Faunal associations with drifting macrophytes and wrack accumulations in the nearshore of South Australian sandy beaches

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Summary

The research in this thesis identifies and addresses some of the knowledge gaps surrounding the role that detached and drifting macrophytes play as habitat and potential food resources in the nearshore of sandy beaches. So far, very little research has been conducted in southern Australia to investigate if important detached macrophytes are to nearshore production. This is surprising considering the large volumes that regularly accumulate as wrack in the surf zone and on sandy beaches, and in some cases wrack is a semi-permanent feature. Very few beach management programs have considered the role of drifting macrophytes and wrack accumulations in coastal ecosystems, which is concerning when beach cleaning or wrack harvesting procedures are in place. Beach cleaning can occur up to multiple times a week along metropolitan Adelaide beaches, particularly during the warmer months. In South Australia, the amounts of wrack removed from beaches varies with approximately 50-110 tonnes of algae and 3000 tonnes of seagrass per year from the South East region of the state (PIRSA 2007).

To establish efficient sampling designs for investigating drifting wrack and associated fauna in surf zones of sandy beaches, I undertook a carefully-planned pilot study to establish optimal-precision estimates for sampling macroinvertebrates and ichthyofauna. I investigated the precision of the mean for various numbers of sub-samples and replicates of seine nets to establish a larger sampling program. The pilot study showed that the processing time for individual seine-net samples could be reduced by 50 % using sub-sampling compared to double the amount of time taken to process the whole sample and the time taken to process replicate seine net samples could be reduced by 25 %, while maintaining acceptable precision. The pilot study and exploratory approaches used in Chapter 2 were essential for establishing precise estimates of flora and fauna associated with very patchy habitats, such as wrack in sandy-beach surf-zones.

The effects of regular storms on drifting marine macrophytes, consequent accumulation of wrack (i.e. seagrass or macroalagae or both) and associated fauna in beach surf zones across three different regions was investigated. Results showed that the influence of storms may be more pronounced in sheltered coastal waters compared to more exposed coastlines, where biota could have adaptations to persist in larger swell conditions. Regional differences were more obvious than the impact of weather, with distinct macrophyte and macroinvertebrate species richness, abundances and assemblages occurring in each region. Fish were less aligned to the regional patterns identified for wrack or invertebrates. This study also showed that beach morphology, specifically grain size and beach slope, may be important to the ecology of surf zones. The new knowledge about the ecology of faunal associations in nearshore waters during storm and calm weather in multiple regions highlights the importance of surf-zone wrack as habitat for many fauna.

A separate study was undertaken to investigate possible trophic pathways associated with wrack accumulations, which are little understood, particularly where wrack compositions vary or where wrack is a semi-permanent feature in sandy-beach surf-zones. In this study, I sampled the gut contents of fish and analysed the $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures of fish, macroinvertebrates and macrophytes. Results showed that fish may be using wrack as habitat but are likely to be foraging widely over multiple habitats away from wrack accumulations. More evidence exists that some invertebrates such as grazers may be using wrack accumulations for both habitat and food. Although preliminary, this study identified baselines for trophic pathways associated with wrack accumulations in these sandy-beach surf-zones, which can be applied to more directed studies in future. More directed studies of specific trophic pathways, other food sources and fauna in nearby habitats (e.g. benthic fauna) would provide better understanding of the trophic pathways within wrack accumulations and also linkages between wrack accumulations and nearby habitats.

Previously, no studies had investigated the surface drift dynamics of detached seagrass. Existing studies have mainly focused on larger macroalgae such as kelps or fucoids in open-ocean systems, rather than along sheltered coastlines. Here, the trajectories of detached natural and artificial seagrass were investigated to establish the drift pathways and short-term colonisation of fauna to drifting macrophytes close to shore. Various release distances from shore in gulf waters in South Australia were compared. Tagged seagrass generally travelled in the same direction as tides but patterns were variable across sampling days and different distances from shore. Many tagged seagrass units released close to shore were stranded on beaches after six hours but the eventual stranding of drifting macrophytes further offshore was more difficult to quantify.

The colonisation of macroinvertebrates and fish to tagged seagrass was compared to fauna found from *in situ* drifting (natural) macrophytes. The results of the drifting macrophyte study also showed that colonisation by fish to drifting macrophytes are more likely to be for habitat, rather than food. Also, more macroinvertebrates may colonise drifting macrophytes at distances closer to shore, possibly due to shallower depths and thus increased proximity of source habitats. This study provides further knowledge about macrophyte drift dynamics, the short-term colonisation of fauna and habitat function along nearshore coastlines. This is essential for further understanding of the ecological significance of allochthonous material arriving on shorelines.

The research in this thesis was strategically planned to investigate and better understand the dynamic movement of nearshore drifting macrophytes, their arrival into surf zones and the fauna that utilise the drifting material as habitat and a food resource. This thesis had an equal amount of research effort placed on the study of macrophytes, macroinvertebrates and fish across multiple regions that were variously dominated by macroalgae and/or seagrasses. The research encompasses some of the few studies anywhere

where much wrack in the surf zone is from seagrasses. Information gained from this research will be useful for future investigation of the ecological function and management of nearshore ecosystems, particularly where processes such as beach cleaning occur. Future management of allochthonous inputs such as wrack in the nearshore zone is particularly important in southern Australia where it has received no attention in previous beach management programs.

Declaration

I certify that this thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma at any university; and to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Ryan Baring

Statement of Contribution

This thesis was prepared as a series of manuscripts (Chapters 2-5) which are either in the process of being, or will in the future be, submitted to various scientific journals. Prof. Peter Fairweather and Dr Rebecca Lester, as my primary supervisors, provided conceptual and methodological input throughout the writing of this thesis. Dr Charlie Huveneers as my secondary supervisor assisted with input into drafting of some chapters at the later stages of writing.

Chapter 2 will be submitted in the near future to a methods based journal, which is yet to be decided. This manuscript is co-authored by my supervisors, Prof. Peter Fairweather, who provided assistance to me with conceptual design, data analyses and editing the manuscript, and Dr Rebecca Lester, who also provided assistance with the writing of *R* script and subsequent data analyses. I reviewed the literature and undertook all field data collection, laboratory processing and species identification, data analyses and manuscript preparation. My proportional contribution to this manuscript was 85 %, Dr Rebecca Lester contributed 10 % and Prof. Peter Fairweather contributed 5 %. .

Chapter 3 has been published in *Journal of Experimental Marine Biology and Ecology* (see Baring et al. 2014) . This manuscript is co-authored by my supervisors, Prof. Peter Fairweather and Dr Rebecca Lester, who provided assistance with conceptual design, data analyses and editing the manuscript. I reviewed the literature and undertook all field data collection, laboratory processing and species identification, data analyses and manuscript preparation. My contribution to this manuscript was 90 %, and Prof. Peter Fairweather and Dr Rebecca Lester contributed 5 % each.

Chapter 4 will be submitted in the near future to *Estuaries and Coasts*. This manuscript is co-authored by my supervisors, Prof. Peter Fairweather and Dr Rebecca Lester, who provided assistance with conceptual design, data analyses and editing the manuscript. Dr Charlie Huveneers provided advice with editing of the manuscript. I undertook all field data collection, laboratory processing, data analyses and manuscript preparation. My contribution to this manuscript was 89 %, with Prof. Peter Fairweather and Dr Rebecca Lester contributed 5 % each and Dr Charlie Huveneers 1 %.

Chapter 5 will be split into two manuscripts in the near future, with one manuscript focusing upon the drift movement of detached macrophytes and the second manuscript focusing on colonisation and biological interactions with associated fauna offshore. The two manuscripts will be submitted to *Estuarine, Coastal and Shelf Science* and *Marine Ecology Progress Series*, respectively. These manuscripts will be co-authored by my supervisors, Prof. Peter Fairweather and Dr Rebecca Lester, who provided assistance with conceptual design, data analyses and editing the manuscript. I undertook all field data collection, laboratory processing, data analyses and manuscript preparation. My contribution to this manuscript was 90 %, and Prof. Peter Fairweather and Dr Rebecca Lester contributed 5 % each.

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After what seemed like a sometimes impossible task in finishing this thesis, I wish to thank many people who have helped along the way in keeping me on track, grounded and alive with only a few scratches.

In the beginning of this project it seemed very ambitious, a little overwhelming, and although it wasn’t an easy road at times, I eventually managed to refine that monolith into an achievable project. For that alone I can only thank my supervisors, Professor Peter Fairweather, Dr Rebecca Lester and Dr Charlie Huveneers. To Prof. Peter Fairweather and Dr Rebecca Lester, I must thank you for your wealth of knowledge, advice and support over these years. I know that you have taught me to be a better scientist along the way.

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So many people helped out in the field and laboratory with this project and I apologise if I miss anyone. Thank you to Graham Baring, June Baring, Mick Drew, George Giatis, Hannah Harbourd, Ben Hamilton, Angela Kennedy, Gavin Lewis, Jacinta Lamacchia, Laura Lewis, Hannah Moloney, Rodney Quinn, Ben Smitheram, Sasha Whitmarsh and Nikki Zanardo.

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I dedicate this thesis to the grandparents that we have lost over the last few years. I wish they were all still around to see me finish this thing. In some ways I know they still are.

Lastly, sometimes the simplest things have kept me motivated to play my part in the protection and conservation of flora and fauna on this planet. One has been the effort that my wife and I have invested in our kids' love for nature. Regularly reading the classic book 'The Lorax' by Dr. Seuss to our kids also reminds me that a few simple words mean so much…

"UNLESS someone like you
cares a whole awful lot,
nothing is going to get better".
"It's not". Dr Seuss (1971)

Chapter One: General Introduction

1. Drifting macrophytes in coastal ecosystems

Drifting macrophytes (such as seagrasses and macroalgae) are a common feature of sandy beaches, where they accumulate as large deposits known as ‘beach-cast wrack’ along and above the intertidal zone. Over time, beach-cast wrack decomposes and can be important in transferring and processing large amounts of nutrients by cycling and re-mineralisation through beach sediments back into the surf zone (McLachlan et al. 1985; Dugan et al. 2011). This process plays a major role in primary production in these typically nutrient-poor zones (McLachlan et al. 1985; Dugan et al. 2011). Also, the energy flow into coastal marine and terrestrial systems associated with this decomposition process provides carbon and nutrients for secondary production (Coupland and McDonald 2008; Christie et al. 2009; Colombini et al. 2009; Cowles et al. 2009). For example, the concentrations of dissolved organic and inorganic nitrogen found in surf-zones can be substantial and are strongly correlated with wrack biomass on sandy beaches (Dugan et al. 2011).

In the surf zones of sandy beaches, where breaking waves form, drifting macrophytes can also provide habitat structure and food in an otherwise sparse water column for a variety of pelagic and mobile demersal macroinvertebrates (Norkko et al. 2000). Subsequently, juvenile fish are attracted to drifting macrophytes as a refuge from predators and to feed on the associated macroinvertebrate fauna (Kingsford 1992). Previous studies have investigated the fish and macroinvertebrate assemblage associated with drifting macroalgae (mainly *Sargassum* spp.) both off- and nearshore in a range of locations worldwide, e.g. eastern Australia (Dempster and Kingsford 2004), Belgium (Vandendriessche et al. 2007) and Japan (Nishida et al. 2008). Fish identified as having close associations with drifting macrophytes tend to be juveniles and are from a wide variety of species (including some recreationally-and commercially-important species; Safran and Omori 1990), yet the temporal and spatial dynamics of these associations over the whole source-to-sink (i.e. offshore to nearshore) gradient are largely unknown.

Further investigation of the different life stages of fish species and the connection of habitats in coastal marine habitats (i.e. linked by macrophytes drifting from source to sink) could contribute immensely to conservation and other environmental managerial decisions. Some of these may include marine park planning or fisheries management by providing an understanding of the reliance that critical life stages of fish have on both temporary (e.g. drifting seagrass) and benthic (e.g. seagrass meadows) habitats. Protection of marine benthic habitats may be critical in South Australia because of the unique diversity, endemism and patch dynamics displayed in this region, particularly of the macroalgae (Phillips 2001). South Australia has 12 seagrass species and many species of large macroalgae growing within the same region. This contrasts with other temperate regions in Australia (Western Australia, which has 19 seagrass species across 7-8 genera and lower diversity of algal species than South Australia; eastern Australia, which has low seagrass diversity [i.e. 2 species in Sydney] and fewer macroalgal species than Western Australia; Womersley 1984, 1987; Carruthers et al. 2007; Short at al. 2007) and the rest of the world (New Zealand, 1 seagrass species, high algal diversity; South Africa, 4 seagrass species; North America, 9 seagrass species, few dominant algal species; Hurd et al. 2004; Carruthers et al. 2007; Short et al. 2007).

In 2003, the South Atlantic Fisheries Management Council USA implemented a management plan for the floating *Sargassum* harvest in South Atlantic waters to conserve the drifting habitats that are used by many marine animals, due to an increased commercial harvest of the algae for fertilisers and other products which is now regulated at 5,000 tons wet weight per year (Comyns et al. 2002; SAFMC 2003). This highlights one example of management starting to recognise coastal marine habitats that have previously been neglected and the importance of having good scientific evidence on which to base ecological management decisions.

In Australia, the commercial harvesting and local council removal of wrack is a common procedure along many beaches, and has been implemented into regional fisheries management plans (e.g. South Australian beach-cast seagrass and marine algae fishery; PIRSA 2007) because there is some concern that this process may impact the nourishment of beaches and alter nearshore production (Kirkman and Kendrick 1997). In South Australia, the amounts of wrack removed from beaches varies with approximately 50-110 tonnes of algae and 3000 tonnes of seagrass per year from the South East region of the state (PIRSA 2007). Conservation of marine habitats and associated biodiversity is a priority for many long-term environmental management strategies, and is evidenced in the development of marine parks nationally (DSEWPC 2012). The affinity that fish have with drifting seagrasses and macroalgae within southern Australia is unknown and there may be fish associations specific to macrophyte types that have not been taken into account in previous studies, highlighting the need for further research in this area.

Research that has investigated attached macrophytes and the role that they play as habitat and food resource for macroinvertebrates and fish has indicated that these are constantly changing habitats that support many trophic interactions (Figure 1.1). Compared to the research effort conducted on the fish assemblages and trophic dynamics associated with attached algal or seagrass beds, the literature about similar research conducted on drifting macrophytes is sparse (Figure 1.1) and mainly concentrated in the northern hemisphere (e.g. USA, Europe; Hobday 2000a-c; Ingolfsson 1995, 1998; Vandendriessche et al. 2006a-b). Some studies have also been undertaken in Chile (Thiel and Gutow 2005), Tasmania (Edgar 1987), along eastern and Western Australian coastlines (Lenanton et al. 1982; Kingsford 1992) and in New Zealand (Langtry and Jacoby 1996) . The following sections provide an overview of the current knowledge of drifting macrophytes and fauna associations and highlight the knowledge gaps that are the focus of this thesis. There are clear knowledge gaps of the drifting movement of macrophytes after detachment from the seafloor and the fauna associating with drifting macrophytes along the drift pathway into the surf zone as shown in Figure 1.1.

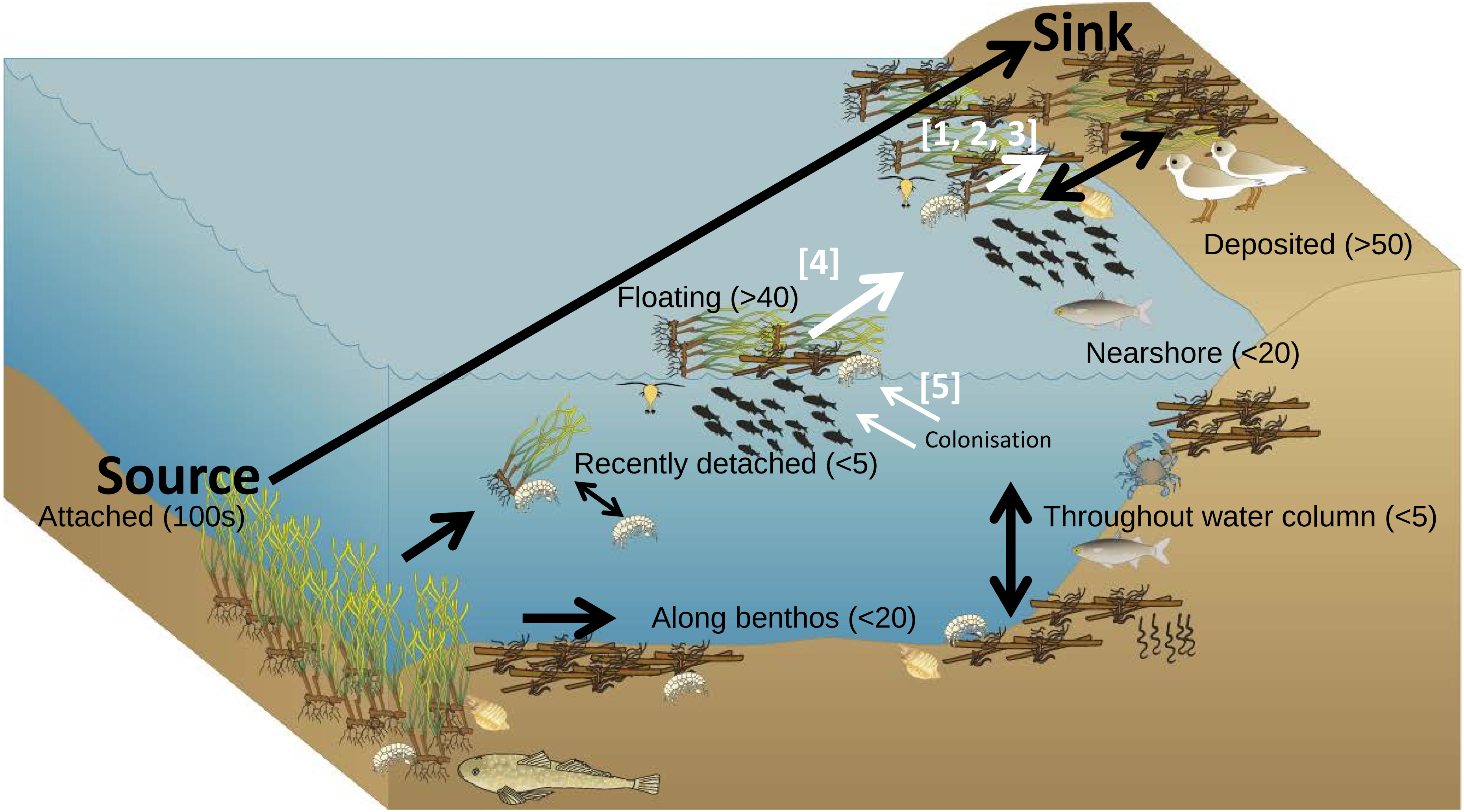


Figure 1.1: Conceptual model of the source-to-sink pathway from detachment to deposit of drifting macrophytes (e.g. seagrass) in a coastal ecosystem, including typical taxa at each point. Surface and benthic drift pathways are shown with emphasis upon transport and cycling throughout water column closer to shore. Black arrows indicate pathways identified in literature searches. White arrows indicate the points along the drift pathway that form the basis of the specific hypotheses examined in this thesis. White numbers in square brackets correspond to the numbered aims outlined in Chapter 1. Approximate numbers of peer-reviewed publications for studies done on specific points along the drift pathway are shown by black numbers in parentheses, based on literature searches.

2. Patchiness in time and space of drifting macrophytes

During heavy storm events or large swells in coastal waters, macrophytes can detach from the substrate and will then drift through the water column and either sink to become lodged in the sediments for burial or later re-suspension, or float to the surface where they continue to drift for days to months with currents and tides until they are finally deposited onshore (Kirkman and Kendrick 1997). Large piles of beach-cast wrack are a common feature on sandy beaches after large storms in many parts of the world (Kirkman and Kendrick 1997). However, no studies have specifically investigated the movement of drifting macrophytes into the nearshore zone of sandy beaches or the fish and macroinvertebrates associated with storm-induced pulses of drifting macrophyte accumulations. Some studies have investigated the deposition of macrophytes on sandy beaches as wrack after storms, but they have generally focused on large one-off storm events (Balestri et al. 2006) or more broadly during stormy periods such as monsoon seasons (Ochieng and Erftemeijer 1999). Larger volumes of seagrass fruit litter (Balestri et al. 2006) and wrack deposits (Ochieng and Erftemeijer 1999) were found on beaches after large storms in both of those studies. In comparison, few studies aim to investigate the arrival of drifting macrophytes into surf zones or deposition of beach-cast wrack specifically with multiple storm pulses versus calm-weather events.

There are many challenges associated with studying a constantly mobile and extremely patchy habitat such as drifting detached macrophytes, which can also interact with multiple benthic habitats close to shore (e.g. identifying the assemblage of fauna when macrophytes are constantly breaking apart or piling up to form large accumulations close to shore; Clarkin et al. 2012). The difficulties associated with investigating such a constantly-changing, mobile habitat may be a contributing factor for the lack of attention that drifting macrophytes have received in ecological studies in the past. The inherent patchiness in both time and space of macrophytes drifting in the marine environment is akin to patches found in freshwater habitats including woody debris after floods (Palmer et al. 1996) and leaf patches in streams (Palmer et al. 2000). In aquatic environments, the main challenge with the study of patchy habitats and associated macroinvertebrate community structure is the inherently large spatial heterogeneity in species abundances (i.e. single individuals of some to thousands of others; Norkko et al. 2000). To deal with this issue, the decision to sub-sample may be chosen in some studies due to restricted time and resources, which do not allow for the sampling of complete habitat patches (Sebastien et al. 1988; Nichols et al. 2006). Sub-sampling in patchy habitats and, more specifically, for macroinvertebrates in aquatic systems, results in reduced sampling precision and can lead to the overestimation of some species and underestimation of others (Andrew and Mapstone 1987; Downing 1989; Riddle 1989). Comparison of precise and time-costly sampling methods (e.g. fish surveys of 1.5 h soak time using baited remote underwater video, BRUVs) versus more efficient ones (e.g. 0.5 h soak time of BRUVs) have been undertaken in previous baseline studies to establish precise sample sizes for large ecological studies of other systems (e.g. Gladstone et. al. 2012). To date, no exploratory investigations have looked into changes in sampling precision estimates associated with sub-sampling of very large, extremely patchy habitats, such as drifting macrophyte accumulations in the surf zone of sandy beaches.

3. Macroinvertebrate assemblages associated with drifting macrophytes

The macroinvertebrate fauna associated with floating macrophytes may change across the drift pathway from detachment through to depositing or sinking locations (Ingolfsson 1995, 1998; Vandendriessche et al. 2006a-b; Clarkin 2012). Soon after detachment, larger sessile invertebrates may be removed from macrophytes due to turbulence (particularly in stormy conditions), while mobile macroinvertebrates are known to evacuate plant structures upon ascent to the ocean surface (Gutow et al. 2009). On ascent and along the drift pathway, detached macrophytes may retain some of the macroinvertebrate community that was present when attached to the substratum (Hobday 2000a). Some evidence exists that rafting on drifting macrophytes acts as a dispersal mode for adult invertebrates such as colonial ascidians and allows for colonisation of new habitats when macrophytes are deposited in nearshore habitats (Worcester 1994). New invertebrate recruits, particularly at the planktonic stage, may be attracted to drifting macrophytes along the entire drift pathway and this provides a vehicle for young invertebrates to disperse to other locations (Ingolfsson 2000; Vandendriessche et al. 2006a-b). There are also other invertebrates without a planktonic larval phase that colonise drifting macrophytes. Olafsson et al. (2001) identified large abundances of benthic harpacticoid copepods, which generally do not have a planktonic larval phase, on anchored clumps of experimental seaweed fronds after 20 days in nearshore waters. These authors suggested that this association may be a seasonal strategy for dispersal by adult harpacticoids.

The attractiveness of macrophyte rafts to macroinvertebrates may be the simple provision of refuge via habitat structure and thus any reduction in algal frond quality with age appears not to deter new colonists (Ingolfsson 1998; Hobday 2000a). The only restriction appears to be the available habitat space (Ingolfsson 1998; Hobday 2000a). The colonisation of drifting macrophytes by otherwise benthic macroinvertebrates may be more apparent at the end of the drift pathway when macrophytes enter the shallower coastal surf zone (Ingolfsson 1995, 1998; Vandendriessche et al. 2006a-b; Clarkin 2012). However, little is known about macroinvertebrate assemblages associated with different compositions of drifting macrophytes (i.e. mainly seagrass versus mainly algae versus a seagrass-algae mix; Figure 1.1).

Close to shore in shallower water (<10 m depth), benthic macroinvertebrates may move into clumps of drifting macrophytes to use the plant structure as a complex habitat for predator avoidance or to graze upon (Norkko et al. 2000; Crawley and Hyndes 2007). Bonsdorff (1992) found that benthic macroinvertebrate abundances were lower in core samples taken from sand under deposited algae clumps as opposed to sand without drifting algae. Norkko et al. (2000) also identified larger abundances of macroinvertebrates in deposited algae compared to the benthos underneath and also found higher levels of anoxia underneath drifting algae in laboratory experiments after three days. The presence of algae on top of the benthos and the subsequent increase in sediment anoxia may reduce the habitat quality for some macroinvertebrates such as amphipods, making the macrophytes a better habitat option, but may favour other macroinvertebrates such as polychaetes (Raffaelli 2000). Further research of drifting macrophytes would provide a better understanding of the role that macrophytes play for macroinvertebrates and the biological connection amongst small-scale habitats.

4. Fish assemblages associated with drifting macrophytes

Since the mid-1900s, it has been well documented that a range of pelagic fish species aggregate around various natural or artificial floating objects in oceans worldwide (Gooding and Magnuson 1967; Hunter and Mitchell 1968). The aggregation of commercially- and recreationally-important fish species around floating objects was quickly acknowledged by many fisheries globally and so Fish Attraction Devices (FADs) are now widely used to optimise return on fishing effort for some species (Gomes et al. 1998; Kingsford 1999; Kingsford and Defries 1999).

Soon after the detachment of macrophytes from the substrate, many fish species are attracted to clumps of macroalgae as a refuge (particularly juvenile stages of fish) and to feed off the associated macroinvertebrate fauna (Kingsford 1992; Vandendriessche et al. 2007). In offshore waters of New Zealand, Kingsford and Choat (1985) found that the colonisation rates of fish to drifting algal clumps appear to be relatively quick (1 to 6 hours) and fish abundances increased exponentially between three and five hours after placement of drifting algal clumps into the water. The association of juvenile fish with drifting macrophytes appears to be stronger closer to shore where macrophytes drift over various shallow-water habitats such as subtidal reefs, in-shore seagrass beds, and un-vegetated surf zones (Kingsford and Choat 1985; Kingsford 1992).

Most studies have identified that a range of juvenile fish species can and do utilise drifting macrophytes in shallower waters (Lenanton and Caputi 1989; Nishida et al. 2008) however, some researchers suggested that this may be an artefact of the methods used to capture fish around drifting objects. For example, Moser et al. (1998) only caught smaller-bodied and juvenile fish in dip nets but also observed larger predatory fish with a remotely-operated vehicle (ROV) camera that filmed around drifting clumps of *Sargassum* in coastal waters of North Carolina. These authors suggested that the larger predatory fish may have been underestimated if net samples were used alone and also mentioned that the fish assemblages associated with drifting macrophytes may be misrepresented in many previous studies that used net samples alone. However, seine net or dip net samples within and around drifting macrophytes usually capture the life stages and species of fish with the strongest affinity to the drifting habitats, which may venture further into the macrophyte matrix rather than flee to open water when disturbed (Kingsford 1999). Any drifting structure may suffice as habitat but, for young fish, the main risk is the potential of being eaten by predators such as large fish or seabirds when occupying less complex habitat structures such as moored buoys versus floating macrophytes (Kingsford 1993). Thus, the role that drifting macrophytes play as a nursery habitat for various fish species may depend on the quality or physical nature of the habitat, the close proximity of adjacent habitats, and the provision of rich food resources.

Initially, the physical presence of a floating structure may be the first visual cue that influences fish to aggregate around drifting macrophytes as a refuge habitat (i.e. for juveniles) and secondary to this may be the presence of better feeding opportunities (particularly for predatory species) (Kingsford 1993). The timing of recruitment for particular species may be synchronous with the timing of large macrophyte accumulations after storms or large swells and thus provide an easily-accessible nursery habitat for these fish (Kokita and Omori 1998). Fish may also be attracted to particular species compositions of drifting macrophytes and the volume of macrophyte clumps or aggregations of clumps may determine the longer-term structure of fish aggregations (Adams et al. 2004). Adams et al. (2004) identified that abundances of one species of pinfish (*Lagodon rhomboides*) were positively correlated with high volumes of drifting algae across eight separate sites in coastal waters of Florida in the USA. In addition, Crawley et al. (2006) identified greater fish biomasses with higher volumes of wrack in surf zones of two beaches in Western Australia and found that sea trumpeter (*Pelsartia humeralis*) were more attracted to floating seagrass than brown algae in aquarium choice experiments. Also, Kingsford (1992) conducted seine net hauls of fish and drifting macrophytes at two offshore stations (10-18 km from shore) in New Zealand and found some evidence of a positive correlation between fish abundances and weight of algae clumps. However, there are few studies that have attempted to investigate the fish assemblages associated with macrophyte accumulations of various species compositions and volumes over multiple sites or regions, particularly in the nearshore zone. Also, in South Australia there have been no previous studies of drifting macrophytes utilising the available regions that have very different macrophyte compositions along the drift pathway and the fish associated with them

5. Trophic interactions associated with drifting macrophytes

Drifting macrophytes support multiple trophic interactions, which can vary along the surface drift pathway through to the surf zone of sandy beaches (Vandendriessche et al. 2007). The few studies that have investigated the trophic interactions of fish associated with drifting macrophytes have shown mixed results that appear to depend upon the fish species and life stage investigated. Vandendriessche et al. (2007) analysed the stomach content of five species of juvenile fish captured from drifting algae and in open water samples in Belgium and found that there were differences in the diets of fish feeding among algae versus open water. Macroinvertebrate fauna were also more often associated with drifting algae compared to being in open water, which provided some rationale for the presence of large juvenile fish associated with the algae (Vandendriessche et al. 2007). Closer to shore, as macrophytes drift over shallow-water habitats (e.g. seagrass beds, subtidal rocky reefs), there may be more opportunity for demersal fish species to opportunistically feed on macroinvertebrates associated with drifting macrophytes. Lenanton et al. (1982) found that the diets of the benthic-feeding, juvenile yellow-eye mullet (*Aldrichetta forsteri*) consisted primarily of one amphipod species (*Allorchestes compressa*) that had a strong association with drifting macrophytes. Diel sampling of fish diets by Robertson and Lenanton (1984) also identified high proportions of the same amphipod species (*A. compressa*) in the stomach of benthic-feeding fishes from beach surf-zones in Western Australia. There is also some evidence of herbivory by benthic fish on detached algae but this appears to be limited to a few specialist species (Wernberg et al. 2006). Furthermore, it is not known whether herbivorous fish are selective grazers on specific algae species (including epiphytes) or on algae at specific stages of decomposition.

Analyses of the stomach contents of fish provide some insight into the dietary composition of drifting macrophyte-associated fishes, yet any further understanding of the trophic pathway is limited with dietary analyses alone. In order to investigate the trophic energy flow from drifting macrophyte to consumer, the use of stable isotope analyses is likely to be useful. A few studies have thus shown evidence for the transfer of energy from detrital material into the foodweb. Hyndes and Lavery (2005) analysed the δ^{13}C and δ^{15}N isotope ratios for drifting algae, seagrass, and associated macroinvertebrates and fish samples captured in nearshore waters of Western Australia. They found that the δ^{15}N values in fish were much more enriched than primary producers (>5 ‰) and δ^{13}C values in fish were similar to that of amphipods and copepods that appeared in large abundances in fish stomachs, indicating that fish were probably assimilating δ^{13}C from these invertebrates. In addition, they also identified that macrophyte-associated amphipods and copepods were most likely to assimilate δ^{13}C from brown algae rather than other forms of algae or seagrass. Rooker et al. (2006) used a combination of stable isotope (δ^{13}C and δ^{15}N) and fatty acid analyses to determine the trophic level of fishes associated with drifting *Sargassum* spp. in the Gulf of Mexico. From the stable isotope analyses, they identified that most of the juvenile fish were secondary heterotrophs whereas adult fish were tertiary consumers, while fatty acid signatures in juvenile and adult fish were similar to phytoplankton, indicating that the fish depended upon phytoplankton production (Rooker et al. 2006). However, there is little evidence to date of the differences in dietary structure of fish associated with drifting macrophytes or trophic interactions associated with drifting macrophytes of different compositions and volumes across multiple regions. In order to demonstrate the importance of trophic interactions associated with various mixtures and volumes of drifting macrophytes in multiple regions, a combination of methods such as dietary analyses of fish and stable isotope analyses of macrophytes, fish and macroinvertebrates should be implemented in drifting macrophyte studies.

6. Source to sink: The drift pathway

Before macrophytes are deposited in the littoral zone, there can be a long drift-time between initial detachment from the benthos (source) to first deposition on land (i.e. islands or mainland) or eventual sinking due to deterioration (Hobday 2000b). The duration of drift is highly dependent on wind current and tidal flow velocities (Biber 2007). Kingsford and Choat (1986) also recognised that surface slicks caused by internal waves create a region for algal accumulation, leading to higher densities of drifting algae and associated invertebrate and fish fauna within surface slicks compared to rippled regions away from slicks.

Relatively little research has focused on the origin of drifting macrophytes and the length of the drifting time, and hence distance travelled, once plants have detached from the substrate. To investigate the previous studies of drifting macrophyte pathways, I repeatedly conducted a comprehensive literature search beginning in 2011 to mid-2014 to keep up to date with any newly published research during the course of my project but citing all of the relevant studies found (Table 1.1). Based on those search results, previous studies have used a variety of techniques to measure the transport dynamics of drifting macrophytes at different stages of the drift pathway from original source through to initial deposit on land or sinking (Table 1.1). Most of the previous tracking studies have been conducted on the larger seaweeds such as species of *Sargassum* or *Macrocystis* and with a large focus on coastal waters of USA or China (e.g. Hobday 2000c; Komatsu et al. 2007). Ranging from small to large spatial (<10 to >1000 km) and various temporal (days to years) scales, there were consistent patterns that have emerged from these various studies (Table 1.1). Four broad tracking methods have been previously used: *in situ* volume or biomass calculations at different stages of the drift pathway; tagging algae at start points but collecting only at end points; real-time tracking across large distances of the surface drift pathway; and satellite imaging or computer modelling of part of the surface drift pathway (Table 1.1).

All authors identified that either major current systems or regional currents and wind stress were the major environmental influences on the surface transport of drifting algae (e.g. Harrold and Lisin 1989; Kingsford 1995; Kirkman and Kendrick 1997; Hobday 2000c; Biber 2007; Komatsu et al. 2007). Kingsford (1995) also highlighted that, to a lesser extent, internal waves had some influence on the surface drift of algae. There are some limitations in the various methods used, but these appear to depend on the time scale of the study undertaken. For example, the studies by Kingsford (1995) and Kirkman and Kendrick (1997) employed visual tags attached to drifting macrophytes, which only provided information about particular stages in time of the surface drift pathway (i.e. recorded at only the start and end-points of the studied portion of the drift pathway). Harrold and Lisin (1989) used radio trackers on detached surface-drifting algae, where the authors could only track the algae over a small time period and could not provide any information about the deposit of wrack onto the shore. In contrast, the real-time satellite-tracking techniques employed by two of the studies were undertaken offshore across large spatial scales (100s to 1000s km) with many trackers eventually lost in current systems well away from coastlines and thus the original source of attached algal beds (Hobday 2000c; Komatsu et al. 2007). This review showed that little is known about the drift dynamics of macrophytes at distances close to shore where oceanographic conditions are amplified and unpredictable due to the interaction of shallow depths with swell, wind waves, and tidal regimes.

Particular sections of the drift pathway of detached macrophytes have received varied amounts of attention in previous research (Figure 1.1). Only one study has investigated the recently detached through to floating at the sea-surface pathway by studying the colonisation or emigration of fauna after detachment from minutes to hours (Gutow et al. 2009). Three studies have investigated the colonisation of fauna of floating macrophytes and along the benthos and interactions between the two (Hair et al. 1994; Salovius et al. 2005; Clarkin et al.

2012). In comparison, nine studies have investigated the drift pathway of detached macrophytes from offshore to nearshore and the faunal compositions associated at those distances (Safran and Omori 1990; Kingsford 1992, 1995; Ingolfsson 1995, 1998, 2000; Olafsson et al. 2001; Vandendriessche et al. 2006a, 2007). The research in this thesis aims to address the lack of knowledge of the drift pathway from the recently detached and floating macrophytes offshore as they travel through to the surf zone and deposit on shorelines and the faunal associations along that drift pathway into the surf zone.

Table 1.1: Summary of the published research on drifting macrophyte pathways (i.e. all macroalagae species and no seagrasses) using various tracking techniques. Environmental influences are numbered according to order of importance as indicated by authors of those papers. This summary is based upon literature searches using the keywords ‘drifting macrophytes’ and the alternatives ‘drifting seaweed’, ‘drifting kelp’, ‘drifting macroalgae’. Multiple searches were conducted within various databases including Biological Abstracts, Google Scholar, Science Direct, Web of Science and Wiley Online and then refined searches of the results for studies of drifting macrophyte tracking studies.

Tracking method used	Algal species	Location studied	Maximum distance tracked	Maximum tracking time	Section of drift pathway	Environmental influences on drift pathway	Limitations of study	Reference
Permanent seine nets at multiple sites along tidal inlet (i.e. used consistent currents)	Various algal species	Florida, USA	< 100 km	8 days	Particular points along a tidal gradient	1) Coastal currents 2) Tidal regimes 3) Wind stress	1) Particular points in time only	Biber 2007
Attached visual tags	*Macrocystis pyrifera*	California, USA	< 10 km	1-2 days	Part of surface drift pathway	1) Wind stress 2) Coastal currents 3) Internal waves	1) Short drift time 2) Two points in time only	Kingsford 1995
	Ecklonia radiata and mimics	Western Australia	2 km	15-23 days	Start and endpoints of drift pathway	1) Winds 2) Coastal currents	1) Two points in time only	Kirkman and Kendrick 1997
Attached radio trackers	*Macrocystis pyrifera*	California, USA	< 50 km	7 days	Complete surface drift pathway	1) Wind stress 2) Coastal currents	2) Short drift time	Harrold & Lisin 1989
Attached satellite-tracked buoys	*Sargassum* spp.	China	< 200 km	58 days	Part of surface drift pathway (i.e. no deposit endpoint)	1) Major current systems 2) Wind stress	1) Loss of trackers 2) No arrival of trackers nearshore	Komatsu et al. 2007
Satellite-tracked drifters	Drifters simulating *Macrocystis pyrifera*	California, USA	>1000 km	89 days	Complete surface drift pathway	1) Major current systems 2) Wind stress	1) No arrival of trackers nearshore 2) Not identical mimics	Hobday 2000c
Satellite imaging	*Sargassum* spp.	Gulf of Mexico, USA	> 1000 km	Years	Each image = 1 position in time.	1) Major current systems	1) Only identified macrophytes at points in time 2) Only detected large algal accumulations	Gower & King 2008
Computer simulation modelling of surface algal-drift pathway	*Sargassum* spp.	China	> 100 km	75-day simulation	Part of surface drift pathway	1) Major current systems	1) Predictions of drift pathway only 2) Relies on known currents	Filippi et al. 2010

7. Aims of this project

The overall aim of this project was to address some of the crucial knowledge gaps of the ecological role that drifting macrophytes play as habitat and food resource for fish and their macroinvertebrate prey, particularly in the typically nutrient-poor surf-zones of sandy beaches. In order to address these knowledge gaps, I proposed a research strategy that prioritised five key areas for investigation of the habitat and trophic function of drifting macrophytes for fish and macroinvertebrates with the following aims, to:

(1) Establish a precise sampling regime for surveying fish, macroinvertebrates and drifting macrophytes in the surf zone of sandy beaches to gain a better understanding of how to efficiently deal with the sampling of extremely patchy habitats (Chapter 2);

(2) Identify fish and macroinvertebrate assemblages found within different volumes and species compositions of drifting macrophytes in separate regions after storm versus calm events (Chapter 3);

(3) Investigate the trophic function of drifting macrophytes of varying composition and the trophic pathways of associated fish fauna and macroinvertebrate in the surf zone of sandy beaches using multiple techniques (i.e. dietary and stable isotope analyses) (Chapter 4);

(4) Track the drift pathways of common drifting macrophyte species within coastal waters at various distances close to shore to identify the processes of macrophytes drifting at the water surface into the surf zone and stranding on sandy beaches(Chapter 5); and

(5) Investigate the rapid colonisation process of fish and macroinvertebrates to surface drifting macrophytes at various distances close to shore to identify the importance of drifting macrophytes as habitat for fauna (Chapter 5).

Thesis structure and outline

This thesis is written as five manuscripts (i.e. Chapter 5 will be split into two manuscripts) for publication in peer-reviewed journals, book-ended by this general introduction (Chapter 1) and a synthesis of findings in a general discussion (Chapter 6). Chapter 2 is a pilot study approach to establishing an experimental design and precise sampling regime for use in extremely patchy habitats such as drifting macrophytes in the surf zone of sandy beaches. Chapter 3 is an investigation of the composition of drifting macrophytes and associated fauna during multiple storm and calm-weather events and across multiple regions of South Australia. Chapter 4 is a study of the trophic structure and pathways associated with drifting macrophytes, macroinvertebrates and fish found in the surf zone of sandy beaches in two regions. Finally, Chapter 5 focuses on the movement of drifting macrophytes and the associated colonisation by macroinvertebrates and fish at different distances away from sandy beach shorelines. Further specific details for each data chapter are also included as tables and/or figures in appendices that are numbered according to each corresponding chapter number. Collectively, this research aims to determine the importance of drifting macrophytes moving into and accumulating nearshore as wrack and the fauna that utilise this allochthonous material as habitat and a food resource.

Chapter 2: Steps for establishing precise estimates of abundance and richness in patchy habitats: a nearshore marine example

Summary

Exploratory investigations of optimal sampling designs are a critical component of the decision-making process in ecology where inherent natural variation can lead to erroneous conclusions if left unexamined. Pilot studies leading to exploratory analyses that investigate the precision of sampling regimes should reduce the chances of erroneous results and can be used to optimise processing time in larger ecological research programs. In my study, I calculated optimal precision estimates for sampling macroinvertebrates and ichthyofauna in surf-zone wrack accumulations by investigating the precision of the mean for sub-samples and replicate numbers of seine nets to guide future sampling regimes. I discovered that the processing time for individual seine net samples could be reduced by 50 % using sub-sampling and that time to process replicate seine net samples could be reduced by 25 %, while maintaining acceptable precision. In future, I suggest that the use of pilot studies with similar exploratory approaches should be less of an exception and more a critical component of ecological investigations, particularly in under-studied or newly-developing areas of research. Further, these types of exploratory approaches are crucially important in a variety of extremely patchy environments where variability is likely to be high.

