointers in regard to stable isotope analysis techniques/protocols (Thanks Janiney). Thanks to Rob Czarnik as well for making sure all the right paperwork and procedures were followed so I could begin my fieldwork and laboratory experiments. Thank you also for the casual employment opportunity, it was a real hoot working with all of you. Thank you to Yvonne Garwood and Lisa Skepper for all their administrative support and keeping me up to date with the correct paperwork.

I would like to take the opportunity to extend my gratitude to my past and present employers from La Vela Restaurant, namely Paul and Mary Wheadon, the team at Bunnings Whitfords, particularly Jenny Sinagra, and the wonderful and recent team at Ningaloo Coral Bay Bayview – Melanie Blake, Jodie & Paul Triner, Deasy, Cairo, Brendan, Adam, Kate, Bernie and Tegan. Thank you for understanding when I needed days off and your constant support throughout my post-graduate degree. To my co-workers at each of these work places, thank you so much for your support, for listening to my incessant rambling about my Masters project and for swapping and or taking my shifts. I have had so much fun working with you all and you are all such wonderful people.

I am indebted to my fellow postgraduate students, the CMER group, colleagues and friends who helped in various field trips, and laboratory and analytical activities. Namely Cairo Rae, Charlie Phelps, Simone Strydom, Leika Vogler, Amber Bennett, Michael Tropiano, Brendan Beard, Lauren Oliver, Zac Born, Roisin McCallum, Carol Sutherland, Jeramie Putman and Jamie Tsakalos– thank you for your assistance on the numerous field trips and in the laboratory. Thank you to Natasha Dunham for your help with GIS; Aiden Fisher, Johnny Lo and James Tweedley for your statistically-inclined minds; and to John Huisman, Kathryn McMahon, Kristina Lemson, Giulia Perina, Federico Vitelli and Aldo Turco for your assistance identifying minute pieces of macroalgae, animal material and other. I would especially like to thank Charlie Phelps and Simone Strydom. Charlie, thanks for making me laugh so much throughout my entire journey. You are a wonderful colleague and friend and I feel so lucky to have had your help in the field and in the office. Simone, thank you so much for your help every step of the way, from my first pilot field trip to Dongara until the last few edits of my written thesis. You are a very inspiring person to work alongside and I appreciate the time and effort you contributed to my project.

Last, but not least, I would like to thank my family. To my amazing parents, Linda and John Rae, thank you for enabling me to go to university in the first place, for the many discussions over my Masters, for the help entering data, getting enthusiastic about marine topics and the environment, and for all the cups of tea and home-cooked meals whilst completing this thesis. I would not have been able to do this without both of you and I love you so much. To my wonderful twin sister Cairo Rae, thank you for being there every step of the way. Thank you for helping in the lab and visiting in the field, for data collection and entry (however hard to understand) and making me laugh whenever over anything. I love you so much and you’re an awesome sister!

Thank you also to my best friend, Zoe Sheffield van Meirlo – you are my rock. Thank you for being there for me throughout the highs and lows. No matter what, I always know you will be there.

I would like to sincerely thank all of you for your support and assistance. This thesis would not have been possible without any of you and stands as a testament to your support.

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1 Introduction

1.1 Ecology of sandy beaches

Sandy beaches are highly dynamic habitats, physically defined by the interaction of sand, waves, and tides (Brown & McLachlan 1994). Beaches dominate the world's coastline, making up around 75% of the globe's land-sea boundaries (Gonçalves & Marques 2011), and form an essential habitat for a diversity of species, including numerous invertebrates, fishes, birds, and mammals (Dugan *et al.* 2000). Although having a terrestrial appearance, organic matter supporting beach food webs comes almost exclusively from the sea (Brown & McLachlan 1994; Gonçalves & Marques 2011). This is particularly the case on dissipative beaches, which are usually flat with breakers far from the intertidal zone dissipating their force gradually along wide surf zones (Branco *et al.* 2010; Short 2012), resulting in large allochthonous inputs of energy and nutrients frequently occurring on these types of beaches (Brown & McLachlan 1994; Short 2012).

Sandy beach food webs are almost completely underpinned by trophic subsidies from the sea, mainly in the form of phytoplankton and the stranding of larger plants and animal carcasses. Conventionally, beach food webs have been categorized into three components: 1) interstitial invertebrates, numerically dominated by small meiofauna within the sand matrix; 2) the microbial loop; and 3) macroscopic organisms comprising larger invertebrates, birds, and fishes (Bergamino *et al.* 2011). Detritus (decomposing organic matter) is an important input to all compartments in beach food webs (Wallace *et al.* 1999). Carbon, fixed by photosynthetic organisms, can be made available to other ecosystem components via herbivores or detritivores (Enriquez *et al.* 1993), where the detrital path acts as a major determinant for the flow of carbon in ecosystems (Enriquez *et al.* 1993). Decomposition of plant detritus is principally conducted by bacteria and fungi and the rate of this process depends on all the factors influencing their activity (Enriquez *et al.* 1993). During decomposition, detritus can be a major food resource for many mobile organisms, including meiofauna such as copepods, and therefore transport of carbon can easily occur across large distances in coastal regions (Enriquez *et al.* 1993).

Detrital inputs can support a diversity of species, and modulate energy fluxes and the dynamics of consumer populations (Moore *et al.* 2004). In beach ecosystems, the movement of detritus and other forms of organic matter across ecosystem boundaries, termed ‘spatial subsidies’, can significantly alter productivity and change the distribution, abundance, and growth rates of consumers at multiple trophic levels (Polis & Hurd 1996; Polis & Strong 1996; Hyndes *et al.* 2014). Cross-boundary spatial subsidies vary enormously among ecosystems and several factors can influence exchange rates (Polis *et al.* 1997). Firstly, the physical characteristics of the recipient habitat (topography and vegetation) and the trophic position at which a subsidy enters a food web can determine how much the recipient habitat will be affected by the subsidy (Anderson & Polis 2004; Witman *et al.* 2004). The level of subsidy can also be influenced by: 1) the rate of consumption of the vector by a population in the recipient system and the mobility of the consumer (Ostfeld & Keesing 2000); 2) the nature of the vector available for transport (e.g. detritus, dissolved nutrients); and 3) the nature of boundaries between habitats (e.g. permeability) (Cadenasso *et al.* 2004; Witman *et al.* 2004). For example, cross-boundary subsidies can easily permeate into sandy beach ecosystems and can strongly affect the recipient system due to its low *in-situ* productivity, i.e. no autochthonous primary production (Power & Dietrich 2002; Liebowitz *et al.* 2016).

Substantial amounts of marine macrophytes regularly become detached from reefs and seagrass meadows, and are transported by waves and tides to the surf zones of beaches (Wernberg *et al.* 2006). Accumulations of this plant material form ‘wrack’ that is a key energy input to many beach food webs. Depending on beach morphodynamics, that is wave height and period combined with sand grain size, wrack can extend beyond the swash zone and foredune, and into the dune swale (Dugan *et al.* 2015). Kelp transported to surf zones has been shown to drive secondary production in shoreline habitats with inputs providing ‘spatial trophic subsidies’ for consumers (Crawley *et al.* 2009). On shores with sizeable amounts of wrack, beach-cast macrophytes can structure faunal assemblages, influencing abundance, biomass, species composition and trophic pathways; most of these effects are positive, generally attributed to wrack providing food and increasing physical habitat complexity (Ince *et al.* 2007; Olds *et al.* 2017).

Movement of nutrients across ecosystem boundaries, including the beach-dune interface, requires a vector and force to move matter (Hyndes *et al.* 2014). On sandy beaches, physical forces that move organic matter onshore are primarily wind, currents, tides, and waves (Lastra *et al.* 2008; Baring *et al.* 2014). These physical forces can deposit large amounts of stranded marine matter (i.e. wrack or carrion) on the shore that forms a crucial resource for beach consumers (Dugan *et al.* 2000; Baring *et al.* 2014). However, it is not only this passive flow of detritus that influences recipient habitats, but the active movement of animal vectors, such as flying insects (e.g. kelp flies), which feed on detritus and extend the influence of the detritus on terrestrial systems (Mellbrand *et al.* 2011).

1.2 Ghost crabs (*Ocypode* spp.)

Ghost crabs (*Ocypode* spp. (Weber, 1795)) are mobile semi-terrestrial invertebrates that normally constitute an important component of beach communities in tropical and subtropical habitats (Lucrezi & Schlacher 2014). They are efficient bioturbators on beaches and are a key link in food webs, frequently being important predators, whilst also providing food for larger vertebrate consumers (e.g. fish, birds) feeding at the land-sea interface (Lucrezi & Schlacher 2014). A characteristic of ghost crabs are their fossorial habits: they create deep and complex burrows and alternate between surface activity and being in underground microhabitats (Lucrezi & Schlacher 2014). They have evolved a range of physiological, morphological and behavioural adaptations that allow them to occupy broad beach to dune gradients (Lucrezi & Schlacher 2014). Ghost crabs can inhabit a range of beaches from sheltered coves and estuarine sandflats to fully-exposed ocean shores (Morrow 2012; Schlacher *et al.* 2013a).

Across the beach-dune gradient, ghost crabs are found in a wide band from the mid to lower intertidal zones to 400 m inland (Lucrezi & Schlacher 2014). Both the distributional extent and the boundaries vary greatly among species: some species can occupy the full dune-beach profile, e.g. *O. quadrata* (Fabricius, 1787), whilst others only occur on the non-vegetated part of the beach seawards of the dunes (e.g. *O. fabricii* (H. Milne Edwards, 1837)), (Lucrezi & Schlacher 2014). Other species, such as *O. ceratophthalma* (Pallas, 1772), can occur in both the supratidal and intertidal zones (Lucrezi & Schlacher 2014). Some species show fairly restricted distributions, such as *O. cordimanus* (Latreille, 1818), which mainly occurs in supratidal areas. *Ocypode convexa* (Quoy & Gaimard, 1824), which occurs in Western Australia, is reported to burrow around high-tide levels with some individuals extending a ‘short distance’ inland (Jones & Morgan 1994). In areas where *O. ceratophthalma* coexist with *O. convexa*, the distribution of the *O. convexa* shifts further upslope towards and into the dune areas (Lucrezi & Schlacher 2014).

Ghost crabs are omnivorous with catholic food choices (Lucrezi & Schlacher 2014), capable of exploiting an extraordinary broad range of food (Chartosia *et al.* 2010; Lucrezi & Schlacher 2014). This broad trophic ambit is reflected in five feeding modes that have been identified in ghost crabs: 1) ‘deposit feeders’ that extract benthic microalgae from the sand with up to 70% efficacy (Lucrezi & Schlacher 2014); 2) ‘carnivores’ that can be an important invertebrate predator on sandy beaches, with up to 90% of their diet consisting of live prey, comprising mostly of shallow-burrowing macroinvertebrates, such as isopods and annelids (Wolcott 1978); 3) ‘detritivores’ that can readily consume plant detritus deposited on beaches, ingesting anything from seagrass and macroalgae to seeds, pods and terrestrial plant matter (Lucrezi & Schlacher 2014); 4) ‘scavengers’: who readily consume animal carcasses, as demonstrated by Schlacher *et al.* (2013b), who showed that they respond rapidly to, and aggregate around, carrion inputs; and 5) ‘cannibals’ which are common especially when other food items are rare (Lucrezi & Schlacher 2014).

Five species of ghost crabs occur in Australia (Jones & Morgan 1994; Sakai & Türkay 2013; Lucrezi & Schlacher 2014): *O. convexa* (Golden ghost crab), *O. ceratophthalma* (Horn-eyed ghost crab), *O. cordimanus* (Smooth-handed ghost crab), *O. pallidula* (Hombron & Jacquinot, 1846) and *O. fabricii* (Figure 1.1). Four species occur along the Western Australian (WA) shoreline (i.e. *O. convexa*, *O. ceratophthalma*, *O. cordimanus* and *O. fabricii*) (Sakai & Türkay 2013). In this region, they have been reported on both sheltered and exposed beaches (e.g. Geraldton, WA) as well as muddy subtidal habitats (Jones & Morgan 1994). Anecdotal evidence does suggest that *O. convexa*, in particular, is the most abundant species within WA.

Many of the more exposed sandy beaches can contain large accumulations of wrack based on deposition of allochthonous inputs of organic matter from the sea, which is known to subsidise beach food webs and include several types of stranded macrophytes in the region (Ince *et al.* 2007; Mellbrand *et al.* 2011). Species of ghost crabs may feed on wrack, with impacts on the provision of spatial/cross-boundary subsidies through the processing of organic detritus and the predation of ghost crabs by other organisms, including higher-order organisms (Lucrezi & Schlacher 2014).

Figure 1.1: Distributions of four of the five species of ghost crabs which occur along the Australian coastline (adapted from Lucrezi and Schlacher (2014)). Although not indicated, *Ocypode pallidula* distributions are constrained to islands off the Queensland coast, such as Lady Elliot and Heron Islands (Sakai & Türkay 2013).