1. Introduction

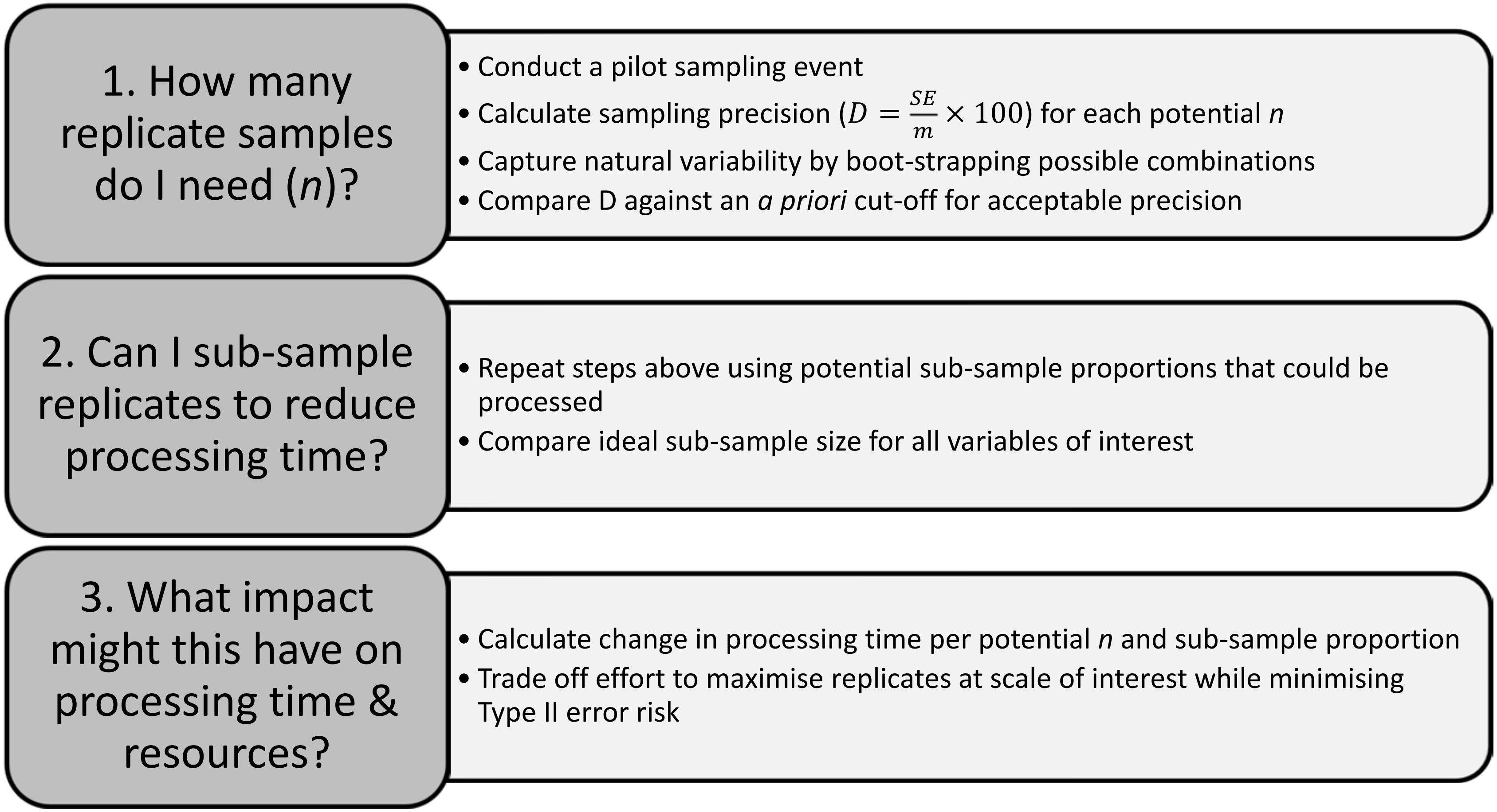
Habitat patchiness is encountered in many terrestrial and aquatic ecosystems (Fahrig 2003; Fischer and Lindenmayer 2007), often a result of habitat fragmentation due to human modification, biological invasions and natural climatic events. This inherent patchiness creates a number of challenges for ecologists who wish to investigate such habitats and the associated fauna, depending on the extent of patchiness within a habitat. Firstly, patchy habitats tend to have inherent habitat heterogeneity that is made up of a mosaic of multiple microhabitats (Robson and Chester 1999). Different microhabitats within a patch may attract different faunal assemblages as has been observed in a variety of ecosystems including terrestrial invertebrates in grasslands (Reid and Hochuli 2007), invertebrates in freshwater streams (Effenberger et al. 2008), and beetles in rainforest canopies (Wardhaugh et al. 2013). The most challenging problem for ecologists is the combined heterogeneity of habitat patches and the associated fauna, particularly when they wish to investigate larger-scale processes at an ecosystem level. This heterogeneity can only be captured by increasing the intensity of sampling. For most ecological sampling programs, it is widely accepted that an increase in the number of replicate samples usually results in, up to a point, lower standard error and improved sampling precision (Andrew and Mapstone 1987; Bros and Cowell 1987). Ideally, in any ecosystem studied, large numbers of habitat patches should be sampled to gain the most precise dataset for habitat structure and the associated fauna but, in reality, this is usually impractical. The majority of research programs are limited by time, resources and funding which constrain the associated sampling efforts, thus an optimal sampling design would only be extensive enough to satisfy sampling precision requirements.

The basis of field ecological studies is an attempt to capture the natural variability in organism abundances at various spatial and temporal scales. Often, large field-based sampling programs can quickly consume allocated time and resources whenever species diversities and abundances are extremely variable. Sampling programs targeting such assemblages often involve sub-sampling whole samples so that some reliable estimate of assemblages can be obtained within the time and resources available (Sebastien et al. 1988). Sub-sampling is a useful way to reduce the time required for laboratory processing of samples but the associated potential for lower sampling precision must be considered and evaluated explicitly. Andrew and Mapstone (1987) highlighted some of the pitfalls associated with sampling for organism abundances using different sample sizes and emphasized the need for pilot studies in order to gain the most precise but also practical estimates from sample data. The pitfalls include the potential inability of small sampling units to obtain a reasonable indication of relative abundances at larger scales and the chance of increased observer fatigue and decreased precision with very large sampling units (Downing 1989; Riddle 1989; Andrew and Mapstone 1987). Both problems can lead to the over-estimation of species with large abundances and under-estimation of rarer ones (Andrew and Mapstone 1987). During the 1980s, multiple researchers (e.g. Pihl and Rosenberg 1982; Andrew and Mapstone 1987; Downing 1989; Riddle 1989) highlighted the need for more forethought to identify optimal sampling designs (e.g. by using pilot studies) and that the use of precision estimates can aid in the decision-making process. More specifically, complacency in sampling design without pre-planned exploration of levels of variability is risky and increases the chances of encountering Type II errors (where no effect is detected due to lack of statistical power when in fact it should be; Fairweather 1991; Mapstone 1995; Zuur et al. 2010). Fairweather (1991, p. 559) highlighted the potential dangers of ignoring statistical power without pre-planned pilot studies, which can “lead to false and dangerous complacency”, particularly where environmental impacts are being investigated. The outcome of this complacency is limited conclusive evidence of ecological relationships and thus a reduced ability to detect environmental effects, which is not only a drain on time and resources but may ultimately lead to significant environmental harm (Fairweather 1991).

In patchy habitats, such as those where organism abundances range from completely absent from some patches through to scarce and to very abundant in others, pilot studies should be an integral part of the process of sampling design. Pre-planning in this way is essential to define a manageable number of whole replicates and sub-sample sizes that will yield appropriate estimates of the population and reduce the chance of making Type II errors. One of the more extreme examples of a patchy habitat in both time and space is the accumulation of detached and drifting macrophytes (commonly referred to as 'wrack') found in the nearshore zone of sandy beaches usually after large storms or swells (Lenanton et al. 1982). Compared to more permanent habitats such as living kelp forests or seagrass meadows, detrital wrack accumulations constantly change structure in space and time, particularly in surf zones where there is constant water movement (e.g. due to wave action, tides and storms). Studies that have investigated wrack arrival into the surf zone highlight the role that such macrophytes play as an important habitat role for fish and macroinvertebrates long after detachment from the seafloor (Robertson and Lenanton 1984; Crawley and Hyndes 2007). Yet, compared to studies of attached macrophytes living *in situ* and the habitat function that they provide for fish and macroinvertebrates, the research effort placed on understanding the role of wrack as a habitat in the nearshore zone has been small (e.g. Van der Merwe and McLachlan 1987; Marin Jarrin and Shanks 2011; Crawley et al. 2006). This may be partly due to the extreme patchiness and temporary nature of wrack accumulations in the nearshore zone which makes it difficult to sample efficiently.

In the few previous studies that have investigated wrack accumulations as habitat in the nearshore zone, seine nets were the preferred method for sampling of fish and macrophyte components (Robertson and Lenanton 1984; Crawley et al. 2006). A benefit of using seine nets is that they enable a large sample of the wrack material to be captured at the same time so that an entire drifting habitat patch can be processed for macrophyte volumes, fish abundances and macroinvertebrate abundances. The shortcomings of sampling entire wrack accumulations include that they are mobile and continuous habitats that vary considerably in volume.. Often, all fish can be identified easily and counted in each replicate seine net haul but the precision of increasing replicate numbers for fish abundances needs to be established in order to provide reliable estimations of fish assemblages associated with surf zone wrack accumulations. The precision of macroinvertebrate abundances and macrophyte volumes of increasing replicate numbers of seine net hauls should also be established for reliable estimations of the material that contributes to wrack accumulations and the associated macroinvertebrate fauna. Also very large wrack volumes often cannot be efficiently processed for macrophyte volumes and macroinvertebrate abundances in the laboratory Therefore, decisions should be made to sub-sample for macrophytes and macroinvertebrates in order to gain precise estimates of relative abundances and distributions, so that sampling effort can be reduced without reducing the ability to answer the hypothesised ecological questions as intended.

The aims of this study were to (1) use a sequence of steps (Figure 2.1) to establish precision estimates of seine-net replication for fish abundances, macroinvertebrates and macrophytes and sub-sample sizes of macroinvertebrate abundances and macrophyte volumes from whole seine net samples and (2) establish baseline data of the detached macrophytes, fish and macroinvertebrate assemblages associated with surf zone wrack accumulations along metropolitan beaches in South Australia. Exploration of the data in this way would provide a baseline of the optimal number of seine net replicates and associated sub-sample sizes required for future studies of wrack and associated fauna in beach surf zones. Also, my study highlights the general importance of exploring preliminary data when the decision to sub-sample is made for any proposed research in other patchy habitats.



1. How many replicate samples do I need (*n*)?

- Conduct a pilot sampling event
- Calculate sampling precision ($D = \frac{SE}{m} \times 100$) for each potential *n*
- Capture natural variability by boot-strapping possible combinations
- Compare D against an *a priori* cut-off for acceptable precision

2. Can I sub-sample replicates to reduce processing time?

- Repeat steps above using potential sub-sample proportions that could be processed
- Compare ideal sub-sample size for all variables of interest

3. What impact might this have on processing time & resources?

- Calculate change in processing time per potential *n* and sub-sample proportion
- Trade off effort to maximise replicates at scale of interest while minimising Type II error risk

Figure 2.1: Flow diagram of the processes used to determine optimal sampling design based on precision estimates and acceptable precision values that have been used in cost-benefit analyses of taxonomic group datasets across sub-samples and replicate numbers. D = % precision, *SE* = standard error, *m* = arithmetic mean, *n* = sample number.

2. Materials and Methods

Study area

Field surveys were conducted at each of five randomly-selected sandy-beach sites along the metropolitan Adelaide coastline in Gulf St Vincent, South Australia from August to September 2011 (Figure 2.2). All of the sites sampled are classified as intermediate beaches (Short 2001) and form part of a 28-km long sandy-beach system that has been highly modified and disconnected over time by the construction of jetties, seawalls, groynes, breakwaters and marinas (Short 2012). Gulf St Vincent has large sub-tidal seagrass meadows that are the dominant form of macrophytes (primarily *Posidonia* spp. but also *Amphibolis* spp. and *Heterozostera tasmanica*, among others) compared to little macroalgae (Edyvane 1999a, 2008), which is proportionally reflected in the wrack that is regularly washed ashore (Duong 2008).

Field surveys

At all sites, sampling was conducted in the surf zone on a sandy bottom with living seagrass meadows at least 30 m away. Replicate seine nets could not be allocated randomly as wrack accumulations are very patchy habitats in time and space and are constantly moving due to the turbulence of the surf zone. Therefore, wrack accumulations were specifically targeted for seine netting but all accumulations were considered available for randomised sampled. Sampling consisted of eight replicate seine-net hauls per site as the maximum number that could be achieved within one sampling day, which were taken to capture whole wrack accumulations and associated fish and macroinvertebrates. However, sorting of macrophytes and macroinvertebrates is much more time consuming, hence the need to sub-sample these two components in this study. A seine net (10 m long, 2 m depth, central 0.5 m bellow, with 4 mm mesh size) was deployed in the surf zone and dragged through wrack accumulations. This size of the seine net, which is slightly smaller than that used in a few other studies (e.g. Crawley et al. 2006) was selected so that the sampling area focused on each individual wrack accumulation and the target biota (i.e. larval and juvenile fish, rather than adults which may have evaded a small net) within it sampled rather than the larger surf zone. The area sampled through wrack accumulations was approximately 70 m^2 on each occasion. The combination of net size and the area sampled through each wrack accumulation was implemented to provide a reliable estimate of the flora and closely associated fauna within each targeted habitat that was sampled. Each net haul was emptied out onto a tarpaulin laid out on the beach to ensure that the entire wrack accumulation could be searched for fish.

All fish were collected from the entire sample and placed in 10-L buckets of aerated seawater before handling for species identification and measurement of standard lengths. Some fish that had lost equilibrium were euthanized with AQUI-S before being preserved in 10 % buffered formalin. After length measurements and identification, all other fish were released back into the surf zone at each site. In order to establish baseline estimates of sub-sample precision for macrophytes and macroinvertebrates, the entire wrack sample from each net haul was evenly laid out onto a tarpaulin then visually split in the field into proportional eighth sub-samples. These eight sub-samples were collected and placed into separate zip-lock bags of various sizes using multiple bags for large samples for transportation in containers of ice to the laboratory.

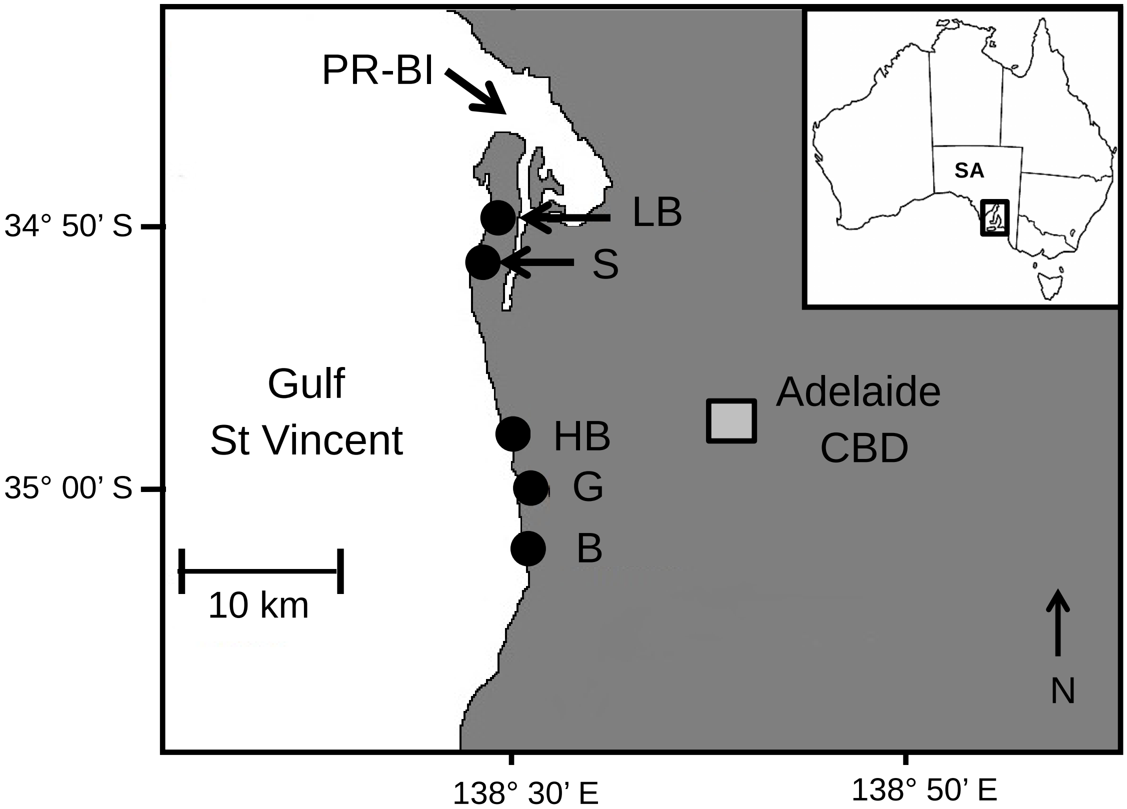


Figure 2.2: Map of sites represented by black circles that were studied along the Adelaide metropolitan coastline in South Australia (SA) during August to September 2011. Sites are B = Brighton, G = Glenelg, HB = Henley Beach, S = Semaphore and LB = Largs Bay. Pr–BI = Port River, Barker Inlet estuary system. Inset map shows the location of the study region in Australia.

Laboratory processing

All eight sub-samples from each replicate were rinsed thoroughly with freshwater to remove macroinvertebrates which were washed into a 500-µm mesh sieve. Macroinvertebrates from each sub-sample were immediately preserved in 70 % ethanol for further identification and abundance counts. Rinsed wrack sub-samples were resealed in zip-lock bags and frozen at -20 °C for storage before volume measurements. Total wrack sub-samples were thawed, drained of excess water and placed in various volumetric cylinders (0.005, 0.1, 0.5 or 2 L) to determine the total displacement volume of each wrack sample. For very large samples that could not fit in volumetric cylinders, 30-L containers with marked volume increments were used. After total volumes for each wrack sub-sample were measured, the wrack was sorted into major macrophyte groups including seagrass, brown algae, red algae and green algae. Macrophytes were identified further to the lowest taxonomic level possible in order to gain information on taxon richness. Materials other than marine macrophytes were assigned to five other groups which included: Porifera; Bryozoa; terrestrial plant matter; anthropogenic litter; and animal fragments. Most macroinvertebrates were identified to family level under a dissecting microscope but other specimens were only identified to order or sub-order due to the poor taxonomic knowledge of some taxa from this region and the difficulty to distinguish between families for juvenile specimens (particularly Gammaridea amphipods).

Data analyses

Macrophyte volumes and macroinvertebrate abundances from sub-samples as increasing eighth fractions from each sample were explored for precision estimates of means calculated from each fraction. Also, macrophyte volumes, fish and macroinvertebrate abundances from each whole-replicate net sample were explored to determine the precision of each increase in replication. Downing (1979, 1989) and Andrew and Mapstone (1987) have highlighted the advantages in using the simple precision of mean calculation to find the precision for a particular sampling unit. The precisions of means (Andrew and Mapstone 1987) were calculated as:

$$D = \frac{SE}{m} \times 100$$

where D = % precision, SE = standard error and m = mean number of individuals per sampling unit, referred to as a ‘precision score’.

From this calculation, precisions of means were plotted to visually explore the data to gain an understanding of the effect of seine-net replicate sample sizes for fish abundances and sub-sample proportions for macrophyte volumes and macroinvertebrate abundances (Figure 2.1). Lower percent values indicate better precision of the mean for that particular sampling unit and, in many studies, a set cut-off value for precise sample sizes is arbitrarily selected *a priori* (Andrew and Mapstone 1987). Several studies have used a cut-off precision value of ≤20 % (Downing 1979; Andrew and Underwood 1989; Bartsch et al. 1998). Therefore, I selected the same cut-off for acceptable precision which could then be applied to further investigations of wrack accumulations in surf zones (Figure 2.1).

Script was written in Tinn-R (Version 2.3.7.1) and run using the R statistical environment (Version 2.14.1) to calculate precision estimates in each eighth fraction for the common wrack and macroinvertebrate groups. For each taxonomic group, I calculated precision estimates for all possible combinations at each eighth fraction for each seine net replicate at each site. At each site, the precision estimates of each fraction were boot-strapped (n = 1000) to capture the nature of the variability in the dataset depending on which possible combinations were included (see also Hewitt et al. 1993 for similar approaches). The mean precision value for each fraction was then calculated and plotted against the pre-determined cut-off value of ≤20 % for each wrack and invertebrate group (Appendix 2, Figure A2.1).

I also calculated precision estimates for the dataset of replicate whole seine-net hauls for each increase in replicate number for common wrack, macroinvertebrate and fish groups. At each site and for each taxonomic group, the calculation of precision estimates for all possible combinations of replicates for each increase in replicate number was undertaken. The mean precision value of each increase in replicate number was calculated and plotted against the pre-determined ≤20 % cut-off value for the common taxonomic groups or species at each site (Appendix 2, Figure A2.2).

Further investigation of the precision estimates from eighth-fraction sub-samples and the whole replicate was undertaken with scatterplots of the number of taxonomic groups that showed acceptable precision (i.e. ≤20 %) at each increase in sub-sample fraction or replicate number (Appendix 2, Figure A2.1,A2.2). To optimise the efficiency of future sampling programs, the percentage of taxonomic groups with acceptable precision for sub-sample fractions and replicate numbers were tabulated with time estimates for field and laboratory processing at each sub-sample or replicate increase.

The species richness and abundances of macroinvertebrates and fish, and percent contributions of macrophyte groups to total volumes of wrack were also plotted to identify descriptive baseline patterns in the data.

3. Results

Wrack contributions and abundance

Overall, there were 18 macrophyte groups and five other groups identified in drifting wrack during seine-net sampling along the surf zones of sandy beaches in the metropolitan Adelaide region in 2011 (Appendix 2, Table A2.1). The largest percent contributions of macrophytes were seagrasses *Posidonia* spp., *Amphibolis antarctica* at >60 %, and unidentified seagrass leaves or rhizomes at all sites (Figure 2.3A, also Appendix 2, Table A2.1). Algae had the largest percent contributions at Brighton (21 %) and Glenelg (10 %), represented by red and brown algae combined (Figure 2.3A). Other groups such as anthropogenic litter and animal fragments were only found in much smaller volumes (<1 %) across all sites (Figure 2.3A). The largest wrack volumes were found at Semaphore but they were highly variable and the smallest wrack volumes were at Largs Bay (Figure 2.3B).

Macroinvertebrate taxon richness and abundance

Invertebrates captured in seine net hauls included 58 taxa with the highest taxon richness found at Brighton, Glenelg and Semaphore (Figure 2.4A; Appendix 2, Table A2.2). Brighton and Glenelg had the largest overall invertebrate abundances compared to other sites (Figure 2.4B). Isopod and gastropod abundances were largest at Brighton and amphipod abundances were similarly most abundant at Brighton and Glenelg (Figure 2.4C-E). Annelid and bivalve abundances were low overall but were greatest at Glenelg (Figure 2.4F-G).

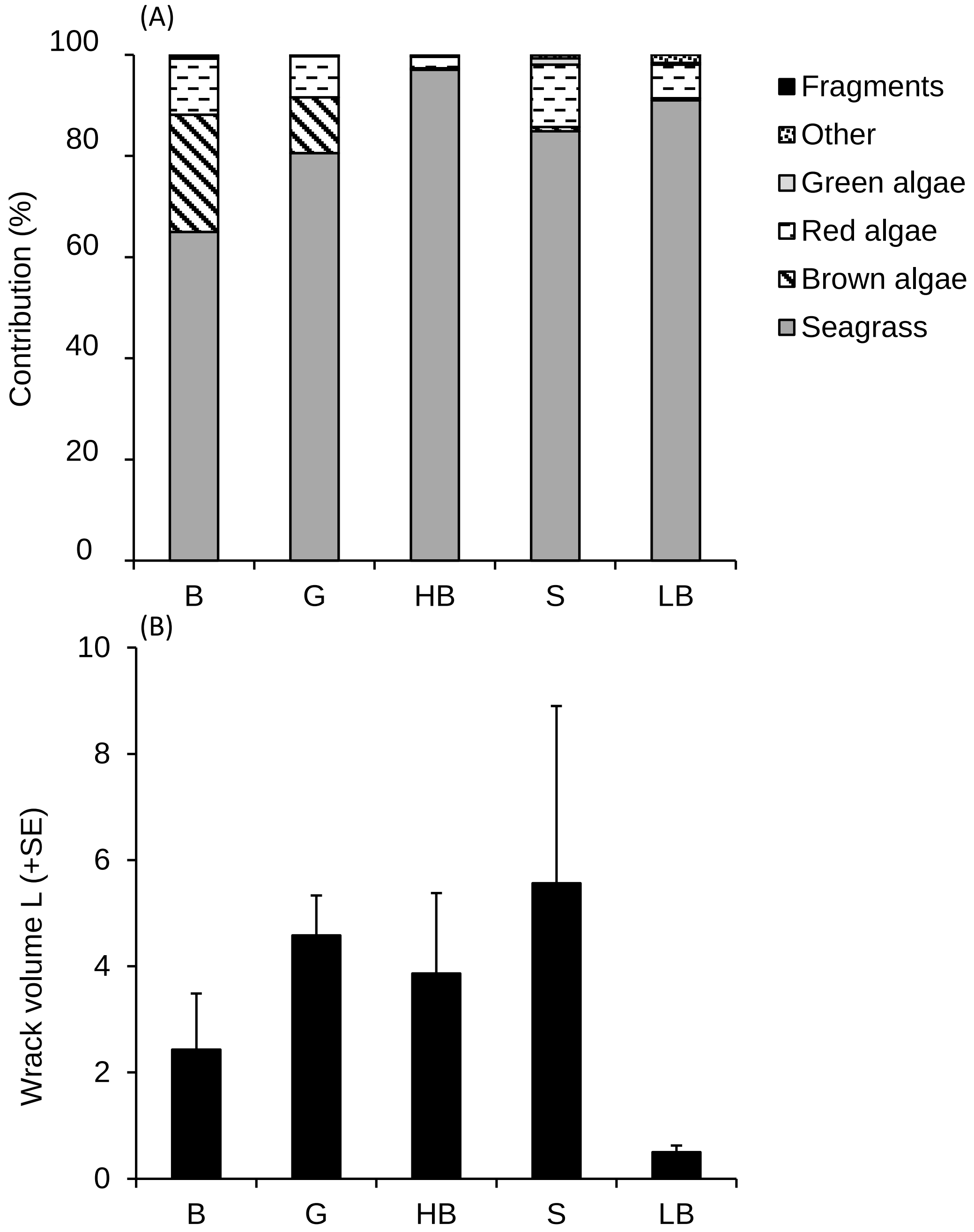


Figure 2.3: Wrack: (A) Percent contribution of the major taxonomic groups of macrophytes and other organisms, and (B) the total mean (+SE) wrack volume (litres) captured in seine net hauls, *n* = 8.

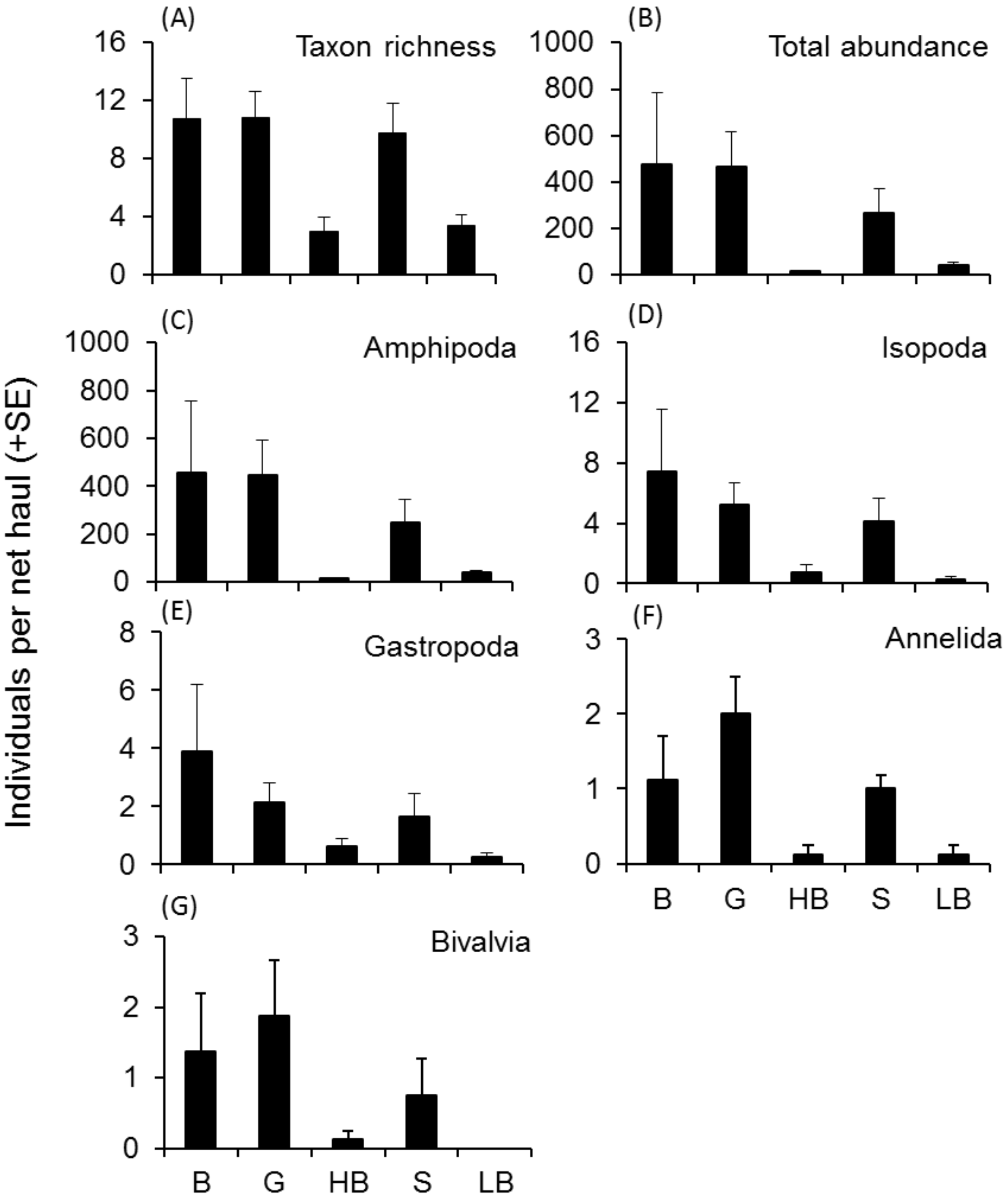


Figure 2.4: Macroinvertebrates: Mean (+SE) (A) taxon richness, and individual abundances of (B) total macroinvertebrate abundances, (C) Amphipoda, (D) Isopoda, (E) Gastropoda, (F) Annelida and (G) Bivalvia captured in seine net hauls during 2011. Sites are B = Brighton, G = Glenelg, HB = Henley Beach, S = Semaphore and LB = Largs Bay. Note the differences in scale on the y-axes across panels, *n* = 8.

Fish species richness and abundance

Fish species numbers captured in seine net hauls totalled 13 and most sites had similar species richness with the exception of Henley Beach (Figure 2.5A; Appendix 2, Table A2.3). Total fish abundances were largest at Largs Bay and all other sites had similar total abundances (Figure 2.5B; Appendix 2, Table A2.3). Abundances of common fish species varied across sites, with the largest abundances of *Aldrichetta forsteri* at Henley Beach, *Leptatherina presbyteroides* at Largs Bay, *Leseurina platycephala* at Glenelg and *Contusus brevicaudus* at Brighton (Figure 2.5C-F, respectively).

Seine-net sub-sample precisions

All of the total wrack and seagrass sub-sample precision scores were below the acceptable pre-selected precision cut-off value of ≤20 % at the one-eighth sub-sample fraction and higher (Figure 2.6A). Total algae sub-sample precisions for the quarter sub-sample fraction had 70 % of scores in the acceptable precision range which increased to >90 % at the half sub-sample fraction (Figure 2.6A; see also Appendix 2, Fig. A2.1).

Total invertebrates and crustaceans had sub-sample precision scores within the acceptable precision cut-off range for >80 % of scores at the quarter fraction (Figure 2.6B). Gastropods and bivalves had ≥50 % of acceptable sub-sample precision scores at the half fraction and only reached 100 % at the seven-eighth fraction (Figure 2.6B). Annelids were highly variable in abundance and had much lower percentages of sub-sample scores within the acceptable precision cut-off range overall and only had 100 % of scores with acceptable precision at the seven-eighths fraction (Figure 2.6B).

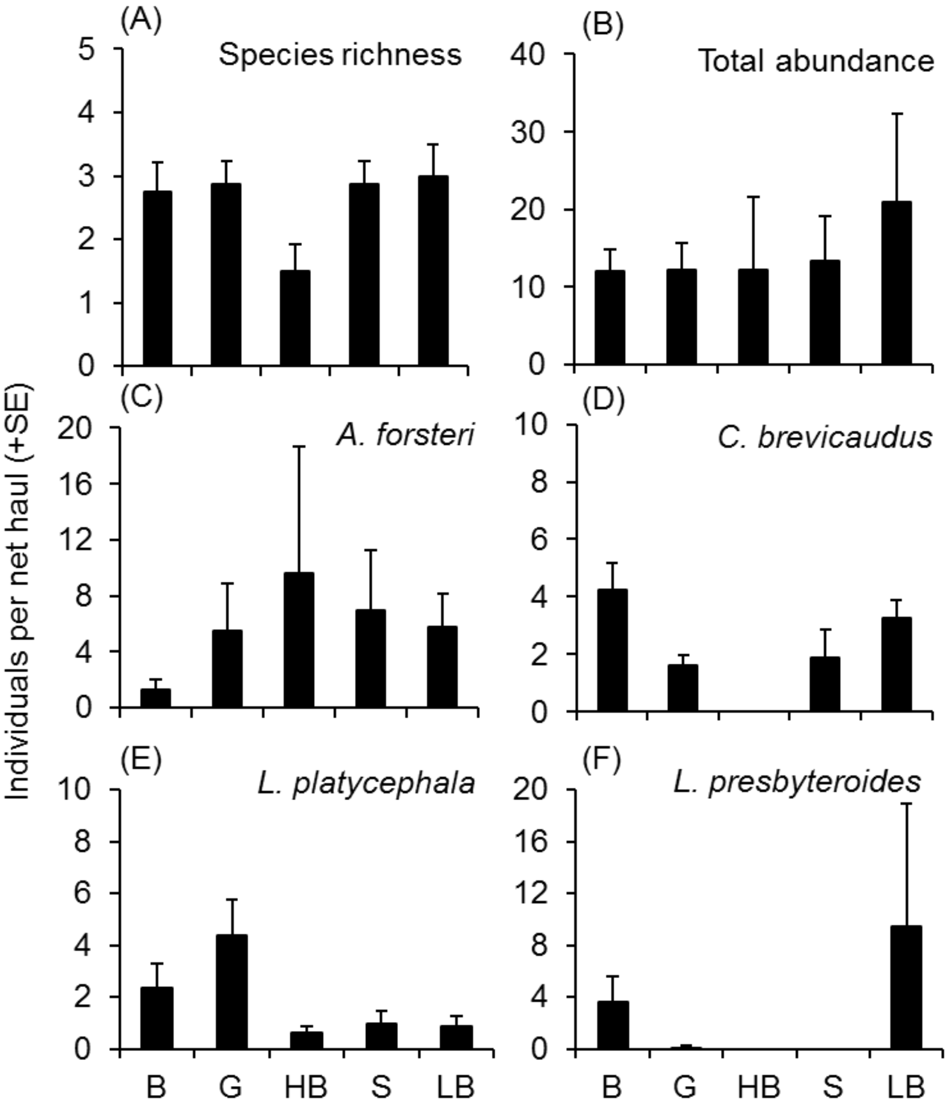


Figure 2.5: Fishes: Mean (+SE) (A) species richness and individual abundances of (B) total fish, (C) *Aldrichetta forsteri*, (D) *Contusus brevicaudus*, (E) *Leseurina platycephala* and (F) *Leptatherina presbyteroides* captured in seine net hauls during 2011. Sites are B = Brighton, G = Glenelg, HB = Henley Beach, S = Semaphore and LB = Largs Bay. Note the differences in scale on the y-axes across panels, *n* = 8.

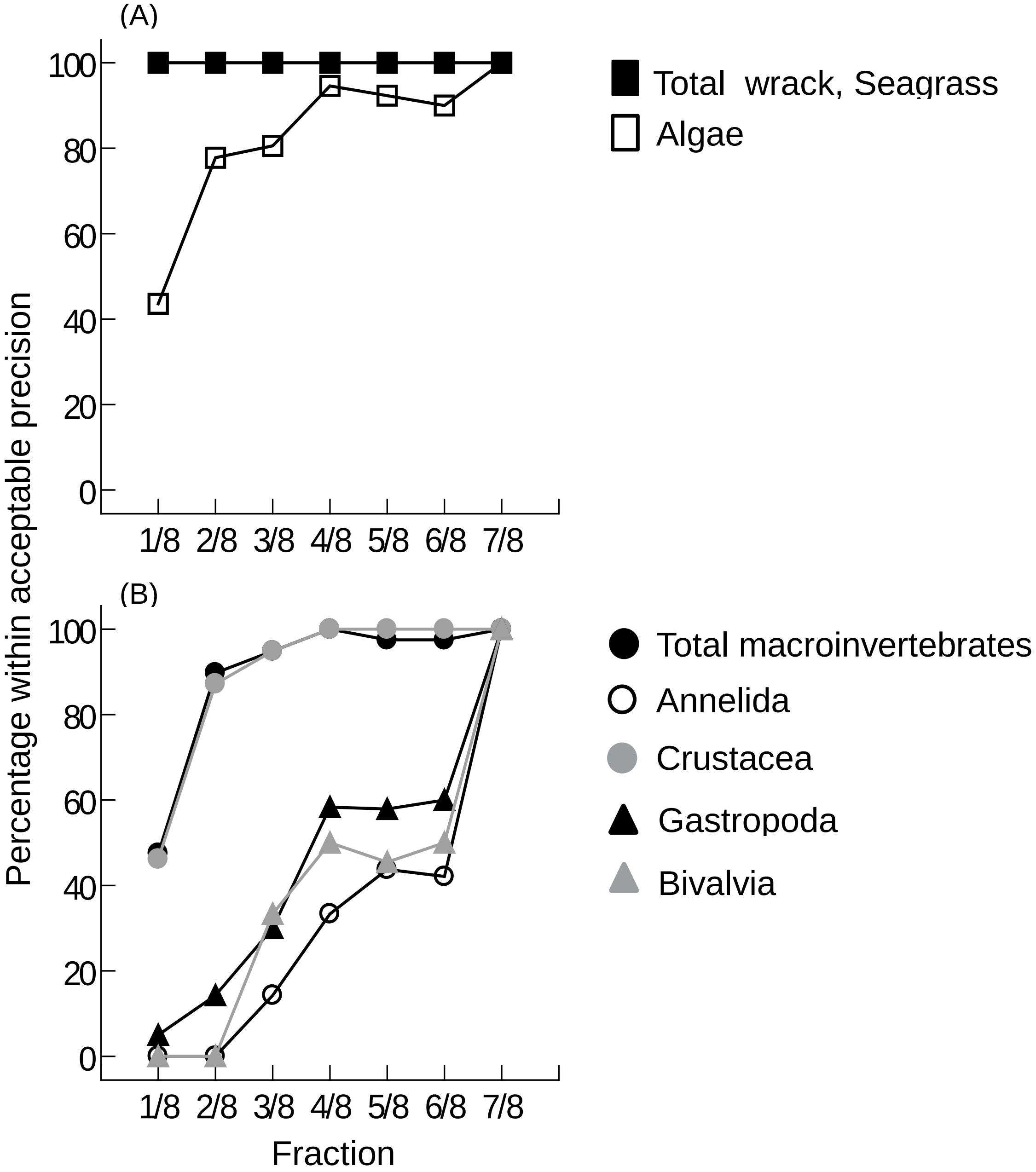


Figure 2.6: Subsampling: Percentage of precision scores that were within the acceptable range (i.e. ≤20 % of the mean) of precision for each sub-sample fraction in the categories of: (A) total wrack and seagrass (black squares on scatterplot representative of both categories that had exactly the same distribution pattern) and algae, and; (B) total invertebrates, Annelida, Crustacea, Gastropoda, Bivalvia.

Seine-net replicate precision

Total wrack, seagrass and algae were within the acceptable ≤20 % precision cut-off range for 60 % of precision scores (i.e. each calculated precision of the mean value) at three replicates, 80 % of precision scores at four replicates and 100 % of precision scores at five replicates (Figure 2.7A, see also Appendix 2, Fig. A2.2).

Total invertebrates were within the acceptable precision cut-off range for 80 % of sample precision scores at three replicates and 100 % of sample precision scores at five replicates (Figure 2.7B). Overall, all five invertebrate groups had ≥60 % of sample precision scores within the acceptable range at five replicates and ≥80 % of sample precision scores at seven replicates (Figure 2.7B). Only three out of the five invertebrate groups had 100% of sample precision scores within the acceptable precision cut-off range for seven replicates, with bivalves and annelids being the exceptions (Figure 2.7B).

Total fish had 80 % of sample precision scores within the acceptable precision range at four replicates and 100 % at six replicates (Figure 2.7C). All four of the most common fish species had ≥65 % of sample precision scores within the acceptable precision cut-off range at five replicates which increased to 100 % at seven replicates (Figure 2.7C).

Sampling precision versus cost

Processing seven-eighths of each sample resulted in all major groups having precisions within the acceptable range and also resulted in an overall reduction in processing time with a saving of 12.6 % compared to processing the full sample (Table 2.1, see also Appendix Figure A2.3).