As illustrated above, ghost crabs can be highly abundant (Schlacher *et al.* 2011), play both a predatory and scavenger role within the food web on sandy beaches (Silva & Calado 2013), and exhibit high mobility across beach systems (Lucrezi & Schlacher

2014). Although the ecology of some species of ghost crab has been explored, very little is known of *Ocypode convexa* (Golden ghost crab). Its general ecology remains unknown, including its distribution and abundance, and its role in food webs on sandy beaches and terrestrial habitats, such as sand dunes (Morrow 2012; Lucrezi & Schlacher 2014). Due to the high biomass of wrack that can accumulate on sandy beaches in temperate Western Australia (Wells 2002), the generalist diet, high abundances, and extensive mobility exhibited by other ghost crab species, *O. convexa* possesses the potential to influence the movement of marine-derived nutrients across the beach-dune gradient.

Beach and coastal dune systems are becoming increasingly exposed to a broad range of anthropogenic pressures from either side of the coastal ecotone, for example, climate change from a marine perspective and urban development from the terrestrial biome (Schlacher *et al.* 2016). To conserve and mitigate these pressures requires interventions, which need to be reinforced by reliable data in terms of severity and frequency of adverse ecological impacts (Schlacher *et al.* 2016). Ghost crabs are recognised as appealing ecological indicators, as they are widespread throughout subtropical and tropical regions, are locally abundant and large. Sampling them, therefore, requires minimal technical methods. In addition, their taxonomy is well known, identification is reasonably simple, and they construct semi-permanent burrows which are clearly visible from a beach perspective (Schlacher *et al.* 2016). Evidence of anthropogenic pressures is often obtained by measuring the response of ‘indicator species’, such as ghost crabs, which is ultimately useful in assessing ecosystem and environmental integrity (Branco *et al.* 2010; Lucrezi & Schlacher 2014; Schlacher *et al.* 2016). Thus, to understand if sandy beach ecosystems are healthy, there is a fundamental requirement to first understand the ecology of such a bio-indicator (Strachan *et al.* 1999). While ghost crabs are recognised as good indicators of beach health, there are some aspects of their ecology which evidently require further investigation. Understanding these aspects would provide access to new metrics for assessment, as well as expose the dynamics between species ecology and human stressors/impacts. Given the putative importance of the trophic ecology of ghost crabs for spatial subsidies in coastal ecotones, and how this remains poorly understood renders it paramount to carry out an investigation to fill such a knowledge gap. Understanding this role is particularly important since crab densities can be significantly impacted by off-road vehicle (ORVs) activities, for example by sand compaction and getting crushed by vehicles on the beach, and via consumption by invasive predators, such as foxes (Brown & McLachlan 1994; Schlacher *et al.* 2012).

1.3 Aim and rationale

The broad aim of this study was to determine the relevance of the Golden ghost crab, *Ocypode convexa*, as a consumer and potential vector for the transport of marine nutrients across sandy beach and dune systems in temperate Western Australia. To establish this, the specific objectives of the study on *O. convexa* were to determine the: 1) patterns in burrow densities along a gradient between the upper tidal and secondary dune zones; 2) diet and sources of production; and 3) feeding preference for marine- and/or terrestrial-derived material.

The outcomes of this research aim to contribute to the building body of knowledge on beach ecology and ghost crab ecology, by providing new information on the trophic ecology of ghost crabs, on their relevance in terms of spatial subsidies, and on the general ecology of a poorly known ghost crab species. The research will also inform decision-making by providing data, which can be used to propose the development of management plans for vulnerable sections of the coastal zone.

2 Materials and methods

2.1 Study sites

The distribution and feeding ecology of *O. convexa* were studied at three beaches in Dongara, Western Australia. Whilst *O. convexa* was the only ghost crab species seen in large densities, other ghost crab species (*O. ceratophthalma* and *O. fabricii*) were occasionally seen (per obs. C. Rae). They are representative of exposed beaches, which are prevalent along much of the west coast of Australia, with moderate to heavy wave action, which, depending on season, causes steep beach slopes. They are intermediate morphodynamic types, with 10 – 30 m wide beaches (surf zone to foredune), backed by primary and secondary dune systems, with exposure to predominately south-westerly winds reaching up to 50 km/hr and 1.5 – 2 m swells from a west to south-westerly direction. Beaches chosen were identified as Meares beach (site 1), Seven Mile beach (site 2) and Getaway beach (site 3) (Figure 2.2). Meares and Seven Mile beaches consisted of wide (25 – 30 m) beach profiles, with low (5 – 10 m high) primary dune systems and high secondary dune systems. In comparison, Getaway beach consisted of a narrow beach profile with steep and high (15 – 20 m) primary dune and secondary dune systems. These beaches were sampled in June 2015, September 2015 and February 2016, and were selected based on their minimum interference to natural distributions and processes by urban development, ORV use and beach visitors.

Figure 2.2: Location of the 3 study sites on the Mid-West coast of Western Australia where samples were collected at Meares (Site 1), Seven Mile (Site 2) and Getaway (Site 3) beaches.

2.2 Distribution and density of *Ocypode* spp.

The relative abundance of ghost crabs in different parts of the beach-dune system was estimated using counts of active burrow entrances as a proxy (Lucrezi *et al.* 2009).

However, since the distinguishing characteristics of different ghost crab species' known also to burrow openings cannot be determined with confidence, all burrow counts were reported at the genus level (*O. ceratophthalma* and *O. fabricii* seen along sampling beaches, per obs. C. Rae).

Based on pilot sampling and observed *O. convexa* activity, burrow entrances were counted in replicate belt transects at five locations along the beach-dune gradient: the upper intertidal [UI], base of primary dune [BPD], top of primary dune [TPD], primary dune swale [PDS], and the top of secondary dune [TSD]) (Figure 2.3). Zones were determined based on morphological features, such as the swash zone, vegetation zones, and swales between the dunes.

At each location and site, six 30 m x 3 m belt transects were positioned, with the longer axis being parallel to the shoreline. At each site, individual belt transects were spaced ca. 200 m apart alongshore. Only active burrow openings were counted, judged by the presence of fresh tracks surrounding the entrance, excavated sediment next to the opening, or both (Lucrezi *et al.* 2009). Counting was done at first light over three days, producing a total of 30 transects per site and sampling time. In addition, ten 1 m^2 quadrats were placed randomly within transects, with two in each zone. This was to collect data on cover of wrack and to determine dominant species within wrack and of dune vegetation (Appendix: Table C).

Soil moisture was also recorded after preforming burrows counts using a digital soil moisture metre (model PMS-714). The sand moisture was measured within each zone at the 15 m mark at each site.

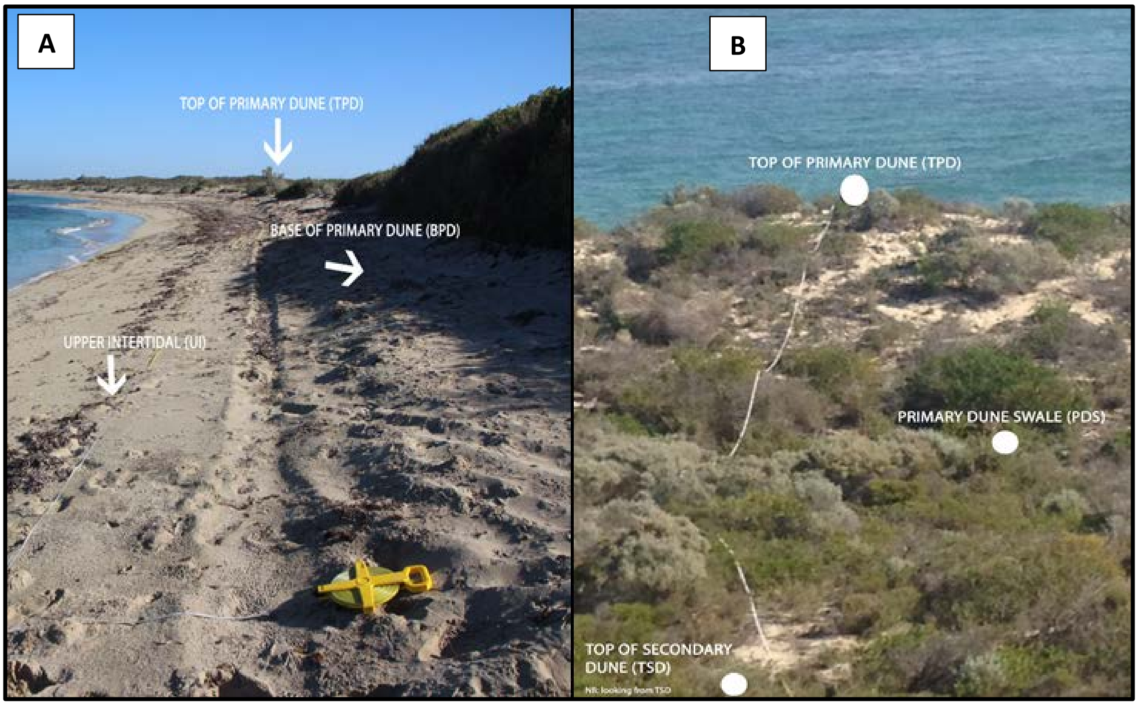

Figure 2.3: A) Illustrates the location of the upper intertidal (UI) and base of the primary dune (BPD) zones; **B)** Location of the terrestrial zones – top of the primary dune (TPD), primary dune swale (PDS) and top of the secondary dune (TSD).

2.3 Dietary composition of *Ocypode convexa*

Both stomach content analysis (SCA) and stable isotope analysis (SIA) were used to identify the principal types and sources of ingested and assimilated food items. For both approaches, I sampled 90 adult *O. convexa* (19 - 26 mm in carapace width) (Fig. 2.4), 30 each in June 2015, September 2015 and February 2016. Surface-active adults were hand-collected from the upper intertidal zone. Adults were selected so that adequate muscle tissues were available for SIA. In the field, individuals were stunned *in-situ* by placing them in an ice slurry; once euthanised, they were injected with 70% ethanol into the stomach to preserve ingested items; this did not affect any muscle tissue outside the stomach cavity (Kolts *et al.* 2013). Specimens were transported on ice to the laboratory and processed for SIA within 72 hours of collection.

Figure 2.4: *Ocypode convexa*: dorsal, ventral and frontal aspects.

To obtain a representative sample of potential dietary items of crabs, the dominant (in terms of biomass, cover, and distribution) of marine and terrestrial autotrophs and invertebrates were collected across zones. As described above, ten 1 m^2 quadrats were placed randomly, two quadrats per zone, at each site. From these, wrack material (algae and seagrass) and live invertebrates were hand-collected and terrestrial vegetation cut above the ground. We analysed three marine autotrophs (*Ecklonia radiata*, kelp; *Amphibolis* spp., seagrass; *Jania rosea*, red alga), two dune plants (S*caevola crassifolia*, thick-leaved fan-flower; *Atriplex* sp., saltbush), and two invertebrates, a snail being widespread in the coastal dunes (*Theba pisana*, sand hill snail) and species of Talitridae (amphipods).

Ninety stomachs were dissected (ten crabs per site x three sites x three sampling times) by first detaching the jaws and then gently removing the stomach whilst holding the oesophagus cartilage with forceps. All stomach content was preserved in 70% ethanol. Forty-five cheliped muscles were also removed (five individuals per site x three sites x three sampling times) from randomly selected male crabs for SIA. Males were chosen because they assimilate a greater proportion of their diet into somatic tissues than females, who direct their diet partly, depending on time of year, to form lipid-rich eggs (Kolts *et al.* 2013).

Samples of potential diet items were rinsed in Milli-Q water, dried (60°C, 48 hr), ground and encapsulated in tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis. Epiphytes were removed from seagrass leaves, and snails extracted from their shells. For $\delta^{13}C$ analysis, amphipods were acid-treated (1N HCl until effervescence ceased) to remove inorganic carbon present in exoskeletons. The untreated portion of amphipods was analysed separately for $\delta^{15}N$ (Crawley *et al.* 2009). Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were measured on a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer at the Stable Isotope Facility at the University of California, Davis. Isotope ratios were calculated as deviations from the international limestone standard Vienna Pee Dee Belemnite (VPDB) ($\delta^{13}C$ and $\delta^{15}N$) in part per thousand (‰): $dX = [(R_{sample}/R_{standard}) - 1] * 1000$, where X is the heavier isotope of the element (^{13}C or ^{15}N) and R is the isotopic ratio ($^{13}C/^{12}C$ and $^{15}N/^{14}N$).

Stomach fullness was visually graded using five broad categories: empty (0%); traces of food to roughly a quarter full (1-25%); a quarter to half full (26-50%); half to three-quarter full (51-75%); and three-quarter to full (>76-100%) (Chartosia *et al.* 2010; MacArthur *et al.* 2011). Stomach contents were placed in a petri dish with 5 millilitres of Milli-Q water and examined with a Leica CLS 150 dissecting microscope at 80x magnification (Kolts *et al.* 2013). Contents were then analysed using the numeric points system (Hyslop 1980), where contents were placed into a petri dish and spread evenly on a grid. The taxon present at each of the 100 systematically placed points were identified to the lowest possible taxonomic resolution (Branco *et al.* 2010), and the percentage of each food item was determined. The percentage of each food item was expressed as a percentage volume based on the number of points on which it was found respectively for each stomach.

2.4 Feeding assays of *Ocypode convexa*

To test whether ghost crabs prefer marine or terrestrial organic matter, a number of laboratory-based feeding assays were conducted that comprised both choice (i.e. food preference) and no-choice experiments. Both types of assays used five food items that were common on the beaches or coastal dunes in the study region: 1) blades of the beach-cast marine kelp *Ecklonia radiata*; 2) leaves of the marine seagrass *Amphibolis* spp.; 3) leaves of thick-leaved fan-flower, *Scaevola crassifolia,* a plant common in the coastal dunes; 4) the flesh from *Theba pisana*, a sand hill snail which was the most abundant in terms of terrestrial fauna within the study region; and 5) the flesh from sandy sprat, *Hyperlophus vittatus*, a typically abundant fish species in the surf zones within the study region (Ayvazian & Hyndes 1995), which was used to represent marine carrion that can wash up onto beaches.

The feeding assays used adults (with carapace widths between 19 - 26 mm) from both the non-vegetated part of the beach (n = 60) and the coastal dunes (n = 60). Assays were established in 10 L aquaria that either housed a single crab (treatments) or no consumer (controls). In the choice experiments, five food items were added, each weighing 10 g (wet weight (ww)) and placed randomly within the aquaria (50 g ww of food in total). In the no-choice experiments, a single food item (10 g ww) was presented per replicate to measure consumption rates.

Food items were randomly collected across the 3 sites within the study region. Food items used in the assays were kept frozen during transit and thawed for 12 hours prior to the commencement of feeding assays. Crabs used in the assays were captured and transported to the laboratory in individual aerated containers housed in a cooler with ice bricks to keep them subdued whilst in transit for 4 hours. In the laboratory, individuals were housed in fourteen 80 L aquaria, which were separated to house individual crabs whilst maximising on space and availability of aquaria. Each aquarium contained 40 L of washed river quartz sand and a 12:12 day and night cycle was also established to mimic their natural environment. In addition, 5 L of seawater was added every 5 hours (or until conditions were dry) to aquaria to feign incoming high tides and prevent crabs from desiccating. A mixture of potential food sources, including brown and red algae, seagrasses (*Amphibolis* spp. and *Posidonia* spp.) and fish carrion, were provided to sustain crab specimens. However, prior to assays commencing, crabs were fasted for 24 hours before being introduced to the arenas and presented with food.

In the choice assay, once each food type was thawed, it was blotted dry and 10 g (ww) of each source placed in both the treatment and control (no crab) experimental units. Twenty crabs were starved for 24 hours before being placed in the experimental arenas, after which consumption in treatments was monitored every 30 minutes over 8 hours, starting at 09:00 each day. Treatments were terminated when ≥50% of the tissue of at least one food source had been consumed. Each food source from each replicate for both treatment and control were rinsed in seawater to remove any sand, then its blotted weight recorded to the nearest 0.01g. Upon completion of the feeding assay, crabs remaining in treatment replicates were released back into the wild at the site of collection.

In the no-choice experiments, a hundred crabs were starved for 24 hours before being placed in the experimental arenas and presented with a single type of food item. Treatment replicates for each of the five food types were randomly allocated to aquariums, as was the sequence in which crabs were offered different food types over the course of the experiment. Termination of no-choice experiments and measurements of consumption rates followed the same procedure as for the choice experiments.

2.5 Data analyses

Spatial patterns in the density of ghost crab burrows were analysed with a mixed-model permutational analysis of variance (PERMANOVA) in PRIMER 7 & PERMANOVA software package using Euclidean distance, with the factors 'ZONE' across the dune-beach gradient (fixed), 'SITE' nested within zone (random), and 'TIME' (random).

A Pearson correlation was also performed in IBM SPSS Statistics 24 to test whether there was an association between *Ocypode* spp. densities and average soil moisture content (%) at each zone. Data were square-root transformed.

PERMANOVA was performed to identify significant differences in stomach content composition of crabs between sites and sampling times, followed by a SIMPER analysis to determine the food items that contributed most to the differences between sites and times. This was further complemented by non-metric multidimensional scaling (nMDS) of volume and frequency of occurrence of diet items across all individuals from whom stomachs were extracted and examined, as well as to illustrate spatial and temporal differences and or similarities in diet composition. The use of non-metric multidimensional scaling in comparison to metric was to minimise the criterion stress and allow for an accurate resemblance scale (Anderson *et al.* 2008).

The Bayesian isotope mixing model framework, MixSIAR, was used to calculate the likely contribution of different food sources to assimilated carbon and nitrogen in the ghost crabs body tissue. MixSIAR estimates probability distributions of source contributions to consumer diets while accounting for uncertainty in source isotope signatures and trophic fractionation (Stock & Semmens 2015). The probability distributions are estimated using a Markov Chain Monte Carlo (MCMC) algorithm (Stock & Semmens 2015).

Trophic fractionation rates are known to vary between species with differences in diet types and dietary studies (Post 2002; Vanderklift & Ponsard 2003). However, fractionation experiments could not be performed within the limits of this project. Fractionation values of decapod crustacean species were obtained from the literature: 1) brown and red algae: $\Delta^{13}C = 2.01 \pm 0.86$, $\Delta^{15}N = 2.80 \pm 0.98$ (Gates 2006); 2) angiosperms and terrestrial plants: $\Delta^{13}C = 1.90 \pm 0.07$, $\Delta^{15}N = 6.00 \pm 0.10$ (Rudnick & Resh 2005); and 3) other diet items: $\Delta^{13}C = 2.17 \pm 0.15$, $\Delta^{15}N = 3.77 \pm 2.42$ (Waddington & MacArthur 2008; Guest *et al.* 2009).

Nutritional values were also calculated based from stable isotope analysis data, which led to the determination of C:N ratios.

For the feeding assays, consumption rates (mg/individual/h/g body weight) were calculated as: $(H_iC_f / C_i) - H_f$, where H_i and H_f were initial and final wet weights, respectively, of food sources presented to crabs, and C_i and C_f were wet weights of paired controls before and after. Replicates in which consumption was zero or the animals died were discarded as they did not provide sensible information on feeding preferences (removal of replicates where total consumption was ≤ zero did not affect statistics) (Goecker & Kall 2003; Crawley & Hyndes 2007).

The choice assays were analysed using a Friedman non-parametric test of ranks (Peterson & Renaud 1989; Jiménez 2015), followed by a *post hoc* Wilcoxon signed-rank test (Wilcoxon 1945) (IBM SPSS Statistics 24). To minimize Type I errors in multiple pair-wise comparisons, a more stringent p-value of 0.02 was used; Bonferroni adjustments were not used as they can increase Type II error rates (Cabin & Mitchell 2000).

The no-choice assay data were analysed using a two-way ANOVA, using the factors food source (random) and zone (fixed). Data was square-root transformed and tested for homogeneity of variance with a Levene's test. The two-way ANOVA was followed by *post hoc* Tukey HSD tests, to test for significant effects for all types of food sources (IBM SPSS Statistics 24).

3 Results

3.1 Patterns in *Ocypode* spp. densities

Burrows of *Ocypode* spp. were present across the entire width of the beach (upper intertidal and base of primary dune zones), where they were recorded in 96% of all transects, but were rarely found in the dune zones (Fig. 3.5). This resulted in a significant Zone effect ($p = 0.001$) (Table 3.1). However, there was also a significant Site (nested in Zone) effect ($p = 0.006$), and Zone by Time ($p = 0.002$) and Site by Time ($p = 0.001$) interactions, indicating that the burrow densities differed across Site, and that the Zone and Site effects were dependent on time of year. These were mainly due to the shifts in densities between the upper intertidal and base of the primary dune zones among times of year (Fig. 3.5). The mean density of crab burrows in the upper intertidal zone in June 2015 were 44 - 115 burrows per 100 m^2, but densities decreased in September 2015 and February 2016 to 22 - 73 and 26 - 64 burrows per 100 m^2, respectively. The average density of crab burrows at the base of the primary dune was at its lowest in June 2015 with 7 - 10 burrows per 100 m^2, however this increased in September 2015 with 10 - 18 burrows per 100 m^2, then again in February 2016 with 27 - 58 burrows per 100 m^2.

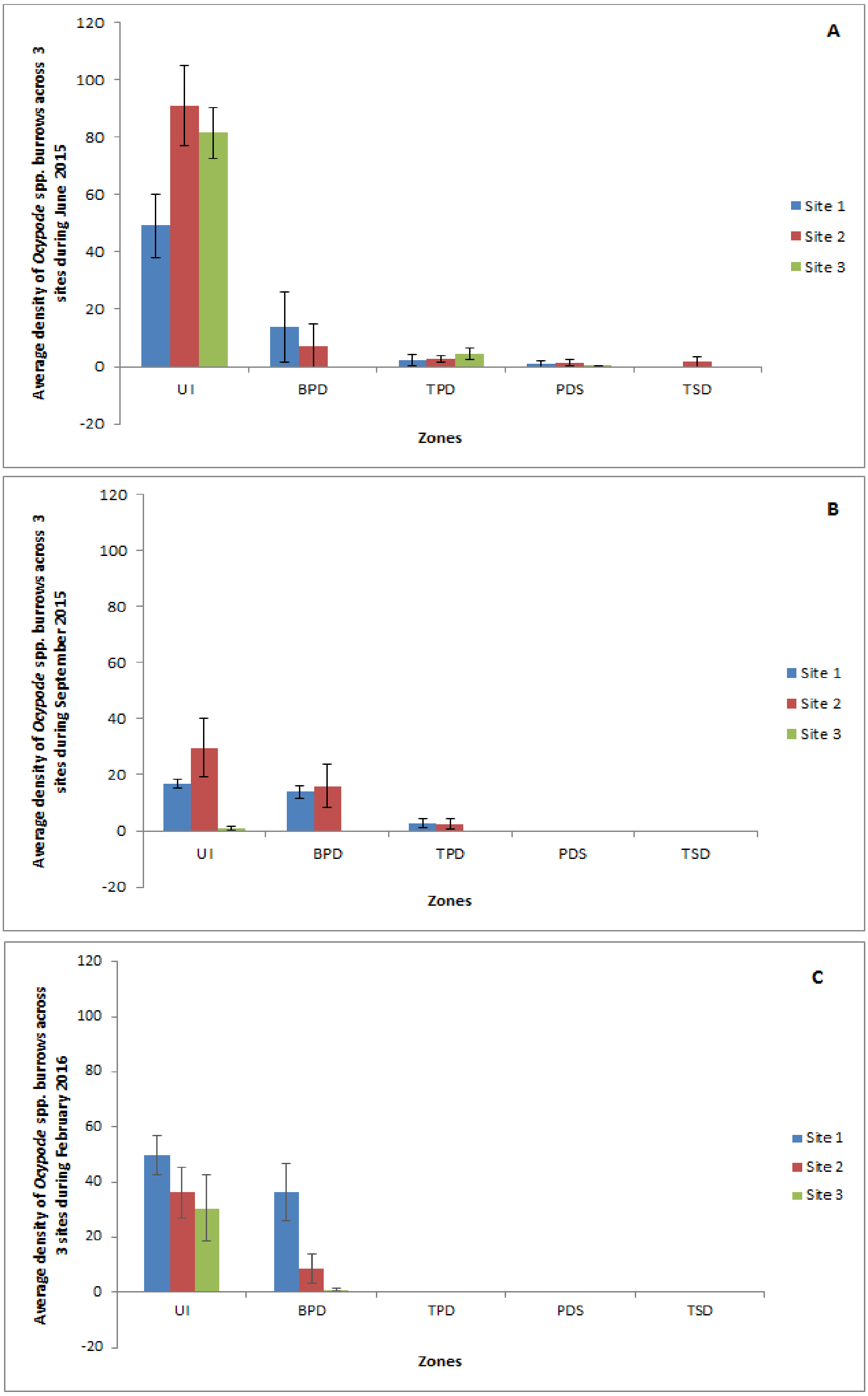

Figure 3.5: Mean density (± SE) of *Ocypode* spp. (burrows/100 m^2) at each of the three study sites across the 5 zones (upper intertidal [UI], base of primary dune [BPD], top of the primary dune [TPD], primary dune swale [PDS] and top of the secondary dune [TSD]) and across 3 different sampling times: June 2015 (A), September 2015 (B) and February 2016 (C).