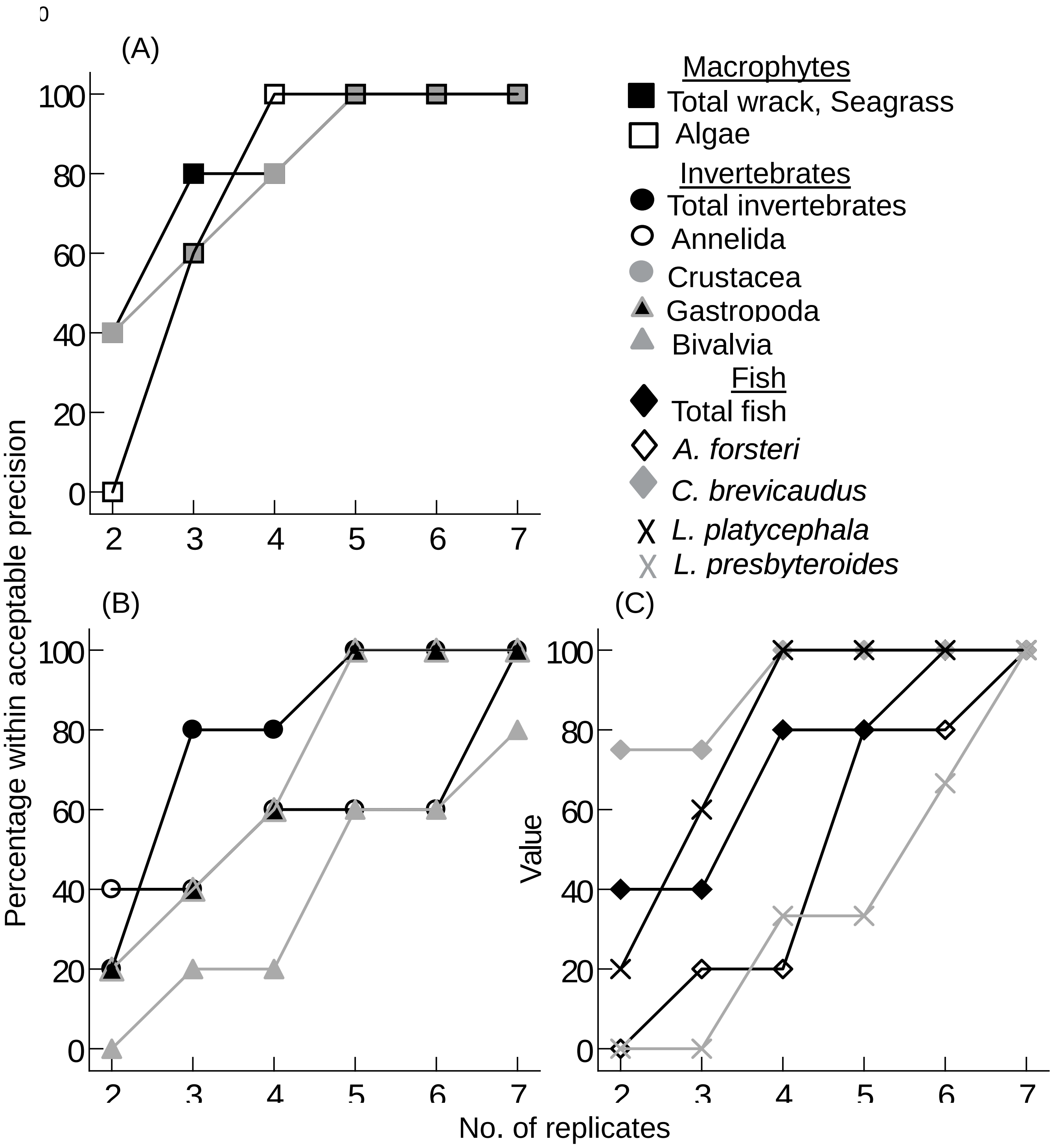


Figure 2.7: Replication: Percentage of scores that were within the acceptable range (i.e. ≤20 % of the mean) of precision for each replicate number in the categories of: (A) total wrack, seagrass and algae; (B) total invertebrates, Annelida, Crustacea, Gastropoda and Bivalvia and; (C) total fish, *Aldrichetta forsteri*, *Contusus brevicaudus*, *Leseurina platycephala* and *Leptatherina presbyteroides*. Dashed lines are presented for clarity on some groups represented in scatterplots.

Table 2.1: Sub-sampling: Numbers of major macrophyte and macroinvertebrate taxonomic groups (out of a possible maximum of 3 and 5 groups, respectively) with scores that had 100 % of possible replicates yielding acceptable precision for each eighth fraction. Approximate times are in hours (h) for processing for field, laboratory and the combination of the two for each eighth fraction. Percent of total time saved shows the overall *pro rata* reduction in time for processing each eighth fraction relative to the time to process the full sample.

Sub-sample	Macrophytes	Macroinvertebrates	Approximate processing time (h)			Time saved
fraction (1/8)	(out of 3)	(out of 5)	Field	Laboratory	Combined	%
0.125	2	0	0.05	0.37	0.42	87.6
0.25	2	0	0.1	0.75	0.85	75.0
0.375	2	0	0.15	1.12	1.27	62.6
0.5	2	2	0.2	1.5	1.7	50.0
0.625	2	2	0.25	1.87	2.12	37.6
0.75	2	2	0.3	2.25	2.55	25.0
0.875	3	5	0.35	2.62	2.97	12.6
Full sample	3	5	0.4	3	3.4	0.0

The relative saving increased with each reduction in sub-sample size. The half fraction had the next highest number of macrophyte or macroinvertebrate groups with 100 % of scores within the acceptable cut-off range (at the smallest possible sub-sample fraction), which would provide a time saving of 50 % for sub-sample processing relative to the whole sample (Table 2.1). However, only two out of five macroinvertebrate groups had 100 % of scores within the acceptable precision cut-off range at the half fraction. But, at the half fraction, the other three macroinvertebrate groups (being Annelida, Gastropoda and Bivalvia) had >50 % of scores within the acceptable precision cut-off range (Figure 2.6).

The number of macrophyte, macroinvertebrate and fish groups that had 100 % of precision scores within the cut-off range increased from five replicate seine-net hauls and above, with the most at seven replicates (Table 2.2). At seven replicates, the time saved for whole replicate sample processing (i.e. compared to all eight samples taken) was 12.5 %, reducing to 25 % at six replicates, without too many groups falling below the threshold of 100 % of scores within the acceptable precision range (Table 2.2, see also Figure A2.3). The two macroinvertebrate and three fish groups that did not have 100 % of scores within the acceptable precision cut-off range at six replicates did have >60 % of scores within the acceptable range (Figure 2.7).

Table 2.2: Replication: Number of major macrophyte, macroinvertebrate and fish taxonomic groups (out of a possible maximum of 3, 5 and 5 groups, respectively) with scores that had 100 % of possible combinations yielding acceptable precision for each replicate number. Approximate times are in hours (h) for processing for field, laboratory and the combination of the two for each replicate number. Percent of total time saved shows the overall *pro rata* reduction in processing time for each number of replicates relative to the maximum number of 8 replicates that can be feasibly sampled in a single field day.

Replicate sample	Macrophytes (out of 3)	Macroinvertebrates (out of 5)	Fish (out of 5)	Approximate processing time (h)			Time saved %
				Field	Laboratory	Combined	
2	0	0	0	1.5	6.8	8.3	75
3	0	0	0	2.25	10.2	12.45	62.5
4	1	0	2	3	13.6	16.6	50
5	3	3	2	3.75	17	20.75	37.5
6	3	3	3	4.5	20.4	24.9	25
7	3	4	5	5.25	23.8	29.05	12.5
8	3	5	5	6	27.2	33.2	0.0

4. Discussion

Implications for designing ecological studies

Constraints of time, resources and funding are an integral part of designing all research programs. Thus decisions often need to be made to reduce the effort of field sampling and subsequent laboratory processing of samples while maintaining confidence in the estimates collected by that sampling program. My study highlights a particular useful process (Figure 2.1) for establishing reliable (precise) estimates for sampling in ecological applications that are often faced with large biological variation. Such variation in community assemblages is particularly pronounced in physically-dynamic, patchy habitats, like the sandy beaches investigated in my case study. Key researchers in this area in the 1980s (e.g. Pihl and Rosenberg 1982; Andrew and Mapstone 1987; Downing 1989; Riddle 1989) explained that preliminary investigation of optimal sampling designs was crucial in the decision-making process for larger ecological studies. One example of where this type of scientific rigour is often overlooked is the monitoring of environmental impacts such as beach nourishment, where very few studies (only 11 out of 46 studies reviewed by Peterson and Bishop 2005) employed any preliminary approaches to ensure that reliable estimates of biological data are obtained. .. Other researchers also flagged the dangers of encountering Type II errors without using preliminary approaches that investigate the statistical power of their sampling regimes (Fairweather 1991; Mapstone 1995; Zuur et al. 2010). The danger of ignoring these types of exploratory approaches and proceeding with a 'business-as-usual' sampling-design approach is that the estimation of variability of richnesses and abundances of ecological communities tend to be under-estimated leading to inaccurate or very wrong conclusions about the rarity of some species and dominance of others (Andrew and Mapstone 1987; Fairweather 1991; Zuur et al. 2010).

Downing (1989) and Riddle (1989) debated the specifics of optimising the precision and cost saving associated with the use of large versus small benthic samplers, but both authors agreed that the continual use of precision estimates would increase our understanding of sampling optimisation. Pihl and Rosenberg (1982) used ≤25 % of the mean as a cut-off to measure the number of replicates needed to achieve acceptable precision when using newly-designed drop traps to capture and investigate abundances of shallow coastal-dwelling macrofauna. Their pilot study found that 30 replicates would provide sufficiently precise estimates for most of the abundant species (except for one fish species), which would not have been determined without preliminary investigation of sampling precision. In the decades since those key scientific publications, however, it seems that fewer, rather than more, ecological studies have overtly implemented this type of pre-planning in their research (but see examples in Bartsch et al. 1998 and Gladstone et al. 2012).

The process used in Figure 2.1 to establish precision estimates for decision making about optimal sampling designs was extremely useful in my study and is one exploratory method that can be implemented into preliminary stages of larger ecological research programs. However, there are multiple other techniques that could also be used, depending on the ecological question being investigated. For example, Downes et al. (2011) used ecologically-important effect sizes to designate a meaningful effect size for power analyses to identify sample sizes for investigations of freshwater stream invertebrates on leaf packs versus sandy bottoms. When investigating ecological communities in this way, any type of preliminary data exploration reduces the chance of misinterpretation of the final data, which then leads to erroneous answers to ecological questions that form the basis of larger scientific research programs. Therefore, exploratory approaches such as the one I, and others beforehand, have used could be applied to many other organisms and ecosystems, particularly where large abundances and inherent heterogeneity in assemblages is encountered. For example, these could include invertebrate assemblages in grasslands, freshwater streams or rivers, rainforest canopies, or soil microbes.

Implications for optimising wrack sampling protocols

The processing of complete seine net samples for detached and drifting wrack volumes and macroinvertebrate abundances can take more than three hours per sample, and so large numbers of replicate samples require time and resources beyond those available for many research programs. Therefore the motivation behind my sub-sampling experiment was to identify whether a reduction in the amount of drifting wrack material that needs to be processed could still provide an acceptable estimate of the whole sample. This would be of benefit because it would reduce the overall resources needed to robustly quantify drifting wrack, macroinvertebrate and fish assemblages from the subtidal region of sandy beaches. This, in turn, could enable additional beaches, for example, to be sampled providing a broader overall assessment of the research question for the same input of resources. In this study, the types and numbers of species of fauna found associated with macrophytes in the surf zone were similar to those found in previous studies (van der Merwe and McLachlan 1987; Crawley et al. 2006; Marin Jarrin and Shanks 2011). Therefore, this sampling provided a useful dataset for estimating the precision of seine net replicates and sub-samples of drifting wrack accumulations captured in the sandy-beach surf zone.

Sub-sample precisions for all wrack and macroinvertebrate groups only reached acceptable precision levels for 100 % of combinations at the seven-eighths fraction, which would only slightly reduce the effort required to process samples (i.e. by 12.6 %). The next best option for a reduction in sub-sample processing would be the half fraction sub-sample hence with a time saving of 50%. Annelids, gastropods and bivalves were macroinvertebrate groups identified that had lower precisions for the half sub-sample category, but >50 % of replicates still reached acceptable precision levels. These three groups are known to be less abundant in drifting wrack accumulations in those surf zones with crustaceans more dominant (Lenanton et al. 1982; Crawley and Hyndes 2007), so it is not surprising that abundances of these groups were extremely variable in my study and that precisions were correspondingly lower. This finding suggests that caution should be used when extrapolating the abundances of rare taxa within any given sample. Nonetheless, I suggest that sorting half of any given seine net would be the most suitable option for future optimised sampling of drifting wrack accumulations in sandy-beach surf zones to provide acceptable precision for the majority of taxa, particularly common taxa. For whole seine-net replicates, the percentage of scores with acceptable precision of all drifting wrack, fish and invertebrate groups was satisfactory (>60 %) at six replicates, relative to the maximum realistic sampling intensity that could be achieved in one day (i.e. 8 seine-net hauls). Thus future sampling effort could be reduced by two replicates below the practical daily maximum and still result in relatively high precision with a time saving of 25 %.

Patterns in these wrack, macroinvertebrate and macrofauna assemblages

This study identified that one site each at the northern and southern ends of the beach system had the largest wrack volumes overall. My study identified that the drifting wrack composition of sandy-beach surf zones along the metropolitan Adelaide coastline in South Australia largely consists of seagrass, which is indicative of the extensive and dense subtidal seagrass meadows of several *Posidonia* species found in this region (Edyvane 1999). The larger number of macrophyte groups represented at southern beaches may be due to the increase in subtidal reef habitats adjacent to the southern coastline (Edyvane 2008). Macroalgae are well represented on these reef habitats and generally increase as coastlines become more exposed to oceanic swells and currents, which also increase further south of metropolitan Adelaide (Edyvane 2008).

Two southern beaches and one northern beach had the most abundant and speciose macroinvertebrates associated with the drifting wrack. The larger abundances and species numbers of macroinvertebrates at the southern beaches found in this study may be due to the presence of macroalgae providing more favourable habitat and food resources. Previous studies have identified that the larger surface area and complex structure of macroalgae, as opposed to seagrass, may be a more favourable habitat for macroinvertebrates (Parker et al. 2001; Vandendriessche et al. 2006b). Particular macroalgal species can also be more palatable for grazing macroinvertebrate species such as the abundant amphipod *Allorchestes compressa* found in my study (Crawley and Hyndes 2007). Alternatively, the prevailing inshore counter-current direction is northward, so southerly sites may be less affected by nutrients and other pollutants associated with runoff from this urban area.

The larger abundances of fish found at the most northerly site of Largs Bay at the northern end of the beach system in this study does not, however, indicate that more fish were present due to larger wrack volumes as has been highlighted in drifting wrack accumulations previously (Crawley et. al. 2006). Instead, the larger fish abundances may be influenced by the close proximity of other complex habitats to the north such as rocky breakwaters, mangroves and the protected waters of the Port River-Barker Inlet estuary system. Future longer-term studies of wrack accumulations in the surf zone along the Adelaide metropolitan sandy-beach ecosystem could indicate how much the associated fauna varies from north to south.

5. Conclusion

Pilot studies are an integral part of the decision-making process in the empirical sciences and they are crucial to ecological science where inherent natural variation can lead to erroneous conclusions without appropriate and thoughtful preliminary data exploration. In my study, I discovered that I could reduce the processing time of seine-net sub-samples by 50 % and the processing time of whole seine-net replicates by 25% relative to practical daily maxima with reasonable precision by following some simple exploratory steps (Figure 2.1). There may have been unknown precision discrepancies as a result if I had avoided the pilot study and continued with a sampling program over larger temporal and spatial scales without this preliminary investigation. If that was the case, then there would be no guarantee that the precision of my macrophyte, macroinvertebrate and fish estimates would have been precise enough. I suggest that carefully-designed pilot studies utilising exploratory approaches with preliminary datasets should become less of an exception and so be brought back to the fore in ecological studies. This type of exploratory pre-planning approach may be of particular importance where new methods are still in their infancy or when aspects of ecosystems with little previous research effort (like this study) are being investigated.

Acknowledgements

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Chapter 3: Storm versus calm: variation in fauna associated with drifting macrophytes in sandy beach surf zones

Summary

New insights about nearshore dynamics came from studying the effects of regular storms in South Australia on drifting marine macrophytes, consequent wrack accumulation and associated fauna in beach surf zones across three different regions. This study examined whether the influence of storms may be more pronounced in sheltered coastal waters compared to more exposed coastlines where biota could have adaptations to persist in larger swell conditions. There were obvious regional differences for wrack species richness, abundances and assemblages that matched the attached floral subtidal landscape in each region. Consequently, invertebrates also differed amongst regions, which highlight the close affinity that some species of invertebrates have with drifting macrophytes. Fish were not so closely aligned to the regional patterns identified for wrack or invertebrates suggesting that many fish are using wrack accumulations as habitat but, being highly mobile, they may actively and constantly move into, out of and within these habitat features. Well-known beach-type models focused upon beach morphology may be more pertinent to the ecology of the surf zones offshore than previously thought, being the most consistent indicator of wrack accumulations and their fauna. This new evidence on the ecology of nearshore waters during storm versus calm weather in multiple regions and the subsequent influence on wrack-fauna associations in sandy-beach surf zones is important for future beach management, particularly when and where large wrack accumulations occur.

1. Introduction

Drifting macrophytes consist of many species of seagrass and algae. During storms or large swell events, seagrass and algae are often ripped from the seafloor by hydrodynamic forcing and either float to the surface and drift, or tumble along the seafloor (Kirkman and

Kendrick 1997). In the nearshore zone of sandy beaches, drifting macrophytes are pushed into the surf zone by wave, tidal and current forcing where they form dense accumulations before being washed ashore (Kirkman and Kendrick 1997). The dense macrophyte accumulations that are formed in the surf zone of sandy beaches may also include many other drifting objects such as animal carcasses and human-sourced litter (e.g. plastics, cans, bottles and lost fishing equipment). Drifting macrophytes may eventually be stranded on beaches and form large piles of beach-cast wrack which can then re-enter the surf zone with subsequent high tides (Kirkman and Kendrick 1997). Eventually, beach-cast wrack begins to decompose over varying amounts of time, depending on the physical structure of particular seagrass (Harrison 1989) or algal (Mews et al. 2006) species.

Drifting macrophyte accumulations and piles of beach-cast wrack are very dynamic habitats and contribute to multiple trophic pathways in marine and coastal terrestrial ecosystems. Drifting macrophytes in the surf zone of sandy beaches provide a habitat matrix and food resource for marine macroinvertebrates, which in turn attract multiple fish species (both fished and non-fished species) to aggregate around the drifting habitats (Lenanton and Caputi 1989; Crawley et al. 2006). The presence of many juvenile fish around drifting macrophytes suggests that they may be an important temporary habitat or nursery for young fish (Lenanton et al. 1982). The question of why juvenile fish are attracted to drifting macrophytes is still not totally resolved but it appears that fish may be using drifting macrophytes as a refuge from larger predators and/or for better food resources due to larger abundances of invertebrate prey than in surrounding clear waters (Lenanton et al. 1982).

Large amounts of wrack are often observed deposited on sandy beaches immediately after large storm events (Kirkman and Kendrick 1997). Some studies have investigated the impact of storm events on attached algae and seagrass but most of these focused on very large events such as hurricanes and none have contrasted storm versus calm periods (Seymour et al. 1998; Cruz-Palacios and Tussenbroek 2005; Filbee-Dexter and Scheibling 2012). Investigations of storm impacts on marine environments have often focused on the immediate change to subtidal habitats including sedimentation (Cruz-Palacios and Tussenbroek 2005) and shifts in macrophyte biomass and associated fauna (Ebeling et al. 1985). Other studies have also investigated the mechanical force required to dislodge algae (Milligan and DeWreede 2000) or seagrass (Rivers et al. 2011) from the seafloor. In contrast, there is very little information on the changes in drifting macrophyte volume or biomass and associated fauna in the surf zone immediately after storms.

One challenge with the study of drifting macrophytes in the surf zone of sandy beaches is the constant changes in physical structure of macrophyte accumulations due to multiple hydrodynamic influences such as changes in tides, swells or wind-induced waves. The physically-turbulent nature of surf zones may be a reason why there are very few studies that have investigated the immediate underlying dynamics of drifting macrophytes moving into and around the surf zone, particularly after storm events. Instead, many studies have focused on the habitat association and community structure of fauna associated with drifting macrophytes without further consideration of the external influences that result in drifting macrophytes to accumulate as wrack in surf-zones.

The composition of drifting macrophytes found in the surf zone of sandy beaches may be a reflection of the type of attached macrophytes that live in subtidal habitats close by. However, little information is known of the composition of drifting macrophyte accumulations (i.e. whether it is predominantly seagrass or algae, or a mixture of the two) in the surf zone of sandy beaches and the role that different compositions might play as potential habitat for fish and invertebrates. Lenanton and Caputi (1989) identified that a prevalence of both red algae and senesced seagrass contributed to an increase in the abundance of the commercially-important fish *Cnidoglanis macrocephalus* from two sandy beach sites in Western Australia. In addition, Crawley et al. (2006) identified that two fish species, *C. macrocephalus* and *Pelsartia humeralis*, preferred either detached clumps of mixed brown algae and seagrass or seagrass alone, respectively, in manipulative habitat-preference trials undertaken in aquaria. Crawley and Hyndes (2007) identified that the common surf-zone amphipod *Allorchestes compressa* used drifting macrophytes as a habitat and food resource but any preference for a particular macrophyte composition was unclear and changed under different laboratory and field conditions. Lenanton and Caputi (1989) and Crawley et al. (2006) also found that fish abundances increased in Western Australian surf zones with an increase in the overall volume of drifting macrophytes.

In eastern South Australia there are three separate bioregions along the coastline that represent very different coastal marine habitats: the protected Gulf St Vincent bioregion consists of dense seagrass meadows; the Coorong bioregion has a mixture of patchy to dense seagrass meadows and patchy subtidal rocky reefs; and the Otway bioregion consists of mainly low-to-medium profile continuous subtidal rocky reefs (Edyvane 1999). These three regions also have distinct detached and drifting or beached macrophyte accumulations: the seagrass-dominated metropolitan Adelaide; the seagrass- and macroalgal-dominated Fleurieu Peninsula; and the macroalgal-dominated South-East region of South Australia (McKechnie and Fairweather 2003; Duong 2008). This study location therefore provides a good model for investigating drifting macrophytes and their associated fish and macroinvertebrate assemblages among very different marine regions. This investigation was designed to quantify drifting macrophyte amount, composition and any associated fauna within the surf zone of sandy beaches across multiple storm and calm events and multiple contrasting regions, without being confounded with smaller-scale temporal and spatial variation.

This study therefore aims to determine whether there are greater volumes of drifting wrack, and greater abundances and species richness of drifting macrophytes and associated fauna in the surf zone of sandy beaches after storms compared to calm-weather events. In addition, I test whether the composition of drifting macrophytes and the abundance and species richness of associated fauna is different between multiple regions regardless of weather events. This provides much-needed information on the compositions of drifting macrophytes and associated macroinvertebrate and fish fauna that coincide with storm pulses over multiple regions. The information obtained also provides further understanding of the productivity and function of sandy-beach ecosystems and their potential role as a habitat for critical life stages of fish and their invertebrate prey.

2. Materials and Methods

2.1 Sampling Regions and Sites

Three separate regions were chosen for this study on the basis of the types of attached macrophytes that are found in each region, which are subsequently found in the wrack washed ashore on beaches (Figure 3.1; Duong 2008). Metropolitan Adelaide (MA) is the coastline adjacent to a metropolitan capital city centre within the large inverse estuary of Gulf St Vincent. This region was classified as seagrass-dominated due to the presence of dense seagrass meadows off shore and few rocky reefs (Edyvane 1999b). Further south, Fleurieu Peninsula (FP) has coastlines within Gulf St Vincent and Encounter Bay and was classified as a seagrass/algae mix due to the presence of both dense seagrass meadows and extensive subtidal reefs (Edyvane 1999b). The most southern region in this study was the South-East (SE), which also has the most open coastline, receiving oceanic swell from the deep Southern Ocean. The South-East was classified as an algal-dominated region due to the presence of many subtidal offshore reefs, large kelps, and sparse seagrass meadows (Edyvane 1999b). Three sandy-beach sites per region were randomly chosen as a subset of a larger number of possible sites. All sites across the three regions are classified as intermediate beaches, which

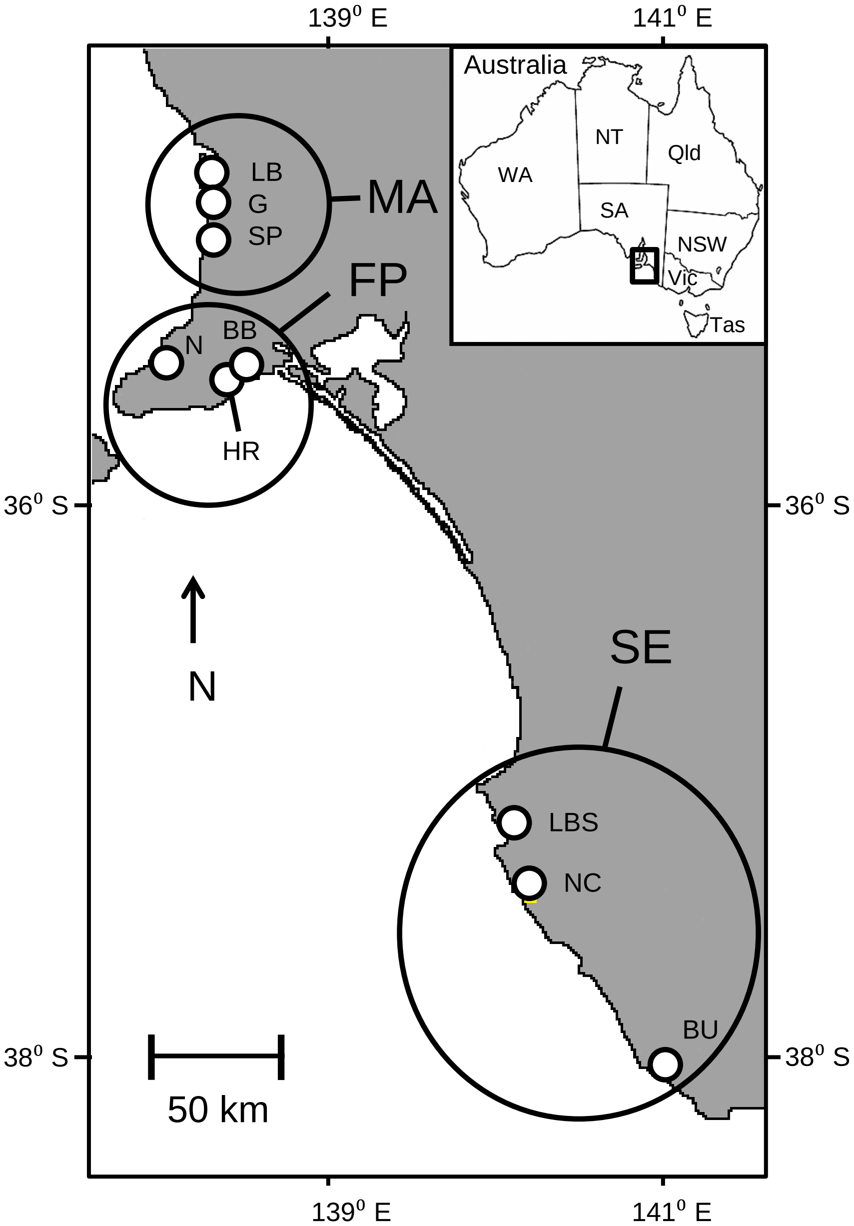


Figure 3.1: Map of the three regions and nine sites represented by large circles and small circles, respectively, that were studied during storm and calm events in 2012. Regions and Sites are MA = Metropolitan Adelaide (LB = Largs Bay, G = Grange, SP = Somerton Park), FP = Fleurieu Peninsula (NV = Normanville, HR = Hindmarsh River, BB = Basham Beach), and SE = South East (LB = Long Beach South, NC = Nora Creina, BU = Bucks Bay).

consist of a shore-parallel bar and trough zone and moderate to steep beach face (Short 2001).

2.2 Field Surveys

Sampling was conducted at all sites during storm and calm weather events in 2012, during the austral summer through winter months when senescence of seagrass occurs locally and wrack is common on beaches (Duong 2008). Storm events were identified once the sea state had reached Beaufort Sea State 7 for more than 24 hours, which is classed as ‘near gale’ according to the international Beaufort Sea State Scale (Met Office 2012). Calm events were identified once the sea state was below Beaufort Sea State 7 for a period of three weeks. In the calm events sampled, the mean wind speeds leading up to the sampling day were always under 44 km/h, which is indicative of calm to fresh or strong sea breezes, compared to the storm events which all had mean wind speeds of > 60 km/hr. Sampling was undertaken at all sites, in all three regions, within one week after a storm had passed or a three-week calm event. For logistical reasons, regions were randomly allocated blocks of days for sampling during each designated event because regions are >100 km apart from each other.

At all sites, sampling consisted of six replicate seine net hauls per site based on sampling efficiencies determined from a pilot study (see Chapter 2 for rationale), which were taken to capture wrack accumulations and associated fish and macroinvertebrates. A seine net (10 m long, 2 m deep, central 0.5 m bellow, with 4-mm mesh size) was deployed in the surf zone of beaches and dragged through wrack accumulations. Each net haul was emptied out onto a tarpaulin laid out on the beach to ensure that the entire wrack accumulation could be searched for fish. All fish were collected from the entire sample and placed in 10-L buckets of aerated seawater before handling for species identification and measurement of standard lengths. Some fish that had lost equilibrium were euthanised with AQUI-S before being preserved in 10% buffered formalin. After length measurements and identification, all other fish were released back into the surf zone at each site.

Wrack samples were visually split into two half sub-samples or, in a few extreme cases of very large wrack volumes, only one quarter or one eighth due to logistical constraints, which was set aside for further processing and the balance of the sample was discarded. In Chapter 2 of this thesis, I established that the precision obtained by processing half sub-samples of wrack and invertebrates was satisfactory but significantly reduced the time and resources taken to process full seine-net samples. The sub-sample kept for further processing was thoroughly rinsed over a 500-µm mesh sieve to remove invertebrates, which were preserved in containers of 70% ethanol for later identification and abundance counts in the laboratory. The rinsed wrack sub-samples were sealed in zip-lock bags and frozen at -20°C for storage before volume measurements.

At each site, various environmental variables were measured to identify whether any were correlated with the presence of macrophytes, macroinvertebrates and fish associated with wrack. For each replicate net haul, the total distance from shore was measured with a 100-m measuring tape and mean depth was calculated from three measurements with an expandable 5-m surveying staff. Water samples of 1 L were taken at mid-depth for each net haul and taken back to the laboratory in containers of ice for further analysis of total suspended solid (TSS). Those environmental variables that were taken in the surf zone were adjacent to each sampled wrack accumulation (i.e. >5 metres away) so as to not disturb fish and macroinvertebrates. Tidal height, weather conditions and the presence of any vessels, human swimmers, or large fauna (e.g. dolphins and seals) were also recorded for each net haul. Beach morphology characteristics were measured three times at each site across the low, mid, and high tide zones at each site using rapid techniques, which included beach slope measured with a clinometer and sand grain sizes determined by comparison to a set of reference grain sizes (Morcom 2007). After each sampling event, the maximum wind speed recorded from each of the preceding seven days in each region was obtained from the Australian Bureau of Meteorology for calculation of mean maximum wind speeds for further analysis of the mean wind speed during the specific time leading up to when that sampling occurred.

2.3 Laboratory Processing

Total wrack sub-samples were thawed, drained of excess water and placed in various volumetric cylinders (0.005, 0.1, 0.5 and 2 L) to determine the total displacement volume of each wrack sample. For very large samples which did not fit into volumetric cylinders, 30-L containers with marked volume increments were used. After total volumes for each wrack sub-sample were measured, they were searched for large pieces of macroalgae or seagrass (>10 cm in length), which were identified to genus or species and measured for separate volumes. The smaller fragments remaining in the sample were sorted into major taxonomic groups. Very large samples (>1 L) of the remaining smaller fragments were visually split into sub-samples and a sub-sample was measured for taxonomic group proportionate volumes. Aside from macrophyte taxa, there were six other categorical groups assigned for various components of the wrack and included Porifera, Cnidaria, Bryozoa, terrestrial plant matter, anthropogenic litter and animal fragments.

Due to the large quantity of macroinvertebrates found in the samples, most were sorted in two stages with a first sort to remove larger (>1 cm in length) and rarer specimens, which were identified and counted to the lowest possible taxonomic level. The remaining samples were then visually divided into sub-samples (i.e. minimum of one sixteenth of sub-sample often with >500 individuals of dominant species) that were small enough to fit into one 100 mm-diameter glass petri dish. Macroinvertebrate sub-samples were sorted under a dissecting microscope with individual specimens identified to the family or species level. Some specimens were only identified to order or sub-order or classified as distinct morphospecies due to the poor taxonomic knowledge of some taxa from this region and the difficulty to distinguish between families for juvenile specimens (particularly copepods and ostracods).

Processing of TSS samples followed the recommended procedure of Stavn et al. (2009) for estuarine and coastal water samples.

2.4 Statistical analyses

A four-factor experimental design of: Weather (Storm, Calm; fixed factor); Region (MA, FP, SE; fixed factor); Sites nested in Region (three levels; random factor); and Event nested in Weather (two levels; random factor) was used to test the full factorial experimental design for analyses of all wrack, fish and macroinvertebrate datasets. Thus there were two sampling Events each for the storm and calm Weather factors (i.e. four Events in total). Theoretically, macroinvertebrates and fish occupy wrack accumulations as a three-dimensional habitat matrix, so the decision was taken to use a cube-root transformation for those abundance and assemblage datasets. Wrack abundance and assemblage data were converted to volume in litres and were left untransformed. Taxa richness data for wrack, macroinvertebrates and fish were also left untransformed. PERMutational ANalysis Of VAriance (PERMANOVA) was used on the full design for each of the univariate and multivariate datasets individually using the PERMANOVA+ version 1.0.6 add-on to PRIMER version 6.1.16 (Anderson et al. 2008).

Both univariate and multivariate analyses were conducted on wrack, macroinvertebrate and fish datasets to test for Weather and Region effects on faunal abundances, species richness or assemblages, respectively. Univariate datasets for total abundances and abundances of major groups for wrack, macroinvertebrates and common fish species were analysed in PERMANOVA using Euclidean distance similarity matrices. PERMANOVA was also used for analyses of wrack, macroinvertebrate and fish assemblages using Bray-Curtis similarity matrices. Pair-wise tests were conducted on the Region factor to determine which regional groupings contributed to differences from PERMANOVA. Analyses on univariate and multivariate datasets were also conducted with the addition of wind speed, total wrack volume and macroinvertebrate abundance as co-variates. PERMANOVA and the addition of these co-variates were used accordingly with: wind speed on wrack, macroinvertebrate and fish; wrack volume on macroinvertebrate and fish; and macroinvertebrate volume on fish datasets. All univariate and multivariate PERMANOVA results are summarised in Table 3.1 and specific details of test outcomes are provided in Appendix 3 (Tables A3.1 to A3.4).

The effects of the main factors of interest for this study (i.e. Weather and Region) were also explicitly tested. Canonical analysis of principal co-ordinates (CAP) was undertaken on all multivariate datasets for Weather and Region and for the interaction of both of these factors. The CAP procedure in PERMANOVA+ is a constrained ordination used for *a priori* hypothesis testing of explicit factors of interest only, as opposed to the PERMANOVA approach that runs analyses on the full design (Anderson and Willis 2003). In CAP, the differences due to the Weather, Region and the interaction of the two were tested for wrack, macroinvertebrate and fish assemblages by obtaining a P value using 999 permutations. CAP was also used to determine the percentage of total variation explained by the first set of principal co-ordinate axes and the allocation success of each group for the previously mentioned factors using wrack, macroinvertebrate and fish assemblage data.

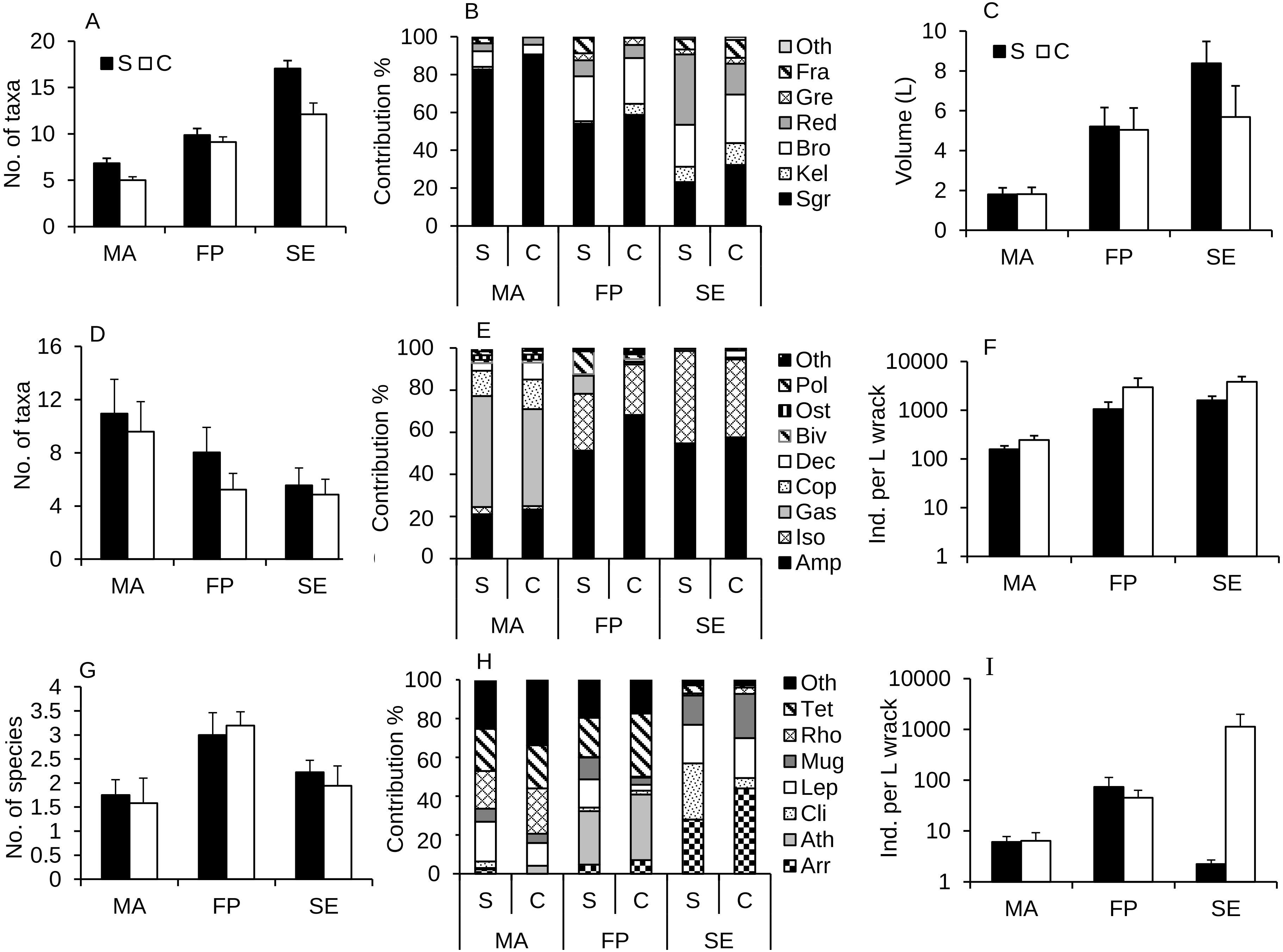
The BEST procedure in PRIMER was used to determine which suite of environmental variables was best correlated with wrack, macroinvertebrate and fish assemblages (Clarke and Warwick 2001). This analysis was intended to identify beach characteristics that were associated with wrack, macroinvertebrate and fish assemblages. Environmental variables of TSS, distance from shore, mean depth, beach slope (low, mid, high shore), wrack volume for macroinvertebrate and fish data and macroinvertebrate abundance for fish data were used. Only the TSS data were log transformed and all environmental variable data were normalised and analysed using the Euclidean distance similarity measure. The RELATE procedure in PRIMER was used to identify the overall correlation between each combination of biological and environmental multivariate datasets.

3. Results

3.1 Wrack

During the four sampling events that took place in each of the three Regions in 2012, a total of 75 macrophyte taxa were found in wrack accumulations captured by seine net hauls (see Table A3.5 in Appendix 3). The macrophytes included at least five green, 37 red and 26 brown algal taxa and seven seagrass species (see Table A3.5 in Appendix 3). Macrophyte taxa richness per sample was similar between stormy and calm Weather and was highest in the South East Region overall (Figure 3.2A). There was a significant interaction between Regions and Events for total macrophyte taxa richness (Table 1). Pairwise tests identified that the regional differences for macrophyte taxa richness were between MA and each of the other two regions (Table 3.1, see Table A3.1 Appendix 3).

For the seven major macrophyte groups identified, only the percent contributions of red algal and kelp groups showed significant differences due to Weather (Table 3.1, Figure 3.2B, see Table A3.1 Appendix 3). Significant regional differences were detected for most of the major groups except green algae and unknown, decomposing macroalgal fragments which were unable to be further identified (hereafter ‘fragments’; Table 3.1, Figure 3.2B). Pairwise tests of major constituents of wrack among Regions again identified that most regional


A
No. of taxa
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15
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Contribution %
100
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Figure 3.2: Summary of the patterns in data for three components (wrack, associated macroinvertebrates and fishes) in terms of taxa richness, proportional contributions of taxa and abundances. Panels A-C represent macrophytes, D-F macroinvertebrates and G-I fish found in wrack. For each of macrophytes, macroinvertebrates and fishes, panels A, D & G represent taxon richness, B, E & H proportional contributions of main taxa and C, F & I abundance (either volume of wrack for macrophytes or individuals per litre of wrack for animals). Means of individual variables are shown for wrack taxon richness, percent contribution of the major taxonomic groups to wrack, and total wrack volume or total abundances are represented. These samples were captured in seine net hauls during storm versus calm-weather surveys in each of three regions during 2012. Weather categories are: S, Storm; and C, Calm. Regions are: MA, Metropolitan Adelaide; FP, Fleurieu Peninsula; and SE, South East. Macrophyte taxon categories are: Sgr, Seagrass; Kel, Kelp; Bro, other Brown algae; Red, Red algae; Gre, Green algae; Fra, Unidentifed macrophyte fragments; Oth, Other groups (coral, sponges, bryozoans, marine animal muscle tissue, terrestrial plant matter, anthropogenic litter). Macroinvertebrate taxon categories are: Amp, Amphipoda; Iso, Isopoda; Gas, Gastropoda; Cop, Copepoda; Dec, Decapoda; Biv, Bivalvia; Ost, Ostracoda; Pol, Polychaeta; Oth, Other groups (Platyhelminthes, Nemertea, Sipuncula, Pycnogonida, Arachnida, Cumacea, Tanaidacea, Polyplacophora, Cephalopoda, Echinodermata). Fish taxon categories are: Arr, Arripidae; Ath, Atherinidae; Cli, Clinidae; Lep, Leptoscopidae; Mug, Mugilidae; Rho, Rhombosoleidae; Tet, Tetraodontidae; Oth, Other families (Diodontidae, Gobiesocidae, Hemiramphidae, Monocanthidae, Odacidae, Plotosidae, Sillaginidae, Sparidae, Syngnathidae, Tetrarogidae, Urolophidae). All error bars show one standard error. Note the differences in scale on the y-axes across panels and the logarithmic scale on the y-axis of two panels (F, I).