Table 3.1: Results of a nested PERMANOVA testing differences ($p \leq 0.05$) in densities of *Ocypode* spp. burrows across 5 zones. Mixed design with Zone (Fixed factor, 5 levels), Site nested within zone (Random factor, 3 levels), and time of the year (Random factor, 3 levels). Data were log-transformed.

	df	**MS**	**Pseudo-F**	**P(perm)**	**Unique perms**
Zo	4	94.001	7.2067	**0.001**	999
Ti	2	3.5875	2.3641	0.128	999
Si(Zo)	10	5.4313	3.5791	**0.006**	997
Zo x Ti	8	7.8228	5.1551	**0.002**	998
Si(Zo) x Ti	20	1.5175	2.9731	**0.001**	999
Res	225	0.51041			

3.2 *Ocypode convexa* stomach content analyses

Ghost crabs ingested a wide variety of food items, with 40 distinct food items being distinguished in stomachs (Table 3.2). Based purely on material found in stomachs, ghost crabs appeared to be overwhelmingly algivores: all but one individual had some type of algal material in the stomachs, whilst a single crab was found to be a pure carnivore (i.e. had no plant material in stomach; Table 3.2). Brown algae (Class Phaeophyceae) were the most frequently-ingested food item and also comprised the highest mean volume (Table 3.2). This included material from the family Sargassaceae and kelp of the genus *Ecklonia* that equally ranked second in terms of the frequency of occurrence and their mean volume (Table 3.2). After brown algae, unidentified plant material from Magnoliophyta ranked fourth, occurring in 29% of stomachs at an average volume of 8.8% (Table 3.2). Animal matter was found in over half of the stomachs analysed for content, beetles were the most frequently observed animal food in the analysed crabs' stomachs, being found in 38% of crabs and making up 5.6% of the crabs' stomach content (Table 3.2). The red alga *Jania rosea* was less common (FO = 27%) compared with either kelp (FO = 60%) or Sargassaceae (FO = 64%) yet ranked as fifth most frequent item. Individual seagrass species were neither very common, nor did they contribute large amounts to the crabs' stomach material (*Halophila spinulosa*: FO = 1%, Vol = 0.1%; *Posidonia ostenfeldii*: FO = 11%, Vol = 1.7%). Food items of terrestrial origin (e.g.

various insects) occurred in half of individuals, comprising on average 12% of stomach volume.

Table 3.2: Frequency of occurrence (%F) and percentage volume (%V) of dietary items (OTU) found in the stomachs (n = 90) of adult *Ocypode convexa* pooled from data summed over 3 sampling times (June 2015, September 2015 and February 2016) and 3 sites.

Higher Taxon	**Operational taxonomic units (OTU)**	**Frequency of Occurrence (%F)**	**Volume (%V) (+/- se)**	**Volume 95% CI**
'Plant Matter'		**99%**	**88.74 +/- 2.55**	**(83.75 - 93.73)**
'Algae'		**99%**	**74.33 +/- 3.09**	**(68.27 - 80.39)**
'Brown Algae'		99%	64.02 +/- 3.34	(57.46 - 70.57)
Ochrophyta, Phaeophyceae	Phaeophyceae	78%	26.47 +/- 2.97	(20.64 - 32.29)
Dictyotales	*Lobophora* spp.	2%	0.05 +/- 0.04	(-0.03 - 0.12)
	Dictyota spp.	7%	0.42 +/- 0.25	(-0.07 - 0.91)
	Distromium spp.	10%	0.77 +/- 0.39	(0.01 - 1.53)
Fucales	*Cystoseira* spp.	1%	0.26 +/- 0.26	(-0.25 - 0.78)
	Sargassaceae	64%	14.55 +/- 2.38	(9.88 - 19.21)
	Sargassum spp.	12%	1.61 +/- 0.53	(0.57 - 2.65)
Laminariales	*Ecklonia* spp.	60%	19.9 +/- 2.89	(14.23 - 25.57)
'Red Algae'		33%	7.65 +/- 2.06	(3.61 - 11.69)
Rhodophyta, Florideophyceae, Rhodomelaceae	*Dasyclonium* spp.	9%	0.38 +/- 0.16	(0.06 - 0.69)
Rhodophyta, Florideophyceae, Corallinaceae	*Metagoniolithon* spp.	3%	1.06 +/- 1.01	(-0.93 - 3.04)
	Jania spp.	3%	0.31 +/- 0.19	(-0.07 - 0.68)
	Jania rosea	27%	5.91 +/- 1.74	(2.49 - 9.33)
'Green Algae' (Chlorophyta)	Chlorophyta	19%	2.67 +/- 0.95	(0.8 - 4.53)
'Vascular Plants'		**49%**	**14.41 +/- 2.36**	**(9.79 - 19.04)**
Seagrass		12%	1.84 +/- 0.86	(0.15 - 3.53)
Posidoniaceae	*Posidonia ostenfeldii*	11%	1.71 +/- 0.86	(0.03 - 3.39)
Hydrocharitaceae	*Halophila spinulosa*	1%	0.13 +/- 0.13	(-0.12 - 0.38)
Magnoliophyta, Poaceae	Poaceae unidentified spp.	8%	0.85 +/- 0.4	(0.07 - 1.63)
Tracheophyta, Alismatales	Alismatales	3%	0.17 +/- 0.14	(-0.1 - 0.43)

Tracheophyta (Phylum)	Tracheophyta	20%	2.72 +/- 1.25	(0.27 - 5.18)
Magnoliophyta (Phylum)	Magnoliophyta	29%	8.84 +/- 1.84	(5.24 - 12.45)
'Animal Matter'		**58%**	**11.26 +/- 2.55**	**(6.27 - 16.25)**
Porifera	Porifera	9%	0.22 +/- 0.08	(0.06 - 0.37)
Mollusca, Gastropoda	Gastropoda	2%	0.05 +/- 0.04	(-0.03 - 0.14)
Crustacea	Crustacea	8%	0.34 +/- 0.17	(0 - 0.68)
'Insects'		49%	10.22 +/- 2.5	(5.32 - 15.13)
Coleoptera	Coleoptera	38%	5.64 +/- 1.46	(2.79 - 8.49)
Hymenoptera	Hymenoptera	13%	0.74 +/- 0.25	(0.25 - 1.23)
Diptera	Diptera	3%	0.1 +/- 0.07	(-0.03 - 0.23)
	Cecidomyiidae	1%	0.02 +/- 0.02	(-0.02 - 0.07)
Blattodea	Blattodea	1%	0.02 +/- 0.02	(-0.02 - 0.05)
Hemiptera	Hemiptera	12%	2.02 +/- 0.87	(0.32 - 3.72)
	Hemiptera - Heteroptera	10%	0.66 +/- 0.29	(0.08 - 1.23)
	Insecta	11%	1.03 +/- 0.37	(0.3 - 1.76)
Arthropoda	Arthropoda	10%	0.31 +/- 0.11	(0.09 - 0.53)
	Unidentified Animalia spp.	4%	0.12 +/- 0.06	(0 - 0.24)
'Marine material'		**99%**	**76.89 +/- 2.99**	**(71.02 - 82.75)**
'Terrestrial material'		**56%**	**11.55 +/- 2.54**	**(6.56 - 16.53)**

PERMANOVA illustrated no significant temporal or spatial differences in the dietary composition, however, there was a significant interaction between sampling time and site (*p* = 0.001) indicating some temporal segregation (Table 3.3, Fig. 3.6). This was particularly evident in the *post hoc* pairwise comparisons. There were significant differences between all sampling times within each site, and between sites 2 & 3 for June 2015, sites 1 & 2 and 1 & 3 for September 2015, and sites 1 & 2 and 2 & 3 for February 2016. The SIMPER analysis indicated that the differences among sites and sampling times were driven by a combination of Phaeophyceae, Sargassaceae, *Ecklonia* spp., Coleoptera, *J. rosea* and Magnoliophyta (seen between sampling times only), with the relative importance of these variables differing according to respective groups (Table 3.4). However, the dissimilarity and standard deviations of the contributions of influential taxa was low, as was their contribution percentages, with all taxa less than 20% (Table 3.4). Therefore, it was difficult to determine strongly influential discriminating species (Clarke & Warwick 1994). The nMDS plot indicated a slight separation of samples between sampling times and sites, with taxon in Ochrophyta (including Sargassaceae) being the dominant item consumed (Fig. 3.6). Separation between June 2015 sampling time and September and February times was apparent, as was a difference between sites 1 and 3 (Fig. 3.6).

Table 3.3: Results of a PERMANOVA testing differences ($p \leq 0.01$) in the diet of *Ocypode convexa* across the 3 different study sites (Si) and sampling times (Sa). Significance level lowered to $p \leq 0.01$, as data were still heterogeneous after square-root transformation. Orthogonal design with sampling time random (3 levels) and site random (3 levels).

	df	MS	Pseudo-F	P(perm)	Unique perms
Sa	2	12354	1.9347	0.096	943
Si	2	17896	2.8025	0.027	946
Sa x Si	4	6385.7	3.6372	**0.001**	998
Res	81	1755.7			

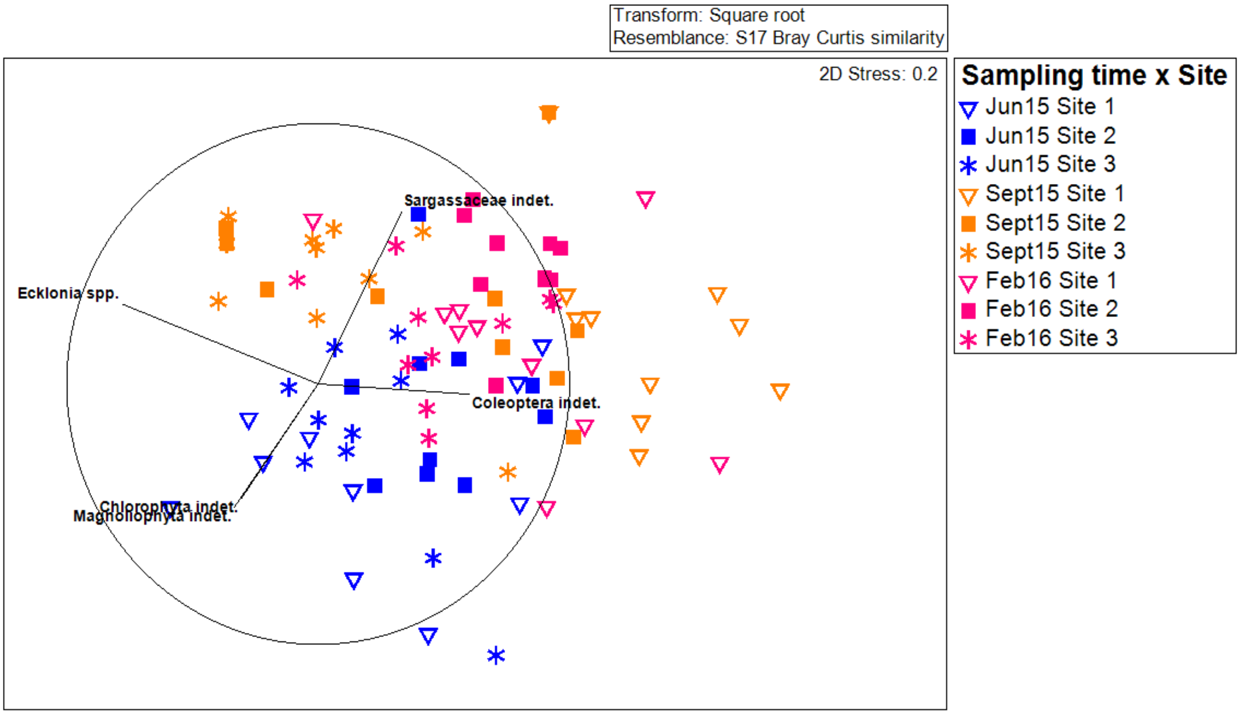

Figure 3.6: nMDS plot based on a Bray-Curtis similarity matrix representing stomach contents of *Ocypode convexa* collected across all sites, highlighting the differences between sites and sampling times (June 2015, September 2015 and February 2016).

Vectors represent the food items characterising the composition of the diet (Pearson correlation = 0.5). Data were square-root transformed.

Table 3.4: SIMPER summary table indicating which taxa contributed to the significant pairwise differences between sites and sampling times (cumulative % cut-off at 50%).