Table 3.1: **S**ummary of results of four-factor PERMANOVA run on univariate or multivariate dependenet variables of wrack macrophytes, macroinvertebrates, fishes and assemblages, showing just the number of significant results (out of 30 PERMANOVA runs) for each source of variation. Examples of the dependent variables for each significant source of variation are also given. Assemblages: W = Wrack; M = Macroinverebrates; F = Fish. Full details are given in Tables A-D in Appendix 1.

Source of Variation	No. of significant results out of 30 analyses	Examples of the dependent variables that were significant			
		Wrack macrophytes (univariate, 9 tests)	Macroinvertebrates (univariate, 10)	Fishes (univariate, 8)	Assemblages (multivariate, 3)
Weather	2	reds, kelp			
Region	14	richness, volume, reds, browns, kelp, seagrass, other	richness, abundance, copepods, isopods, amphipods		W, M
Event(Weather)	9	richness	copepods, isopods, decapods, gastropods	abundance, *L. presbyteroides*	M, F
Sites(Region)	12	greens	ostracods, isopods, gastropods	richness, *A. truttaceus*, *L. presbyteroides* *T. glaber*	W, M, F
We x Re	0				
We x Si(Re)	0				
Re x Ev(We)	6	richness	decapods	abundance, *A. truttaceus*	M, F
Ev(We) x Si(Re)	24	richness, total volume, greens, reds, browns, kelp, seagrass, fragments, others	richness, abundance, copepods, ostracods, amphipods, gastropods, bivalves	richness, *A. forsteri*, *C. brevicaudus*, *L. platycephalus*, *T. glaber*	W, M, F
	Σ = 67 out of 240				

differences were between MA and each of the other two regions, except for red algae and kelp which were only significant different between MA and SE (Table 3.1). For all seven major groups there were significant interactions between small-scale factors of Events and Sites.

Macrophyte total volumes were largest in SE, particularly during storms, and smallest in MA (Figure 3.2C). Total volumes were significantly different among Regions with the largest difference identified between MA and SE based on pairwise tests (Table 3.1, see Table A3.1 Appendix 3). The interaction between Event and Site was also significant for total wrack volumes (Table 3.1, see Table A3.1 Appendix 3).

Wrack assemblages, when analysed as a multivariate dataset, were significantly different among Regions and those differences were between MA and both of the other two regions (Table 3.1, see Table A3.2 Appendix 3), which was consistent with the univariate results presented above.

3.2 Macroinvertebrates

Across all sampling events, a total of at least 101 macroinvertebrate taxa were identified from wrack accumulations in beach-seine net hauls (see Table A3.6 in Appendix 3). Taxon richness was higher after storms in all three regions but was not significantly different for the Weather factor (Figure 3.2D, Table 3.1, see Table A3.3 Appendix 3). Across all sampling events, taxon richness was greatest in MA and smallest in SE, opposite to wrack volumes (Figure 3.2D). There were also significant differences for Regions and Sites, with regional differences between MA and SE from pairwise tests (Table 3.1). There was a significant interaction for taxa richness of Event by Site (Table 3.1).

Percent contributions of major taxa were similar within each region between stormy and calm Weather (Figure 3.2E). Isopods and amphipods contributed most to macroinvertebrate percent contributions in SE and FP (Figure 3.2E). In comparison, gastropods and amphipods contributed most to macroinvertebrate percent contributions in MA (Figure 3.2E).

Macroinvertebrate total abundances were higher in calm periods for all regions but this effect was not statistically significant (Figure 3.2F, Table 3.1, see Table A3.3 Appendix 3). Across all sampling events, total macroinvertebrate abundances differed among Regions, and were greatest in SE and smallest in MA (Figure 3.2F, Table 3.1). Abundances of some of the common macroinvertebrate groups were greater after storms in all three Regions (e.g. polychaetes, ostracods and amphipods, see Figure A3.1 Appendix 3 for individual abundances). Other macroinvertebrate groups were more abundant after storms in FP but the same set of taxa were all more abundant during calm periods in SE (e.g. copepods, isopods and gastropods). However, PERMANOVA tests on the abundances of all of the macroinvertebrate groups showed that differences between the two Weather types were not statistically significant (Table 3.1). Across sampling events, isopods and amphipods were more abundant in SE and FP and copepods were more abundant in MA which contributed to the differences among Regions (Table 3.1). There was also a significant interaction between Regions and Events for decapods (Table 3.1). Finally, most of the macroinvertebrate groups had a significant interaction between Events and Sites, except for polychaetes, isopods and decapods (Table 3.1).

For macroinvertebrate assemblages, there were significant differences between Regions, Events and Sites, and significant interactions between Region by Event plus Event by Site (Table 3.1, see Table A3.2 Appendix 3). Pairwise tests identified that the Region differences were between MA and both of the other two regions (Table A3.2 Appendix 3), which was also consistent with the univariate results presented above.

3.3 Fishes

Across all regions and sampling events, a total of 39 fish species from 21 separate families were captured from seine net hauls in the surf zones of these sandy beaches (Table A3.7 Appendix 3). Most of the fish captured were juveniles but also included some sub-adults and adults that were mainly small-bodied (e.g. atherinids and clupeids) or cryptic species (e.g. syngnathids) (see Table A3.7 Appendix 3 for size ranges). The fish captured included 12 species that are targeted by commercial and/or recreational fisheries and nine species that are protected in multiple Australian states (all syngnathids). Fish species richness was similar between the two levels of the Weather factor in all regions (Figure 3.2G, Table 3.1, see Table A3.4 Appendix 3). For Regions, fish species richness was highest at FP and lower for MA and SE which had similar number of species to each other (Figure 3.2G), but this trend was not statistically significant (Table 3.1). There was a significant interaction between Events and Sites for fish species richness (Table 3.1).

Percent contributions of fish families were mostly similar between stormy and calm Weather within each region (Figure 3.2H). One notable exception was the lower percent contribution of Clinidae in calm compared to stormy Weather in the South East of South Australia. Different sets of fish families were more common in each region (Figure 3.2H). Leptoscopidae, Rhombosoleidae and Tetraodontidae and Other categories were the main contributors within surf-zone wrack in MA. Atherinidae, Tetraodontidae and Other categories contributed most in FP, while Arripidae, Clinidae, Leptoscopidae and Mugilidae contributed most to the South East Region (Figure 3.2H).

Total fish abundances were low for both Weather types in all regions except for a large increase in abundances during calm weather in SE only (Figure 3.2I, see Figure A3.1 Appendix 3 for individual abundances). Fish abundances were significantly different among Events and there was also a significant interaction between Regions and Events (Table 3.1, see Table A3.4 Appendix 3). For the most common fish species, there were no significant differences in abundances for Weather or Region (Table 3.1). The only significant differences for fish species abundances were at the Event and Site levels for *L. presbyteroides* and the Site level only for *A. truttaceus* and *T. glaber* (Table 3.1). Also, there were significant interactions for *A. truttaceus* between Regions and Events (Table 3.1) and for four fish species between Events and Sites (*A. forsteri*, *C. brevicaudus*, *L. platycephalus*, *T. glaber*; Table 3.1).

Fish assemblages were significant between Events and Sites and significant interactions between Region by Event plus Event by Site (Table A3.2 Appendix 3), which was also consistent with the univariate results presented above.

3.4 Wrack and faunal assemblages

For wrack assemblages, canonical analysis of principal co-ordinates (CAP), using Weather as the discriminant factor, indicated a significant difference between distributions of the canonical scores for storm and calm Weather with high overall allocation success (Table 3.2). There were also significant differences between wrack assemblage canonical scores for Region with high overall allocation success (Table 3.2). The small percentage of misclassified canonical scores was attributed to a few samples with close similarities in wrack assemblages at MA with FP and SE with FP. CAP ordination of the discriminant Weather by Region factor (i.e. six groups) revealed better distinction in wrack assemblage canonical scores between Weather for FP compared to the other two regions (Figure 3.3A).

Table 3.2: Results of canonical analysis of principal co-ordinates examining differences in wrack, fish and invertebrate assemblages for constrained hypotheses concerning just Weather by Region interactions. The percentage of the total variation (%Var) explained by the set of principal co-ordinate axes selected (*m*) is shown. Allocation success is the percentage of points that are correctly allocated to each group. Q*m*'HQ*m* = the trace statistic or sum of squared canonical correlation; δ^2 = first squared canonical correlation.

					$Q_m'HQ_m$	δ^2
Taxonomic group	Factor	*m*	%Var	Allocation success (%)	*P*	*P*
Wrack	Weather	38	99	70	0.001	0.001
	Region	36	98	84	0.001	0.001
	Weather x Region	39	99	61	0.001	0.001
Macroinvertebrates	Weather	13	88	73	0.001	0.001
	Region	6	68	86	0.001	0.001
	Weather x Region	19	98	65	0.001	0.001
Fish	Weather	13	95	59	0.008	0.008
	Region	13	95	78	0.001	0.001
	Weather x Region	14	98	42	0.001	0.001

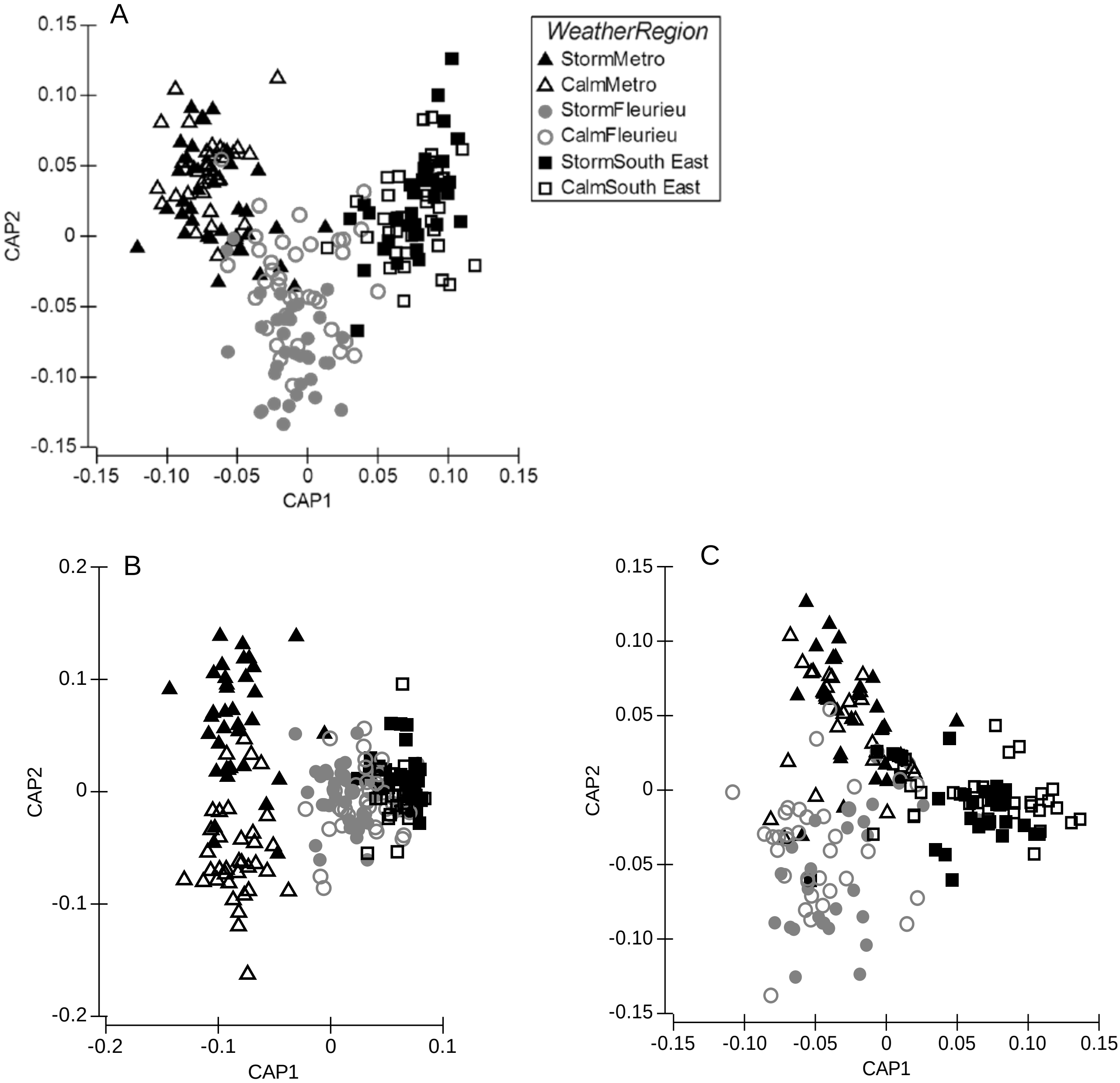

Figure 3.3: CAP analyses for the interaction of Weather and Region acting on assemblages of (A) wrack macrophytes, (B) macroinvertebrates and (C) fishes captured in seine net hauls during storm versus calm-weather surveys in each of three regions during 2012. Weather categories are Storm; and Calm. Regions are Metropolitan Adelaide; Fleurieu Peninsula; and South East.

The overall allocation success for Weather by Region for wrack assemblages was satisfactory (Table 3.2) and the best allocation was for the MA calm Weather (80%) followed by storm Weather for SE (77%). The misclassified canonical scores for each Weather category were allocated to the opposing Weather category within the same Region (e.g. MA storm misclassified to MA calm).

For macroinvertebrate assemblages, CAP with Weather as the discriminant factor indicated a significant difference between distributions of the canonical scores for storm versus calm Weather with high overall allocation success (Table 3.2). There were also significant differences among macroinvertebrate assemblage canonical scores for Region with high overall allocation success (Table 3.2). The small percentage of misclassified canonical scores was attributed to a few samples with close similarities in macroinvertebrate assemblages at MA with FP and SE with FP. CAP ordination of the discriminant Weather by Region interaction revealed better distinction in macroinvertebrate assemblage canonical scores between Weather for MA compared to the other two regions (Figure 3.3B). The overall allocation success for Weather by Region for macroinvertebrate assemblages was reasonably good (Table 3.2) and the best allocation was for the MA storm and calm Weather (80% and 88%, respectively). Also, the misclassified canonical scores for each Weather category were mainly allocated to the opposing Weather category within the relevant Region (e.g. MA storm misclassified to MA calm).

For fish assemblages, CAP with Weather as the discriminant factor indicated a significant difference between distributions of the canonical scores for storm and calm Weather with lower overall allocation success than compared with either wrack or macroinvertebrate CAP results (Table 3.2). There were also significant differences among fish assemblage canonical scores for Region, which had the highest overall allocation success out of all CAP for fish (Table 3.2). The percentage of misclassified canonical scores was mainly attributed to a few samples with close similarities in fish assemblages at MA with FP and SE. CAP ordination of the discriminant Weather by Region interaction revealed some distinction in fish assemblage canonical scores between Weather for SE and very little distinction between Weather for the other two regions (Figure 3.3C). The overall allocation success for Weather by Region for fish assemblages was low (Table 3.2) and the best allocation was for the calm Weather in FP (58%) and stormy Weather in SE (56%). However, the overall allocation success for Weather by Region was still well above the percent allocation success that would be observed by chance for this design (17%). The misclassified canonical scores for each Weather category were mainly allocated to the opposing Weather category within the relevant Region (e.g. MA storm misclassified to MA calm), except for the stormy Weather in SE which was misclassified to storms in MA.

3.5 Wrack, fauna and environmental influences

3.5.1 Co-variates of wind speed, wrack volume and total invertebrate abundance

For PERMANOVA analyses of wrack taxa richness, total volume and group volumes, the co-variate of wind speed only changed the results of the full design at the Site level for the seagrass and fragments groups (see Table A3.1 Appendix 3). Analyses of wrack assemblages with the inclusion of wind speed as a co-variate only changed the results for the Event factor (Table A3.2 Appendix 3).

Macroinvertebrate taxa richness results were not affected by the co-variates of wind speed and wrack volume (see Table A3.3 Appendix 3). Results of the full design were influenced by the wind speed co-variate for four macroinvertebrate groups and results for another two macroinvertebrate groups were influenced by the wrack volume co-variate (see Table A3.3 Appendix 3). Macroinvertebrate assemblage analyses results did not change with the addition of either wind speed or wrack volume as co-variates (see Table A3.2 Appendix 3).

Fish species richness results did not change with the addition of wind speed, wrack volume or macroinvertebrate abundance as co-variates (see Table A3.4 Appendix 3). Total macroinvertebrate abundance was the only co-variate that changed the effect of Event by Site for fish abundances and influenced the Region factor for *T. glaber* (see Table A3.4 Appendix 3). The macroinvertebrate abundance co-variate also had some influence on the results for *A. truttaceus* and *C. brevicaudus* for the Event by Site interaction and Event factor, respectively (see Table A3.4 Appendix 3). Fish assemblage PERMANOVA results were influenced by the wrack volume co-variate for the Region factor (see Table A3.2 Appendix 3).

3.5.2 Synergistic effects of wrack, fauna and environmental influences

There was a significant correlation between ordinations of wrack assemblages and environmental data (RELATE; rho = 0.161, $P < 0.01$) and the best correlation was for the combined environmental variables of turbidity, distance from shore, beach slope and sand grain size (BEST; rho = 0.161, $P < 0.05$). For invertebrate assemblages there was a significant correlation with the overall ordination of environmental data (RELATE; rho = 0.181, $P < 0.01$) and the best correlation was for the combined environmental variables of beach slope, sand grain size and wind speed (BEST; rho = 0.187, $P < 0.05$). Fish assemblages were also significantly correlated with the ordination of environmental data (RELATE; rho = 0.293, $P < 0.01$) and the best correlation was for the environmental variables of distance from shore, beach slope and sand grain size (BEST; rho = 0.3, $P < 0.05$). Overall, the correlations identified by the BEST analyses tended to be weak, as identified by the low rho values obtained for wrack, macroinvertebrate and fish assemblages with the ordination of environmental data.

4. Discussion

In the full design for this study, weather conditions only influenced red algal and kelp volumes out of all of the wrack, invertebrate and fish groups or species measured. However, under the constrained analysis of the Weather by Region interaction, there were significant effects on whole assemblages of wrack, invertebrates or fishes. Regional differences were most notable between Metropolitan Adelaide and South East for wrack and invertebrate taxa richness, total abundances, abundances of several taxa and whole assemblages. Additional co-variates of wrack volume or wind speed had some influence on invertebrate abundances and fish assemblages. Overall, the environmental variables of beach slope and sand grain size were consistently correlated with wrack, invertebrate or fish assemblages.

4.1 Drifting macrophytes in the surf zone

Larger volumes of red algae were found after storms, indicating that storms with sea states of Beaufort Sea State 7 or 8 may provide enough hydrological force to break off fragments or dislodge whole algae. This result is not surprising considering that the fragile structures of many red algae species have some of the smallest mechanical break forces required to fragment or dislodge them (Thomsen and Wernberg 2005).

This study also found that the weather differences for kelp were more complex and generally opposite to that for red algae, with an increase in kelp volumes during calm periods. Thomsen et al. (2004) previously identified that *Ecklonia radiata*, the most common kelp found in this study, was more susceptible to breakage for early life stages and kelps that are attached to soft limestone substrates. This would explain the presence of kelp after storms (i.e. opposite to the pattern observed here) but there may be a lag time after storm activity before older *E. radiata* is dislodged due to cumulative damage over time. In turn, this may result in larger volumes of kelp arriving in the nearshore zone during a later calmer period, some multiple weeks after a storm had passed through.

Bettignies et al. (2012) indicated that damage to stipes, primary lamina and secondary laterals of *E. radiata* increased and became larger over the spring through summer period in Western Australia, thus reducing the mechanical force required for fragmentation or dislodgement. Bettignies et al. (2012) also found that the sustained damage to the structure of *E. radiata* resulted in larger volumes breaking off in autumn through early winter, which could be due to natural senescence. My study was undertaken over the summer through winter period but future research could investigate the processes of macroalgal fragmentation and dislodgement over multiple seasons and years. This would provide more information that could be used to detect whether patterns of drifting macrophyte occurrence were associated with particular weather patterns and/or natural senescence and whether such patterns were consistent through time. This would be particularly helpful in addressing the paucity of information on the little-known process of senescence for macroalgal species in general.

4.2 Weather effects on macroinvertebrates and wrack in the surf zone

Differences between Weather states were most obvious from CAP (Figure 3B) for invertebrate assemblages in Metropolitan Adelaide. The less obvious differences for wrack and fish assemblages were indicative of large amounts of small-scale spatial and temporal variation in those data. The relatively-sheltered Metropolitan Adelaide sites in Gulf St Vincent appear to be subjected to more pronounced storm effects on biota compared with sites along the more exposed coastlines of Fleurieu Peninsula and South East, particularly under storm conditions with a Beaufort Sea State 7 or 8, as sampled in this study. Therefore, even larger storm intensities that have Beaufort Sea State 9 or above may result in more pronounced effects on particular biota of Fleurieu Peninsula and South East, which are more likely to receive large and regular oceanic swells from the Southern Ocean (Hemer and Bye 1999, Middleton and Bye 2007).

Most of the previous studies that have investigated the effect of storms on various marine biota have focused on one-off episodic events such as severe storms or tropical cyclones (Dobbs and Vozarik 1983, Posey et al. 1996). One previous study of a one-off storm on coastal marine fauna in the Northern Hemisphere (Long Island Sound, USA) identified distinct increases in macroinvertebrate abundance, species number and different assemblages in the water column post-storm (Dobbs and Vozarik 1983). In contrast, observations on benthic macroinvertebrate assemblages before and after single large storm events have found very little change or only notable differences for abundances of specific taxa such as benthic surface feeders (Dobbs and Vozarik 1983, Posey et al. 1996). Very few studies have investigated the effects of multiple storms with intensities similar to my study, or greater, on marine biota. Those few have focused on mussels and attached macrophytes and found an increase in dislodgement as storms intensified (Witman 1987, Reusch and Chapman 1995). The pulse from storms with a Beaufort Sea State of 7 or 8 may be only slightly larger than some of the regular swell conditions that arrive on the exposed Fleurieu Peninsula and South East coastlines, compared to the protected gulf conditions of the Metropolitan Adelaide coastline (Hemer and Bye 1999, Middleton and Bye 2007). Therefore, it is likely that there may be some pre-adaptation of particular flora and fauna to large swells in the Fleurieu Peninsula and South East regions (e.g. aggregation of *Ecklonia radiate*, where holdfasts of adjacent thalli are fused and less solitary kelp than found in protected waters; Wernberg 2005). In this study I did not have the facility to measure local wave conditions throughout the study period due to a lack of permanent oceanographic instrumentation in South Australian coastal waters near where sampling occurred. Future deployment of wave measurement instrumentation along this coastline would help establish a more consistent record of swell conditions for South Australian waters and thus assist in determining the relative difference between storm surges and common swell conditions.

4.3 Regional perspectives of macroinvertebrate and wrack associations

The macrophyte groups found in the nearshore wrack in this study were a reflection of the species pools of living, attached forms found in various subtidal habitats within each region (i.e. seagrass meadows, Metropolitan Adelaide; seagrass meadows and sub-tidal rocky reefs, Fleurieu Peninsula; continuous rocky reefs, South East; Edyvane 1999). The multiple differences found between wrack volumes, taxa richness and assemblages between the Metropolitan Adelaide and South East regions is not surprising considering the stark contrast between sub-tidal features in each of those regions.

In contrast, differences found for macroinvertebrate abundances, taxa richness and assemblages between the Metropolitan Adelaide and South East regions were more complex. The larger abundances of macroinvertebrates and dominance of certain taxa such as the isopod *Exosphaeroma* spp. in South East may be due to the greater amount and richness of macroalgae. This diversity may provide more palatable food and/or enhanced three-dimensional habitat structure resulting in a larger surface area for macroinvertebrates to graze and hide from predators. In comparison, the more simple seagrass available in wrack accumulations in Metropolitan Adelaide may provide less palatable food material, structural complexity and surface area for some species. These results tend to follow similar patterns to other aquatic vegetation studies that show positive correlations between macroinvertebrate abundance and vegetation surface area (Parker et al. 2001, Vandendriessche et al. 2006).

However, I found no clear correlation of macroinvertebrate abundance, taxa richness or assemblages with total volume of wrack accumulations. Other studies have found mixed results, with correlations between macroinvertebrates and drifting macrophytes either being species specific (Vandendriessche at al. 2006) or consistent over a number of different taxa (Ingolfsson 1995). Manipulative studies of drifting macrophyte volumes across multiple nearshore marine ecosystems and hydrodynamic regimes would determine how consistent these patterns really are.

In this study, the abundant invertebrate fauna were members of a broad range of taxa indicative of shallow-water species. Drifting macrophytes may move through multiple macroinvertebrate source habitats along the drift pathway from detachment through to deposition in the surf zone. Previous studies have highlighted the complex emigration and immigration dynamics of some macroinvertebrates associated with drifting macrophytes along portions of the pathway from detachment through to the nearshore zone (Ingolfsson 1998, Norkko et al. 2000). For example, Gutow et al. (2009) identified that large numbers of highly mobile macroinvertebrates such as amphipods and isopods left the brown alga *Ascophyllum nodosum* immediately after being experimentally detached from the seafloor in Iceland. Clarkin et al. (2012) indicated that isopods of the genus *Idotea* could either passively or actively colonise macroalgal rafts either from the water column or transfer among contacted macroalgae rafts. In my study, there were large numbers of the *Exosphaeroma* and *Euidotea* isopods and the amphipod *Allorchestes compressa* found associated with macrophytes accumulated in the surf zone. All of these taxa are known to be shallow coastal-dwelling species that can be found in a wide range of subtidal habitats, which makes it very difficult to determine the source from which colonisation may have occurred, but it may be that drift material is the prime habitat for them (Robertson and Lucas 1983, Harrison and Ellis 1991, Poore and Lew Ton 1993). Previous studies have identified *A. compressa* as an important coloniser of drifting macrophytes in the surf zone in Western Australia, but any preference for a particular macrophytic habitat is complex (Robertson and Lucas 1983, Crawley and Hyndes 2007).

Less mobile species such as gastropods and bivalves may be more inclined to raft on drifting macrophytes to arrival in the surf zone, rather than to show more dynamic movement patterns. In my study, there were large abundances of some benthic gastropods (i.e. *Phasianella* spp. and sand-dwelling naticid snails) that are normally associated with attached macroalgae or seagrass habitats. Thus, these findings suggest that rafting on drifting material over large distances may be an important recruitment strategy and survival function for some species. However, the mechanisms behind rafting and colonisation are very complex and further work is required to investigate the relative importance of differing recruitment strategies and whether such processes vary over the complete drift pathway from detachment to arrival in the surf zone.

4.4 Fish and wrack in the surf zone

I found no clear correlation between wrack volume and fish under storm or calm conditions and across multiple regions. Differences in fish assemblages in some regions were influenced by wrack volume but there were no consistent correlations through time and across all regions. Other studies have found that fish abundances can increase with an increase in macrophyte volume, although these patterns may be species specific (Lenanton and Caputi 1989, Crawley et al. 2006). The differences in fish assemblages among regions/weather events found in my constrained analyses highlight that large variation over space and time masked such effects in the full PERMANOVA analyses. This suggests that the movement of fish into, out of, and within surf zones is constant and may be a reflection of the oscillating nature found of surf zones. My study did sample only storm and calm events in the first half of the 2012 year and therefore may have some limited power in detecting variation in fish recruitment over multiple seasons and years. Also, the storm strengths in future years may be different to the storms that I studied, which may have some influence to any variation in fish recruitment over multiple years.

The types of fish species, relatively low incidence of abundant species, and total number of species captured in my study were all comparable with other studies of wrack accumulations in the surf zone of sandy beaches (Lenanton et al. 1982, Robertson and Lenanton 1984, Lenanton and Caputi 1989, Crawley et al. 2006). Most of the fish captured were juvenile, opportunistic feeders that may have the ability to move quickly within and between wrack accumulations in the surf zone. Some of the fish species captured have a close affinity to macrophytes (e.g. Syngnathidae and Clinidae) and may passively move with macrophytes along the drift pathway into the surf zone. My study builds on previous studies that suggest sandy-beach surf zones provide a nursery function for juvenile fish, habitat for small-bodied fish, food sources for opportunistic feeders, and in turn a feeding ground for predatory fish (Lenanton et al. 1982, Robertson and Lenanton 1984, Lenanton and Caputi 1989, Crawley et al. 2006). The longevity of fish association with wrack accumulations in surf zones needs to be investigated further with manipulative studies to determine the level of affinity involved.

4.5 Wrack, associated fauna and beach morphologies

In this study, there was a general pattern of wrack, macroinvertebrate and fish assemblages correlating with beach slope and grain size. These two variables are key components in beach morphodynamic models (McLachlan et al. 1993, Short 2001). Beach morphology models have mainly been used in previous studies from geomorphological or coastal management perspectives (e.g. Short and Hesp 1982) or to investigate ecological features of beach infaunal communities (e.g. McLachlan et al. 1993). In comparison, very few studies have investigated the influence of beach morphology on macroinvertebrates inhabiting the surf zone (but see Neves et al. 2007) or fish (Nakane et al. 2013). Further evidence also suggests that surf-zone fish abundance and richness may be greater off dissipative beaches than reflective beaches, which may be a reflection of differences in turbulence with varying beach types (Nakane et al. 2013).

The consistency of correlation of wrack, macroinvertebrates and fishes with these two aspects of beach morphology identified here suggests that previously-used beach models and classifications may also be applicable to surf-zone ecology. These findings suggest that the inclusion of subtidal habitats in the existing models may be warranted. Future research into macroinvertebrates and fish assemblages in sandy-beach surf zones should incorporate targeted, detailed beach profiling across all beach types over time to encapsulate any change in beach morphologies and subsequent classification type.

5. Conclusion

In this study, there were some influences of weather on particular taxa (e.g. red algae) but the effect of storms on surf zone wrack assemblages was not consistent and varied among regions. However, this study does provide new evidence on the influence of storms on nearshore waters across multiple regions and how the hydrodynamics and wrack-fauna associations contribute to the ecology of sandy-beach surf zones. This is important for understanding the importance of wrack assemblages to the productivity of the beach surf zone by means of habitat provision, food resource and nursery function. Such information is essential for ecological decisions about future beach management where beach cleaning practices or commercial wrack harvesting occur.

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Chapter 4: Trophic structure within surf-zone wrack accumulations at sandy beaches

Summary

In parts of southern Australia and elsewhere, wrack accumulations are common in surf zones and in some locations are semi-permanent features. But, very few studies have investigated the trophic pathways associated with wrack accumulations in sandy beach surf-zones, despite their potential importance to nearshore food webs. I sampled macrophytes, macroinvertebrates and fish from wrack accumulations at two sites with different macrophyte compositions (i.e. algae versus algae/seagrass mix). I also sampled the gut contents of fish and analysed the $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures of fish, macroinvertebrates and macrophytes. I identified that fish may be using wrack accumulations predominantly as shelter but may be foraging over multiple habitats for food. In comparison, there was more evidence that grazing macroinvertebrates may be feeding on and around macrophytes within the wrack accumulations, as well as using them as habitat. This study established a baseline of the trophic pathways associated with wrack accumulations in sandy beach surf-zones. Given the modest evidence for use of wrack as a food source, the lower trophic levels of the food webs identified remain unknown and must be an area for future research. In future, more directed studies should also be conducted on the function and wider foraging and feeding ecology of fishes across multiple habitats through time.

1. Introduction

In the surf zone of sandy beaches, the presence of drifting macrophytes accumulating as wrack can increase macroinvertebrate abundances of those taxa that use wrack as habitat and food (Lenanton et al. 1982). Juvenile fish also utilise wrack in the surf zone as a nursery habitat and can feed on macroinvertebrates associated with wrack (Lenanton et al. 1982). The dominant macroinvertebrates found to have close association with wrack accumulations in beach surf zones are the smaller crustaceans such as amphipods and isopods. For example, in southern Western Australia, the amphipod *Allorchestes compressa* is the most abundant macroinvertebrate species found in wrack accumulations along surf zones and is an important grazer on macrophyte tissue (Crawley and Hyndes 2007). In turn, small crustaceans such as *A. compressa* are the most common food item found in the stomachs of various species of wrack-associated fishes captured along sandy-beach surf-zones in southern Western Australia (Robertson and Lenanton 1984; Crawley et al. 2006). Aside from a few studies (Hyndes and Lavery 2005; Crawley et al. 2009), the role of wrack in food webs of sandy-beach surf zones has received less attention compared to habitat function.

Investigations of the feeding ecology of fishes in coastal marine food webs have incorporated various techniques, which include gut content (e.g. Hollingsworth and Connolly 2006), stable isotope (e.g. Leakey et al. 2008) and fatty acid (e.g. Crawley et. al. 2009) analyses, to establish diets of particular species or group feeding guilds (e.g. herbivores versus carnivores). Gut content analysis is widely used in ecological studies and has been useful for determining the diets of fish as a snapshot in time, such as rivers during dry versus flood periods (Balcombe et al. 2005) and saltmarshes across varying tidal regimes (Hollingsworth and Connolly 2006). In comparison, stable isotope analysis is used to establish consumer-resource discrimination and the diets of animals over much longer periods (i.e. weeks to months) (Peterson and Fry 1987; Fry 2008; Boecklen et al. 2011; Hyndes et al. 2013). Stable isotope analysis relies on the fractionation of the heavy isotopes of, say, $\delta^{13}C$, which varies among primary producers, and $\delta^{15}N$, which become enriched with each increase in trophic level. These changes are typically consistent or well-ordered and are the basis for establishing trophic steps (Peterson and Fry 1987, Post 2002). This process enables the deduction of trophic levels organisms and links between primary producers and consumers, so that food webs can be constructed for particular habitats or ecosystems (Peterson and Fry 198;, Post 2002; Fry 2008).

To establish an understanding of both the recent and long-term (over weeks to months) feeding ecology of fishes, a combination of techniques such as gut content and stable isotope analysis can be used. This combined approach is particularly insightful when investigating species, habitats or ecosystems that have had little research effort to date, so as to provide preliminary information of trophic pathways and food webs as a guide for more directed future investigations (e.g. Pasquaud et al. 2008; Cresson et al. 2014). For example, preliminary investigation of the most common benthic, demersal and pelagic fish using both gut content and stable isotope analyses identified a baseline trophic web for the Gironde Estuary in France (Pasquaud et. al. 2008). Also, the combination of gut content and stable isotope analyses was helpful in determining the trophic position of Mediterranean reef fishes within different feeding guilds (Cresson et al. 2014), particularly when fish consume a large range of different food items. The approach of using multiple techniques is particularly useful with omnivorous and herbivorous fish where the actual fractionation of $\delta^{15}N$ can be higher than the standard fractionation mean of 3.4 ‰ per trophic level (Post 2002) due to different digestive processes among herbivorous fishes (Wyatt et al. 2010; Cresson et al. 2014).

Changes in fish foraging behaviour with movement among multiple habitats and over time can be determined for particular species when both gut contents and stable isotope techniques are used, whereas such patterns can be difficult to identify when only one technique is used (Lugendo et al. 2006; Hadwen et al. 2007; Vaslet et al. 2012). Aside from fish, the combination of gut content and stable isotope analyses has also been used on various other animals and ecosystems such as aquatic invertebrates in rivers (Jardine et al. 2005) and green turtles in the Gulf of Mexico (Williams et al. 2014). The multiple technique approach is essential to begin establishing trophic levels and food webs so that we can understand the ecological function of particular species, which can then act as a baseline for more detailed and directed studies.

To date, only a few studies have investigated trophic pathways associated with wrack accumulations in sandy-beach surf-zones. Hyndes and Lavery (2005) investigated the trophic pathways associated with wrack, fish and invertebrates found in beach surf zones along the southern Western Australian coastline with the use of both stable isotope signatures and fish dietary (gut) analyses. Hyndes and Lavery (2005) obtained stable isotope signatures from attached macrophytes in adjacent offshore habitats, detached macrophytes drifting as wrack, and fish and invertebrates from unvegetated surf zones. Their study highlighted the importance of algae as a food source for small crustaceans and, more specifically, that amphipods are most likely assimilating carbon from brown algae (Hyndes and Lavery 2005). Crawley et al. (2009) also compared the stable isotope values of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ for detached macrophytes, macroinvertebrates and fishes from sandy-beach surf-zones. They confirmed that $\delta^{13}C$ and $\delta^{15}N$ were useful in building a food web for coastal nearshore surf-zones where wrack accumulations were present (Crawley et al. 2009).

Beach-based studies have investigated the contribution of allochthonous marine-derived material to food webs between the swash zone and into beach dunes to identify the extent of marine-terrestrial connection. Bessa et al. (2014) investigated the trophic pathways among semi-terrestrial crustaceans and stranded wrack on sandy beaches in Portugal and found seasonal shifts in consumer diets from terrestrial- to marine-based sources. Colombini et al. (2011) identified that allochthonous marine-derived material is an important food source on sandy beaches in Italy for many marine or semi-terrestrial macroinvertebrate consumers but is less important for more terrestrial macroinvertebrate species found in beach dunes. Other studies in South America have found that there are clear trophic differences between reflective and dissipative sandy beaches with more complex food webs and trophic pathways identified at more-speciose dissipative beaches (Bergamino et al. 2011; Bergamino et al. 2013). Apart from those few studies, the trophic dynamics associated with wrack accumulations in other sandy-beach surf-zones worldwide is still relatively unknown, particularly where large semi-permanent wrack accumulations with different compositions (i.e. algal dominated versus a seagrass/algae mixture) are present. Furthermore, any differences in the trophic dynamics of surf zones with wrack accumulations of differing macrophyte compositions have yet to be explored.

The main aims for this study were to investigate the trophic pathways of drifting macrophytes and associated invertebrates and fishes, found in the surf zone of South Australia, focussing upon one sandy beach in each of two separate regions according to wrack composition (i.e. algal dominated versus a seagrass/algae mixture). Therefore based on the two separate regions with differing wrack compositions, I hypothesised that there would also be distinctly different trophic structures between the two sites with either algal dominated or seagrass/algal-mixture wrack compositions. Analyses of carbon $\delta^{13}C$ and nitrogen $\delta^{15}N$ stable isotopes provides an understanding of trophic pathways, consumer group partitioning and productivity (Fry 2008) of surf zones that have wrack as a semi-permanent feature. Fish diets also provide further insights into the feeding ecology of fish species found within or close to drifting macrophytes to determine whether this association is influenced by the availability of food. Baseline information on the trophic structure associated with different wrack accumulations along sandy beaches will thus identify whether consumers (e.g. fish and macroinvertebrates) are feeding on and around drifting macrophytes.

2. Materials and Methods

Study area

During March 2012, the surf zones of two sandy beaches were sampled for drifting macrophytes and associated fish and macroinvertebrates: Basham Beach on the Fleurieu Peninsula; and Long Beach South in the South-East Region of South Australia (Figure 4.1).

During February 2012, there was a high-temperature weather anomaly, which resulted in a rapid increase in coastal water temperatures over multiple days that led to subsequent fish die-off along various parts of the South Australian coastline (PIRSA 2013). Similar anomalies have also been identified over multiple years along the Western Australian coastline that also resulted in fish and invertebrate mortalities (Pearce and Feng 2013). Initially, I had planned to sample six sandy-beach surf-zones in this study but only two of these sites could be sampled due to a noticeable lack of fish and macroinvertebrates at the other four sites after this extreme weather event.

These beaches were chosen for sampling because drifting macrophytes were a semi-permanent feature of the embayment at both beaches compared to the heterogeneous abundance of drifting macrophytes at other beaches. Basham Beach, on the southern side of Fleurieu Peninsula, is close to a mixture of small offshore subtidal reefs and dense seagrass meadows in nearby Encounter Bay (Edyvane 1999b). Long Beach South is at the western end of the South-East Region of South Australia, which is characterised by large subtidal reefs that feature high macroalgal diversity due to the presence of nutrient-rich upwelling along that coast (Edyvane 1999b). The drifting macrophyte compositions found at both sites are a reflection of those subtidal habitats found nearby in each region with a seagrass and algae mixture predominating at Basham Beach and a dominance of macroalgae at Long Beach South (Chapter 3 this thesis; Duong 2008).

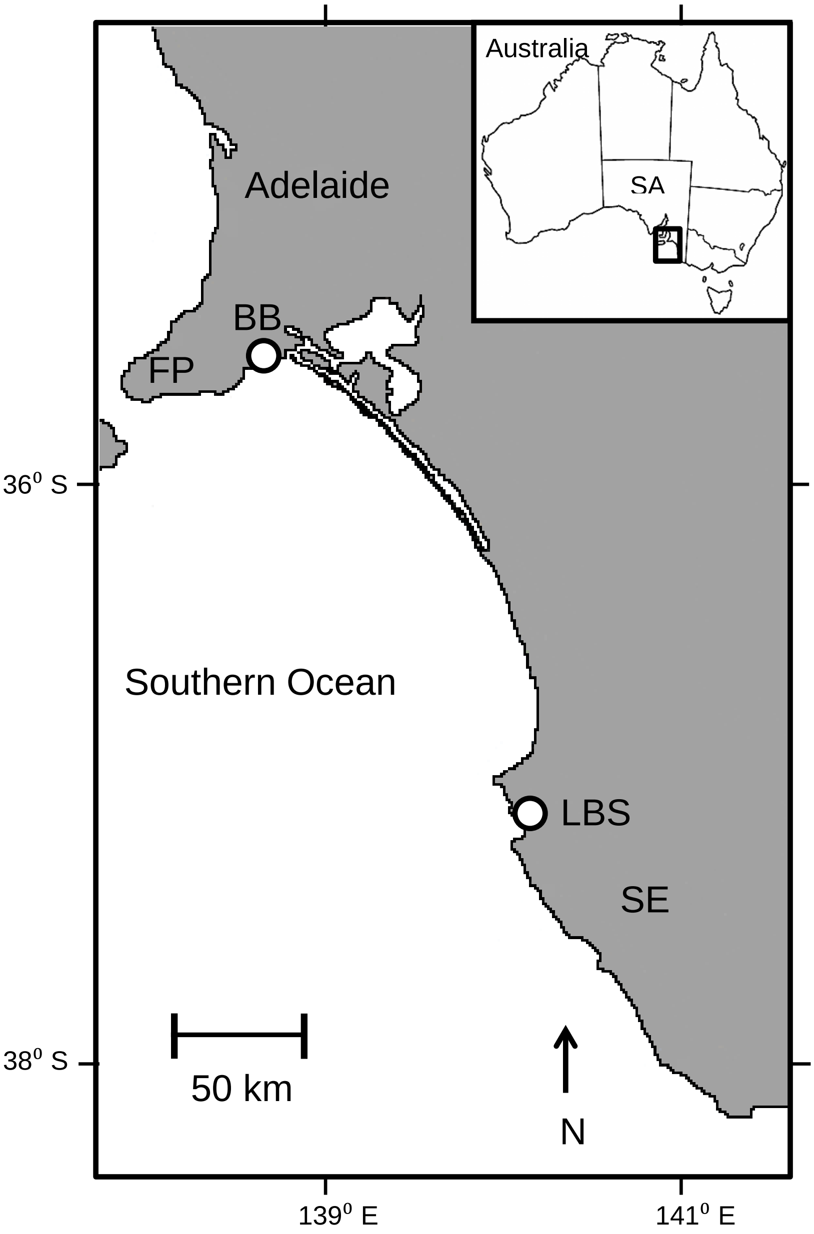


Figure 4.1: Map of study sites, Basham Beach (BB) and Long Beach South (LBS), sampled with seine nets in two regions, Fleurieu Peninsula (FP) and South-East (SE), south of Adelaide. Sampling occurred in March 2013.

Field sampling

At each site, six seine-net hauls were undertaken to capture wrack accumulations and their associated invertebrates and fish during March 2013. The wrack obtained from each seine-net haul was processed on the beach to identify the six most-common macrophytes. Samples of each of the six most-common species of macrophyte and of large invertebrates such as decapods and gastropods found in each net haul were placed in zip-lock bags and frozen in a portable freezer. Smaller macroinvertebrates such as amphipods and isopods were rinsed from half of each replicate wrack sample (Chapter 2), placed in sealed sample jars and frozen. All macrophyte and invertebrate samples were placed in a -20 ^{0}C freezer in the laboratory until processing for stable isotope analysis.

All fish from each replicate seine-net haul were placed in a series of six 50-L bins containing aerated seawater so that all fish from each net haul could be kept until the end of each sampling session. The two most-abundant fish species were then identified at each site and only individuals from those species were sacrificed for stable isotope and dietary analysis, in accordance with animal ethics approval. Up to 20 individual fish from each of the two most abundant species per site were randomly selected for dietary analysis, because Lenanton et al. (1982) found that 20 stomachs of each fish species associated with wrack was sufficient to describe the diet of each species. All fish kept for further processing were euthanised with an overdose of AQUI-S solution and kept in zip-lock bags on ice before being processed in the laboratory at the end of each sampling day. Remaining fish that were not required for stable isotope or dietary analysis were returned alive back into water of the surf zone.

At the end of each sampling day, all fish samples were blotted dry, weighed for whole body weights (±0.01 g) and measured for standard body length (±1 mm). Ten of each fish species were randomly selected for stable isotope analysis, for which they were rinsed with de-ionised water, after which dorsal muscle tissue was dissected with a scalpel and forceps, placed in a zip-lock bag and frozen at -20 ^{0}C. All fish stomachs were kept for dietary analysis. A 10 % formalin/seawater solution was injected by syringe and hypodermic needle into the stomach cavity to ensure fixation of each stomach and its contents. All fish were placed in jars of 10 % formalin/seawater solution and, after 48 hours, were thoroughly rinsed with water to remove excess formalin before being preserved in jars of 70 % ethanol.

Stomach content analysis

All fish were dissected to remove the stomach or the first third of the gut for fish species without true stomachs, to ensure that stomach contents from all species were comparable and only included food items that were at the earliest stage of digestion (Lenanton et al. 1982). Each full stomach or gut section was rinsed with water and blotted dry to remove excess formalin before being weighed (±0.001 g). Stomachs and gut sections were dissected longitudinally to enable light scraping with a spatula and feather forceps to remove entire contents and rinsed with water to remove any residual food items. Empty stomachs and gut sections were blotted dry to remove excess water and weighed (±0.001 g). Stomach and gut section contents were placed in a petri dish and sorted under a binocular dissecting microscope. All food items were sorted to the finest taxonomic level possible. Percent volumes of each food item from each gut were determined by evenly spreading them on graph paper (1 mm^2) with scores obtained by the area covered (Robertson 1977).

To determine the feeding intensity for each fish species, a gut fullness index (GFI) was calculated as a dimensionless ratio: total food weight x 1000 / total fish weight (Hynes 1950). Also, the percent frequency of each food item for each fish species was determined with the Occurrence Index, which was determined by the number of fish that had a particular food item present in their gut as a percentage of all fish processed per species (Hynes 1950). The Occurrence Index was chosen as a complementary technique to percent volume contributions of food items and GFI because it provides robust and interpretable models of the overall importance of food items for each fish species (Baker et al. 2013).

Stable isotope analysis

Macrophytes were defrosted, scraped for removal of epiphytes with a scalpel and rinsed with de-ionised water. Epiphytes present were only red algae and only found with enough material to satisfy minimum volumes for stable isotope analysis for macrophytes from Basham Beach. Invertebrate samples were defrosted and smaller crustaceans from each separate replicate sample were sorted and pooled into major taxonomic groups, such as Isopoda and Amphipoda. The pooling of smaller macroinvertebrates such as Amphipoda to broad taxonomic groups was to ensure that enough biological material is available for stable isotope analysis (Hyndes and Lavery 2005). Isopod and amphipod samples were rinsed with de-ionised water and oven dried at 60 ^{0}C for 24 hours. Samples were then split into halves with one half treated with a drop-by-drop application of 1 M hydrochloric acid (HCl) until cessation of bubbling to remove $CaCO_3$ for $\delta^{13}C$ (Jacob et al. 2005; Carabel et al. 2006; Mateo et al. 2008). All $\delta^{13}C$ samples were then re-dried at 60 ^{0}C for 24 hours without any post-acid treatment rinse with distilled water to reduce the chance of undesirable changes in $\delta^{13}C$ values (Jacob et al. 2005; Carabel et al. 2006; Mateo et al. 2008). The remaining half of each sample did not undergo any pre-preparation with acidification and was instead left untreated for $\delta^{15}N$ analyses (Jacob et al. 2005). Larger invertebrates such as gastropods and portunid crabs were selected using individuals as replicates from each sample. Gastropods were removed from their shells and portunid crabs were dissected with only white muscle tissue obtained, which was rinsed with de-ionised water. Fish muscle tissue samples were defrosted and rinsed with de-ionised water. All macrophyte, invertebrate and fish samples were placed into tin-foil containers of various sizes, oven dried at 60 ^{0}C for 24 hours (re-dried for HCl treatments) and then ground into a fine powder using a mortar and pestle.

Dried and ground macrophyte, invertebrate and fish samples were weighed into tin cups (300-500 µg for δ^{13}C and 2-3 mg for δ^{15}N) and analysed with an IsoPrime stable isotope mass spectrometer (GV Instruments, UK) at Flinders University Advanced Analytical Laboratory, Bedford Park, SA. Duplicate re-runs of random samples were undertaken for quality assurance to ensure homogeneity of individual samples. Sample values of carbon δ^{13}C and nitrogen δ^{15}N were expressed as per mil (‰) differences between sample isotopic ratios and the conventional standards of Peedee belemnite limestone and N_2 in air, respectively. Reference standards of sucrose and urea were also used to establish analytical precision for δ^{13}C and δ^{15}N, respectively.

Data analyses

To test for differences by site in fish standard lengths and gut fullness indices for selected groups of species, univariate PERMANOVAs were conducted on untransformed raw data based on Euclidean distance matrices (PRIMER Version 6 & PERMANOVA+ Version 1.0.6; Clark and Warwick 2001; Anderson et al. 2008). Pearson Chi-Square contingency tests were undertaken in SYSTAT Version 13.0 to determine whether there were differences by site in the number of individual fish with empty stomachs. Percent volume data of food items obtained from fish guts were averaged for each fish species per site and compared in terms of similarities in diet composition between fish species by site using a Bray-Curtis similarity matrix in PRIMER.

Plausible trophic levels were investigated as shifts in isotopic discrimination based on differences in centroid values between diet and consumer. The mean standard fractionation increase in δ^{13}C and δ^{15}N of 0.4 ‰ and 3.4 ‰, respectively, for each trophic level step is widely used in many trophic studies (Post 2002). However, discrimination of δ^{13}C can range between -1 to +1‰ for each trophic step (Minagawa and Wada 1984; Vanderklift and Ponsard 2003; Crawley et al. 2007). For consumers, the fractionation shift in δ^{13}C can change depending on whether whole body or just muscle tissue is analysed with the average shift for muscle tissue determined as +1.3 ‰ (McCutchan et al. 2003). Further consideration was also given to the possibility of negative shifts in δ^{13}C, which has been identified in herbivorous invertebrates (Vander Zanden and Rasmussen 2001). I also considered the wider ranges in fractionation shifts of δ^{15}N of -1 to +5 ‰ per trophic level as identified in previous studies (Minagawa and Wada 1984; Vanderklift and Ponsard 2003; Crawley et al. 2007). Therefore, I also selected the larger ranges in δ^{13}C between -1 to +1.3 ‰ and δ^{15}N between -1 to +5 ‰ per trophic level to further investigate possible discrimination between consumers and producers and hence trophic level positions.

3. Results

Fish abundances and size frequencies

During seine-net sampling around wrack accumulations in sandy-beach surf-zones, a total of 197 fish from 13 families and 14 species were captured (Table 4.1). Only three fish species occurred at both sites: f*Aldrichetta forsteri*, *Tetractenos glaber* and, in much lower abundances, *Leseurina platycephala*. The most abundant fish species captured at Long Beach South were *T. glaber* and *A. forsteri* (Table 4.1). In comparison, *Enoplosus armatus* and *T. glaber* were the most common fish species found at Basham Beach (Table 4.1). Standard length measurements of *A. forsteri* captured at Long Beach South indicated that they were mostly juveniles (Figure 4.2A) (Chubb et al. 1981). The lengths of *E. armatus* at Basham Beach were distributed across a much narrower range and all individuals appeared to be juveniles (Figure 4.2B). Individuals of *T. glaber* captured at the two sites had no overlap in size ranges with only juveniles (as defined by Booth and Schultz 1999) captured at Basham

Table 4.1: Total abundances of all fish species captured during seine netting in two regions south of Adelaide: Fleurieu Peninsula, Basham Beach (BB); and South-East, Long Beach South (LBS). Sampling occurred in March 2013. A blank indicates that zero individuals were caught. Total of *n* = 6 net hauls at each site. Species in bold were chosen for further analysis of guts and tissue stable isotopes.

		Site		
Family	Species	Basham Beach	Long Beach South	Total
Arripidae	*Arripis truttaceus*	2		2
Atherinidae	*Leptatherina presbyteroides*		4	4
Clinidae	*Cristiceps australis*	2		2
	Heteroclinus sp.1		3	3
Diodontidae	*Diodon nicthemerus*		6	6
Enoplosidae	***Enoplosus armatus***	18	1	19
Leptoscopidae	*Leseurina platycephala*	3	4	7
Monacanthidae	*Scobinichthys granulatus*	2		2
Mugilidae	***Aldrichetta forsteri***	9	19	28
Platycephalidae	*Platycephalus speculator*	1		1
Plotosidae	*Cnidoglanis macrocephalus*	3		3
Syngnathidae	*Vanacampus* sp.1		1	1
Terapontidae	*Pelates* sp.1	2		2
Tetraodontidae	***Tetractenos glaber***	89	28	117
	Total catch	131	66	197
	No. of species	10	8	14

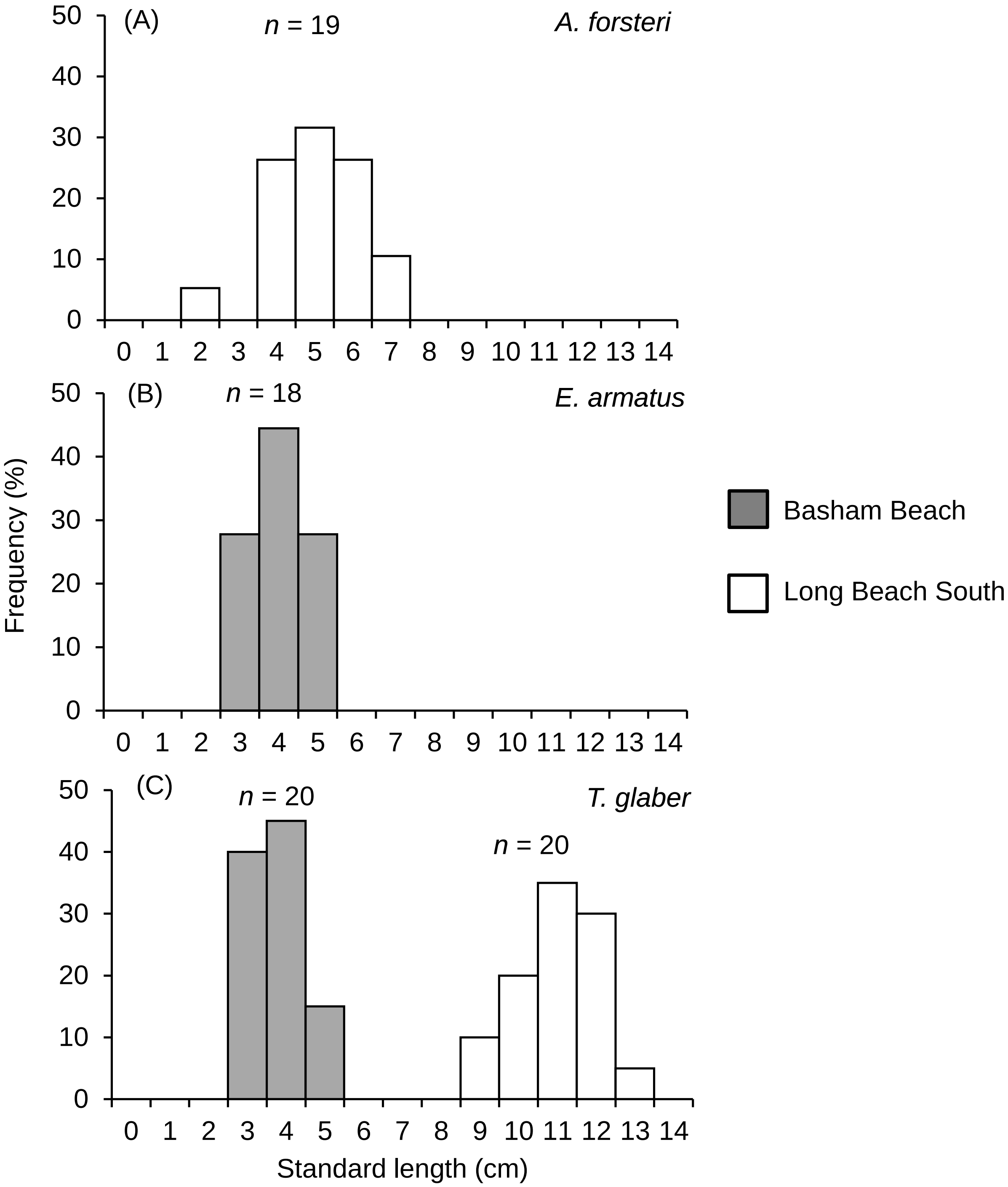


Figure 4.2: Standard length-frequency distributions of the most common fish species (A) *Aldrichetta forsteri*, (B) *Enoplosus armatus* and (C) *Tetractenos glaber* associated with wrack accumulations in sandy-beach surf-zones of Basham Beach and Long Beach South. *n* = number of guts examined

Beach and only adults at Long Beach South (Figure 4.2C). Mean lengths of fish were significantly different for the species by site groups (Pseudo-$F_{3, 1}$ = 292.02, P = 0.0001) for all pair-wise combinations, except for the comparison of *T. glaber* and *E. armatus* at Basham Beach.

Fish dietary composition

Gut fullness indices, represented as the percent contribution of ingested food weight to total body weight, were broadly similar for all three fish species but lowest for *T. glaber* at Long Beach South (Figure 4.3). These differences were not statistically significant (Pseudo-$F_{3, 1}$ = 1.27, P = 0.29). Two out of the three fish species had only a small portion of individuals with completely empty stomachs (i.e. *E. armatus* 11 % and *A. forsteri* 16 %, Figure 4.3, Appendix 4, Table A4.1) but no stomachs were empty for *T. glaber* (although these differences were not significant by contingency tests, Chi-square = 6.1, P = 0.109).

All three fish species had omnivorous diets with animal, seagrass, algal and detrital matter found in varying percentages within their stomachs (Figure 4.4A; see also Appendix 4, Table A4.1). The widest diet range was identified for individuals of *E. armatus* and *T. glaber* captured at Basham Beach (i.e. 12 and 11 food groups represented, respectively, Appendix 4, Table A4.1). Isopods (Sphaeromatidae and *Euidotea*) contributed the largest percent volume to the diets of *E. armatus* at Basham Beach and *T. glaber* at Long Beach South (Figure 4.4A). Unidentified animal fragments (i.e. animal muscle tissue of unknown origin), which are likely to be from brachyuran crabs, followed by isopods and brachyuran crabs contributed most to the diets of *T. glaber* at Basham Beach (Figure 4.4A). Unidentified animal fragments, which are likely to be from mollusc mantle tissue, contributed most to percent volumes in *A. forsteri* diets (Figure 4.4A). In comparison, polychaetes, amphipods, algae, seagrass and detrital matter contributed much less to dietary volumes overall (Figure 4.4A). Only trace amounts of various groups, such as other crustaceans, gastropods, bivalves and sand grains, were identified in stomachs of the three fish species (Appendix 4, Table A4.1). Average percent volume contributions of food items for fish species by site were most similar between *T. glaber* from both sites and *E. armatus* at Basham Beach (Table 4.2). In contrast, the percent volume compositions of food items between *A. forsteri* and two other species were dissimilar (*T. glaber* from Long Beach South and *E. armatus* from Basham Beach, Table 4.2).

Frequency of occurrence indices had similar patterns to percent volume contributions, where the largest percent frequencies and largest percent contribution values in each fish species were represented by the same food items (i.e. isopods, brachyuran crabs and unidentified animal fragments, Figure 4.4B). Food items with some of the lowest percent contribution volumes also had low frequencies of occurrence in all fish species (Figure 4.4B).

Macrophytes and macroinvertebrates caught in seine nets

The macrophytes captured in seine nets at Basham Beach mainly consisted of brown and green algae and the two seagrass species *Amphibolis antarctica* and *Amphibolis griffithii*. At Long Beach South, macrophytes mainly consisted of various species of red and brown algae. Only three brown algae, *Cystophora* spp., *Ecklonia radiata* and *Sargassum* spp., were found at both sites. Macroinvertebrates captured in seine nets at Basham Beach only consisted of crustaceans and included sphaeromatid isopods, gammarid amphipods and the portunid crab *Ovalipes australiensis*. However, even when pooled, there were not enough amphipods for stable isotope analysis from Basham Beach samples. Sphaeromatid isopods and *O. australiensis*, *Euidotea* spp. isopods and the two grazing gastropod species *Phasianella australis* and *Prothalotia lehmanni* were also captured at Long Beach South.

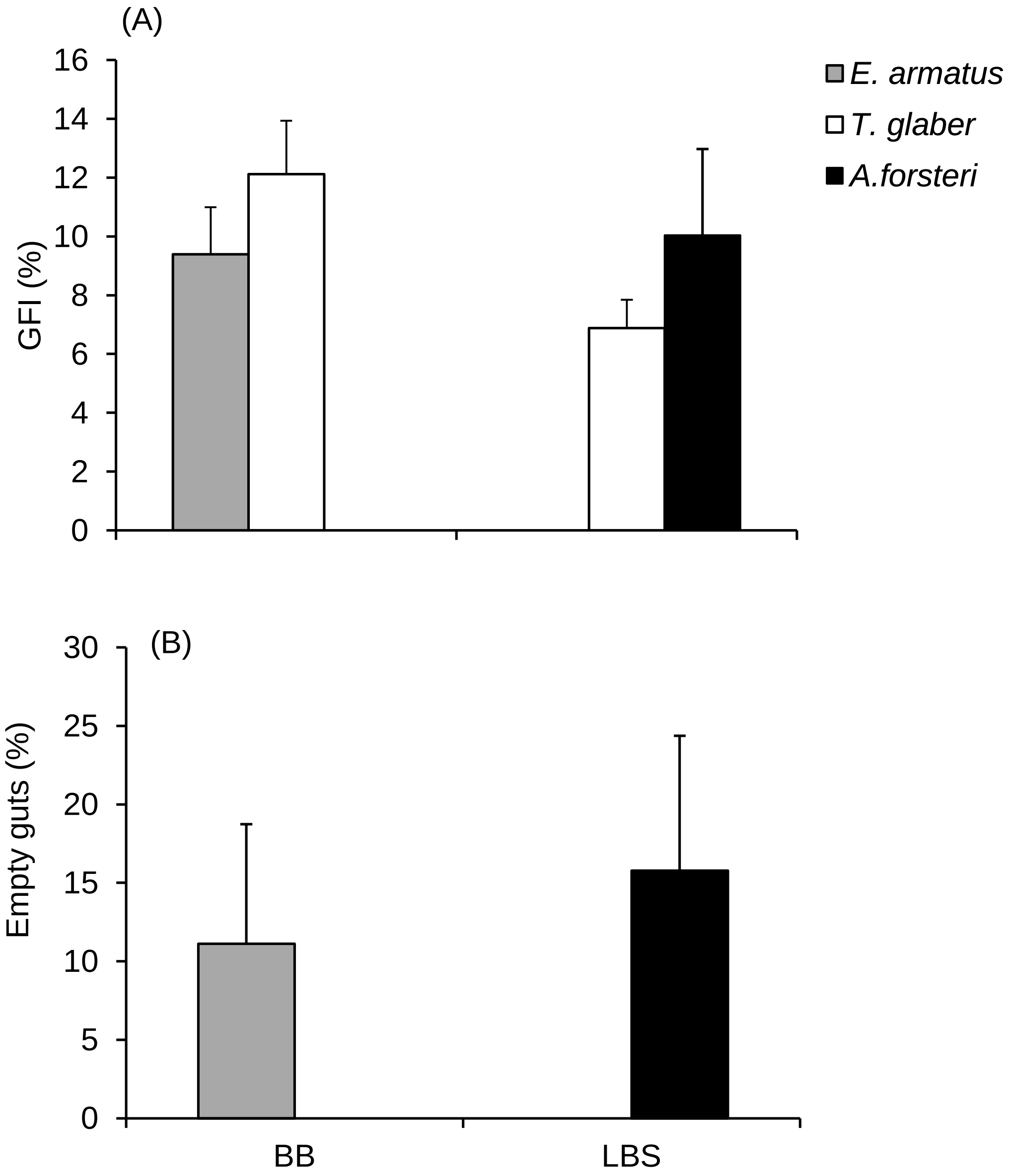


Figure 4.3: (A) Gut fullness index (GFI) and (B) percentage of empty guts of common fish species captured in sandy-beach surf-zones at Long Beach South (LBS) and Basham Beach (BB). *Tetractenos glaber* is not shown in (B) because zero individuals had empty guts. *n* values are given in Figure 4.2.

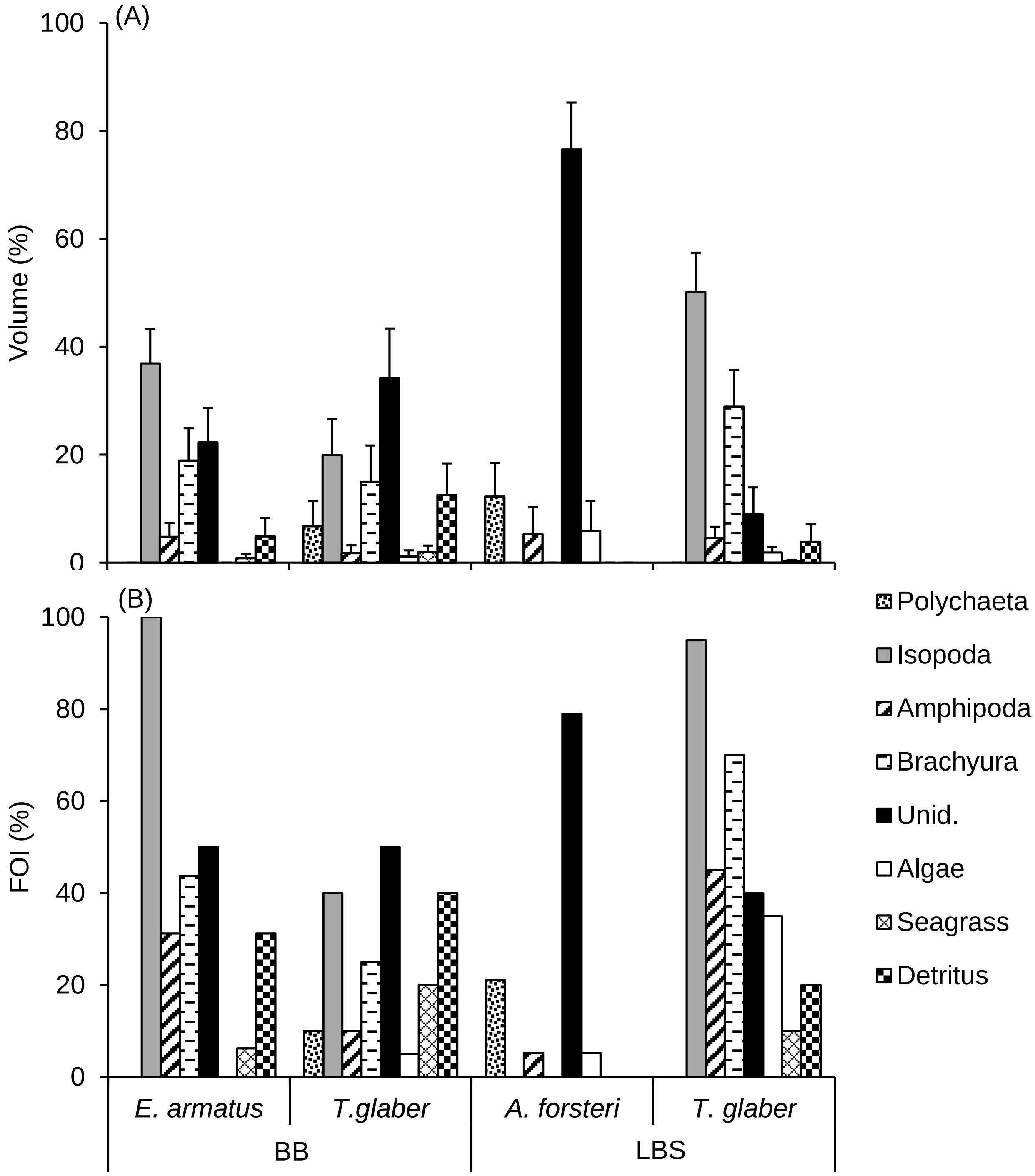


Figure 4.4: Food items obtained from guts of common fish species captured in sandy-beach surf-zones at Long Beach South (LBS) and Basham Beach (BB). The six most-common food items are shown for (A) mean ± SE (*n* = 18-20) percent volume contribution (Volume %) and (B) Frequency of Occurrence Index (FOI %). Unid. = all unidentified animal fragments, Detritus = all unidentified macrophytic material.

Table 4.2: Comparison of fish diets from food items obtained from guts of the two most common fish species captured at each of Basham Beach (BB) and Long Beach South (LBS). Bray-Curtis similarity values (%) based on percent volume contributions of dietary food items. *n* = 18 to 20 guts of each fish species.

Fish species (site)	*E. armatus* (BB)	*T. glaber* (BB)	*A. forsteri* (LBS)
T. glaber (BB)	67.6		
A. forsteri (LBS)	27.1	43.9	
T. glaber (LBS)	74.9	52.2	15.5

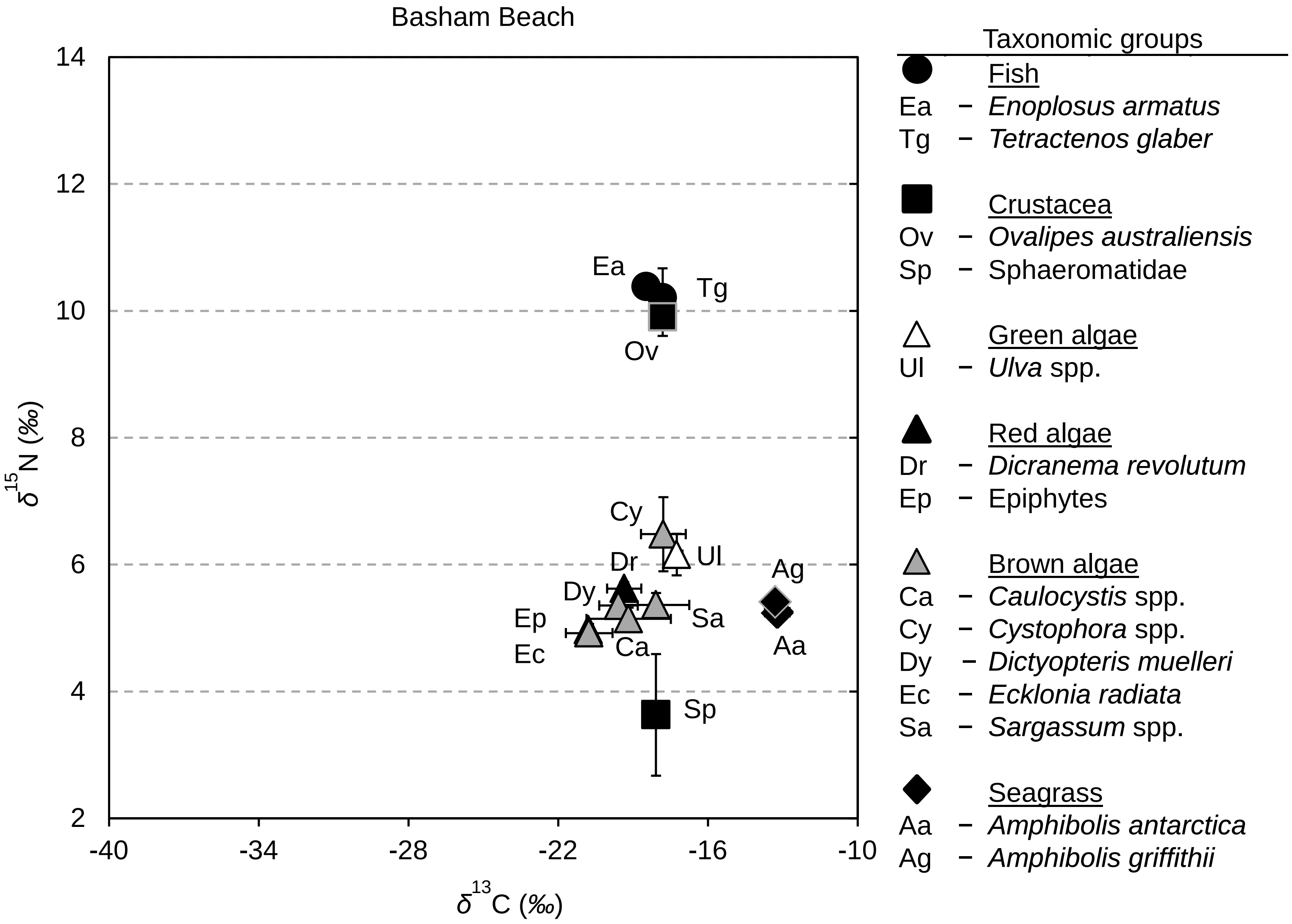
Stable isotope composition

Comparison of the range in stable carbon and nitrogen isotope values for both sites across all macrophytes and macroinvertebrates indicated that the trophic web as a whole tended to be more depleted in $\delta^{13}C$ at Long Beach South (BB ‰ range of -20.7 to -13.2 $\delta^{13}C$ versus LBS ‰ range of -33.7 to -17.8 $\delta^{13}C$ across all groups) but more depleted in $\delta^{15}N$ at Basham Beach (BB ‰ range of 3.6 to 10.4 $\delta^{15}N$ versus LBS ‰ range of 5.8 to 13 $\delta^{15}N$ across all groups) (Figure 4.5). In contrast, fish had similar values across the two sites. Species or taxonomic groups in common at both sites were significantly different in $\delta^{13}C$ and $\delta^{15}N$ between sites, except for $\delta^{13}C$ of *T. glaber* and *Ecklonia radiata*, and $\delta^{15}N$ of all Crustacea (Table 4.3).

At Basham Beach, carbon and nitrogen stable isotope values were obtained from 10 macrophyte, two macroinvertebrate taxonomic groups or species, and two fish species (Figure 4.5A). Out of all macrophytes, both *Amphibolis antarctica* and *Amphibolis griffithii* were most enriched for $\delta^{13}C$ and *Cystophora* spp. was most enriched for $\delta^{15}N$ (Figure 4.5A). In comparison, epiphytes and *E. radiata* were the most depleted for $\delta^{13}C$ overall. The red algae *Dicranema revolutum* and the two brown algal taxa *Dictyopteris muelleri* and *Caulocystis* spp. had a similar range in $\delta^{13}C$ but *D. revolutum* was slightly more enriched in $\delta^{15}N$ (Figure 4.5A). Sphaeromatid isopods were the most depleted in $\delta^{15}N$ and had the widest range overall (Figure 4.5A). The portunid crab *Ovalipes australiensis* and the two fish *T. glaber* and *E. armatus* were similar in $\delta^{13}C$ and $\delta^{15}N$, except *E. armatus* was slightly more depleted in $\delta^{13}C$ (Figure 4.5A).

At Long Beach South, carbon and nitrogen stable isotope values were obtained from eight macrophyte, four macroinvertebrate taxonomic groups or species, and two species of fish (Figure 4.5B). Overall, the two red algae *Cryptonemia* spp. and *Phacelocarpus* spp. were the most depleted for $\delta^{13}C$ and sphaeromatid isopods were the most depleted in $\delta^{15}N$ overall (Figure 4.5B). Out of all macrophytes, *Cystophora* spp. and *Gracilaria* spp. were the most enriched for $\delta^{13}C$ (Figure 4.5B). Out of all macroinvertebrates, the portunid crab *O. australiensis* was the most enriched for $\delta^{15}N$ and $\delta^{13}C$ (Figure 4.5B). Gastropods and *Euidotea* isopods were similar in $\delta^{13}C$ but gastropods were slightly more enriched in $\delta^{15}N$ (Figure 4.5B). The two fish *T. glaber* and *A. forsteri* had similar $\delta^{13}C$ values and *T. glaber* was only slightly more enriched in $\delta^{15}N$ (Figure 4.5B).

(4.5A)


Basham Beach
14
12
10
8
6
4
2
-40
-34
-28
-22
-16
-10
δ^{15}N (‰)
δ^{13}C (‰)
Ea
Tg
Ov
Cy
Ul
Dr
Dy
Ep
Ec
Ca
Sa
Ag
Aa
Sp
Taxonomic groups
● Fish
Ea – *Enoplosus armatus*
Tg – *Tetractenos glaber*
■ Crustacea
Ov – *Ovalipes australiensis*
Sp – Sphaeromatidae
△ Green algae
Ul – *Ulva* spp.
▲ Red algae
Dr – *Dicranema revolutum*
Ep – Epiphytes
△ Brown algae
Ca – *Caulocystis* spp.
Cy – *Cystophora* spp.
Dy – *Dictyopteris muelleri*
Ec – *Ecklonia radiata*
Sa – *Sargassum* spp.
◆ Seagrass
Aa – *Amphibolis antarctica*
Ag – *Amphibolis griffithii*

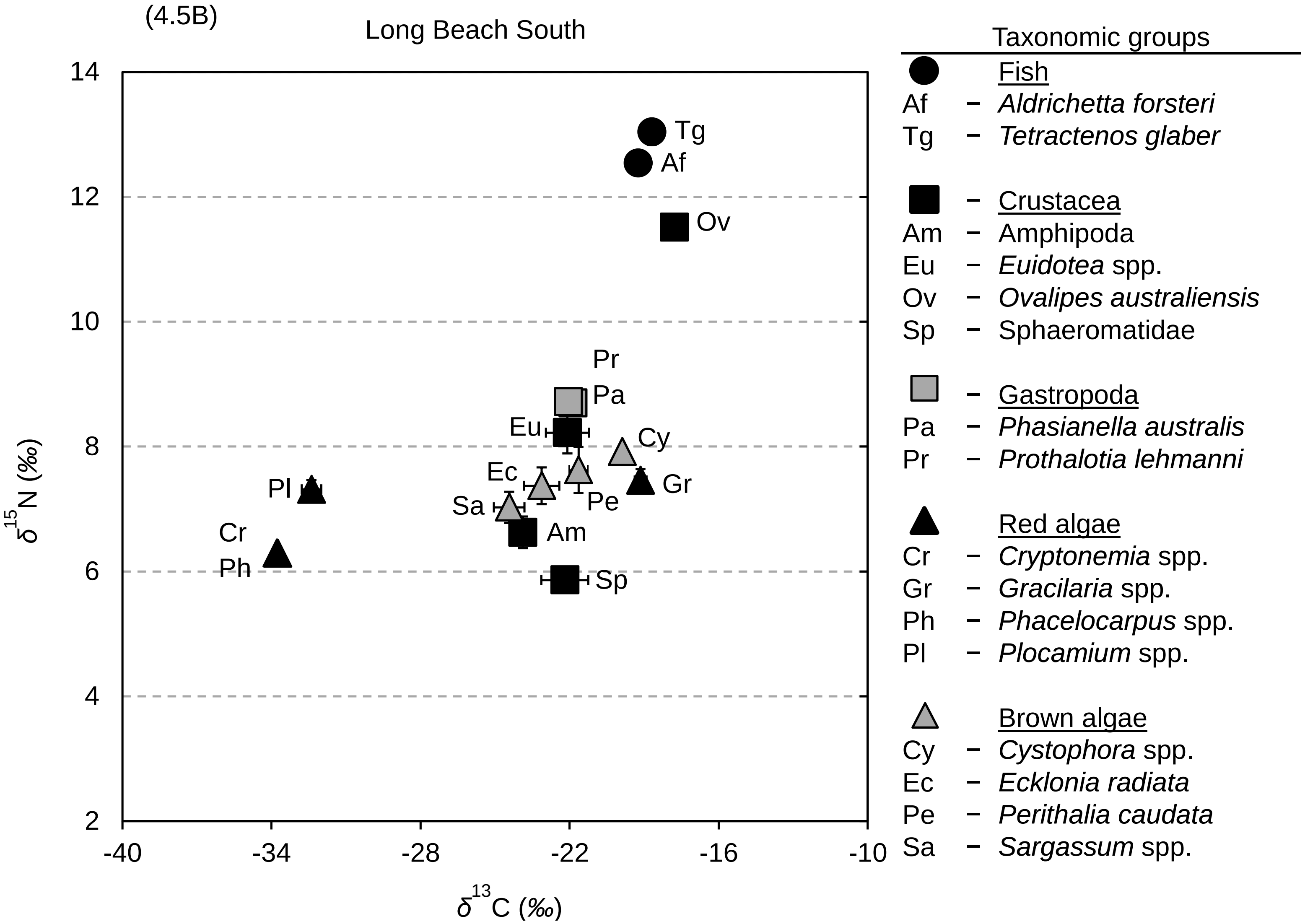


Figure 4.5: Stable isotope ratios of δ^{13}C and δ^{15}N (plotted as centroids with standard errors) for macrophyte (*n* = 1-6), macroinvertebrate (*n* = 1-10) and fish (*n* = 10) taxa captured during seine netting of wrack accumulations in sandy-beach surf-zones at (A) Basham Beach and (B) Long Beach South. The symbol for epiphytes is included under red algae at Basham Beach.

Table 4.3: Univariate PERMANOVAs comparing δ^{13}C and δ^{15}N for species in common between the sites of Basham Beach (BB) and Long Beach South (LBS) and the site with higher values for each isotope. PERMANOVAs were based on Euclidean distances of the stable isotope values. Significant results are indicated by * <0.05, ** <0.01, *** <0.001. Blank cells = non-significant. Where significant, the site with the higher enrichment according to δ^{13}C and δ^{15}N is given.

Taxonomic group	δ^{13}C		δ^{15}N	
	Significance	Site with higher value	Significance	Site with higher value
T. glaber			***	LBS
Sphaeromatidae	*	BB	*	LBS
Ecklonia radiata			**	LBS
Sargassum spp.	**	BB	**	LBS

Trophic pathway determinations

Overall, no clear trophic pathways could be identified when using just the strict standard fractionation values of 0.4 ‰ for δ^{13}C and 3.4 ‰ for δ^{15}N. At Basham Beach, based on the discrimination range for trophic source shifts of -1 to +1.3 ‰ for δ^{13}C and of -1 to +5 ‰ for δ^{15}N for trophic level shifts, *E. armatus* could be obtaining C and N from *Ulva* spp., *Dicranema* spp. and three brown algal species. Similar patterns were identified for *T. glaber* and *O. australiensis*, except that they may not be obtaining C and N from the brown algae *Dictyopteris muelleri* (Table 4.4A, Figure 4.5A). None of the consumers appeared to be obtaining C and N from seagrass. The portunid crab *O. australiensis* was unlikely to be a food source for both fish species as they were all in a similar trophic-level range (Table 4.4A, Figure 4.5A), but this pathway was plausible based on the discrimination range used here.

At Long Beach South, based on the same discrimination range, *A. forsteri* may be obtaining δ^{13}C and δ^{15}N from the brown algae *Cystophora* spp. and, less likely, *T. glaber* from *O. australiensis* (Table 4.4B, Figure 4.5B). Similar to Basham Beach, both species of fish and the portunid crab *O. australiensis* appeared to be within the same trophic level range and utilising similar trophic sources (Table 4.4B, Figure 4.5B). The crustacean *Euidotea* and both gastropod species may be obtaining C and N from the brown algae *Ecklonia radiata* and *Perithalia caudata* (Table 4.4B, Figure 4.5B). Amphipods may be obtaining C and N from *Ecklonia radiata* and other brown algae, e.g. *Sargassum* spp. (Table 4.4B, Figure 4.5B). The portunid crab *O. australiensis* and Sphaeromatid isopods do not appear to be obtaining C and N from any of the primary producer groups (Table 4.4B, Figure 4.5B).

Table 4.4: Plausible consumers and potential food pathways established by the difference in fractionation of ΔC and ΔN between each consumer and potential food source pair. Consumers and food items were obtained from seine-net sampling of the surf zone at (A) Basham Beach and (B) Long Beach South. Values shown are based on the difference in centroid values for carbon (ΔC) or nitrogen (ΔN) isotopes obtained from potential food item values subtracted from consumer values and then compared with a coarse range in discrimination of δ^{13}C at -1 to +1.3 ‰ for each trophic source and δ^{15}N at -1 to +5 ‰ for each trophic level step. Underlined values = plausible assimilation of only one of either δ^{13}C or δ^{15}N from potential foods to consumers. Bold values = plausible assimilation of both δ^{13}C and δ^{15}N from potential foods to consumers. Blank cells are consumers that were considered to be within the same trophic level and so unlikely to be feeding on each other.