Groups	Taxa identified	Mean value*	Mean value	Dissimilarity/ Square Difference (SD)	Contribution %
Site 1* vs. Site 2	Phaeophyceae	3.83	5.34	1.27	16.02
	Sargassaceae	2.21	3.88	1.13	15
	Ecklonia spp.	1.8	2.42	0.93	13.14
	Coleoptera	2.65	0.32	0.91	10.3
Site 1* vs. Site 3	Phaeophyceae	3.83	3.1	1.19	11.83
	Sargassaceae	2.21	1.89	0.92	9.6
	Ecklonia spp.	1.8	5.16	1.32	17.66
	Coleoptera	2.65	0.61	1.01	10.27
	J. rosea	0.76	1.75	0.71	8.61
Site 2* vs. Site 3	Phaeophyceae	5.34	3.1	1.14	16.79
	Sargassaceae	3.88	1.89	1.04	14.09
	Ecklonia spp.	2.42	5.16	1.23	18.63
	J. rosea	0.6	1.75	0.64	9.1
Jun 2015* vs. Sept 2015	Magnoliophyta	4.09	0	1.46	14.19
	Phaeophyceae	3.84	3.15	1.19	12.17
	Sargassaceae	1.44	2.56	0.94	9.44
	Ecklonia spp.	2.94	3.47	1.04	11.4
	J. rosea	0.7	2.01	0.86	8.02
Jun 2015* vs. Feb 2016	Magnoliophyta	4.09	0.41	1.42	14.78
	Phaeophyceae	3.84	5.28	1.29	13.1
	Sargassaceae	1.44	3.97	1.33	12.42
	Ecklonia spp.	2.94	2.97	1.09	10.64
Sept 2015* vs. Feb 2016	Phaeophyceae	3.15	5.28	1.5	18.7
	Sargassaceae	2.56	3.97	1.2	16.42
	Ecklonia spp.	3.47	2.97	1.05	16.28

3.3 Stable isotope analysis

Stable carbon isotopes of potential food items and consumers covered a broad range of values, from the most depleted signatures in thick-leaved fan-flower (*Scaevola crassifolia*, δ^{13}C = -24.76 ± 0.24‰, mean ± se; Fig. 3.7) to the most enriched signatures in beach casts of the red alga *Jania rosea* ($\delta^{13}C$ = -11.96 ± 0.22). Tissues of *Scaevola crassifolia* had the lightest stable nitrogen ratios ($\delta^{15}N$ = 0.43 ± 0.44), whilst the most enriched signatures were recorded in sandy sprat (*Hyperlophus vittatus*; $\delta^{15}N$ = 10.87 ± 0.05). The carbon isotope ratios of ghost crabs ($\delta^{13}C$ = -17.30 ± 0.10) broadly straddled the middle of the range of producers and wrack material (Fig. 3.7), and were similar to talitrid amphipods ($\delta^{13}C$ = -18.18 ± 0.29). Nitrogen ratios of ghost crabs ($\delta^{15}N$ = 8.20 ± 0.12) were the second most enriched after sandy sprat and heavier compared with both talitrid amphipods ($\delta^{15}N$ = 3.40 ± 0.16) collected from the beach and sand hill snails collected from the dunes ($\delta^{15}N$ = 3.91 ± 0.17; Fig. 3.7).

Isotope ratios for both carbon and nitrogen in ghost crabs were remarkably invariant in space and time (Table 3.5). For carbon, there were no significant differences between sites and times, except for June 2015 when carbon ratios were slightly lower at site 3 ($\delta^{13}C$ = -18.12 ± 0.31‰) compared with other sites ($\delta^{13}C$ = -16.80 to -16.85‰; Table 3.5). Nitrogen ratios were equally invariant among sites and over time, with the only significant (p = 0.03) difference between means being slightly elevated values at site 2 in June 2015 ($\delta^{15}N$ = 9.66 ± 0.48‰). At other times, mean $\delta^{15}N$ values were similar among all three sites (range of $\delta^{15}N$ means: 7.54 to 8.26‰), and no significant temporal variation was evident between all crabs collected during September 2015 and February 2016 (Table 3.5).

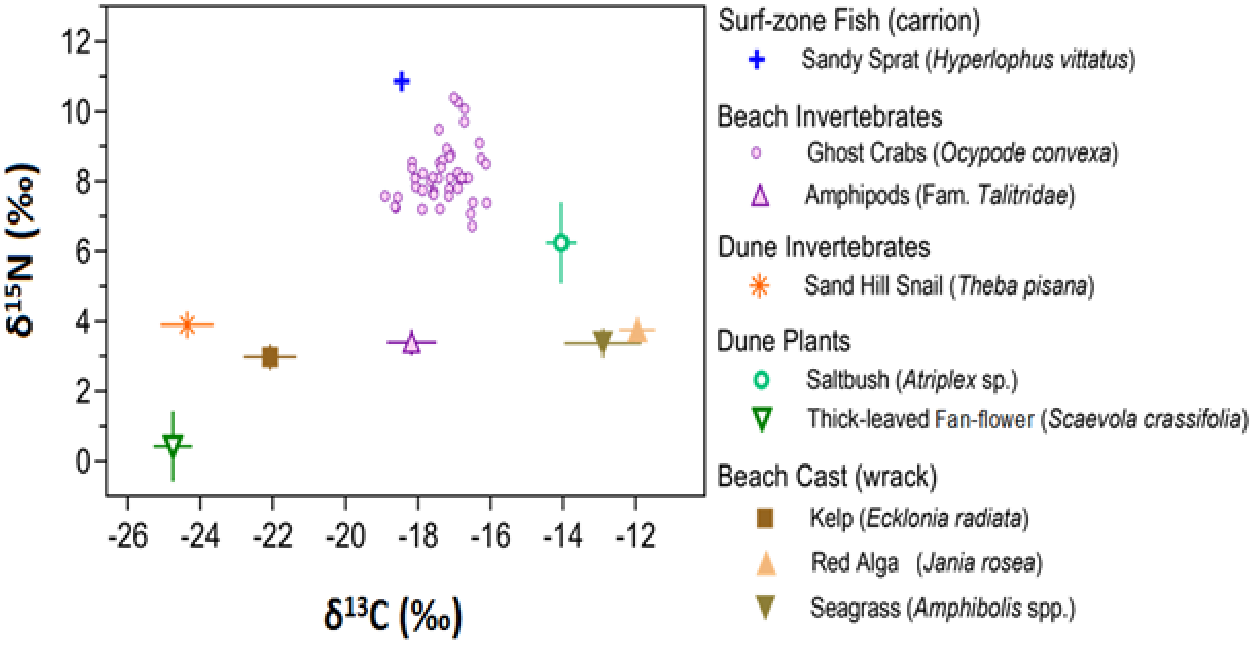

Figure 3.7: Bi-plot of average δ^{13}C and δ^{15}N values of a range of primary producers and consumers (including *Ocypode convexa*) (Appendix: Table B).

Table 3.5: Variation in stable carbon and nitrogen ratios of ghost crabs (*Ocypode convexa*) (n = 45) from Dongara, Western Australia.

δ^{13}C (‰)	Meares Beach		Seven Mile Beach		Getaway Beach	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
June '15	-16.80	(0.23)	-16.85	(0.05)	-18.12	(0.31)
Sep. '15	-17.24	(0.22)	-17.15	(0.23)	-17.66	(0.39)
Feb. '16	-16.84	(0.24)	-17.74	(0.23)	-17.33	(0.36)

δ^{15}N (‰)	Meares Beach		Seven Mile Beach		Getaway Beach	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
June '15	8.40	(0.21)	9.66	(0.48)	8.14	(0.25)
Sep. '15	7.81	(0.18)	7.54	(0.18)	7.90	(0.17)
Feb. '16	8.10	(0.35)	8.26	(0.36)	7.99	(0.35)

Isotope mixing models suggest that *O. convexa* assimilates carbon and nitrogen from a range of marine and terrestrial sources, with no clear dominance by any single source, or by a group of sources (Fig. 3.8). Marine kelp (*Ecklonia radiata*), available to ghost crabs as stranded wrack on the upper beach, and the thick-leaved fan-flower (*Scaevola crassifolia*), growing in the dunes, both had modelled median contributions of 16% (Fig.

3.8). Another dune plant, saltbush (*Atriplex* sp.) and sand hill snails (*Theba pisana*) had slightly lower median contributions at 11% each (Fig. 3.8). All other diet sources included in the mixing models had median contributions of 8 to 9% (Fig. 3.8). Overall, the inter-quartile ranges of all potential food sources included in the mixing models indicated a mixed diet made up of algae/plant and animal matter of both marine and terrestrial provenance.

However, the nutritional values of food sources illustrated a distinct difference (Table 3.6). I found that the nitrogen content of animal prey was, on average, nine times higher than that of algae and vascular plants, with the most nutritious prey being fish carrion, followed by the soft tissues of snails and amphipods (Table 3.6).

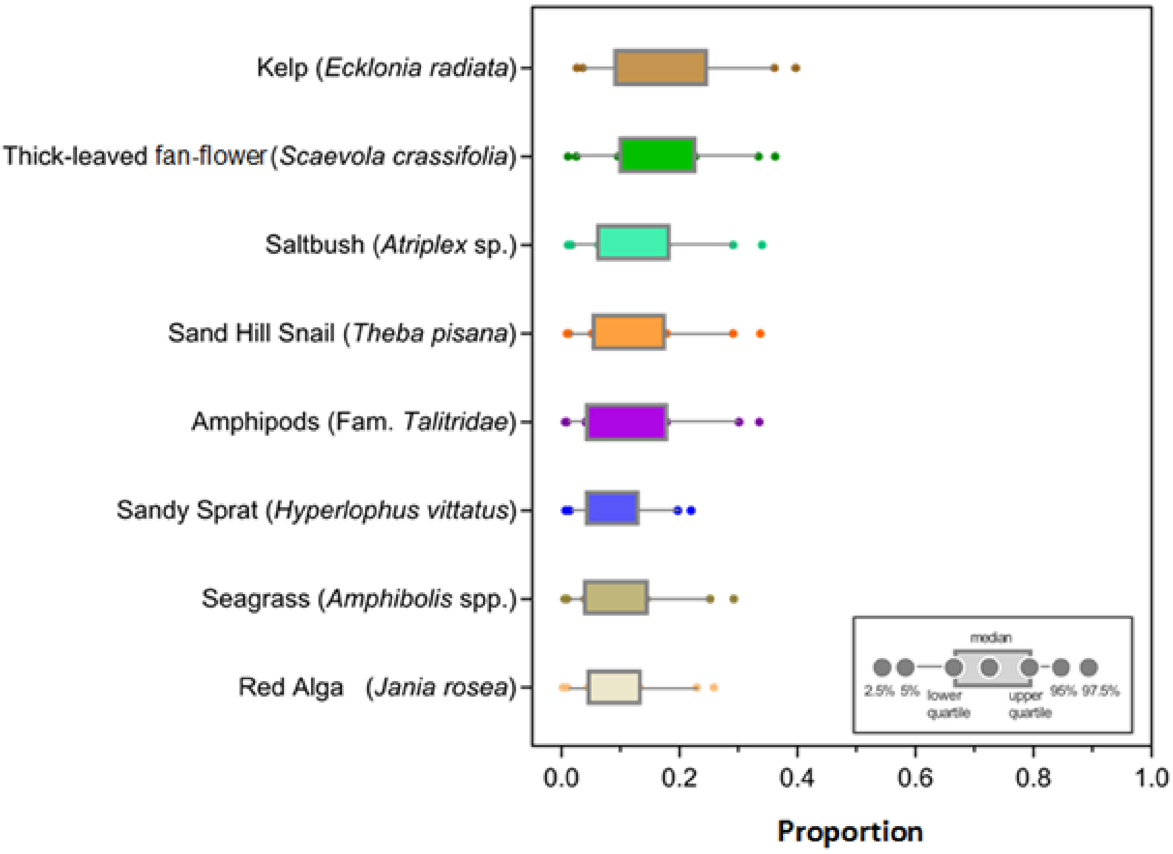

Figure 3.8: Box-whisker plots for the contributions of eight potential food sources for *Ocypode convexa* (sampling times and sites combined). Based on dual-isotope (δ^{13}C and δ^{15}N) mixing model (MixSIAR) outputs illustrating 3rd/98th (dots), 5th/95th (line), 25th/75th (box) and 50th (median) percentiles.

Table 3.6: Nutritional values (indexed by nitrogen content and C/N ratios) of a range of potential food items for *Ocypode convexa* (n = 45).