(4.4A)

Consumers:	*E. armatus*		*T. glaber*		*O. australiensis*		Sphaeromatidae	
Taxonomic group Potential foods	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN
Macroinvertebrates								
O. australiensis	**-0.7**	**0.5**	**0.0**	**0.3**				
Sphaeromatidae	-0.4	6.8	0.3	6.6	0.3	6.3		
Green algae								
Ulva spp.	**-1.2**	**4.2**	**-0.6**	**4.0**	**-0.6**	**3.7**	-0.8	-2.5
Red algae								
Dicranema spp.	**0.9**	**4.8**	**1.5**	**4.6**	**1.5**	**4.3**	1.3	-2.0
Epiphytes	2.3	5.4	3.0	5.2	3.0	4.9	2.7	-1.3
Brown algae								
Caulocystis spp.	0.7	5.2	1.4	5.1	1.4	4.8	1.1	-1.5
Cystophora spp.	**-0.7**	**3.9**	**0.0**	**3.7**	**0.0**	**3.4**	-0.3	-2.8
Dictyopteris muelleri	**1.1**	**5.0**	1.8	4.9	1.8	4.5	1.5	-1.7
Ecklonia radiata	2.3	5.5	2.9	5.3	2.9	5.0	2.7	-1.3
Sargassum spp.	**-0.4**	**5.0**	**0.3**	**4.8**	**0.3**	**4.5**	0.0	-1.7
Seagrasses								
Amphibolis antarctica	-5.2	5.1	-4.6	5.0	-4.6	4.7	-4.9	-1.6
Amphbibolis griffithii	-5.2	5.0	-4.5	4.8	-4.5	4.5	-4.9	-1.6

(4.4B)

Consumers:	*A. forsteri*		*T. glaber*		*O. australiensis*		Amphipoda		*Euidotea*		Sphaeromatidae		*P. australis*		*P. lehmanni*	
Taxonomic group Potential foods	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN	ΔC	ΔN
Macroinvertebrates																
O. australiensis	-1.5	1.0	**-0.9**	**1.5**												
Phasianella australis	2.6	3.8	3.2	4.3	4.1	2.8										
Prothalotia lehmanni	2.8	3.8	3.4	4.3	4.3	2.8										
Amphipoda	4.6	5.9	5.2	6.4	6.1	4.9										
Euidotea	2.8	4.3	3.4	4.8	4.3	3.3										
Sphaeromatidae	2.9	6.7	3.5	7.2	4.4	5.6										
Red algae																
Cryptonemia spp.	14.5	6.2	15.1	6.7	16.0	5.2	9.9	0.3	11.7	1.9	11.6	-0.4	11.9	2.4	11.7	2.4
Gracilaria spp.	-0.1	5.1	0.5	5.6	1.4	4.1	-4.7	-0.8	-2.9	0.8	-3.0	-1.6	-2.7	1.2	-2.9	1.3
Phacelocarpus spp.	14.5	6.2	15.1	6.7	16.0	5.2	9.9	0.3	11.7	1.9	11.6	-0.4	11.9	2.4	11.7	2.4
Plocamium spp.	13.1	5.2	13.7	5.7	14.6	4.2	8.5	-0.7	10.3	0.9	10.2	-1.5	10.5	1.4	10.3	1.4
Brown algae																
Cystophora spp.	**0.6**	**4.6**	1.2	5.1	2.1	3.6	-4.0	- -1.3	-2.2	- 0.3	-2.3	-2.1	-2.0	0.8	-2.2	- 0.8
Ecklonia radiata	3.9	5.2	4.4	5.7	5.3	4.1	**-0.8**	**-0.7**	**1.0**	**0.9**	0.9	-1.5	**1.3**	**1.3**	**1.1**	**1.3**
Perithalia caudata	2.4	4.9	2.9	5.4	3.9	3.9	2.2	1.0	**-0.5**	**0.6**	-0.6	-1.8	**-0.2**	**1.1**	**-0.4**	**1.1**
Sargassum spp.	5.2	5.5	5.7	6.0	6.6	4.5	**-0.5**	**0.4**	2.3	1.2	2.2	-1.2	2.6	1.7	2.4	1.7

4. Discussion

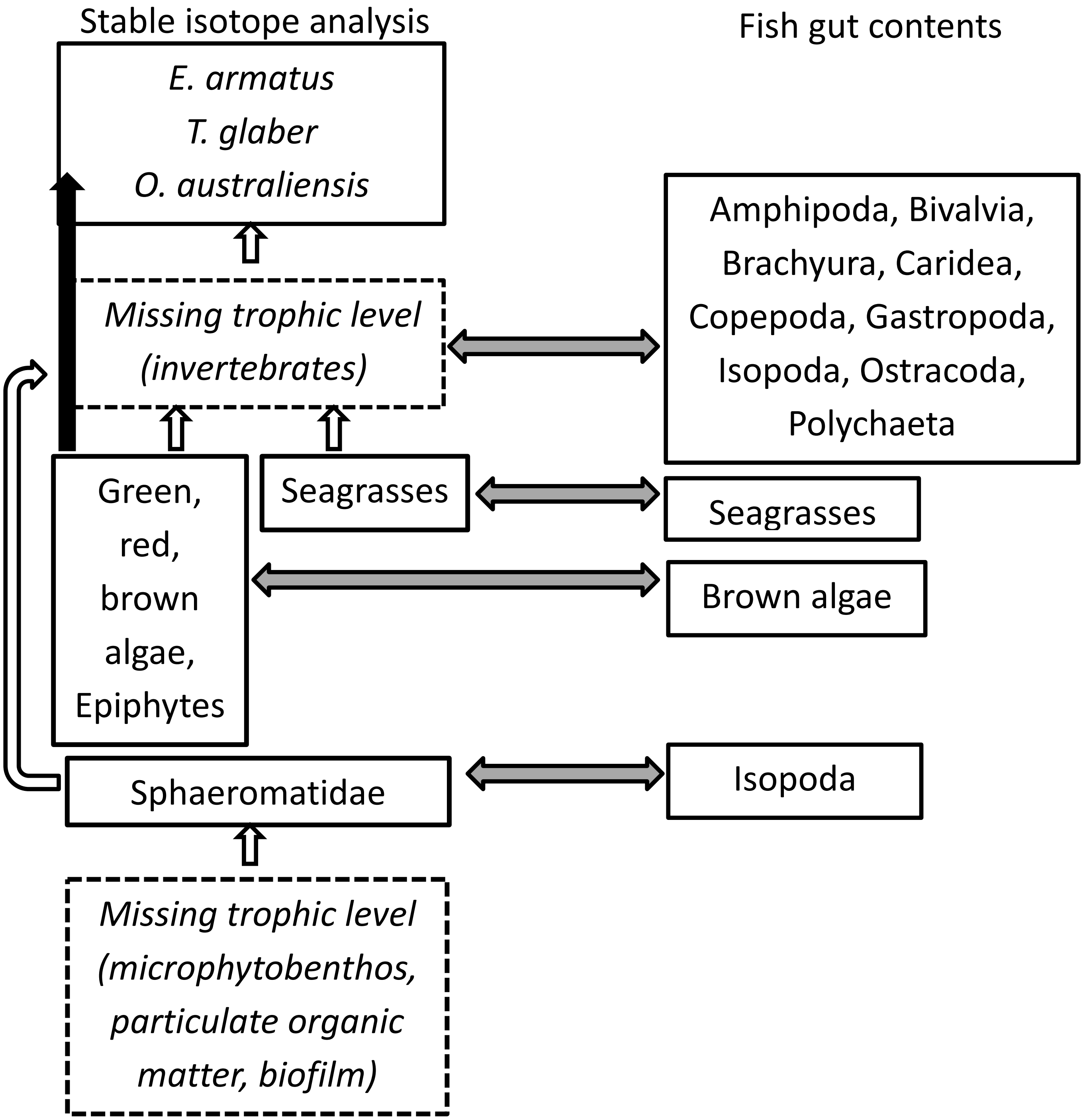
T. glaber at both sites and *E. armatus* at Basham Beach were omnivorous but the main contributing food items were crustaceans consisting of mainly sphaeromatid and *Euidotea* isopods and brachyuran crabs. The exception to this pattern was *A. forsteri* at Long Beach South, which had mainly unidentified animal muscle tissue and polychaetes in their guts. In previous studies, amphipods and polychaetes were identified as the major prey item for juvenile fish (including *A. forsteri*) from surf-zone wrack accumulations in Western Australia (Lenanton et al. 1982; Hyndes and Lavery 2005). However, for many fish species, diet composition may vary between size classes of fish, between day and night, and among different habitats such as drifting macrophytes or bare sand (Robertson and Lenanton 1984). The small amounts of algae and seagrass in fish gut contents in my study suggest that these items may not necessarily be a food item targeted by these fish species, which has also been suggested by Hyndes and Lavery (2005) for fish found among wrack accumulations in Western Australia.

A large diversity of food items was found in the guts of fish sampled. Similar types and diversity of food items were found in previous studies in wrack accumulations of sandy-beach surf-zones in Western Australia (Robertson and Lenanton 1984; Hyndes and Lavery 2005). The exception in my study was the presence of just four different food types in the guts of *A. forsteri*, which mainly consisted of unidentified animal tissue and polychaetes. This suggests that this species is more selective by feeding from the benthos rather than directly among the drifting wrack material. In previous studies, *Aldrichetta forsteri*, whiting (Sillaginidae) and flounder (Rhombosoleidae) species have also shown more selective and less diverse diets than other species in wrack accumulations off Western Australian sandy beaches (Lenanton et al. 1982; Robertson and Lenanton 1984; Hyndes and Lavery 2005). Future targeted investigation over time of particular feeding guilds (e.g. benthic foragers) along sandy-beach surf-zones in the presence or absence of wrack accumulations would be beneficial in understanding the feeding ecology of these fishes and their use of floating wrack assemblages.

Synthesis of the stable isotope and gut content data identified that there are many possible macroinvertebrate food sources found in fish guts that could fill the missing trophic level niche between algae and fish or larger crustaceans (e.g. *O. australiensis*) at both sites (Figure 4.6). At both sites, the links between fish gut contents to possible trophic levels show that fish could be feeding throughout most trophic levels but the only links detected by stable isotope analysis were between fish and algae, and between some of the invertebrate species and algae at Long Beach South only (Figure 4.6). The position of Sphaeromatidae highlights that isopods as a group seem to cover a large trophic range but also provides further evidence that they may also be feeding on primary producers (e.g. diatoms) from a missing lower trophic level (Figure 4.6).

In my study, I found there was a clear separation in trophic levels at both sites based on δ^{15}N values, particularly between the fish and a portunid crab versus all other groups. However, the large separation between the trophic levels of macrophytes and fish and portunid crabs at both sites indicates that there may be a trophic level missing from the isotope results, especially at Basham Beach (Figure 4.6). Given that gut contents provided plausible items for this trophic level, the fish may not yet have assimilated N and C from these foods, as it can take weeks to months for isotopic signatures to show up in muscle tissue (Boecklen et al. 2011; Hyndes et al. 2013). Also, fish may not be just foraging within wrack accumulations but may also be foraging over a wider range of habitats, which can make it very difficult to ascertain the origin of dietary food items (Nagelkerken and Van der Velde 2004; Wyatt et al. 2010). This may be the case if certain fish species (particularly juveniles) have only recently

(4.6A)


Stable isotope analysis
Fish gut contents
E. armatus
T. glaber
O. australiensis
Missing trophic level
(invertebrates)
Amphipoda, Bivalvia, Brachyura, Caridea, Copepoda, Gastropoda, Isopoda, Ostracoda, Polychaeta
Green, red, brown algae, Epiphytes
Seagrasses
Seagrasses
Brown algae
Sphaeromatidae
Isopoda
Missing trophic level
(microphytobenthos, particulate organic matter, biofilm)

(4.6B)

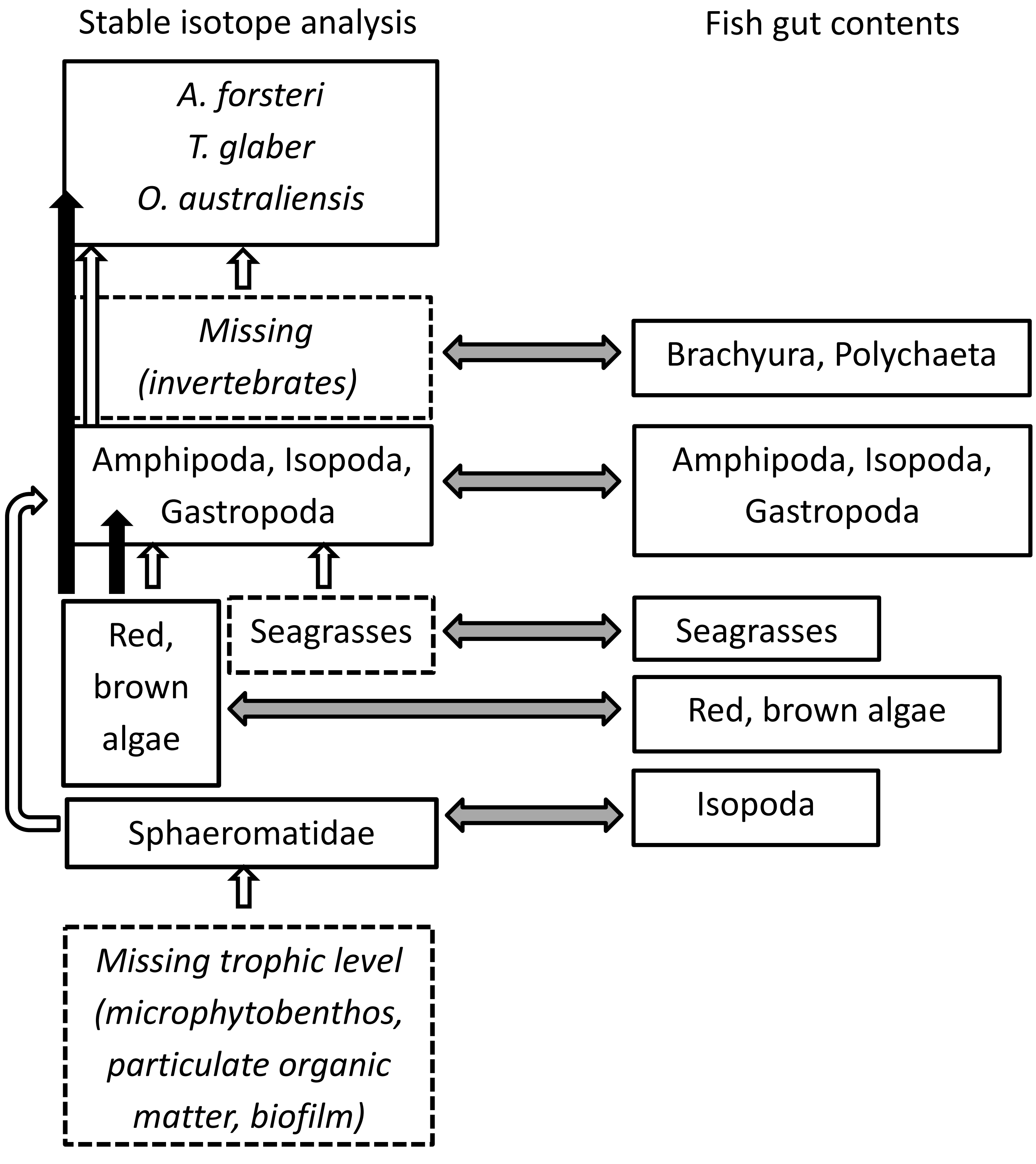


Figure 4.6: Plausible trophic pathways established from stable isotope (left) and gut content analysis (right) of wrack accumulations in sandy-beach surf zones of (A) Basham Beach and (B) Long Beach South in March 2013. Black filled arrows indicate plausible carbon and nitrogen flow pathways and assimilation of potential diets according to δ^{13}C and δ^{15}N values from stable isotope analysis (SIA). Open vertical arrows indicate likely consumption according to previous studies. Grey filled horizontal arrows indicate the most likely trophic position of food items found in fish gut contents inferred from previous studies. Boxes with dashed lines indicate possible position of missing trophic levels or, in the case of Long Beach South seagrass, that was not present in wrack samples used for stable isotope analyses. The dashed line box labelled 'missing invertebrates' for Long Beach South indicates that some unknown subset of macroinvertebrates could fill that niche but still be part of the same trophic level directly below it. All information in dashed line boxes was established from isotope values from other previous studies. All information from previous studies was obtained from literature cited herein.

moved into wrack accumulations in the surf zone where they were caught, meaning that the isotopic signature measured may be a reflection of food sources from an entirely different habitat, such as the benthos. Alternatively, more transient fish species may regularly move into and out of wrack accumulations and amongst other nearby habitats with tidal movement and/or to forage for food (Lugendo et al. 2006). For example, fish may have been voraciously feeding upon isopods among wrack accumulations at the particular point in time that I sampled but not have had enough time for those $\delta^{15}N$ and $\delta^{13}C$ signatures to show up in muscle tissues. Instead, the $\delta^{15}N$ and $\delta^{13}C$ signatures of fish muscle tissue may be more representative of foods obtained from other nearby habitats that I did not sample, or food items that were temporally transient. Also, as the fish were only sampled at one point in time, there may have been food items consumed within wrack accumulations that were not present at the time that I conducted my field sampling and so plausible food items may have been missed.

Initially, I thought that the semi-permanent presence of wrack accumulations along sandy-beach surf-zones at Basham Beach and Long Beach South would provide both nursery habitat and important food resources for juvenile fish. Instead, it appears that fish may be using these wrack accumulations primarily as habitat and only as a secondary foraging habitat with preferences likely for other nearby foraging grounds that may have more foraging opportunities or higher quality food resources, assuming that the patterns observed here are not as a result of the transient nature of some food sources within the wrack itself. Similar behavioural patterns have been identified in juvenile fish that use mangroves as shelter and/or habitat but primarily forage over adjacent seagrass beds (Nagelkerken and Van der Velde 2004; Vaslet et al. 2012).

In this study, sphaeromatid isopods at both sites did not appear to be assimilating N from drifting macrophytes in wrack accumulations and were lowest in $\delta^{15}N$ at both sites indicating that there may be a lower trophic level that I did not capture. Instead, they could be feeding on other items such as microphytobenthos, particulate organic matter and biofilms (Figure 4.6) that have lower δ^{15}N isotope values as identified in previous studies among mangrove habitats (Bouillon et al. 2002; Vaslet et al. 2012) and on sandy beaches (Colombini et al. 2011; Bessa et al. 2014). In my study, the possibility of grazing isopods (*Euidotea*), gastropods and the omnivorous portunid crab *O. australiensis* feeding on, and assimilating N and C from, brown algae is likely but difficult to ascertain and further investigation into the diets of these consumers over time would be needed to determine the relative importance of that food source. Previous research indicates that allochthonous brown algae is an important dietary item for the surf-zone-inhabiting amphipod *Allorchestes compressa*, which is commonly found among wrack accumulations in Western Australia (Crawley and Hyndes 2007; Crawley et al. 2009). In contrast, very little is known about the feeding habits of the other macroinvertebrates that I found within surf-zone wrack accumulations at Basham Beach and Long Beach South, which highlights an important avenue for further research.

Here, I identified notable differences in the overall range of δ^{15}N and δ^{13}C values for trophic webs between the two sites, with Basham Beach more enriched in δ^{13}C and Long Beach South more enriched in δ^{15}N. I found that δ^{15}N and δ^{13}C values from macroalgae, macroinvertebrate and fish at both sites were within a similar range to those found in wrack accumulations off Western Australian sandy-beaches (Hyndes and Lavery 2005; Crawley et al. 2009) and macroinvertebrates and fish from surf zones of Uruguayan beaches (Bergamino et al. 2011) but the Long Beach South site in my study was slightly more depleted in δ^{13}C. The ranges in δ^{15}N for all macrophytes that I observed were also well within the values highlighted by Raven et al. (2002) in their exhaustive review of carbon isotope values for marine macroalgae and seagrasses. The enriched δ^{13}C values of seagrasses at Basham Beach and the detection of three species of red algae with very depleted δ^{13}C values at Long Beach

South indicated that none of the consumers that I sampled were grazing on those groups, even with consideration of a much wider fractionation range (Minagawa and Wada 1984; McCutchan et al. 2003; Vanderklift and Ponsard 2003; Crawley et al. 2007). In previous studies, site-to-site variation of $\delta^{15}N$ and $\delta^{13}C$ of primary producers and consumers has been identified across various subtidal habitats such as limestone reefs and seagrass beds and within surf-zone wrack accumulations (Crawley et al. 2009; Hyndes et al. 2013). In my study, the site-to-site variation in $\delta^{15}N$ and $\delta^{13}C$ of primary producers and consumers is not surprising considering that these are two regions with different macrophyte compositions at Basham Beach (a seagrass and algae mix) and Long Beach South (algae dominated) and differences in the taxa collected at each of the two sites. However, there may also be other site-specific environmental influences contributing to the variability in $\delta^{15}N$ and $\delta^{13}C$, such as the nutrient-rich cold-water upwelling that occurs along the South-East coastline where Long Beach South is located (Lewis 1981).

Isolating any direct link from lower to higher levels along a putative trophic pathway is challenging, particularly in detrital-dominated habitats such as wrack accumulations where macrophytes can be either still living or in various stages of decomposition. The very few relevant previous studies suggest that the effects of decomposition of seagrass and macroalgae on stable-isotope ratios can be complex, inconsistent and species specific, with either enrichment, depletion or no change in $\delta^{15}N$ and $\delta^{13}C$ over time all possible (Lehmann et al. 2002; Moloney 2013). With the onset of decomposition in macrophytes, $\delta^{15}N$ values can fluctuate through time due to microbial activity. Fellerhoff et al. (2003) identified that microbial activity caused variability in $\delta^{15}N$ of ± 6 ‰ during the decomposition of freshwater wetland macrophytes in short-term (21 days) and long-term (100 days) in mesocosm experiments in Brazil. In comparison, decomposition litter bag experiments with the seagrass *Thalassia testudinum* and mangrove leaves found that $\delta^{15}N$ values fluctuated over time but, over a year-long period of decay, there was a decrease of 2 ‰ for both plants (Fourqurean and Schrlau 2003). Background environmental conditions can also contribute to the rate of change in δ^{15}N. In freshwater lake sediments, oxic versus anoxic conditions contribute to differences in the type, timing and degree of microbial activity and subsequent differences in δ^{15}N of organic matter (Lehmann et al. 2002). I did identify some variability in δ^{15}N and δ^{13}C for macroalgal and seagrass species at both sites but it is difficult to determine their age or condition of decomposition based on field samples (Moloney 2013).

There are many challenges associated with the use of the stable isotopes δ^{13}C and δ^{15}N to identify trophic pathways (Peterson and Fry 1987; Vander Zanden and Rasmussen 2001; Vanderklift and Ponsard 2003; Boecklen et al. 2011). The passage of isotopic δ^{13}C and δ^{15}N from diet to consumer is often unpredictable, particularly when isotopic ranges can vary for particular species over space and time and when a large number of sources are involved (Crawley et al. 2007). In many cases, establishing trophic pathways with the standard fractionation means for δ^{13}C and δ^{15}N of 0.4 ‰ and 3.4 ‰, respectively, can be problematic due to a wider range in δ^{13}C or δ^{15}N than predicted (Peterson and Fry 1987; Post 2002). Simply relying on these standard fractionation-discrimination values can lead to erroneous conclusions. Therefore, when the standard fractionation values are used to calculate shifts in trophic levels and sources, careful interpretation is needed and the wider fractionation ranges should also be referred to and taken into account. In my study, I considered the possibility of wider ranges in fractionation discrimination in δ^{13}C of -1 to +1.3 ‰ and δ^{15}N of -1 to +5 ‰ as identified previously in other studies (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001; McCutchan et al. 2003; Vanderklift and Ponsard 2003; Crawley et al. 2007). Exploring the variability in fractionation in this way is not ideal as there is no definitive trophic pathway identified, but it does provide further insights into the needed next phase of research, which could include manipulative studies in the field or feeding trials in the laboratory, for example. Some longer-term manipulative studies could resolve causes of variability in the data and provide helpful insights into identifying more specific trophic pathways. This is particularly important in the case of wrack accumulations in sandy-beach surf-zones where the investigation of trophic web structures is still in its infancy.

5. Conclusion

This study has established a baseline of the trophic function associated with wrack accumulations in two sandy-beach surf-zones. The preliminary investigation of the trophic pathways associated with wrack accumulations in sandy-beach surf-zones identified that fish may be using these semi-permanent features as a food resource and habitat, but that the latter usage may be more important. It is likely that fish associated with wrack accumulations in sandy-beach surf-zones may be foraging over multiple habitats for higher quality foods. Grazing macroinvertebrates may be feeding on macrophytes within wrack accumulations as well as using them as habitat. In future, investigations should span multiple, large-scale (i.e. seagrass beds versus surf zones) and small-scale (i.e. macrophytic versus bare-sand patches) habitats in close vicinity, so as to provide a better understanding of how diets relate to isotopic $\delta^{15}N$ and $\delta^{13}C$ values in fish. Also, more experimental manipulative field or laboratory studies are required to investigate the effects of decomposition on the isotopic signatures of macrophytes in wrack accumulations. More recently, the inclusion of fatty-acid techniques has become useful as a tool to isolate and discriminate particular signatures in common between producers and consumers to detect more specific trophic pathways (Rooker et al. 2006; Crawley et. al. 2009). The baseline trophic pathways that I have identified in wrack accumulations in sandy-beach surf zones could be elucidated further with more explicit approaches such as fatty acids and/or manipulative laboratory experiments in future.

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Chapter 5: Drift dynamics of natural versus artificial seagrass at various distances from shore and initial colonisation by invertebrates and fish

Summary

Drifting macrophytes such as seagrass and macroalgae are commonly found washed ashore in large volumes on beaches in southern Australia. Few studies have investigated the drift trajectories of macrophytes whilst in nearshore coastal waters, and the associations of fishes and invertebrates with and short-term colonisation throughout the drift pathway. This four-month study investigated the surface drift trajectories of natural and artificial tagged seagrass released at various distances from shore over separate days in gulf waters in South Australia. The colonisation of macroinvertebrates and fish to tagged seagrass was compared to fauna found from *in situ* surface drifting macrophytes netted at different distances from shore. Surface drift trajectories of natural and artificial tagged seagrass were generally in the same directions as tides but trajectories were variable across three sampling days and when released at different distances from shore. Only tagged seagrass units that were released closest to shore stranded on sandy beaches within 6 hours of observation, so it would be difficult to predict the eventual stranding location on shorelines for macrophytes released further offshore.

Colonisation by fish to drifting macrophytes is more likely to be for habitat and shelter rather than food resources. There is some evidence that more macroinvertebrates may colonise drifting macrophytes at distances closer to shore (i.e. ≤0.25 km) due to shallower depths and increased availability of source habitats. Particular fauna may stay with macrophytes as they arrive and accumulate as surface and/or benthic wrack in the surf zone, while many others may leave for more suitable habitats. This study provides some evidence of tidally-induced macrophyte surface drift dynamics, the short-term rapid colonisation of fauna and habitat function of detached macrophytes along nearshore coastlines. This is

essential for further understanding the ecological significance of allochthonous material arriving on shorelines, which should be implemented into future research and management of sandy-beach ecosystems.

1. Introduction

Drifting macrophytes such as seagrass and macroalgae detach from the benthos after storms or in large swells (Kirkman and Kendrick 1997). After they detach from the seafloor, drifting macrophytes can be moved around by various hydrodynamic forces such as tides, currents and wind-induced wave action (Harrold and Lisin 1989; Kirkman and Kendrick 1997, Komatsu et al. 2007). Detached macrophytes can drift at the water surface for months at a time and be displaced over distances of more than 1000 kilometres (Hobday 2000a). Eventually, drifting macrophytes may deteriorate and sink to the seafloor or end up stranded as beach-cast wrack along coastlines (Johnson and Richardson 1977; Hobday 2000b). In some regions, drifting macrophytes form large accumulations close to shore and eventually pile up along beaches in very large volumes (Kirkman and Kendrick 1997). Yet there is still little information known about the movement of drifting macrophytes moving into and eventually stranding on sandy-beaches.

Previous surveys have assessed the composition and volume of drifting macrophytes along point transects at the sea surface offshore (Kingsford 1995; Komatsu et al. 2014; Mizuno et al. 2014). Other studies have investigated drifting macrophytes along the seafloor by diver census (Wernberg et al. 2006), mapping with acoustic echo sounding equipment (Riegl et al. 2005) and surveying with remotely-operated vehicles (Britton-Simmons et al. 2012) offshore. Few studies have investigated the drift dynamics of macrophytes closer to shore (e.g. 2 km offshore, Kirkman and Kendrick 1997; 0.2 to 4.6 km offshore, Harrold and Lisin 1989) and most have focused on brown algae species (particularly *Sargassum* or

Macrocystis spp.) from coastal regions in the Northern Hemisphere (Harrold and Lisin 1989, Kingsford 1995, Komatsu et al. 2007). The methods used in previous studies to record drift trajectories of drifting macrophytes at the sea surface are varied and include the attachment of visual (Kingsford 1995; Kirkman and Kendrick 1997), radio (Harrold and Lisin 1989) or satellite tags (Komatsu et al. 2007) to algal clumps. Other studies have also used satellite imagery of very large drifting macrophyte accumulations at the sea surface in the Gulf of Mexico (Gower and King 2011) or modelled the paths of particles to determine drift dynamics and trajectories of macrophytes in the East China Sea (Filippi et al. 2010). Most studies that have included physical tracking investigated large drifting macrophyte accumulations that were square metres in area or multiple kilograms in weight (Kingsford 1995; Harrold and Lisin 1989; Komatsu et al. 2007). In comparison, the drift dynamics of small clumps (<1 kg) of detached macrophytes close to shore (i.e. ≤3 km) are still relatively unknown. In comparison, there are no previous studies of tracking drifting seagrass, only plastic drifters that were released at the sea surface as a mimic of seagrass leaves and macroalgae (Kirkman and Kendrick 1997). Also, less is known about the movement of drifting macrophytes in sheltered or semi-enclosed systems such as estuaries or gulfs.

In the marine environment, juvenile fish and macroinvertebrates have been observed to use various drifting structures as a habitat and/or food resources. These include seagrasses, macroalgae, terrestrial vegetation, drift ice in polar regions (Macfarlane et al. 2013), jellyfishes and man-made debris such as styrofoam and plastics (Kingsford 1993; Bravo 2011). When seagrass and algae detach from the seafloor, some macroinvertebrates living amongst them will move to, raft upon or stay close to the drifting habitat, while others rapidly relocate to other (predominantly benthic) habitats (Gutow et al. 2009; Clarkin et al. 2012). Rafting on drifting macrophytes can be an important dispersal mechanism for macroinvertebrates without a pelagic larval stage, such as direct developers that have few alternatives for dispersal over large distances (Ingolfssen 1995; Clarkin et al. 2012). Specific families of fish that have a close habitat association with attached macrophytes, such as monocanthids and syngnathids, may also raft with drifting macrophytes for extended time periods and over large distances (Dempster and Kingsford 2004). Juveniles of pelagic fish species including commercially-important carangids have also been found to aggregate around drifting macrophytes and artificial drifting structures (Dempster and Kingsford 2004).

Most of the previous studies of drifting macrophytes at the sea surface have focused upon surveys of *in situ* drift algae and the associated fauna over various temporal and/or spatial scales (Safran and Omori1990; Ingolfsson 1995; Vandendriessche et al. 2006, 2007). More specific studies have used colonisation experiments to investigate the attractive role that drifting macrophytes play as habitat for macroinvertebrates and fish. Ingolfsson (1998) used anchored buoys with tethered fronds of the brown alga *Ascophyllum nodosum* in nearshore waters of Iceland over weekly intervals to identify that colonisation of macroinvertebrates can occur through the transfer between clumps of drifting macrophytes. Clarkin et al. (2012) used laboratory-based experiments and a field colonisation experiment with *A. nodosum* tethered to anchored buoys over six weeks to determine that different isopod species (*Idotea* spp.) may either passively or actively colonise drifting macrophytes. Dempster and Kingsford (2004) found that drifting fish aggregation devices (FADs) constructed from plastic strips and mops attracted the most fish species after six hours and larger abundances of fish were captured at FADs that also had an odour source. Soria et al. (2009) also found that FADs enhanced the schooling behaviour of the small pelagic fish *Selar crumenophthalmus* and acted to retain individual fish to form larger groups. However, there is still little understanding of the initial colonisation of both macroinvertebrates and fish to recently detached surface drifting macrophytes over short time frames (e.g. the first six hours after detachment).

The aims of this study were to investigate the short-term surface drift trajectories of small clumps that were mimics of individual macrophytes using either naturally-occurring or artificial drifting macrophytes (<1 kg) with attached radio tags released at various distances from the shoreline (≤3 km) within sheltered gulf waters of Southern Australia. The initial colonisation of radio-tagged natural and artificial drifting macrophytes by macroinvertebrates and fish was also investigated. Natural baselines of the macrophyte, macroinvertebrate and fish compositions associated with *in situ* drifting macrophyte clumps were also established. Thus, this experiment provides further understanding of drifting macrophyte movement, the initial colonisation of macroinvertebrates and fish, and the likely deposition of macrophytes as wrack on beaches. The information obtained will aid in future management of coastal zones and highlight the important function that drifting macrophytes provide as habitat and food resource for juvenile fish and their invertebrate prey.

2. Methods

Study site

Tracking of radio-tagged natural and artificial seagrass was undertaken during the austral spring/early summer period from September to December 2013 in Gulf St Vincent, South Australia. Gulf St Vincent is a large inverse estuary where evaporation exceeds rainfall and has a surface area of 7,000 km^2 and a maximum depth of 40 m (De Silva Samarasinghe and Lennon 1987). Sandy beaches totalling 28 km in length overall are the main coastal fringe along the eastern coastline of metropolitan Adelaide along Gulf St Vincent (Short 2001).

Tagged seagrass units were deployed from the coastal waters off West Beach along the metropolitan Adelaide coastline (Figure 5.1). West Beach is between the two main waterways that flow into the coastal waters along Adelaide’s metropolitan beaches, the Torrens River mouth on the northern side and the Patawalonga River/Barcoo Outlet on the southern side. The reasons for the selection of West Beach as the deployment site for this study were that: (1) coastline urbanisation from West Beach through to Glenelg in the south has expanded dramatically in recent years with the construction of multiple coastal developments such as marinas, groynes and breakwaters (Short 2012); (2) large accumulations of wrack often become trapped along the beaches from West Beach through to Brighton (Figure 5.1), particularly in the vicinity of man-made structures; and (3) the beaches along the metropolitan coastline are regularly cleared of wrack with earthmoving equipment by local councils for aesthetic reasons with still relatively unknown impacts to nearshore ecology.

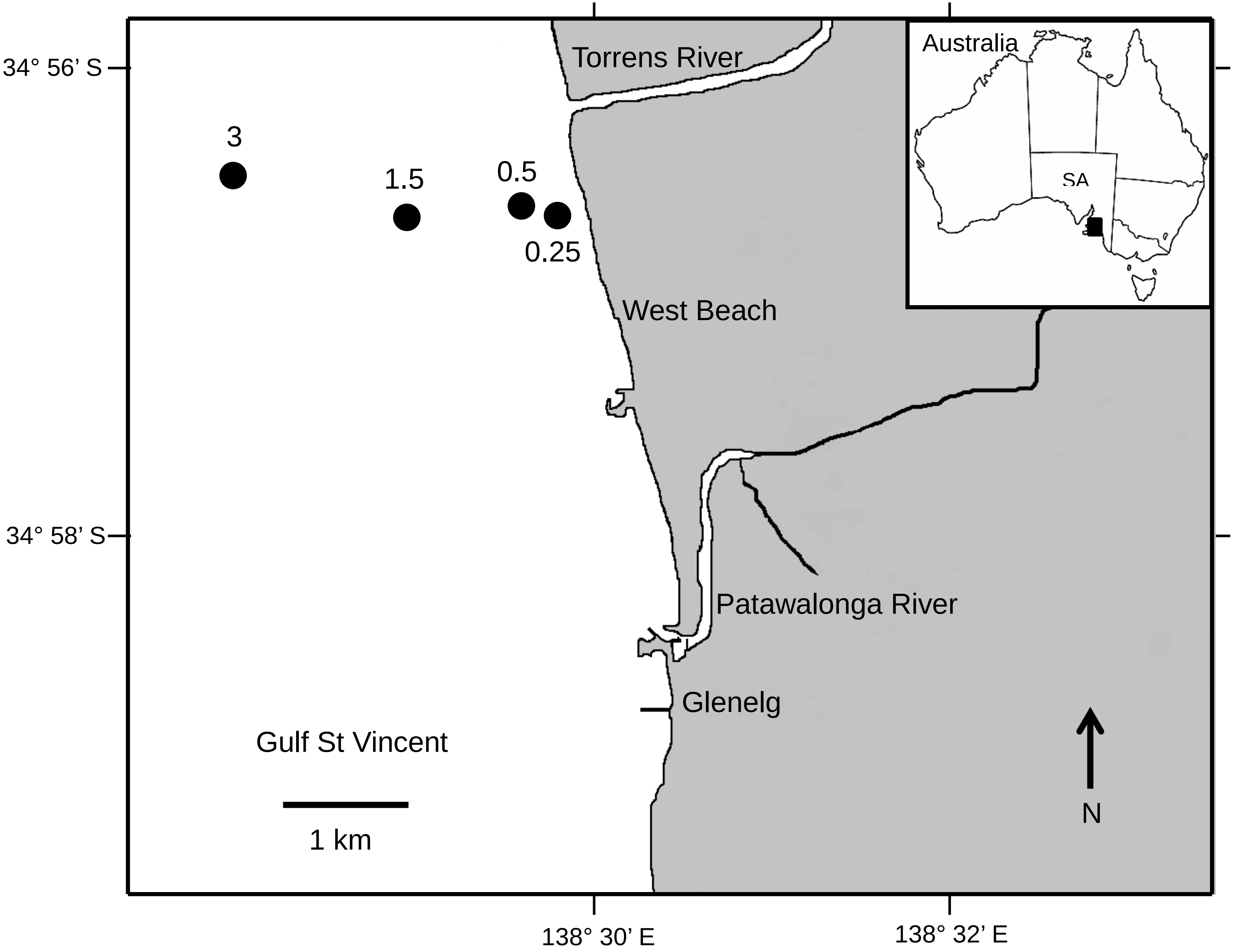

Figure 5.1: Map of study site at West Beach along the metropolitan Adelaide coastline during drifting seagrass tracking during September to December 2013. Release points at different distances from shore (km) are shown as black circles.

Preliminary testing of radio-transmitters

SIRTRACK Ltd. 2-stage VHF waterproof radio-transmitters set at individual frequencies were selected as the most robust, cost-effective and reliable option for tracking seagrass in this marine environment. The Biotrack Ltd. Sika Ultra Receiver unit (150-154MHz bandwidth) was used in conjunction with a Folding Yagi 3 Element Antenna (145-155MHz bandwidth) to scan for receiver pulses (rate of 30 pulses per minute), so that tagged macrophytes could be located. The SIRTRACK radio transmitters transmit at maximum capacity in air and have a signal radius of up to 2 km which can be lower in rough seas. In order to obtain the best radio signal from radio transmitters, counter-weighted floating cage units were constructed from Gutter-Guard plastic mesh (Figure 5.2). Each radio-transmitter was placed inside a cage unit along with a high-density polystyrene float and a 15 g counter-weight to ensure that they were small and lightweight as possible to reduce any cage influence on seagrass drift trajectories (mean weight of cage unit = 80.82 ± 0.62 SE g). This counter-weighted float design also ensured that the cage unit remained upright at the sea surface, half of the cage unit below the water and the antenna in the air when seagrass was attached to the base (Figure 2).

Before the tracking study was undertaken, a series of field tests were used to determine the ability to detect and locate radio-transmitters. To minimise float-induced drag, various volumes of seagrass without rhizomes were attached to cage units and observed to determine an ideal seagrass clump volume that mimicked single plants that had detached from the seafloor. Various volumes of fresh seagrass (*Posidonia* spp.) were attached to cage units using zip ties (i.e. treatments were blank cages = 0 L attached, otherwise 0.05, 0.1, 0.2, 0.3, 0.4 and 0.5 L attached) and their small-scale drift trajectories were observed and compared over a short time (e.g. 5 minutes) with multiple re-runs. The 0.1 L volume was the smallest

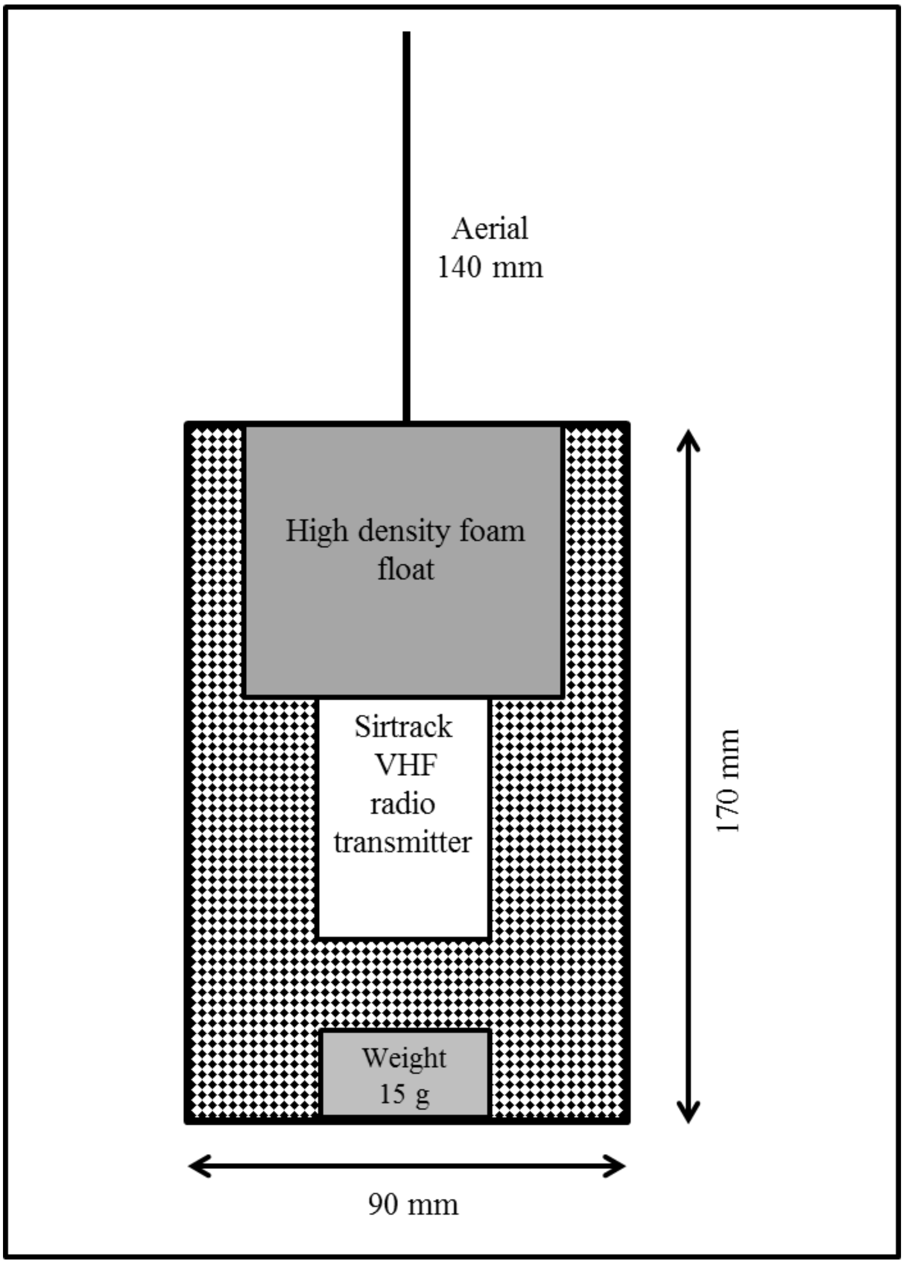

Figure 5.2: Counter-weighted floating cage design used for tagged seagrass units with radio transmitters installed as used during field experiments in the austral spring/summer of 2013. Either natural or artificial seagrass clumps were attached to the base of each cage unit.

volume that had a similar drift trajectory and distance to all of the larger volumes and so was selected as the seagrass volume for the main study.