	%N		**C:N**	
Algae and Vascular Plants	mean	se	mean	se
Wrack				
Kelp (*Ecklonia radiata*)	1.11	0.04	39.30	1.40
Seagrass (*Amphibolis* spp.)	0.85	0.15	72.10	9.60
Red algae (*Jania rosea)*	0.55	0.04	36.20	2.20
Dune plants				
Thick-leaved fan-flower (*Scaevola crassifolia*)	1.61	0.07	33.40	1.40
Saltbush (*Atriplex* sp.)	1.45	0.10	24.90	1.70
Animals				
Amphipods (Fam. Talitridae)	5.19	0.31	7.90	0.70
Sand hill snail (*Theba pisana*)	9.77	0.60	5.00	0.20
Sandy sprat (*Hyperlophus vittatus*)	15.23	1.26	3.70	0.00

3.4 Feeding assays

Ghost crabs strongly and consistently preferred meat over algal and plant food (Fig. 3.9). This pronounced penchant for feeding on animal flesh was evident irrespective of whether crabs were given a choice of food items (Figure 3.9a; Friedman, $\chi^2 = 125.07$, df = 2, $p < 0.001$), or whether the animals in the feeding assays originated from the non-vegetated beach or from the dunes (Table 3.7, Zone x Source $p = 0.83$; Fig. 3.9b). In the choice assays, crabs consumed 55 times the amount of fish carrion than the average of algal or plant food, and 17 times the amount of snail carrion (Fig. 3.9a). In fact, mean consumption rates of seagrass (0.70 ± 0.28 mg/individual/h/g body weight), kelp (0.21 ± 0.19) and dune plants (0.04 ± 0.04) were substantially lower compared with snail flesh (3.77 ± 0.85) and fish flesh (17.52 ± 0.85), which were significantly ($p < 0.001$) higher than the other material offered. This pattern of intense feeding on necromass and negligible intake of vegetable matter was mirrored in the no choice experiments (Fig. 3.9b). Fish carrion was consumed by crabs at rates 21 times exceeding intake of algae and plants, and snails were devoured 7 times more (Fig. 3.9b). Conversely, consumption of any of the three types of plant food was equally low (Fig. 3.9b).

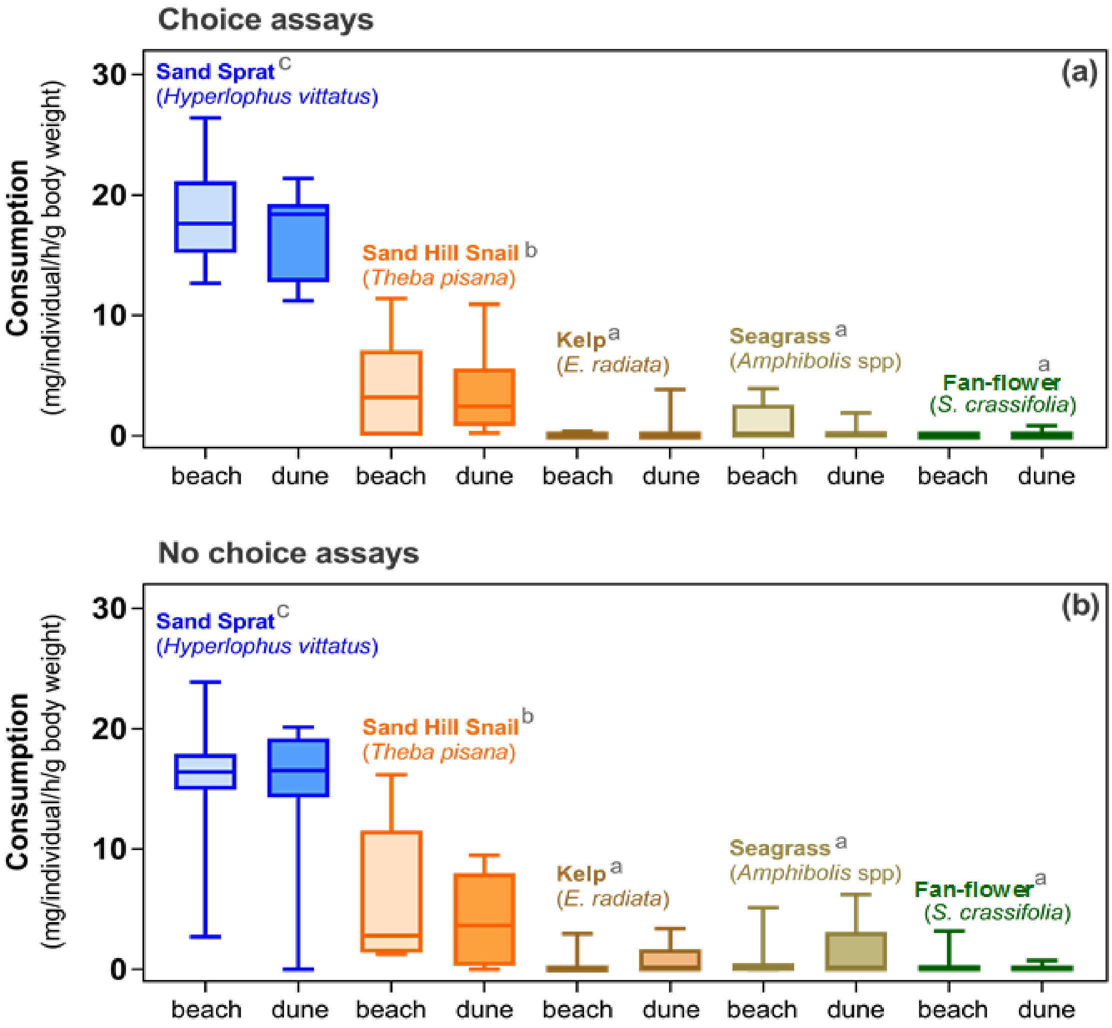

Figure 3.9: Mean consumption (± SE) of *Ocypode convexa* found on beach and dune zones for Choice (**a**) and No-choice (**b**) assays for each of the 5 potential food sources - *E. radiata*, *Amphibolis* spp., *S. crassifolia*, *H. vittatus* and *T. pisana*. Bars labelled with the same letter do not differ significantly (Choice assay *post hoc*, Wilcoxon signed-rank test and No-choice assay *post hoc* Tukey HSD, $p \leq 0.05$).

Table 3.7: Two-way ANOVA testing the no-choice consumption rates for *Ocypode convexa* found in beach and dune zones for the 5 different food sources - *E. radiata*, *Amphibolis* spp., *S. crassifolia*, *H. vittatus* and *T. pisana*.

Source of Variation	**df**	**MS**	**F**	**Sig.**
Zone	1	0.12	0.40	0.53
Source	4	6.74	22.61	**0.00**
Zone x Source	4	0.11	0.37	0.83
Error	59	0.30		

4 Discussion

This study is the first account of the ecology of the Golden ghost crab *Ocypode convexa*, a species endemic to the west coast of Australia. By investigating the densities and distributions at three beaches in the Mid-West region of Western Australia, I have shown that most of the population of ghost crabs occur on the non-vegetated beach, seawards from the base of the primary dunes. With regards to distribution patterns across the beach-dune gradient, my results concur with other studies showing that the bulk of the population typically is distributed at or near the strandline between the upper tidal limit and the foredunes (Jones & Morgan 1994; Dugan *et al.* 2000; Chartosia *et al.* 2010; Corrêa *et al.* 2014).

The diet of *O. convexa*, as gauged by stomach content analysis, appears extraordinarily varied. This melange of diverse food items consumed by ghost crabs is also reflected by stable isotope mixing models, suggesting assimilation of a broad range of material comprising detrital algae and vascular plants from marine and terrestrial sources, and animal carrion of invertebrate and fish carcasses being consumed in roughly similar proportions. However, this catholic diet of ghost crabs under field conditions may be a constraint of limited carrion availability on beaches rather than a continual penchant for a mixed diet that includes plants. In the feeding assays, I have conclusively shown that when animal carcasses are available, ghost crabs behave almost exclusively as scavengers, consistently selecting animal carrion over plant material (Schlacher *et al.* 2013b). Therefore, ghost crabs are unenthusiastic consumers of vegetables, feeding on algae and plant matter only when animal carrion or live animal prey is sparse.

4.1 *Ocypode* spp. densities and distribution across beach-dune gradient

Ghost crab burrows were significantly more abundant in the upper intertidal zone at all sites and during all sampling times. By contrast, densities were consistently much lower in the dunes. This spatial pattern is likely to reflect the burrowing pattern of *O. convexa* since it was the only dominant species collected on those beaches during the crab sampling for dietary studies. These distributions across the beach are similar to those reported by Corrêa *et al.* (2014), for *Ocypode quadrata* in south eastern Brazil, and by

Quijón *et al.* (2001) for *Ocypode gaudichaudii* in Chile, both reporting consistently higher densities on the non-vegetated part of the beach seawards of the dunes.

Higher abundance of ghost crabs closer to the sea do appear to be positively correlated with higher moisture content of the sediment, thus seems to be one factor influencing their distribution (Appendix: Fig. A; Table A; Fig. B). Additionally, other influential factors could be greater food availability at or near the wrack line or behaviour associated with reproduction. Sand moisture has been shown to influence burrow position and depth (Wolcott 1984; Schlacher & Lucrezi 2010b; Lucrezi & Schlacher 2014). One of the functions of burrows is to provide crabs with a moist environment, enabling them to take up oxygen and avoid desiccation during high temperatures (Lucrezi & Schlacher 2010). Another function of burrows is to act as a refuge during storms or hot weather, and considering deeper burrows are constructed in drier environments (Lucrezi & Schlacher 2014), such as dune zones, this could explain higher distributions of crabs closer to dune zones in June 2015 (winter) compared to September 2015 (spring) and February 2016 (summer) (significant interaction between zones and sampling times). Burrows are also important for moulting, sex-specific signalling, and egg development during the reproductive season of ghost crabs (Lucrezi & Schlacher 2014), potentially being another contributing factor to the higher densities observed within the upper intertidal zone across all sampling times.

Although few ghost crabs occurred in the dune zones, this does not necessarily imply that coastal dunes are lesser habitats. On the contrary, coastal dunes are critically important as refuges during storms (Lucrezi *et al.* 2010; Harris *et al.* 2011). In fact, populations of ghost crabs on beaches where dunes have been replaced with urban structures take significantly longer to recover after storms (Walker & Schlacher 2011). Thus, the importance and value of dunes to ghost crabs is likely to be a ‘pulsed’ one, strongest during and after storms (Walker & Schlacher 2011). This was supported in the current study where more burrows were recorded in the dunes during winter (June 2015) compared with the warmer months (September 2015 & February 2016). However, to provide a greater understanding of the extent of nutrient transfer from the marine to the terrestrial environment, investigations regarding ghost crab movements into dune zones would be beneficial.

The bulk of the *O. convexa* population occurring between the upper intertidal and base of the primary dune zones has implications to human disturbance. This is the area where off-road vehicles (ORVs) drive along the beach, and due to this spatial overlap, it is well established that these vehicles cause substantial and widespread environmental harm to beach ecosystems, including negative impacts on ghost crabs (Wolcott & Wolcott 1984; Lucrezi & Schlacher 2010; Schlacher & Lucrezi 2010a, b). Such impacts include being crushed at night by ORVs, which severely impact ghost crabs densities since they are most active at night and feed at the shoreline, as well as altered habitat quality (Moss & McPhee 2006; Schlacher & Thompson 2007; Lucrezi & Schlacher 2010; Schlacher *et al.* 2016). It is, therefore, likely that the popular use of off-road vehicles on this beach zone in the Mid-west region (Moss & McPhee 2006; Carter & Schlacher 2009) will impact the population of *O. convexa* through crushing of crabs or destruction of burrows and compaction of sand in heavy ORV usage areas. In addition, the limited distribution of this species across the beach-dune interface and geographically makes it susceptible to a range of other human disturbances, such as global warming, altered precipitation and pollution, i.e. debris and chemicals, but little is known about these effects on ghost crabs (Schlacher *et al.* 2016). Ghost crabs represent a powerful model organism for detection of such ecological impacts in sub-tropical and tropical coastal systems (Jones & Morgan 1994; Schlacher *et al.* 2016). Therefore, accurately measuring and predicting the environmental risks that these elements pose for beach and other ecosystems is a research priority.

4.2 Diet of *Ocypode convexa*

Ocypode convexa in the Mid-West of Western Australia is an opportunistic feeder, consuming a remarkably wide variety of food items. Based on stomach content analyses, the diet composition of *O. convexa* showed some variation across sites and times, but was typically dominated by brown algae, complemented by some vascular plants including seagrass, and arthropods (various insects and amphipods). Stable isotope analysis, which indicates diet over a longer time period compared with stomach content analysis (weeks cf. daily) (Hyslop 1980; Layman *et al.* 2012), also indicated a mixed diet, including material commonly found in wrack (e.g. seagrass, kelp), detritus from dune plants, and arthropods from the beach and dunes (Ince *et al.* 2007; Laidre 2013). My findings of a varied diet that included both marine and terrestrial matter are broadly similar to other ghost crab species whose food intake has been examined (Chartosia *et al.* 2010; Lucrezi

& Schlacher 2014). For example, Chartosia *et al.* (2010) found that food intake of *O. cursor* comprised 67% drift algal material and 33% of animal material, mostly terrestrial insects dominated by ants (Myrmicinae). In comparison, 89% plant and 11% animal matter were identified in *O. convexa* for the present study, in which marine algae, Phaeophyceae and Rhodophyta, and terrestrial fauna predominantly from the Class Insecta, formed the majority of the diet. Whilst there have been few recent studies on the diet of ghost crabs, species from the superfamily Ocypodoidea (*Uca* spp., *Scopimera inflata*, *Ocypode quadrata* and *Ocypode cursor*) appear to feed opportunistically on both marine and terrestrial plants and fauna (Wolcott 1978; Robertson & Pfeiffer 1982; Wolcott & O'Connor 1992; Wolcott 1999; Chartosia *et al.* 2010). These opportunistic diets reflect those morphological and physiological characteristics seen in the Infraorder Brachyura that allow them to forage on a range of food types (Bellwood 2002; Josileen 2011; Lee 2015).