Other trials included testing of the signal strength of radio-transmitters under different scenarios in the surf zone and onshore along sandy beaches. The various scenarios in the surf zone and onshore revealed that signals of radio-transmitters could still be detected at a distance of 200 m away but the signal became very weak at a distance of 400 m, particularly when buried in sand and/or wrack. Radio-transmitters could also be detected up to 90 m away with only one quarter of the aerial in air and the remainder of the transmitter underwater. The results of these trials indicated that these radio-transmitters would be sufficient for small time-scale tracking studies with high potential success rates of locating radio-transmitters under the harshest conditions (i.e. buried in sand or wrack or partially underwater).

Field tracking

The most common macrophytes found stranded on sandy beaches of metropolitan Adelaide is the seagrass *Posidonia sinuosa*, with little algae by comparison to other regions worldwide (Duong 2008, also see Chapter 3). However, there is often a mixture of *Posidonia angustifolia* and *P. sinuosa* found growing together in seagrass meadows in Gulf St Vincent, which makes it difficult to discriminate between the two. Identification of the two seagrass species is particularly difficult from leaves alone when rhizomes are absent (Cambridge and Kuo 1979), which is how they are normally found when large amounts of senesced leaves wash up along metropolitan Adelaide beaches. Therefore, rather than discriminate between the two species, they were grouped together and so are referred to herein as *Posidonia* spp.

Before the tracking study began, enough seagrass samples for the entire study were obtained by snorkelling along the easily accessible, shallow subtidal region of Second Valley in Gulf St Vincent and were removed by hand to mimic natural removal by storms or large swells. All of the seagrass was taken back to the laboratory, rinsed thoroughly with freshwater to remove any invertebrates, measured into clumps of 0.1 L volumes, placed in zip-lock bags and frozen at -20^{o} C until required. Artificial seagrass was constructed by cutting PVC surveyor flagging tape (dark green in colour) into strips that were 40 cm length x 0.7 cm width which were then combined into clumps and measured out to 0.1 L volumes and placed in zip-lock bags until ready for use. The day before each field day, five of each of natural seagrass and artificial seagrass samples were placed in freshwater to de-frost the natural frozen seagrass and to leach any potential chemicals in the artificial seagrass.

Investigation of the drift dynamics of seagrass were undertaken by boat with starting points 0.25, 0.5, 1.5 or 3 km offshore during daylight hours over a six-hour period per sampling day, with three replicate days used per release distance. The average water depths for each starting point were 4.3, 6.3, 5.3 and 9.5 m for the 0.25, 0.5, 1.5 or 3 km distances, respectively, and most release locations had seagrass beds as the dominant benthic habitat, except for the 0.25 km distance that was mostly a sandy bottom. For each sampling day, the natural seagrass and artificial seagrass samples were attached with zip-ties to separate randomly-selected cage units, herein classified as either natural seagrass (NAT) or artificial seagrass units (ASU) tag types, respectively. For logistical reasons and to ensure that seagrass units were not lost during tracking, only one distance was allocated to each separate tracking day. However, tracking days were randomly allocated to starting point distances to reduce any bias in distance selection for a particular day. All of the tracking days were undertaken in calm weather with wind speeds ≤15 knots for safety reasons and to ensure that all seagrass units could be found at the end of each tracking day. Thus this study represents wrack surface drift behaviour under calm conditions and light winds only.

At the starting point of each day, all NATs and ASUs were released at the same time and location and their GPS co-ordinates recorded. All seagrass units were tracked and located using the radio receiver and visually at subsequent time points of 0.5, 1, 1.5, 2, 4 and 6 h after initial release with a GPS location recorded for each unit. At the 6 h point, a dip net (35 cm diameter, 500 µm mesh size) was used to capture each seagrass unit, which was searched for fish and/or cephalopods. All fish and cephalopods were identified and /or photographed, counted and immediately released back into the sea, as per animal ethics permission. The natural or artificial seagrass was removed from the cage unit and rinsed with seawater to remove any other invertebrates through a 500 µm sieve, which were then preserved in jars of 70 % ethanol for further identification and abundance counts in the laboratory. During the field tracking if and when seagrass units were beached, their GPS positions and times of arrival on the beach were recorded as an end point and the natural or artificial seagrass was removed immediately and processed in the normal way. On the first day of the 3 km release distance, large swells and bad weather reduced visibility at the six hour point resulting in the loss of two artificial seagrass units with no end point distance recorded for one and no fauna samples from both units.

Throughout each tracking day, up to ten replicates of *in situ* drifting macrophyte clumps (when available) and open water (free of drifting objects) were sampled with the dip net to investigate the fish and invertebrates naturally found along each tracking distance from shore. All net samples were searched for invertebrates, which were preserved in jars of 70 % ethanol. Identification of macroinvertebrates was undertaken in the laboratory and individuals were identified to the finest taxonomic level possible and counted for abundances. Any incidental injuries to fish resulted in euthanasia with immersion in AQUI-S solution and all such mortalities were preserved in 10 % formalin. All other fish that were unharmed were released alive back into coastal waters where they were obtained. All natural drifting macrophytes captured in the field were identified to the finest taxonomic level possible and measured for displacement volume using various-sized volumetric cylinders filled with water.

Weather conditions, wind speeds and direction (using an anemometer, AZ Instruments Model No: 8906), photographs of Beaufort sea state and presence of any flotsam near seagrass units and the vicinity of physical structures (i.e. jetties or breakwaters) were also recorded to aid in interpretation of seagrass-unit movement patterns. Oceanographic and meteorological data including tidal cycles (semi-diurnal during this study), swell conditions and wind speeds were also obtained from the Australian Bureau of Meteorology and Willy Weather for further analyses of seagrass unit movements (BOM 2013, Willy Weather 2013).

Data analyses

Multiple regression tests, of cumulative distance travelled of tagged seagrass (as the dependent variable) versus the independent variables of tide height, wind speed, elapsed time since last tide change, and elapsed time since start of experiment, were undertaken to detect if there were any relationships in travel distance with those variables. Multiple contingency tables using Pearson chi-square analyses were used to detect the likelihood of tagged seagrass units changing direction or stranding on shorelines in relation to the variables of distance-from-shore release points, tide heights, wind directions and wind speeds in these contingency tests.

A simple Pearson correlation of straight line distance from start to finish versus total distance travelled had a moderately positive correlation (r = 0.593, p = <0.001). Therefore, only results based on the total distance travelled are presented here. A second Pearson correlation of cumulative distance through time and point-to-point distance between pairs of time points had a strong positive correlation (r = 0.715, p = <0.001). Therefore, only results based on the cumulative distance travelled are presented in analyses of tracking trajectories through time.

A four-factor experimental design of: Tag type (Artificial, Natural seagrass; fixed factor); Distance (0.25, 0.5, 1.5, 3 km; fixed factor); and Day nested in Distance (three levels; random factor) was used for analyses of cumulative distance travelled with Time as the repeated measure (0.5, 1, 1.5, 2, 4, 6 h). The factor of Time was removed for the experimental design used to analyse the colonising fauna datasets as abundances were only obtained from the last time point (at 6 h). A reduced two-factor experimental design of: Distance (0.25, 0.5, 1.5, 3 km; fixed factor); and Day nested in Distance (three levels; random factor) was used for the *in situ* macrophyte and fauna datasets. Macroinvertebrate and fish abundance data were converted to individuals per L and cube-root transformed before statistical analyses (see Chapter 3 this thesis). Macrophyte volumes and assemblage data were converted to volume in litres and was left untransformed. PERMutational ANalysis Of VAriance (PERMANOVA) was used on the full design for each of the univariate and multivariate datasets using the PERMANOVA+ version 1.0.6 add-on to PRIMER version 6.1.16 (Anderson et al. 2008).

Tagged macrophyte cumulative distance travelled datasets were analysed in PERMANOVA using Euclidean distance similarity matrices for these univariate data. The removal of the highest-order interaction of cumulative distance travelled datasets was undertaken as required for repeated measures PERMANOVA (Anderson et al. 2008). Univariate datasets for total abundances and abundances of major groups for macrophytes, macroinvertebrates and common fish species were analysed in PERMANOVA+ using Euclidean distance similarity matrices. PERMANOVA was also used for analyses of macrophyte, macroinvertebrate and fish assemblages using Bray-Curtis similarity matrices. Multiple pairwise tests were conducted if fixed factors or interactions were significant to identify which groupings contributed to differences from PERMANOVA. Analyses on cumulative distance travelled datasets were also conducted with the addition of either wind speed or tide height as a co-variate. Analyses of *in situ* macroinvertebrates and fish were conducted with the addition of total macrophyte volume on macroinvertebrates and fish; and total macroinvertebrates on fish datasets.

Canonical analysis of principal coordinates (CAP) was undertaken on all *in-situ* multivariate datasets for the factor of Distance from shore separately because it was the main factor of interest for *in situ* samples. The CAP procedure in PERMANOVA+ is a constrained ordination used for testing *a priori* hypotheses of explicit factors of interest, as compared to the PERMANOVA approach that runs analyses on the full sampling design (Anderson and Willis 2003). In CAP, the difference due to Distance from shore was identified for macrophyte, macroinvertebrate and fish assemblages by obtaining a *P* value using 999 permutations. CAP was also used to determine the percentage of total variation explained by the first set of principal co-ordinate axes and the allocation success of each group within the factor of interest (Distance from shore). The RELATE procedure in PRIMER was used to identify the overall correlation between each combination of macrophyte, macroinvertebrate and fish multivariate datasets.

3. Results

Drift trajectories of natural and artificial tagged seagrass units

Total distances travelled of all tagged seagrass units were different for particular days and tag types (Pseudo-$F_{1,8} = 4.9$, $p = 0.0001$) and ranged between 0.25 km to 5.3 km (Figure 5.3). The cumulative distance travelled over time increased by a larger number after two hours due to a change in sampling from half hour intervals to two hour intervals (Figure 5.3). The distance travelled for natural and artificial tagged seagrass units at each release distance from shore only diverged for the 0.25 km distance after four and six hours and at the 3 km distance after six hours where wind speed increased from 9-11 to 18-25 km/h (Figure 5.3).

Most tagged seagrass units initially drifted in a southerly direction with the receding tide, with exception of an initial northerly drift direction on only one sampling day for the 0.5 km distance-from-shore release-point (Figure 5.4). The drift trackline of tagged seagrass units released at different distances from shore only crossed paths on two occasions between the 0.25 and 0.5 km distances (Figure 5.4). Tagged seagrass units completely changed direction on eight days and stranded on beaches on four days out of 12 sampled.

Both wind speed and tidal height significantly influenced the cumulative distance travelled by tags across time points (Table 5.1), but their inclusion as co-variates did not influence the significance of other factors in the design. Analyses including either a co-variate of tidal height and wind speed had multiple significant high-order interactions with Distance x Tag type x Time, the highest-order significant interaction (Table 5.1), indicating that patterns in drifting macrophyte movement are variable through distance from shore across time. Many of the pairwise differences in cumulative distance travelled between timepoints for both tag types were significantly different for the 1.5 km release distance with both tide height and wind speed as co-variates (Table 5.2; Appendix 5, Table A5.1). Pairwise differences were also for the 0.25 km and 0.5 km distances from shore when wind speed was a covariate, and for the 3 km distance from shore when tidal height was a covariate (Table 5.2; Appendix 5, Table A5.1).

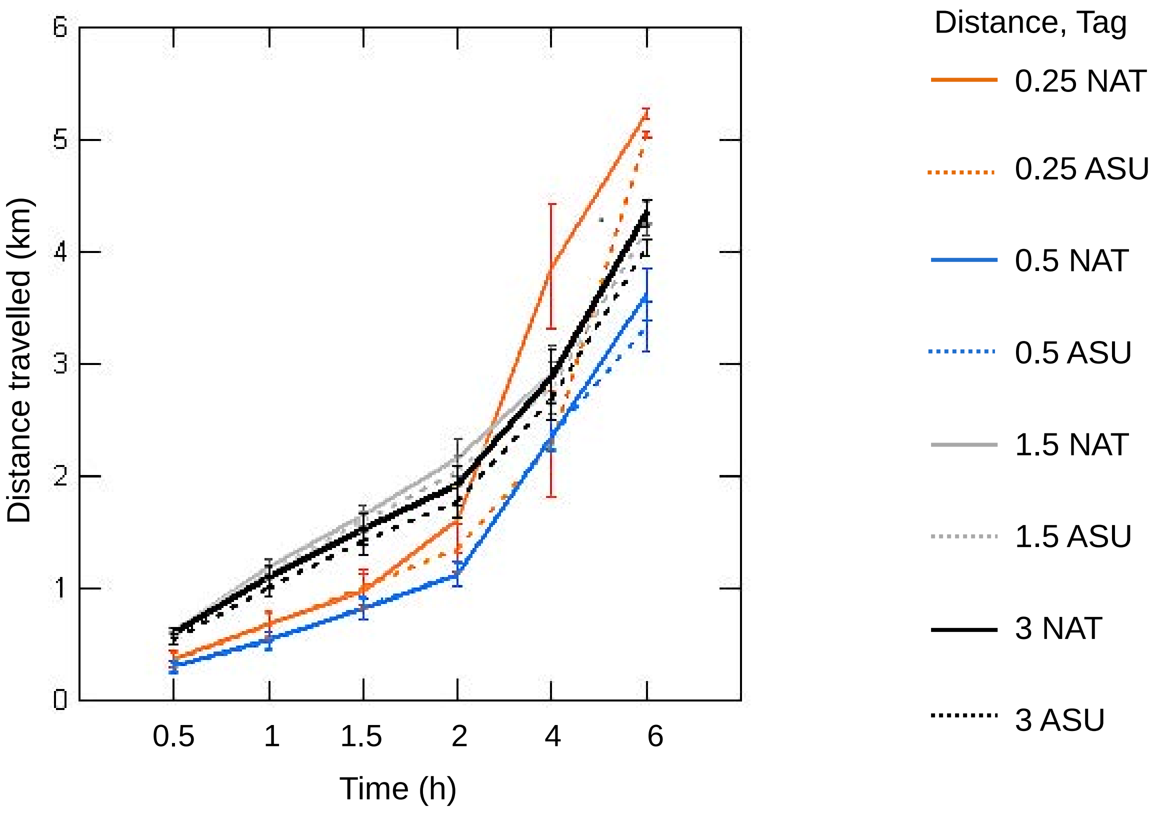

Figure 5.3: Cumulative distances travelled over six hours for both tag types, natural (NAT) or artificial (ASU) seagrass at each distance-from-shore release-point during field tracking experiments (*n* = 15 for each distance, except *n* = 14 for 3 km).

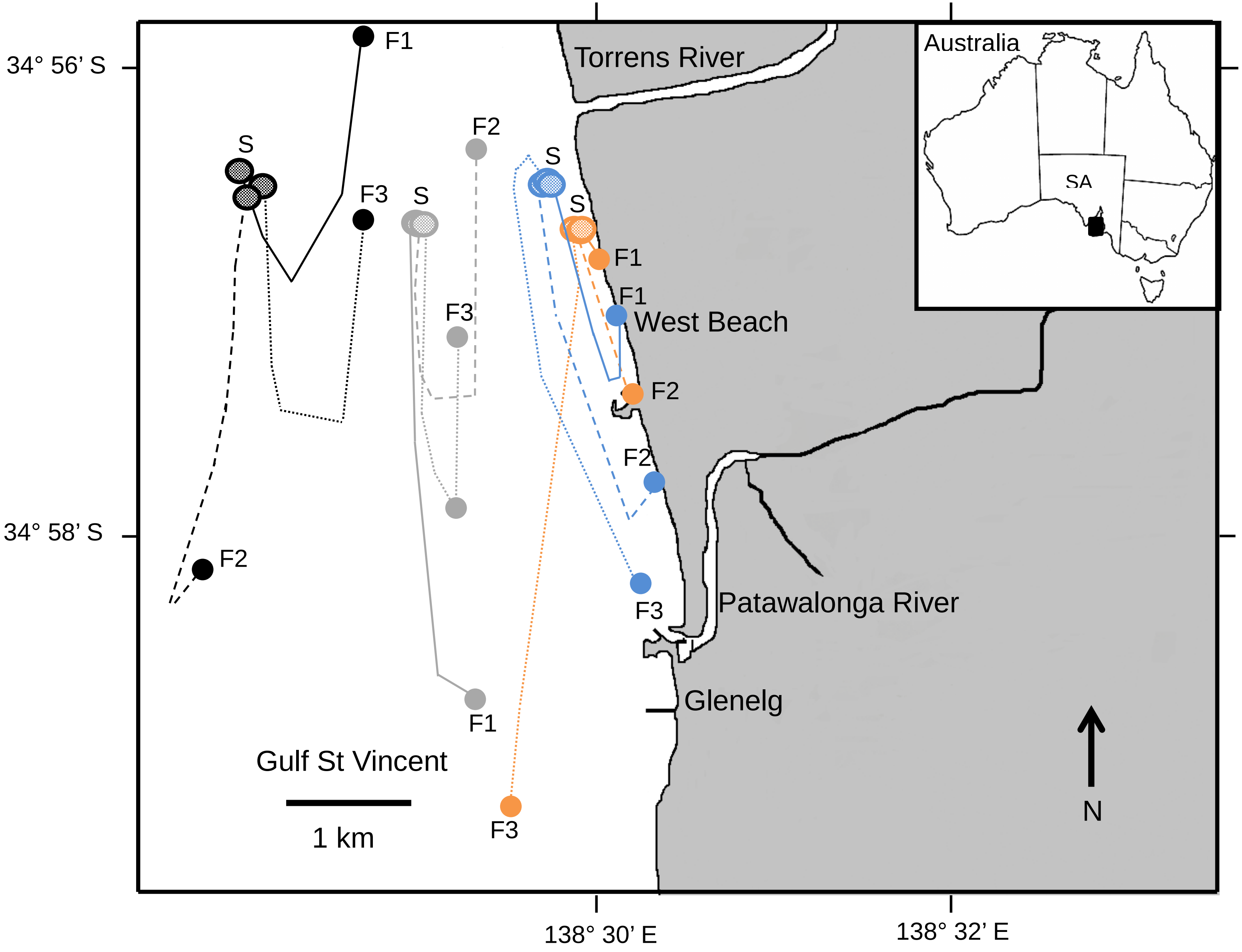

Figure 5.4: Mapped tracklines of drift trajectories for both tag types at all distances from shore. Orange lines and circles = 0.25 km, Blue lines and circles = 0.5 km, Grey lines and circles = 1.5 km, Black lines and circles = 3 km. Solid line = Day 1, Dashed line = Day 2, Dotted line = Day 3. Start points at each distance (S). Finish points are F1 = Day 1, F2 = Day 2, F3 = Day 3.

Table 5.1: Analyses of cumulative displacement distance through time for the factors distance from shore (Distance) and Tag type over Time points and sampling Day (nested within Distance) from tagging experiment. Results are from repeated measures PERMANOVA based on Euclidean distance similarity matrices with a co-variate of either wind speed or tidal height included in the design. (n = 30 for all distances except n = 29 for 3 km).

Source	*df*	Wind speed co-variate			Tide height co-variate		
		MS	*F*	*p* (perm)	MS	*F*	*p* (perm)
Co-variate							
Wind	1	19.48	3.82	0.06			
Tide	1				568.08	106.2	<0.01
Distance	3	27.17	2.28	0.17	11.86	0.88	0.48
Tag	1	0.79	5.45	0.05	2.04	14.92	<0.01
Time	5	182.88	69.96	<0.01	79.22	24.06	<0.01
Day (Distance)	8	11.66	1662.5	<0.01	13.69	1952.5	0.70
Distance x Tag	3	$7.45E^{-2}$	0.63	0.60	5.09E-2	0.47	0.99
Distance x Time	15	0.50	0.20	0.99	0.50	0.20	<0.01
Tag x Time	5	0.34	12.78	<0.01	0.30	11.96	<0.01
Tag x Day(Distance)	8	0.12	16.61	<0.01	0.11	15.23	<0.01
Time x Day(Distance)	37	2.49	354.31	<0.01	2.44	348.39	<0.01
Distance x Tag x Time	15	$1.63E^{-2}$	2.32	<0.01	1.63E-2	2.32	<0.01
Residual	570	$7.01E^{-3}$			7.01E-3		
Total	671						

Table 5.2: The number of significant PERMANOVA pairwise tests out of a possible 240 pairs for the variable cumulative distance travelled between time points for each release distance from shore (km) for all tag types resulting from the significant interaction term of Distance from shore (Dfs) x Tag type x Time point.

Distance	Tide height	Wind speed
0.25	1	4
0.5	0	6
1.5	11	12
3	9	2

Table 5.3: Results of the dependant variable cumulative distance travelled overall predicted from the independent variables of tidal height, wind speed, hours since last tide change and elapsed time since release of tagged units, from multiple regressions. Adjusted R^2 and multiple regression coefficient are presented. Tolerance measures varied from 0.21 to 0.96, where inter-correlations among independent variables where a satisfactory result > 0.1. All values shown coincide with significance values of $p < 0.001$. Bold values represent the variables that had the strongest relationship to distance travelled by tagged seagrass units.

Variable	Distances from shore (km)				
	All	0.25	0.50	1.5	3
Adjusted R^2	0.81	0.90	0.95	0.86	0.90
Constant	0.34	3.71	-0.31	0.03	-1.59
	Coefficient	Coefficient	Coefficient	Coefficient	Coefficient
Tide height	**-0.26**	**-1.91**	0.05	0.22	0.45
Wind speed	0.04	0.17	-0.06	0.06	0.09
Tide turn	0.06	-0.27	0.24	-0.01	0.22
Elapsed time	**0.58**	0.39	**0.51**	**0.67**	**0.77**

The variable with the strongest relationship with cumulative distance travelled by tagged seagrass units was inconsistent and changed depending on the distance released from shore (Table 5.3). The cumulative distance travelled by tagged seagrass units showed a significant positive relationship with elapsed time overall for all variables investigated at most distances from shore (Table 5.3). The one exception was the cumulative distance travelled by tagged seagrass units released from the 0.25 km distance from shore, which had a significantly negative relationhsip with tidal height, indicating that distance travelled increased with a decrease in tide height (Table 5.3).

Across all time points, tagged seagrass units were travelling in the same direction as tides (82 %) more than wind (58 %) (Table 5.4). All tagged seagrass units completely changed direction for the 0.5 km and 3 km distance from shore release points but only a third changed direction for the 1.5 km distance (Table 5.5). No tagged seagrass units changed direction for the 0.25 km distance from shore (Table 5.5). Two thirds and half of the tagged seagrass units were stranded on sandy beaches when released from the 0.25 and 0.5 km distances from shore, respectively (Table 5.5). No tagged seagrass units were stranded on the shore when released at the 1.5 and 3 km distances from shore (Table 5.5). Across all distances and time points tagged seagrass units completely changed direction during low to mid wind speeds, west to south-westerly directions of winds, and during ebb and flood tides (Table 5.6). The stranding of tagged seagrass units mainly occurred during low speed, westerly winds and during ebb tides (Table 5.6).

Fauna colonising with natural and artificial tagged seagrass units

During the tagging experiment, a total of 18 macroinvertebrate taxa consisting of one polychaete, 14 crustacean, two gastropod and one cephalopod species were captured around tagged seagrass units (Appendix 5, Table A5.2). Total macroinvertebrate abundances were

Table 5.4: The percent of time that tagged seagrass units were travelling in the same or opposite direction as wind or tides based on all time point observations.

Direction of environmental variable versus tag drift direction	Percent of time
<u>Wind direction</u>	
No wind	3
Same	58
Opposite	39
<u>Tide direction</u>	
Between tides	12
Same	82
Opposite	6

Table 5.5: Contingency tables of the percentages of units that either did (Y) or did not (N) change direction or hit the beach for each distance-from-shore release-point. Pearson Chi-square statistics (χ^2) for the test of the number of tags either turning or hitting beach as fates are shown (*n* = 30 for all distances except *n* = 29 for 3 km).

Distance from shore (km)	Percent turned		Percent hit beach	
	Y	N	Y	N
0.25	0	100	67	33
0.5	100	0	53	47
1.5	33	67	0	100
3	100	0	0	100
χ^2	89.12		52.01	
p	<0.001		<0.001	

Table 5.6: Contingency tables of the percentages of units that did change direction or hit the beach for wind direction, wind speed (low, 0.1-9; mid, 9.1-14.6, high, >14.6 km/h) and tide stage. Pearson Chi-square statistics (χ^2) for the test of the number of tags either turning or hitting beach as fates are shown (*n* = 30 for all distances except *n* = 29 for 3 km).

Distance from shore (km)	Percent turned	Percent hit beach
Wind direction		
North-East	12.5	0
North-West	12.5	35
South	12.5	0
South-West	37.5	47
West	25	18
χ^2	38.5	41.2
P	<0.001	<0.001
Wind speed		
Low	37.5	74
Mid	50	5
High	12.5	21
χ^2	24.9	20.8
P	<0.001	<0.001
Tide stage		
In-between tides	12.5	7
Ebb	37.5	82
Flood	50	11
χ^2	111	2.7
P	<0.001	ns

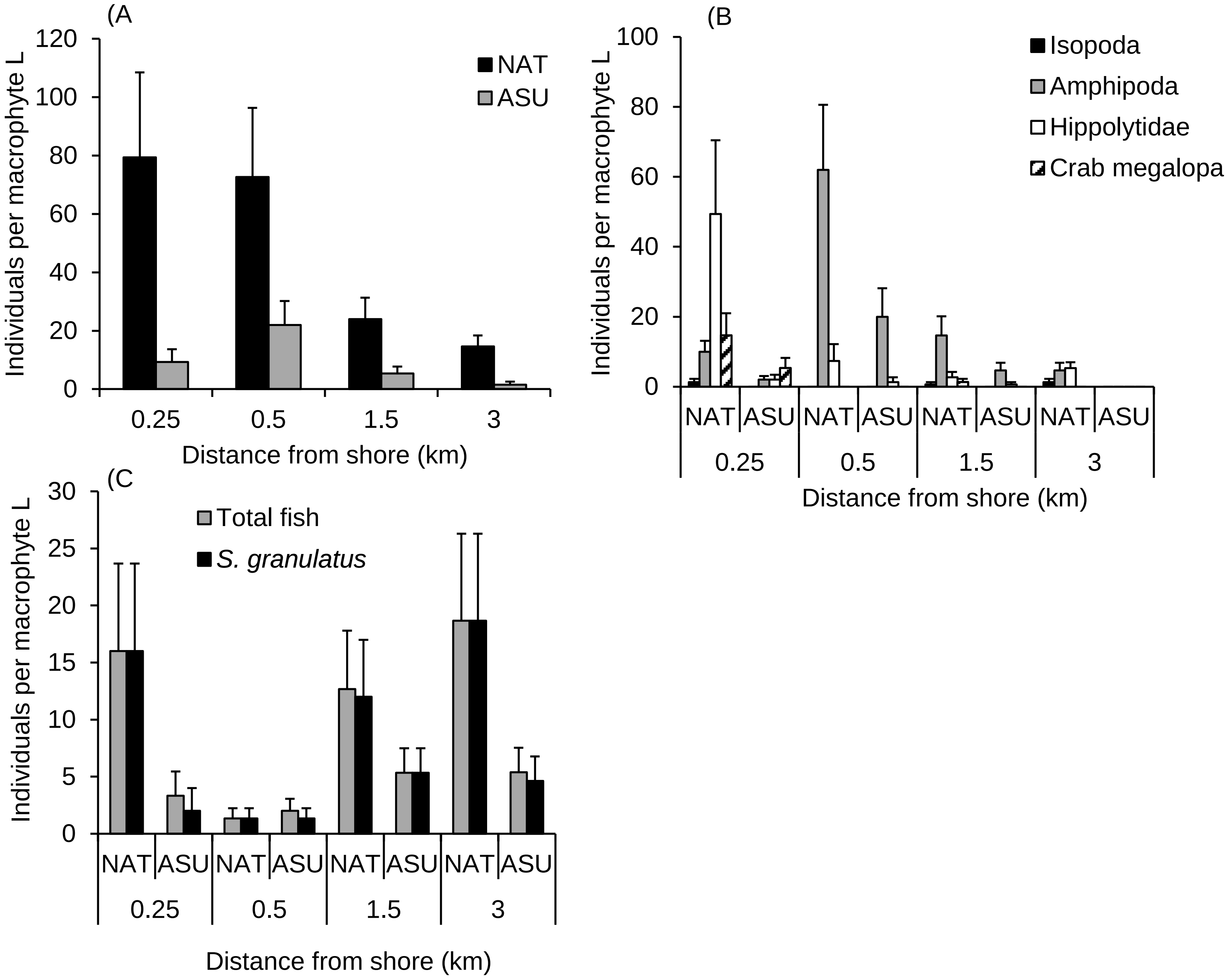

Figure 5.5: Abundances (+SE, *n* = 15 for all distances except 3 km *n* = 13) of (A) total invertebrate, (B) Isopoda, Amphipoda, Hippolytidae (shrimp), and crab megalopa, and (C) total fish and *Scobinichthys granulatus* recovered from tagged natural (NAT) and artificial (ASU) seagrass units after being released at a range of distances from shore on separate days (nested in Distance from shore) for six hours. Natural seagrass units were defaunated before seagrass was attached to each tag unit and deployed.

Table 5.7: Univariate (total abundance) and multivariate (assemblage) PERMANOVA results for colonisation by invertebrates and fishes, captured from tag types of either natural or artificial seagrass units after being released at different distances from shore on separate days (nested in Distance) for six hours. No factors were significant for groups not displayed here, including Polychaeta, Copepoda, Isopoda, *Idiosepius notoides*, Gastropoda, *Arripis georgianus*, *Heteroclinus* Sp.1, *Hippocampus breviceps*, *Pseudocaranx georgianus*, *Stigmatopora argus*. Significant values * <0.05, ** <0.01 and *** <0.001. Blanks show NS outcomes.

Source of variation: Dependant variable group	Distance	Tag type	Day (Distance)	Tag x Distance	Tag x Day (Distance)
Total invertebrates abundance		***	***		
Amphipoda abundance		***	***		
Hippolytidae abundance			***		***
Crab megalopa abundance			***		***
Invertebrate assemblages		**	***		
Total fish abundance		*	***		
Scobinichthys granulatus abundance		*	***		*
Fish assemblages		*	***		

largest, but with large variation for the 0.25 and 0.5 km distances from shore (Figure 5.5A, Table 5.7). Tagged natural seagrass units had significantly higher total macroinvertebrate abundances than artificial seagrass (Figure 5.5A, Table 5.7), despite being defaunated prior to release. There was a general trend for the most common macroinvertebrate groups to have higher abundances at tagged natural seagrass units compared with artificial seagrass, but only amphipod abundances were significantly different (Figure 5.5B, Table 5.7).

For the natural seagrass units, isopod abundances were similar at all distance-from-shore release-points, except the 0.5 km distance where isopods were absent (Figure 5.5B). For both the natural and artificial seagrass units, amphipod and crab megalopa abundances were higher for the 0.5 km and 0.25 km distances, respectively (Figure 5.5B). The natural seagrass units had higher Hippolytidae (shrimp) abundances for the 0.25 km distance-from - shore release-point but artificial seagrass had similarly low abundances of Hippolytidae at all distances, with the exception of the 3 km distance where it was absent (Figure 5.5B). There was a significant interaction between tag type and sampling day for Hippolytidae and crab megalopa (Figure 5.5B, Table 5.7), indicating that preference for any particular tag type was variable through time. Macroinvertebrate assemblages were significantly different between tag types (Table 5.7). The higher abundances of the gammarid amphipod sp.1 from natural tags contributed most to the dissimilarity between tag types (contribution = 36.74%, by SIMPER).

During the tagging experiment a total of five fish species including two Syngnathidae, and one species from each of the families Arripidae, Carangidae and Monocanthidae, were captured around tagged seagrass units (Appendix 5, Table A3). Total fish abundances from natural seagrass units were significantly higher overall than those from artificial seagrass (Figure 5.5C, Table 5.7). Abundances of the most common fish species *Scobinichthys granulatus*, varied depending on the day of sampling (Figure 5.5C, Table 5.7). The 0.5 km distance had lower fish abundances overall, but there was no significance in those differences in fish abundances among distances (Table 5.7). All other fish species captured were sparse in abundance and highly variable, and there were no significant differences amongst distances, tag types or sampling. Fish assemblages were significantly different between tag types and sampling days (Table 5.7). The higher abundances of the fish species *S. granulatus* from natural tags contributed most to the dissimilarities between tag types (contribution = 89.32%, by SIMPER).

In situ *drifting macrophytes and associated fauna*

Overall, three brown algal groups, four seagrass species, 43 invertebrate taxa and six fish species were identified from *in situ* (i.e. natural) drifting macrophyte clumps across all distances from shore (Appendix 5, Tables A5.4-A5.6). Volumes of *in situ* drifting macrophytes were largest for the 0.25 and 3 km distances from shore but there was large variation among sampling days (Figure 5.6A). Brown algae contributed most to *in situ* drifting macrophyte clumps compared with seagrass (Figure 5.6B). There were very few open water samples (*n* = 3) that captured fauna and those that did were only single individuals of certain taxa (i.e. crab megalopa, Hippolytidae) so were not analysed further.

Total invertebrate abundances obtained from *in situ* drifting macrophytes were highest for the 0.25 km distance from shore but with large variation among sampling days (Figure 5.7A). The most commonly occurring macroinvertebrates were Amphipoda and Hippolytidae, with ranges of 20 to 2000 and 50 to 3000 individuals per macrophyte L, respectively (Figure 5.7A). Crab megalopa abundances were significantly higher at the 0.25 km distance from shore compared to both 0.5 and 1.5 km distances (Figure 5.7B, Table 5.8). Total macrophyte volume as a co-variate did not have any influence on the results with this analysis and was not a significant factor in itself.

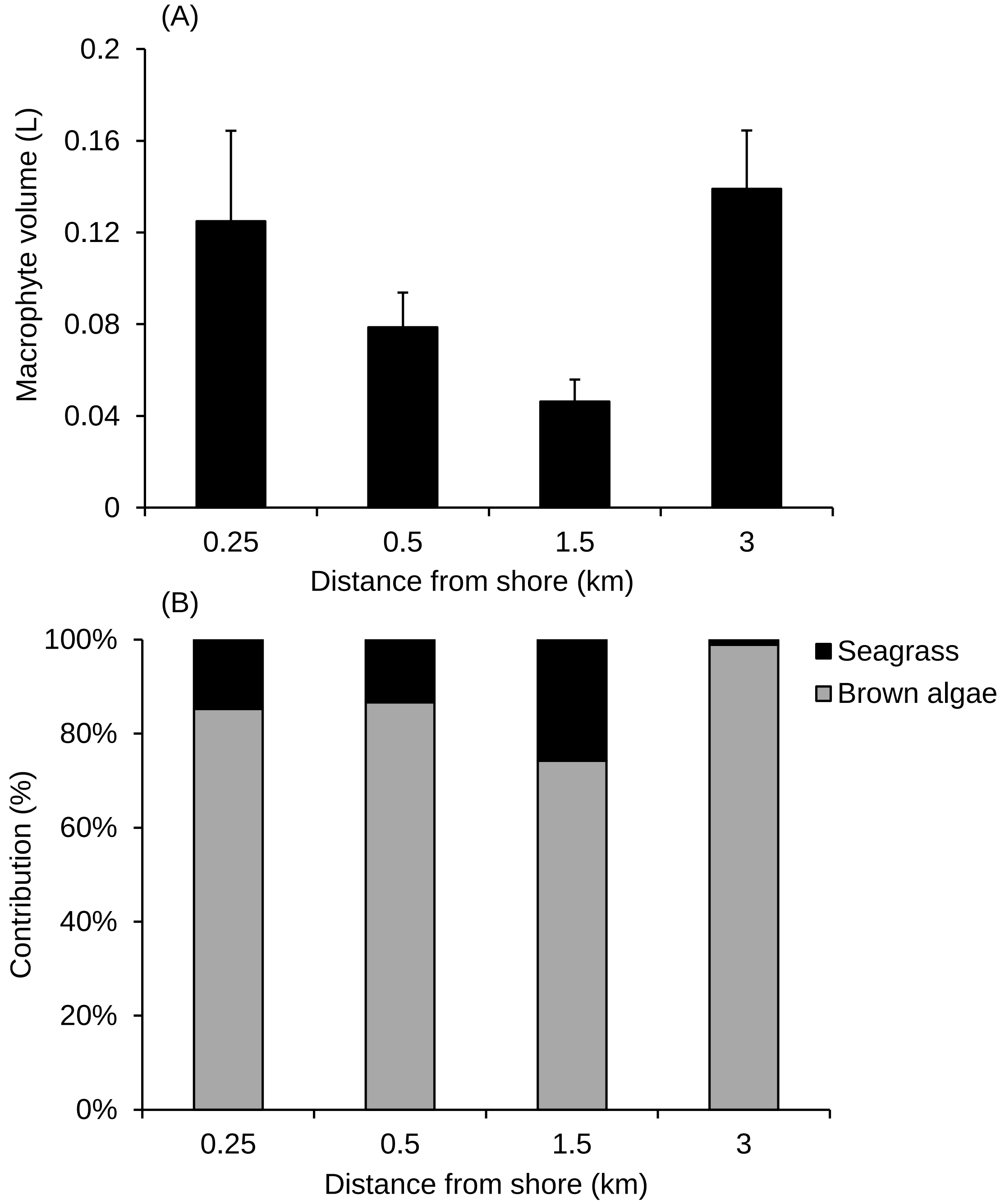

Figure 5.6: (A) Total macrophyte (+SE, *n* = 3-10) volume and (B) percent contribution of seagrass and brown algae of *in situ* drifting macrophyte clumps netted at a range of distances from shore on three separate days each.

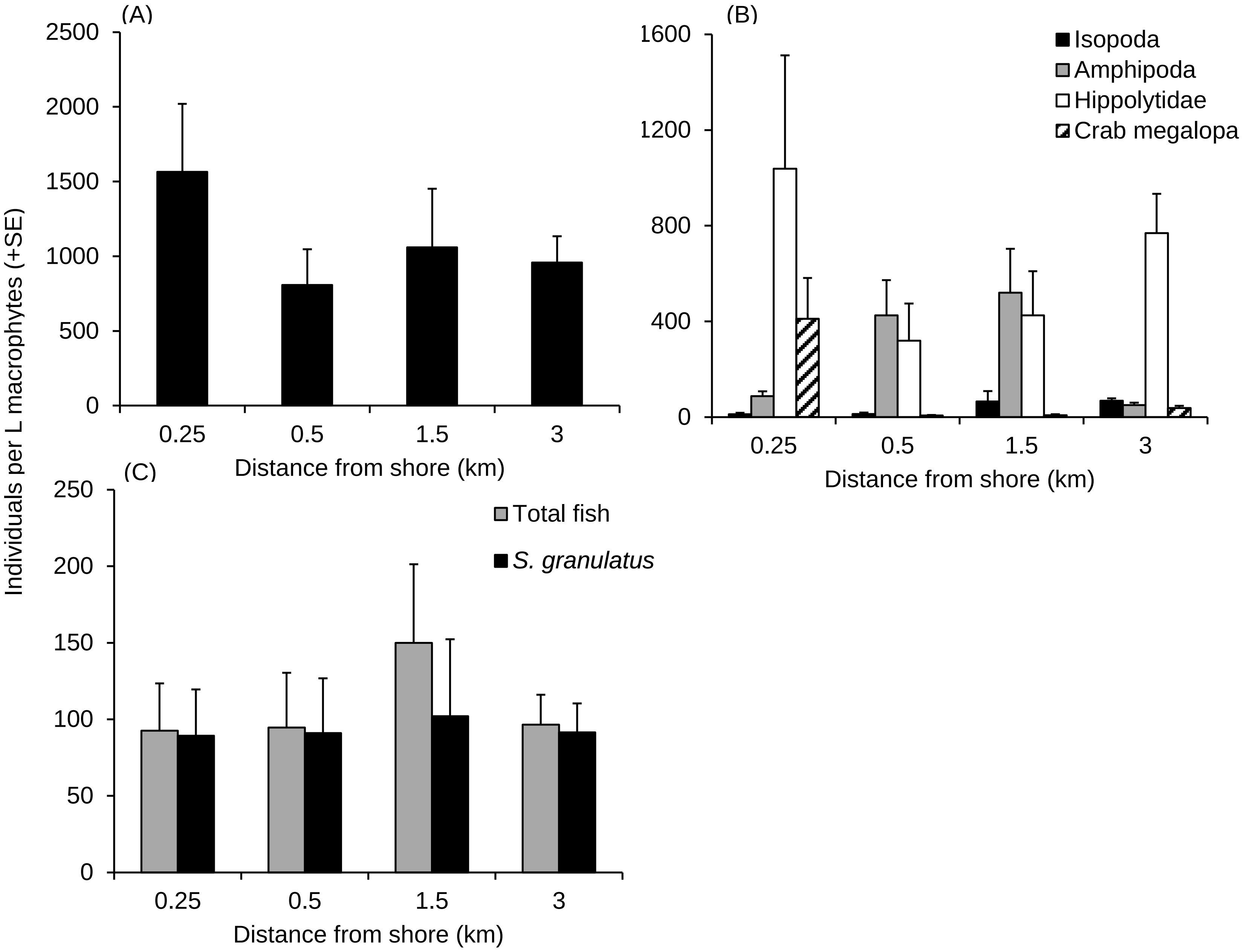

Figure 5.7: Abundances (+SE, *n* = 3-10) per litre of wrack of (A) total invertebrates (B) Isopoda, Amphipoda, Hippolytidae (shrimp), and crab megalopa, and (C) total fish and *Scobinichthys granulatus* from *in situ* drifting macrophyte clumps netted at a range of distances from shore on three separate days each.

Table 5.8: Analyses of total volume of macrophytes, and macroinvertebrate and fish abundances associated with *in situ* drifting macrophyte clumps netted at a range of Distances from shore on separate days (nested in Distance). Univariate PERMANOVA models with co-variates of either total macrophyte volume for both macroinvertebrates or fish, or total macoinvertebrate abundances for fish only were included in the analysis. Macrophyte data consisted of percentages of brown algae or seagrass in the macrophyte clumps by volume. Taxonomic groups for which neither factor were significant are not displayed here, including total macrophyte volume, Polychaeta, Copepoda, Gastropoda, Bivalvia, *Heteroclinus* Sp.1, *Hippocampus breviceps* and *Trianectes bucephalus*. Significant values are shown as * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$. ≠ is shown for significant groupings from pairwise tests of differences between distances from shore ($p < 0.05$). Blank cells indicate no significant differences ($p > 0.05$).