Ghost crabs are commonly reported to be efficient, frequent, and common scavengers of animal carcasses on sandy beaches and dunes worldwide (Lucrezi & Schlacher 2014). This contrasts with data from my stomach content analyses indicating that algal and plant material, particularly algae stranded as wrack, are the main food source. This may suggest that feeding is largely opportunistic on wrack deposits (Appendix: Table C). However, whilst not observed *in-situ*, *O. convexa* is likely to respond rapidly to both live animal prey and carrion inputs. This behaviour was demonstrated in the feeding assays, where the species almost exclusively fed on invertebrate and fish carcasses, shunning algae, seagrass and dune plants. Ghost crabs are frequently reported to actively predate, hunting prey as large as turtle hatchlings and the unfledged chicks of ground-nesting birds (Schlacher & Lucrezi 2010a; Peterson *et al.* 2012; Lucrezi & Schlacher 2014).

Stomach content analysis (SCA) is a traditional approach in diet studies, but only provides a short-term (hours to days) ‘snapshot’ of recently ingested items (Hyslop 1980). It can also be misleading if diet items are digested at different rates and may not reflect what is assimilated into the animal’s tissues (i.e. a mismatch between food *ingested* and food assimilated). In this study, SCA would strongly point towards ghost crabs being mainly herbivorous based on the large amounts of plant material (mostly brown algae) in the crabs’ stomachs. Plant material, particularly vascular plants, is recalcitrant during digestion due to it containing complex structural molecules (e.g. cellulose), tannins and phenolics, resulting in slower digestion compared to animal material (Wolcott & O'Connor 1992; Chartosia *et al.* 2010). These differences in digestibility can bias interpretations of stomach content data and can over-estimate the contribution of plant material.

Stable isotope analyses from this study provided a more integrated picture of assimilated dietary items. Stable isotope analyses are one of the primary means to analysing the structure of food webs, where $\delta^{13}C$ is often used to link consumer to food source and $\delta^{15}N$ is typically used as a proxy for trophic position (Gannes *et al.* 1998; Layman *et al.* 2012). Based on $\delta^{13}C$ and $\delta^{15}N$ signatures and isotopic mixing model results, *O. convexa* assimilates nutrients from a broad range of food sources, including animal material in similar amounts to plants. The food sources analysed in this study were representative of a range of food items available to *O. convexa* within the study region. Carbon and nitrogen isotope values for food sources of *O. convexa* were similar to that of Ince *et al.* (2007), where macroinvertebrates (amphipods and dipteran flies) consuming wrack material had $\delta^{13}C$ values from -22.3 to -17.3‰ and $\delta^{15}N$ values ranging between 7.5 to 14.3‰, in comparison to primary producers ($\delta^{13}C$ = -24.8 to -12.0‰; $\delta^{15}N$ = 0.4 to 6.3‰) and faunal ($\delta^{13}C$ = -24.1 to -18.2‰; $\delta^{15}N$ = 3.4 to 10.9‰) food sources from this study. Moreover, a low $\delta^{15}N$ value (‰) for *O. convexa* ($\delta^{15}N = 8.2 \pm 0.1$) in comparison to *H. vittatus* ($\delta^{15}N = 10.9 \pm 0.1$) was unsurprising due to ghost crabs being omnivores and sandy sprat being invertivores, thus making ghost crabs first to second order consumers (MacArthur *et al.* 2011; Hyndes *et al.* 2013). This was similarly seen in MacArthur *et al.* (2011) where the mean $\delta^{15}N$ value (‰) for the Western Rock Lobster was 8.3 ± 0.3 in comparison to invertebrate prey, i.e. gastropods and polychaetes ($\delta^{15}N = 5.9 \pm 0.3$).

The limitations of SCA have led to an increasing emphasis on stable isotope analysis (SIA) as a tool to assess food web structure and function (Layman *et al.* 2012; deVries *et al.* 2015). However, interpretation of an animal's diet from its stable isotope composition is calculated based on knowledge of fractionation values of the food source assimilated into the tissues of consumers (deVries *et al.* 2015). Known fractionation values are limited for many consumer species and tissues (Waddington & MacArthur 2008), and are often based on assumed values (Caut *et al.* 2009; Bond & Diamond 2011). Thus, a degree of uncertainty must be acknowledged when using SIA. In addition, SIA depends on being able to locate, identify and sample a full range of dietary items that the consumer may devour. Missing critical dietary items is likely to increase the uncertainty around the outcomes from SIA and the associated mixing models. However, the relatively close distributions of the potential contributions of the range of dietary items used suggest that uncertainty was not a major issue in the current study. Rather, it confirmed the varied diet of *O. convexa* shown through SCA. By combining these two techniques for dietary studies, this study has further provided a more robust short- and long-term estimate of the diet of *O. convexa*.

Whilst ghost crabs can ingest a very broad range of food items in the field, my feeding assays demonstrated conclusively that crabs are almost exclusively scavengers in the situation where animal carcasses are available. This proclivity for animal flesh, is likely to be related to the greater nutritional value of protein-rich animal material (Pearson *et al.* 2011). The nitrogen content of animal prey was higher than that of algae and vascular plants and even amphipods, the prey items with the lowest nitrogen content amongst the analysed animal prey, had three times more nitrogen than the plant material with the highest nitrogen values. These substantial differences in the nutritional value are closely related to food selection in ghost crabs, with 99% of the variation in feeding rates for different food items being explained by the nutritional value of food (Fig. 3.10). Crabs, therefore, appear to strongly and consistently select animal carrion over plant matter, and this active choice behaviour is closely linked to the nutritional value of food.

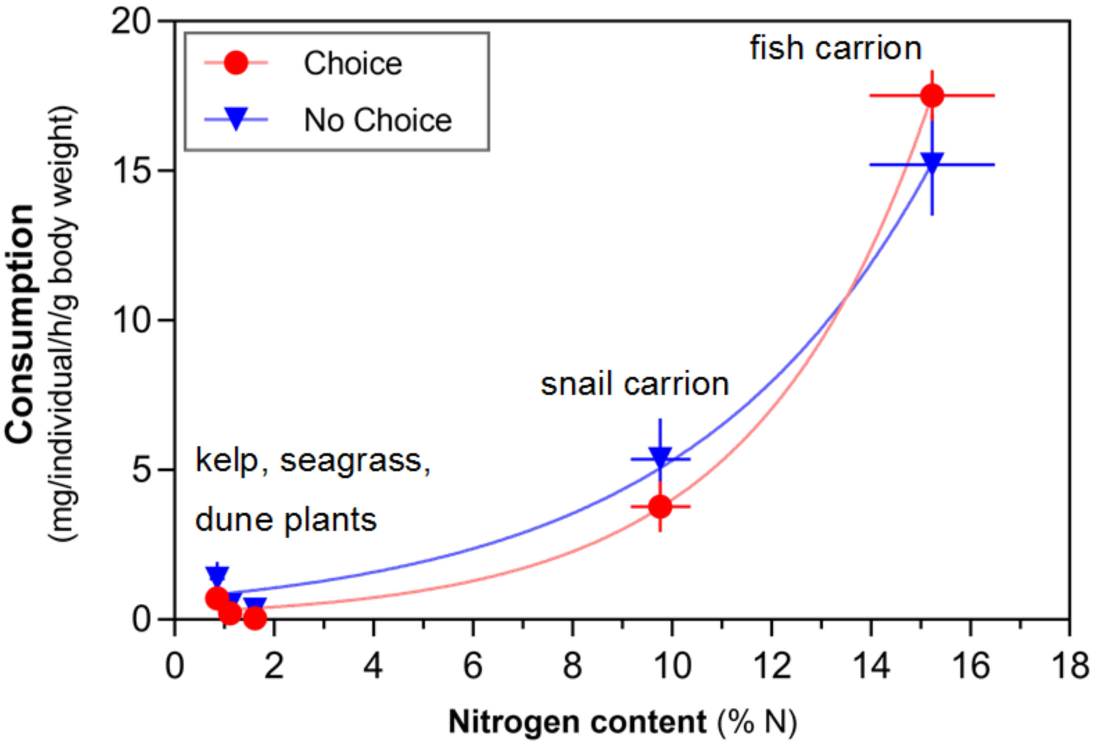

Figure 3.10: The relationship between feeding rate of *Ocypode convexa* and the nutritional value (indexed by nitrogen content) of different food items in feeding assays.

The potential animal material on beaches can be in the form of carrion, i.e. animal carcasses (Schlacher *et al.* 2013b), however, little is known about the input or quantity of this material on West Australian beaches (possibly because it is consumed rapidly). In addition to animal carcasses, ghost crabs may also predate on living animals, most likely species that are associated with wrack. In particular, arthropods (e.g. amphipods, dipteran flies, spiders, beetles) can be abundant at the strandline and are found throughout coastal dunes (Ince *et al.* 2007; Mellbrand *et al.* 2011). It is, however, unclear to what extent ghost crabs actively hunt for live prey or whether consumption of live prey occurs coincidentally whilst scavenging. Active hunting behaviours have been reported for some ghost crab species on larger vertebrate prey (e.g. turtle hatchlings, unfledged chicks of ground-nesting birds) and benthic invertebrates (e.g. mole crabs) (Strachan *et al.* 1999; Wolcott 1999; Laidre 2013). However, it is unknown whether ghost crabs can detect and capture smaller and swiftly-moving animals, such as talitrid amphipods and other arthropods. Based on the interpretation of all three dietary techniques used in this study, the most plausible trophic mode of *O. convexa* appears to be an omnivore of catholic tastes, foraging opportunistically on a wide range of both animal and plant matter from the marine and terrestrial provenance.

4.3 Trophic implications of *Ocypode convexa* on sandy beaches

This study further supports the conclusion that cross-boundary subsidies, such as algae, seagrass and animal carrion from the sea, underpin food webs of sandy beaches in the region (Ince *et al.* 2007; Mellbrand *et al.* 2011) and elsewhere (Barreiro *et al.* 2012; Tran 2014; Claudino *et al.* 2015). Ghost crabs show distinct trophic plasticity (Lucrezi & Schlacher 2014), but as shown in the present study, consume high proportions of marine-derived material. Since crustaceans can process a sizeable amount of this material (Lastra *et al.* 2014), and *O. convexa* is highly abundant in the region, it is likely to play a pivotal role in the energy pathway in beach food webs, as concluded for ghost crabs by Wolcott (1978). Furthermore, the occasional foray of *O. convexa* into the dune system suggests that it can act as a conduit of carbon transfer further inland.

From the stomach content analyses, I demonstrated that *O. convexa* consumes high proportions of beach-cast macrophytes, particularly kelp. The impacts of climate change, i.e. increasing sea temperatures, on the abundance of seaweeds such as kelp (Wernberg *et al.* (2013), has the potential to produce a negative effect on *O. convexa* populations due to its existing diet composition and also its restricted range. The food web structure on beaches in the Mid-West of Western Australia is also likely to change if macroalgae disappears as a food source. For example the wrack-associated amphipod, *Allorchestes compressa*, has a preference for brown algae (Crawley *et al.* 2009), which could have a flow-on effect on ghost crab densities and distributions if kelp was impacted by climate change. Furthermore, Rodil *et al.* (2015) found that changes in the type of wrack on beaches, and alterations to its basic biochemical traits due to environmental shifts, i.e. increase in temperature, affected associated macrofaunal assemblages. In addition to range retractions of macroalgae due to climate change (Wernberg *et al.* 2013; Phelps *et al.* 2017), harvesting and/or removal of wrack for commercial purposes or beach grooming can impact beach ecosystems (Kirkman & Kendrick 1997; Fairweather & Henry 2003; McKechnie & Fairweather 2003; Ince *et al.* 2007; Baring *et al.* 2014). The strong link between ghost crabs and food sources in the wrack indicate that removal of beach wrack is likely to impact its populations. Thus, there is a need to educate multiple sectors of society about the importance of wrack deposits and the conservation of strandlines.

Whilst a complementary pathway of marine carbon can be transferred via nutrient translocation of ghost crab's faecal matter (i.e. crabs feeding on algae and defecating in the dunes), the predators of ghost crabs are likely to provide a direct trophic link, relaying marine matter to terrestrial ecosystems. Ghost crabs are often important invertebrate consumers on sandy shores, however, they are also preyed upon by higher-level vertebrate consumers (e.g. birds, reptiles and mammals) (Lucrezi & Schlacher 2014). Although there is minimal data on vertebrate predators on beaches within the Mid-West region, potential predators to ghost crabs in the region include feral cats (*Felis catus*), Red foxes (*Vulpes vulpes*), the Silver (*Chroicocephalus novaehollandiae*), Kelp (*Larus dominicanus*) and Pacific (*Larus pacificus*) gulls, the Eastern osprey (*Pandion cristatus*), Brahminy kites (*Haliastur indus*), Nankeen kestrels (*Falco cenchroides*), corvids such as the Australian raven (*Corvus coronoides*), and the Northern quoll (*Dasyurus hallucatus*). These predators are all likely to use beaches and coastal dunes as foraging sites (Ambrose & Murphy 1994; Risbey *et al.* 1999; Burbidge *et al.* 2000; Burbidge & Morris 2002; Surman & Nicholson 2009; Debus 2012), and thus contribute to the transfer of marine matter through the terrestrial food web.

Mammals are the most widely recorded vertebrate consumers of ghost crabs, with predation being intense in some settings (Lucrezi & Schlacher 2014). Mammal predation on ghost crabs is a pivotal mechanism in beach food webs (Lucrezi & Schlacher 2014). For example, cascading top-down effects were observed in Florida, USA when racoons were controlled to protect turtle eggs (Barton & Roth 2008). Instead there was a population increase of ghost crabs (*Ocypode quadrata*) and a resultant increase in predation of turtle nests due to racoon populations controlling ghost crab populations (Barton & Roth 2008). Vertebrates, for example birds of prey and foxes, can also suppress aggregative responses of ghost crabs around carcasses as a result of competition for food, higher risk of predation for crabs, and actual crab predation by birds and mammals that are facultative scavengers (Schlacher *et al.* 2013a; Schlacher *et al.* 2013b). Thus, predation on ghost crabs provide an important functional pathway for the spatial coupling of marine and terrestrial ecosystems (Lucrezi & Schlacher 2014). Additionally, human impacts negatively affecting ghost crab densities and behaviour would ultimately affect these predators too, further interfering with this pathway. More studies on this topic in regard to the West Australian coastline would further assist in understanding the trophic importance of ghost crabs within the region.

In summary, the ghost crab, *O. convexa*, is an abundant generalist feeder, residing more on the intertidal beach profile than in the dune systems, thus demonstrating a clear intake of marine material over terrestrial, as well as a preference for fauna or carrion instead of plant material, further indicating their potential in transferring marine material into terrestrial environments.

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6 Appendix

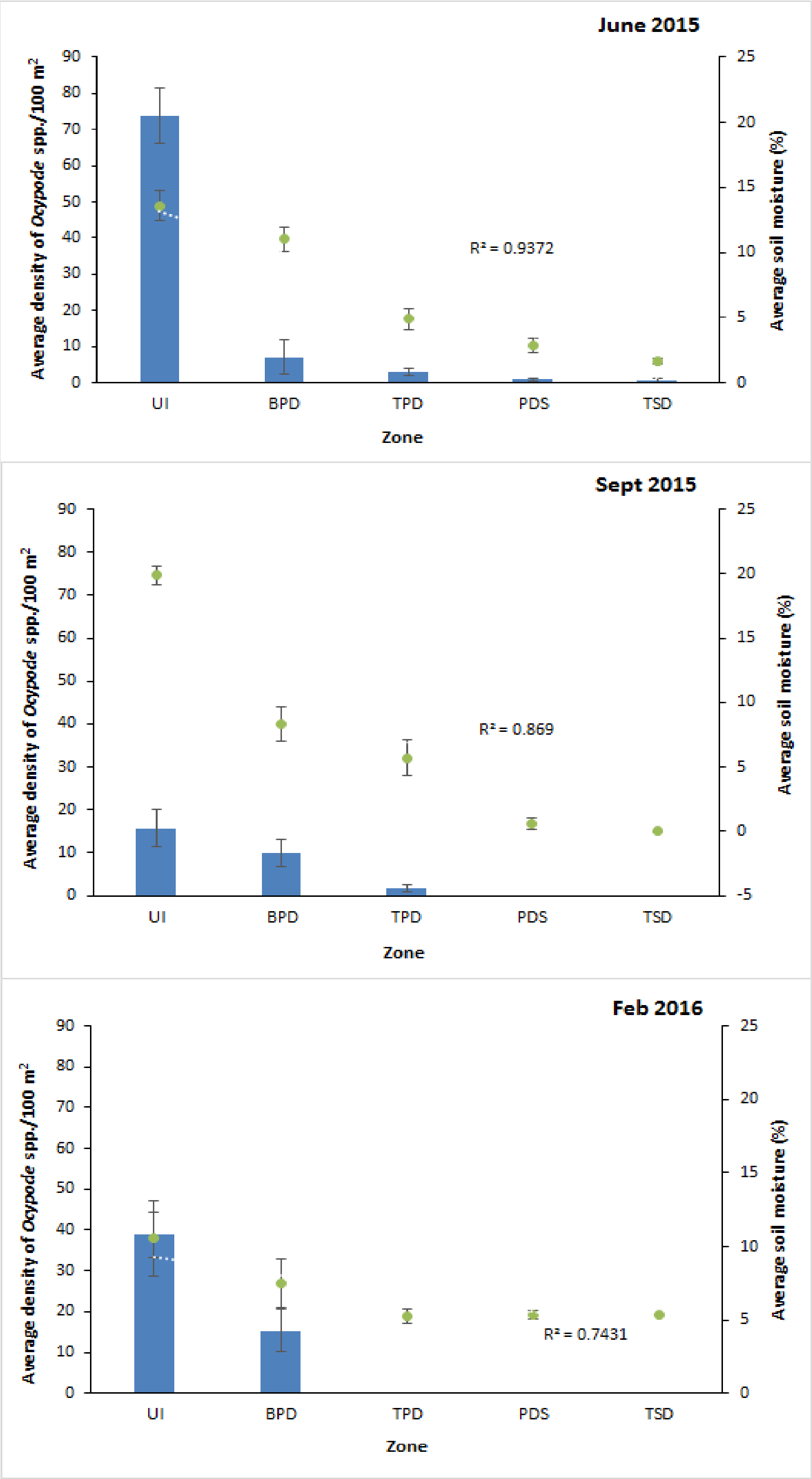

Figure A: Average density of ghost crab (*Ocypode* spp.) burrows per 100 m^2 (±SE) (sites combined) (indicated by the blue bars) in correlation to average soil moisture (%) (±SE) (indicated by green dot points) across zones and sampling times.

Table A: Pearson correlation results for *Ocypode* spp. densities and soil moisture (n = 270) across zones and sampling times (June 2015, September 2015 and February 2016). All three correlation coefficients were $p < 0.01$. Data were square-root transformed.

	Abundance	**Moisture**
Zone	-0.66	-0.78
Abundance		0.60

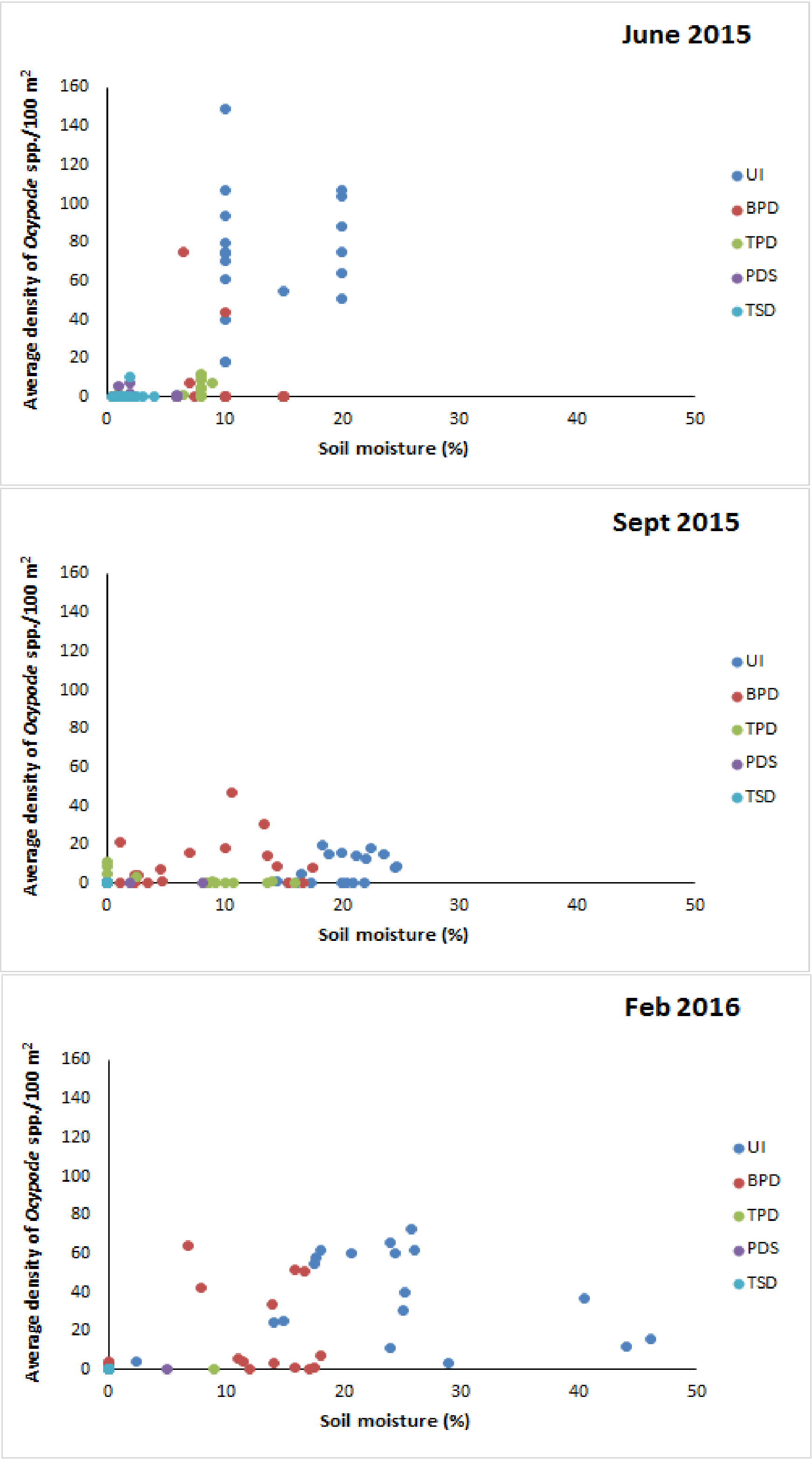

Figure B: Scatterplots illustrating differences between zone, average density of *Ocypode* spp. and soil moisture across sampling times (June 2015, September 2015 and February 2016).

Table B: Sample sizes (n), mean and standard error values for δ^{13}C and δ^{15}N of a range of primary producers and consumers (including *Ocypode convexa*).

Item	Sample size (n)	δ^{13}C Mean	δ^{13}C SE	δ^{15}N Mean	δ^{15}N SE
"Surf-zone Fish (carrion)"					
Sandy sprat (*H. vittatus*)	5	-18.46	0.04	10.87	0.05
"Beach Invertebrates"					
Ghost crabs (*O. convexa*)	45	-17.30	0.10	8.20	0.12
Amphipods (Fam. Talitridae)	8	-18.18	0.29	3.40	0.16
"Dune Invertebrates"					
Sand hill snail (*T. pisana*)	10	-24.37	0.32	3.91	0.17
"Dune Plants"					
Saltbush (*Atriplex* sp.)	10	-14.06	0.19	6.25	0.06
Thick-leaved Fan-flower (*S. crassifolia*)	10	-24.76	0.24	0.43	0.44
"Beach Cast (wrack)"					
Kelp (*E. radiata*)	10	-22.08	0.32	2.98	0.16
Red alga (*J. rosea*)	10	-11.96	0.22	3.77	0.16
Seagrass (*Amphibolis spp.*)	10	-12.91	0.46	3.38	0.19

Table C: List of genera/species identified along the beach and dune systems across all sites and sampling times in Dongara, Western Australia.

Wrack/plant Identification
Dune vegetation
Carpobrotus virescens
Coast Bone Fruit (*Threlkeldia diffusa*)
Scaevola crassifolia
Spinifex longifolius
Ruby Saltbush (*Enchylaena tomentosa*)
Bromus diandrus
Olearia axillaris
Acacia rostellifera
Alyxia buxifolia
Atriplex sp.
Tetragonia decumbens
Wrack material
Ecklonia radiata
Sargassum spp.
Brown algae mix
Posidonia sinuosa
Posidonia australis
Posidonia spp.

Amhibolis spp.
Halophila spp.
Jania rosea
Red algae mix
Green algae mix