Source of variation: Dependant variable group	Distance	Day (Distance)	Pairwise outcome for sig. effect of Distance
Macrophytes			
Brown algae		**	
Seagrass		**	
Invertebrates			
Total invertebrates		***	
Isopoda		*	
Amphipoda		***	
Hippolytidae		***	
Crab megalopa	*	**	0.25 ≠ 0.5, 1.5 km *
Idiosepius notoides		***	
Fish			
Total fish		***	
Scobinichthys granulatus		***	
Gymnapistes marmoratus		***	
Stigmatopora argus		*	

Abundances of total fish or the most common fish species *Scobinichthys granulatus* (> 90% of all fish were from this species) were similar across all distances from shore (Figure 5.7C, Table 5.8). All five of the other fish species were much lower in abundance overall (Appendix 5, Table A5.6). The co-variate of total macroinvertebrate abundances was significant (PERMANOVA, Pseudo-$F_1 = 5.01$, $p = 0.03$) but did not have any influence on the significance of other factors within this design.

Overall, the most common fish and macroinvertebrate species found around *in situ* drifting macrophytes were similar to, but were found at higher abundances than those found around natural tagged seagrass units (compare Figures 5.5 and 5.7). The macroinvertebrate groups Hippolytidae, Amphipoda and crab megalopa, and the fish species *S. granulatus* were all commonly found associated with *in situ* and tagged drifting seagrass in coastal waters of Gulf St Vincent (Figures 5.5 and 5.7).

Macrophyte, macroinvertebrate and fish assemblages were not significantly different among distances from shore. Canonical analysis of principal co-ordinates of macrophytes, macroinvertebrates and fish for the factor of distance from shore identified that the amount of variation explained (62, 46 and 65 %, respectively) was satisfactory considering that 25 % is better than chance for this model (Figure 5.8, Table 5.9) (Anderson et al. 2008). For macrophytes and fish, the allocation success (31 and 28 %, respectively) at the different distances from shore was poor with high mis-classification rates overall (Figure 5.8, Table 5.9). Macroinvertebrate assemblages had slightly better allocation success over the different distances from shore (58 %, Figure 5.8, Table 5.9). There was a weak but significant relationship between the multivariate datasets of macrophytes versus macroinvertebrates and fish, and macroinvertebrates versus fish (RELATE; $Rho = 0.2$, $p = 0.\ 0005$; $Rho = 2.3$, $p = 0.02$; $Rho = 0.3$, $p = 0.0001$; respectively).

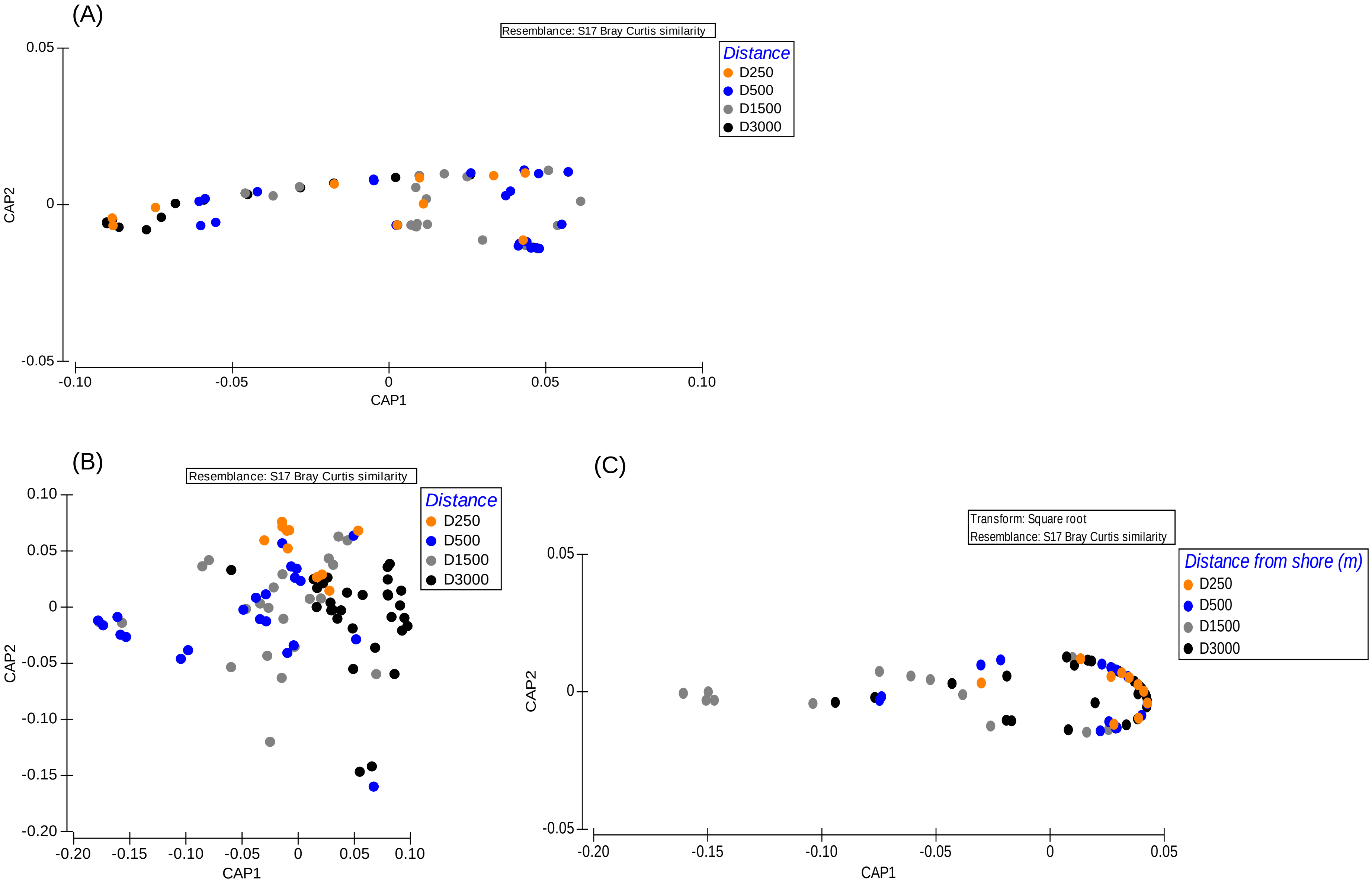

Figure 5.8: Analyses of (A) macrophyte (B) invertebrate and (C) fish assemblages from *in situ* drifting macrophyte clumps among distances from shore according to canonical analysis of principal co-ordinates (CAP) analyses.

Table 5.9: Results of differences in macrophyte, fish and invertebrate assemblages associated with natural drifting macrophytes among distances from shore as identified by canonical analysis of principal co-ordinates (CAP). The analysis is based on a constrained hypothesis that assemblages will vary with distance from shore (excluding other potential factors). The percentage of the total variation (%Var) explained by the set of principal co-ordinate axes selected (m= 2 in each case) is shown. Allocation success is the percentage of total data points that are correctly allocated to each group. Qm'HQm p shows = significance for the trace statistic or sum of squared canonical correlation (both axes) and δ^2 p shows = significance based on the first squared canonical correlation (first axis only) based on randomisation tests.

Taxonomic group	%Var	Allocation success (%)	$Q_m'HQ_m$ p	δ^2 p
Macrophytes	62	31	0.002	0.001
Macroinvertebrates	46	58	0.001	0.001
Fish	65	28	0.003	0.003

4. Discussion

Drift trajectories of tagged seagrass units

In this study, I aimed to mimic the movement of recently-detached seagrass at different points from shore and identify drift patterns over the short term (i.e. six hours). Most previous studies that have physically tracked drifting macrophytes have been undertaken over much longer time frames (i.e. days to months, Harrold and Lisin 1989; Hobday 2000a; Komatsu et al. 2007). One exception was a study that investigated the drifting pathways of *Macrocystis pyrifera* in the Southern California Bight over 50 m, showing that those pathways were mainly influenced by onshore winds, particularly closer to shore (Kingsford 1995).

The movement of drifting seagrass at the sea surface in Gulf St Vincent appeared to be influenced primarily by tidal movement in calm conditions, but winds increasingly influenced drift when wind speed changed rapidly, as was observed on two sampling days at the 0.25- and 3-km release distances. There were clear daily differences at all release distances which highlight the complexities associated with varying timings and strengths of tidal currents and winds. From this study, it appears that the likelihood of macrophytes changing direction tends to coincide with the change from tidal movement from ebb to flood. Studies that have investigated the pathway of drifting macrophytes over days or months identified that wind, wind-driven surface water, wind waves (Harrold and Lisin 1989), and/or large offshore current systems (Komatsu et al. 2007) primarily contributed to macrophyte movement. Previous tracking studies have mostly been undertaken along coastlines that were adjacent to uninterrupted open-ocean influences such as oceanic swells and large-scale current systems. In contrast, my study was undertaken in a sheltered inverse estuary away from the open ocean. Gulf St Vincent has a unique semi-diurnal tidal cycle with large spring and neap tidal ranges resulting in regular but moderate tidal oscillation (De Silva

Samarasinghe and Lennon 1987). Therefore, in this study, it was not surprising to identify a strong tidal influence on the drift trajectories of tagged seagrass units. This was particularly noticeable with tagged seagrass units turning with the change between ebb and flood tides. Those tidal oscillation characteristics of Gulf St. Vincent may influence the movement of drifting macrophytes back and forth along the same section of coastline repeatedly over multiple tidal cycles. This aspect should be investigated further in future to understand the arrival and accumulation of drifting macrophytes that eventually pile up on beaches as stranded wrack.

There may also be other influences, such as changes in current direction throughout the year, which could only be observed in longer-term studies and so were not identified here. For example, in Western Australia, plastic drifters that were mimics of seagrass and macroalgae released 2 km from shore travelled in a northerly direction during summer and south-easterly direction in winter (Kirkman and Kendrick 1997). Similarly, the local nearshore coastal counter currents in Gulf St Vincent change throughout the year, with a mean circulation that is predominantly northerly in direction during summer and southerly in circulation during winter, due to changes in wind stress and water density gradients (Bye and Kaempf 2008). I did not measure currents nor investigate the drift trajectories of tagged seagrass at different times of the year, but different drift trajectories due to these changes in circulation are possible in this system.

The ultimate fate of drifting macrophytes reaching the shoreline has been investigated by releasing drifting macrophytes at various distances from shore and identifying strandings on shorelines over days to months (Harrold and Lisin 1989; Kirkman and Kendrick 1997; Hobday 2000a). In this study, the number of tagged seagrass units stranding on beaches decreased with the distance released from shore. Westerly winds at low to mid speeds (up to 14.6 km/h) may have had some influence on the tagged seagrass units stranding on beaches but once drifting macrophytes arrive into the surf zone, the hydrodynamic influence of waves takes over and pushes them into shore. Similar observations were made in a study of drifters in the Southern California Bight, where the probability of arrival at shorelines of drifting macrophyte mimics was related to release distance from shore and coastline topography (Hobday 2000a). The short timeframe of my study made it difficult to predict the fates of tagged seagrass stranding on shorelines at the 1.5 and 3 km release distances as it would take longer for them to reach shorelines, highlighting the need for longer-term tracking from those distances.

Few studies have investigated the drifting of detached macrophytes along the seafloor, which was also beyond the scope of my study. The low volumes of seagrass found as a part of *in situ* drifting macrophyte clumps during my study suggests that seagrass may be tumbling along the seafloor rather than being suspended at the water surface. This may be an explanation for the stark contrast to large volumes of seagrass found in previous studies of wrack accumulations in surf zones (Chapters 2 and 3) and on beaches (Duong 2008) along the Adelaide metropolitan coastline. Only a few studies have investigated the fate of drifting macrophytes that do not reach shorelines, using collection by divers (Wernberg et al. 2006), remotely-operated vehicles (Britton-Simmons at al. 2012) or acoustic echo-sounding (Riegl et al. 2005). In Western Australia, 5000 individually-tagged kelp (*Ecklonia radiata*) fronds that were released 2 km from shore drifted for up to 23 days (Kirkman and Kendrick 1997). Only 1 % of the kelp was found stranded on beaches, but it was difficult to predict the fate of the remaining kelp given that it tends to drift below the surface (Kirkman and Kendrick 1997). In Puget Sound, Washington State, large densities of drifting macrophytes on the seafloor at more than 90 m depth were observed using remotely-operated vehicle (Britton-Simmons et al. 2012). Seasonal patterns in the presence of macroalgae or seagrass drifting along the benthos and accumulating on bare substrates and within dense seagrass meadows have also been documented in the Indian River Lagoon in Florida, USA (Riegl et al. 2005).

One challenge associated with investigating the ultimate fate of drifting macrophytes is that some macrophytes move throughout the water column by drifting to and at the surface for a period of time before losing buoyancy, eventually sinking to the seafloor (Johnson and Richardson 1977; Hobday 2000b). The drift dynamics of detached macrophytes at the surface, throughout the water column and along the benthos may also vary through time adding to the difficulties in capturing such movement in field-based ecological studies. The methods used in my study focused on the surface drift pathway nearshore over the short-term to establish some baseline for detached macrophyte drift trajectories in sheltered gulf waters, which there is little information. Further investigation should investigate the benthic-pelagic movement of drifting macrophytes in these systems.

Fauna associated with drifting natural and artificial tagged seagrass versus in situ *drifting macrophytes*

In this study, colonisation of drifting natural and artificial tagged seagrass units by macroinvertebrates and fish was measured after six hours. Other studies that have investigated the colonisation of drifting fish attraction devices (FADs) in New South Wales (Dempster and Kingsford 2004) or drift algae in New Zealand (Kingsford and Choat 1985; Kingsford 1992). These studies identified rapid colonisation by fish after the first hour and the largest abundances and species numbers had accumulated after five to seven hours (Kingsford and Choat 1985; Kingsford 1992; Dempster and Kingsford 2004). Dempster and Kingsford (2004) used a series of one-off experiments and identified relatively large, but highly-variable fish abundances (ranging from < 5 to > 60 individuals per FAD) and mean species numbers of up to 6 species per FAD after six hours. During the same timeframe, my study found between one and 29 individuals per 0.1 L wrack volume and a maximum of three species per 0.1 L on any given day. The compact design of my tagged seagrass units and the small clump size (0.1 L volume) aimed to mimic single plants that had recently detached from the seafloor, as are commonly found in the surf zones and on sandy beaches locally. Dempster and Kingsford (2004) used much larger FADs (15 cm buoys) with plastic strips and a mop head attached to 1 m of rope below the water surface. The disparity in results between this study and that of Dempster and Kingsford (2004) may indicate that larger drifting structures with more surface area may support higher abundances of fish (Safran and Omori 1990) and macroinvertebrates (Ingolfsson 1995) to use as shelter and/or habitat, even in the short term.

Abundances of macroinvertebrates have previously been shown to be positively correlated with macrophyte volume in other studies but these patterns may be species specific (Ingolfsson 1995, 1998). In my study, macrophyte volume as a co-variate in various analyses showed there was no evidence of an increase in fish or macroinvertebrate abundances with an increase in drifting macrophyte clump size from *in situ* samples. Furthermore, I also found no relationship between macroinvertebrate and fish abundances with macrophyte size in surf-zone wrack accumulations (see Chapter 3 this thesis). Differences in patterns between faunal abundances and drifting macrophyte volume seen across different studies may be due to bio-regional characteristics and/or associated oceanographic conditions (Ingolfsson 1995, Vandendriessche et al. 2006).

Natural tagged seagrass attracted higher abundances and more diverse macroinvertebrate taxa than artificial seagrass at all distances from shore. Larger abundances of fish were attracted to natural than artificial seagrass units for most distances from shore, except for 0.5 km. This suggests that both visual and olfactory cues may be important for macroinvertebrates and fish to be attracted to drifting objects, but this needs to be investigated further. However, the presence of fauna even in low numbers from artificial seagrass units within six hours indicates that any drifting object provides at least some habitat (Kingsford 1992, Druce and Kingsford 1995). Also, similar macroinvertebrate and fish species were found around *in situ* drifting macrophytes and tagged seagrass units which suggests that some fauna may be utilising the macrophytes as habitat, rather than food resources (Kingsford 1992). However, any differences associated between the fauna associated with *in situ* drifting macrophytes and that on tagged seagrass units may also be influenced by the differences in physical structure provided by the mainly brown algae found *in situ* versus the tagged seagrass units.

The paucity of previous studies investigating colonisation of untethered drifting macrophytes is likely to be a result of the challenges associated with tracking detached and drifting structures, particularly where they may move over large distances. In one previous study, a choice experiment found similar abundances of macroinvertebrates inhabiting natural and artificial floating macrophytes that were anchored to the seafloor for up to 20 days (Ingolfsson 1998). Also, artificial seagrass units attached to the seafloor over multiple days have been shown to attract post-larval juvenile crustaceans and fish in similar compositions to natural seagrass (Kenyon et al. 1999). Hair et al. (1994) found that there were only species-specific preferences of fish to artificial seagrass units that were either stationary or mobile but still tethered to buoys at the water surface or above the seafloor. Furthermore, there are also complexities involved with studying macrophytes on the drift such as the higher likelihood of immigration or emigration of fauna as drifting material travels over nearby multiple habitats in shallower waters (Ingolfsson 1995, 2000).

Abundances of macroinvertebrates colonising natural seagrass units increased close to shore, but this pattern was not observed for fish from tagged seagrass units nor for either macroinvertebrates or fish captured from *in situ* macrophyte clumps. My results suggest that nearshore drifting macrophytes may be colonised by macroinvertebrates from a greater range of sources such as the benthos, water column or other drifting macrophytes closer to shore. Similar patterns have been identified previously in Northern Ireland with macroinvertebrates colonising drifting macrophytes from the water column, passive marooning on clumps as a result of contact with other drifting material, or from a wide range of benthic habitats that may be passed over during the drift pathway (Clarkin et al. 2012). At distances further than 1.5 km from shore, colonisation is more likely to be occurring only from the water column or other drifting macrophytes due to an increase in water depth (Clarkin et al. 2012). Colonisation of drifting algae by macroinvertebrates has also been shown to decrease with distance from shore in Finland, and to be delayed at 0.4 km compared to distances at or under 0.2 km from shore (Salovius et al. 2005), suggesting that this pattern may be short-lived.

In comparison, harpacticoid copepod assemblages around floating algae in Iceland were not influenced by distances from shore between 0.2 and 14 km; rather macrophyte composition and size were more important (Olafsson et al. 2001). Particular taxa may also show species-specific colonising behaviour, as has been identified in isopods (genus *Idotea*), where different species showed either a preference for or against colonisation of drifting algae rafts (Clarkin et al. 2012). The colonisation by macroinvertebrates of drifting macrophytes and the longevity of their stay may depend on whether those species are adapted to hiding within the matrix of drifting macrophytes or clinging to them over long periods of time, such as amphipods and isopods (Ingolfsson 1995).

In this study, I did not find any fish and only a few individual macroinvertebrates in open water free of drifting macrophytes. The use of a small dip-net to capture fish and macroinvertebrates in open water in this study only sampled a small volume of water compared to the use of much larger seine-nets (Kingsford 1992). However, other studies have also found very sparse faunal abundances in open water samples (Vandendriessche et al.

2007), suggesting that colonisation between separate drifting macrophyte clumps (i.e. rather than from the open water) may be more likely at greater distances from shore. Colonisation at greater distances from shore may also occur when drifting macrophytes pass through oceanographic features. For example, these may include windrows or surface slicks caused by internal waves, where other drifting macrophytes and colonising fauna may be more concentrated (Kingsford and Choat 1986; Kingsford 1990). Aggregations of drifting macroalgae and higher abundances of small fish have been previously observed in surface slicks compared to outside of these features (Kingsford and Choat 1986). Oceanographic features such as windrows may play an important role in drift pathways and faunal colonisation but it is challenging to repeatedly sample and capture those dynamics close to shore where environmental conditions such as winds and small-scale currents may change rapidly.

The composition of common fish and macroinvertebrate species found on *in situ* drifting macrophytes and colonising tagged seagrass units had some similarities to fauna associated with surf-zone wrack-accumulations in the same region (see Chapter 3 this thesis). For example, some macroinvertebrate taxa such as gammarid amphipods and sphaeromatid isopods were common on both drifting macrophytes and surf-zone wrack (Chapter 3). In comparison, hippolytid shrimps and crab megalopa were regularly found on *in situ* drifting macrophytes in this study, consistent with other studies (Kingsford and Choat 1985; Hobday 2000c), but were not regularly found in high numbers on surf-zone wrack-accumulations (Chapter 3). The most common fish species on drifting macrophytes in this study, *Scobinichthys granulatus*, was rarely found from surf-zone wrack (Chapter 3). However, the timing of this study in the austral spring/summer period was different to the summer/winter period in Chapter 3, so there may also be differences in timing of recruitment. If there is no difference in the timing if recruitment, however, then these patterns suggests that some macroinvertebrate taxa may raft all the way into the surf zone, while other macroinvertebrates and some fish species, potentially such as *S. granulatus*, may leave for more favourable habitats before macrophytes drift into the surf zone.

Future directions

This study identified that the movement of drifting macrophytes at the surface in coastal waters of Gulf St Vincent can be influenced by tidal and, to a lesser extent, wind forces. The stranding of drifting macrophytes onto shorelines becomes less likely with increasing distance from shore. Thus, the movement of drifting macrophytes is complex, particularly away from the coastline. The fate of macrophytes further from the shore, could be investigated with longer-term radio, satellite tracking or satellite imagery of macroalgae and seagrass at distances of more than 10 km offshore. I conducted this study during calm conditions but there is also a need to investigate the movement of drifting macrophytes during, or soon after, storms, to capture potential influences from wind induced waves. More studies are also needed to investigate the drift trajectories of detached macrophytes along the benthos and within the water column below the surface to establish an understanding of benthic-pelagic interaction.

There is some evidence that drifting macrophytes are more likely to be colonised by macroinvertebrates closer to shore due to a greater range of potential source habitats. There is also evidence that only particular fauna will stay with the macrophytes as they arrive in the surf-zone, while others may leave for more suitable habitats. Further manipulative studies that provide habitat choices such as a range of artificial macrophytes at different depths or distances away from source habitats should investigate the colonisation and later emigration of fauna closer to shore and interactions with other nearby habitats. The benthic-pelagic interaction associated with drifting macrophytes may be stronger closer to shore when water depths are smaller and this should be investigated with the experimental addition of different volumes and types of macrophytes throughout the water column at different depths. Finally, this study only investigated the short-term colonisation of fauna in calm conditions and it would be beneficial to examine how this might change under a range of weather conditions and over longer timeframes.

5. Conclusion

Detached macrophytes move rapidly, mainly driven by tidal cycles, in the nearshore waters of a sheltered gulf system. These drifting macrophytes appear to be important for colonising fauna, given that colonisation occurred in as little as 6 h in this study, which is comparable to the study by Kingsford (1992) who also identified colonisation by fish in similar timeframes. There is also evidence that faunal associations change at different stages (i.e. distances from shore) of the drift pathway into shore and accumulation as wrack nearshore, which has profound importance to nearshore ecology and function. Thus, loss of drifting habitats due to beach cleaning or harvesting processes may lead to removal of habitat and food resource for multiple fauna at particular crucial life stages (i.e. juvenile fish and larval stages of macroinvertebrates) Therefore, future beach management decisions, such as those regarding the cleaning of wrack from beaches, need to consider better the habitat function of drifting macrophytes arriving close to shore, the accumulation of wrack in the surf zone and eventual deposition on beaches.

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Chapter 6: General Discussion

The research that forms this thesis was strategically planned to unravel some of the complexities of detached macrophytes that drift into and accumulate as wrack in sandy-beach surf zones and the fauna associated with those macrophytes. This approach would be important for further understanding of wrack supply to sandy-beach surf zones or onto beaches, which could then be applied to future nearshore and beach management. The fieldwork involved with studying patchy habitats such as drifting macrophytes is very challenging and therefore a sampling strategy that was able to tackle those challenges was implemented across the four separate studies in this thesis. A pilot study was used to determine precise baselines with a pre-determined precision of the mean cut-off value of ≤20 % for optimal sampling of macrophytes, macroinvertebrates and fishes associated with wrack accumulations of sandy-beach surf zones (Chapter 2). With a baseline sampling regime established for surf-zone wrack accumulations, a much larger investigation of multiple storm and calm-weather events across multiple regions aimed to determine regional differences in the composition and abundances of macrophytes, macroinvertebrates and fish with the arrival of storms (Chapter 3). I also hypothesised that there would be larger volumes of wrack accumulations soon after storms versus calm weather periods (Chapter 3). Then sandy-beach surf zones in two of those regions (Fleurieu Peninsula with a seagrass-algae mix; South East, algal dominated) were investigated to establish baseline information of trophic pathways associated with semi-permanent wrack accumulations (Chapter 4). Finally, the simulated drift trajectories of macrophytes that had detached relatively close to shore (≤3 km), the rapid colonisation of fauna into natural and artificial seagrass, and the fate of macrophytes stranding on sandy beaches over the short term (6 hours) were also investigated to identify the nearshore drift dynamics of macrophytes (Chapter 5). I also hypothesised that there would be higher abundances of fauna colonising natural seagrass versus artificial seagrass over the short term. Also, tagged seagrass drifting at the water surface that was released at smaller distances from shore (≤0.5 km) versus further away from shore (≥1.5 km) would be more likely to strand on beaches in the short term (Chapter 5).

1. Key findings

The main findings from this research are summarised in a modified version of the conceptual diagram of the source-to-sink pathway that was designed at the beginning of this project (Figure 6.1). Soon after macrophytes detach from the seafloor, they may drift at the sea surface (Hobday 2000c) and I found that this surface drift pathway can be complex and unpredictable, with multiple potential drift directions, particularly at greater distances (>1.5 km) from shore (Chapter 5). In calm weather, the movement of drifting macrophytes may be mainly tidally driven but large increases in wind speed (>27 km/h) may influence drift trajectories (Figure 6.1). The likelihood of drifting macrophytes changing direction was mainly associated with the turn of tide from ebb to flood. The likelihood of drifting macrophytes arriving on beaches is greater closer to shore (<0.5 km) under the influence of onshore (westerly) winds, but as those macrophytes entered the surf zone, it was likely to be wave action that then promoted movement onshore.

The colonisation of drifting macrophytes by macroinvertebrates and fish is likely to change along the drift pathway with accumulation of different source populations possible (Chapter 5; Clarkin et al. 2012). Greater distances from shore (>1.5 km) and greater depths (>9 m) may limit the source pool of colonising fauna to those found in open water (e.g. within windrows) or to macrophyte raft-to-raft transfer (Figure 6.1; Kingsford and Choat 1986; Kingsford 1990; Clarkin et al. 2012). Closer to shore (<0.5 km), the source pool is also likely to include fauna moving up from the benthos to drifting macrophytes given shallower water depths (<6 m) (Figure 6.1; Salovius et al. 2005; Clarkin et al. 2012).

In the calm versus storm events that I studied, it appeared that wrack, fish and macroinvertebrates in the surf zone were not strongly influenced by weather. There were clear and consistent differences in the regional surf-zone wrack composition (Figure 6.1), which variously included seagrass-dominated, a seagrass/algae mixture, or algal-dominated wrack as the coastline changed from a sheltered gulf to open ocean (Chapters 2-4). There were also some repeatable differences in macroinvertebrate assemblages between the seagrass-dominated and algal-dominated regions in the surf zone (Chapter 3). I found that the presence of wrack and fauna in surf zones was correlated with beach morphology, suggesting that beach profiles extend into the surf zone and might contribute more to the ecology of surf zones than previously thought (Chapter 3; Defeo and McLachlan 2005; Neves et al. 2007; Manning et al. 2013; Carcedo et al. 2014).

Investigations of fish gut contents and carbon and nitrogen stable isotopes showed that wrack accumulations in surf zones may play a more important role as habitat rather than primary food resources, particularly for fish (Figure 6.1, Chapter 4), although this conclusion may have been influenced by the limited amount of sampling that was able to be achieved for this study (i.e. two of the intended six beaches, sampled once). The swift colonisation of artificial and de-faunated natural drifting seagrass by macroinvertebrates and fish within 6 hours suggested that drifting macrophytes are attractive predominantly as habitat, particularly for fish where any drifting structure may suffice as desirable habitat (Figure 6.1, Chapter 5). Thus, the aims of this project (Chapter 1) were largely fulfilled by the data collected, but there were some exceptions. Predictions of the occurrence of storm-induced pulses of wrack in the surf-zone, and subsequent faunal abundance increases, were not supported for the categories of storms that I studied (Chapter 3). Also, trophic levels were not as well-defined within wrack accumulations as predicted and it is likely that trophic pathways include

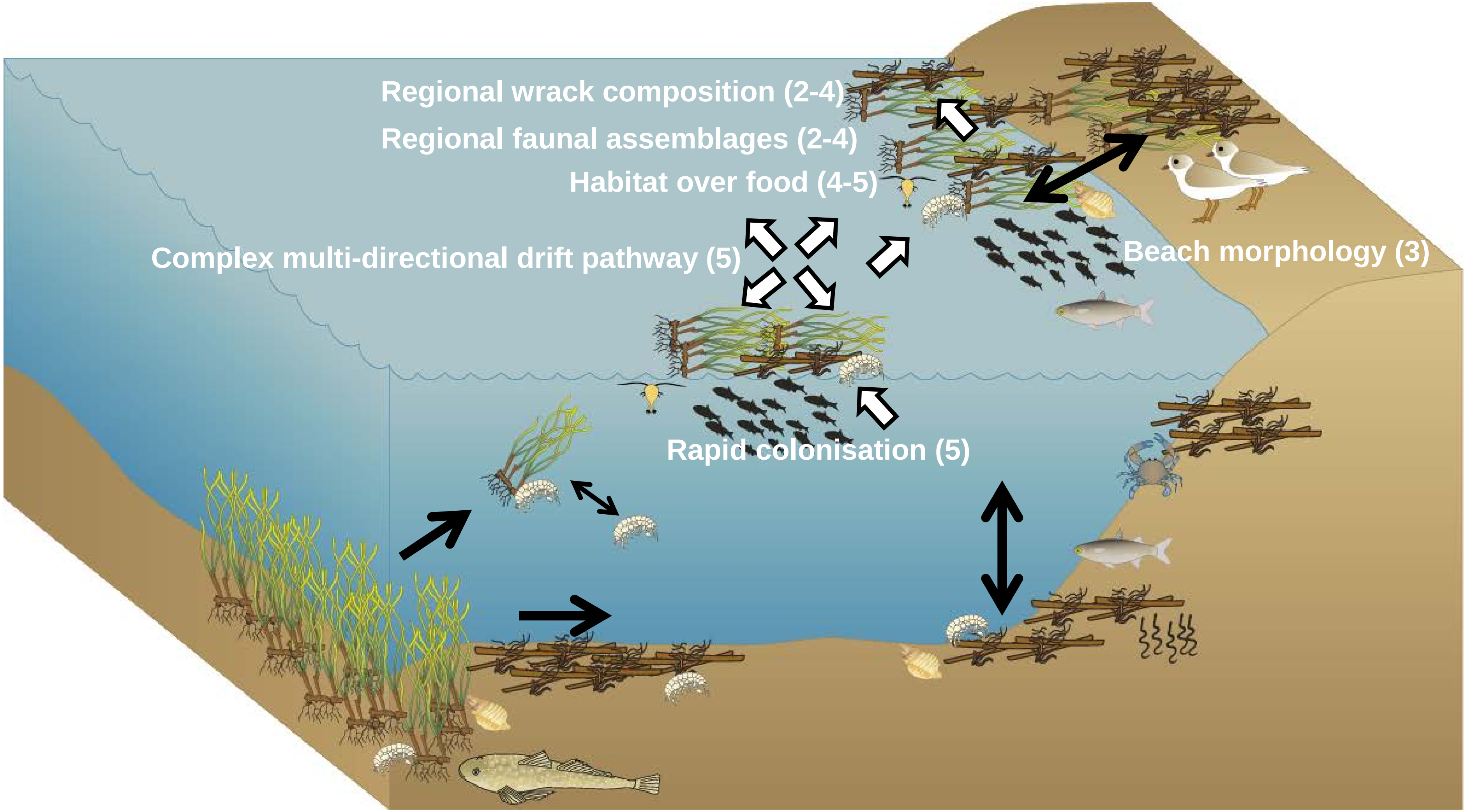

Figure 6.1: Conceptual model of the source to sink pathway from detachment to deposit of drifting macrophytes in coastal ecosytems. Specific points along the drift pathway that were studied are shown with the main findings from a series of investigations. White arrows with black outline indicate the sections of the drift pathway that were investigated as part of the original aims and hypotheses of this thesis. Directions of arrows depict the drift pathway found in this study. The fauna associated with studies in this thesis are shown in surf zone wrack accumulations and floating macrophytes in diagram. Black arrows indicate pathways identified in literature searches throughout entire study period. Numbers in brackets correspond to thesis chapters.

possibly unidentified food sources from other habitats in the surf zone or nearshore environment (Chapter 4).The movement of drifting macrophytes offshore was not influenced by relatively higher recorded wind speeds on some days but overall my experiments were conducted in relatively calm weather for short periods of time (i.e. hours; Chapter 5). Also, the study described in Chapter 3 showed that wrack, macroinvertebrate and fish assemblages were consistently correlated with aspects of beach morphologies, specifically to sand grain sizes and beach slopes.

During this study, I also identified and implemented an optimal and precise sampling regime that could capture the inherent natural variation found in the floral and faunal distributions of patchy habitats such as wrack in surf zones (Chapter 3). In subsequent studies (Chapter 3 and 5), I implemented multi-factorial experimental designs to encapsulate the small-spatial natural variation that is inherent with patchy habitats such as drifting macrophytes and wrack accumulations.

Composition and movement of drifting macrophytes

The research within this thesis contributes much to the body of knowledge of macrophyte compositions within wrack accumulations along sandy-beach surf zones in southern Australia (Chapters 2-5). Macrophyte compositions found in separate regions consistently matched the available pool of macrophytes that grow subtidally in each of those regions (i.e. metropolitan Adelaide, with few headlands, is seagrass-dominated; Fleurieu Peninsula, a seagrass/algae mixture; South East, with mostly rocky reefs, is algal-dominated; Chapters 2-4). These findings also agree with those previous studies of macrophyte compositions found within wrack accumulations in sandy-beach surf zones and deposited on beaches in southern Australia (Kirkman and Kendrick 1997; Duong 2008). Duong (2008) and Kirkman and Kendrick (1997) demonstrated that the composition of macrophytes found in beach-cast wrack was similar to the macrophytes in nearby subtidal habitats (i.e. either seagrass meadows or macroalgae beds on offshore reefs).

There was a large amount of natural site-to-site variation found within wrack accumulations in each region, particularly along metropolitan Adelaide and Fleurieu Peninsula beaches (Chapters 2-3). Even though all beaches sampled in this series of investigations were classified as intermediate in morphodynamics (Short 2001), there appear to be subtle site-to-site differences that may be due to small-scale variation in factors such as beach morphology, eddies or currents, or subtidal habitats nearby. Small-scale site-to-site variation of wrack accumulations has also been identified in other studies of wrack accumulations on beaches in southern Australia, where wrack can pile-up in large amounts (i.e. metres high) on some beaches, and be very low in volume or non-existent on others (McLachlan 1985; Kirkman and Kendrick 1997; Duong and Fairweather 2010). Volumes of beach-cast wrack can vary through time, are unpredictable and may accumulate and stay in the nearshore system for long periods of time, i.e. of days to weeks before being deposited onshore or buried in sand (Kirkman and Kendrick 1997; Colombini and Chelazzi 2003; Barreiro et al. 2011). For example, Barreiro et al. (2011) found large seasonal variation in wrack supply to six sandy beaches in Spain, which was influenced by wave exposure and coastal topography. In my study, there was variation in the amounts of wrack in surf zones across all sites through time and it would be very interesting to define the build-up, recycling and longevity of these accumulations in future.

Based on the research in this thesis, patterns in macrophyte composition did not appear to change substantially over time (Chapters 2-4) and were similar during calm and stormy weather (Chapter 3). Larger volumes of many red algae appeared after storms, compared to calm periods, suggesting that the fragile structure of red algae may be more susceptible to breakage under Beaufort Sea State 7 or 8 storms. In comparison, the presence of other macrophyte groups in surf-zone wrack accumulations was more complex and did not appear to be influenced by the storm pulses that I studied. Larger and rarer storm pulses of higher than Beaufort Sea State 8 may result in the dislodgment of more macrophyte species and in larger wrack volumes, which has been found from very large one-off storms elsewhere (Balestri et al. 2006, Filbee-Dexter and Scheibling 2012). For other macrophytes such as larger kelps, there may be cumulative impacts over multiple storm events resulting in escalating damage and eventual dislodgement. Bettignies et al. (2013) found that *Ecklonia radiata* tissue wounds progressed over seasons resulting in breakage with the onset of storms after summer, which they suggest could be due to damaged tissues caused by temperature effects or natural senescence. However, untangling the effects of hydrodynamic forces produced by storms, temperature effects or the processes of natural senescence of growing macrophytes would require further investigation over multiple seasons and years for each key component of the wrack.

The composition of macrophytes found drifting *in situ* at various distances from shore or within surf-zone wrack accumulations along metropolitan Adelaide beaches showed that there are differences in composition along the drift pathway (Chapters 2, 3 and 5). Wrack found on beaches (Duong 2008) and in surf zones (Chapters 2-3) was comprised predominantly of seagrasses (especially *Posidonia* spp.) along Adelaide metropolitan beaches. In comparison, macrophytes drifting *in situ* at the water surface offshore mainly consisted of brown macroalgae (mainly *Sargassum* spp.) during short-term, calm-weather surveys (Chapter 5). This suggests that larger volumes of seagrass might be tumbling along the seafloor or drifting within the water column, rather than drifting at the surface. Other studies in USA (Riegl et al. 2005; Britton-Simmons et al. 2012) and Western Australia (Wernberg et al. 2006) have identified large amounts of drifting macroalgae along the seafloor, and in some cases well away (i.e. up to 90 m depths; Britton-Simmons et al. 2012) from potential macroalgal bed sources. Also, seagrasses might be drifting at the water surface in larger volumes when conditions change to larger swells or during large storm events, rather than during the calm conditions sampled here. Future investigations into possible differences in surface and bottom currents under different weather or swell conditions, although challenging to do, may lead to better understanding of the hydrodynamics influencing drifting macrophyte movement and pulses of arrival along sandy beaches.

I found that macrophytes drifting at the surface very close to shore (≤0.5 km) were more likely to arrive into the surf zone and eventually deposit on beaches than those further from shore, at least in the time frame investigated (Chapter 5). The fate of drifting macrophytes further offshore (≥1.5 km) was less predictable due to tidal oscillation and changes in wind speed (Chapter 5). Some of the macrophytes found in surf-zone wrack accumulations in my studies (Chapter 2 and 3) may be from localised benthic sources close to shore in the immediate vicinity of beaches but, based on the trajectories that I recorded, many more may be derived from unknown locations some distance from where they were sampled, as was demonstrated by Kirkman and Kendrick (1997). Long-distance drift is even more likely along coastlines that are adjacent to the open ocean such as the South East region of South Australia, rather than the sheltered coastlines studied here (Chapter 5). Such long-term drifting patterns have previously been found in China (Komatsu et al. 2007) and USA (Hobday 2000c) with drifting macroalgae tracked over 100s to 1000s of kilometres and over longer timeframes of 2-3 months. Along open-ocean coastlines, oceanic influences such as large swells and current systems would make it even more difficult to predict the benthic sources of drifting macrophytes. My study of tracking drifting macrophytes with radio transmitters was undertaken over very short time frames (i.e. six hours) and in relatively calm weather, so the results may differ over longer time frames and under varying weather conditions. Under those scenarios, a combination of larger satellite transmitters for tracking in real time and radio transmitters for locating and retrieving tagged macrophytes at the end of tracking experiments would be helpful in further understanding of long-term drift trajectories (see Hobday 2000c; Komatsu et al. 2007) under differing conditions.

Drifting macrophytes as habitat

The research in this thesis provides additional evidence to that in the literature that total volumes of wrack (either in accumulations in the surf zone [Chapters 2-3] or drifting offshore [Chapter 5]) did not influence the type or numbers of colonising fauna. Other studies have found positive correlations between faunal abundances and macrophyte volumes or weights but they are usually species specific (Ingolfsson 1995, 1998; Vandendriessche et al. 2006). Instead, it is likely that the composition of drifting macrophytes is more important than volume *per se* (Chapters 2 and 3) but my research also provides some evidence that the mere presence of any drifting structure is attractive as habitat for some fishes and macroinvertebrates (Chapter 5). Larger numbers of small pelagic fish have been found around Fish Attraction Devices (FADs) that can act as a meeting point for conspecifics (Soria et al. 2009). Macrophytes drifting offshore and wrack accumulations in the surf zones of sandy beaches are particularly important for juvenile fish (Chapters 2-5). This evidence agrees with previous studies that have highlighted the importance of drifting macrophytes as nursery habitat for young fish (Lenanton et al. 1982; Robertson and Lenanton 1984; Lenanton and Caputi 1989; Colombini and Chelazzi 2003; Crawley et al. 2006). There was also some evidence in two of my studies that the more complex structure of some macroalgae, compared to seagrasses, may be more attractive for macroinvertebrates to move into and hide amongst the matrix provided (Chapters 2-3).

In all of the studies in this thesis, crustaceans such as gammarid amphipods and isopods were the most abundant macroinvertebrate taxa found in macrophytes drifting offshore and in the surf zone (Chapters 2-5). These results are comparable to other studies undertaken in either surf zones or surface waters further away from shore (Van der Merwe and McLachlan 1987; Crawley et al. 2006; Vandendriessche et al. 2006; Marin Jarrin and Shanks 2011). In Belgian coastal waters, Vandendriessche et al. (2006) commonly found gammarid amphipods, isopods (*Idotea* spp.) and crab megalopae in surface-drifting algal clumps. In surf zones of Western Australia the amphipod *Allorchestes compressa* (Crawley and Hyndes 2007) and fish species such as *Aldrichetta forsteri*, *Cnidoglanis macrocepahalus* and atherinids (Robertson and Lenanton 1984; Crawley et al. 2006) were commonly found in high abundances. In my research the types of fauna commonly found along the drift pathway (Chapter 5) and into the surf zone (Chapters 2-3) were similar to those previous studies.

My research provides further evidence to the literature (Kingsford and Choat 1985; Ingolfsson 1995, 1998; Hobday 2000c) of a change in faunal assemblages (particularly for fish) along the drift pathway (Chapter 5) into the surf zone (Chapters 2-3). There were noticeable differences in assemblages once drifting macrophytes accumulate as wrack in the surf zone (i.e. more benthic taxa including gastropods and bivalves). However, in Chapters 3 and 5, there may be a number of methodological influences at play such as different net types, and sampling times (i.e. austral summer/winter versus spring/summer) that may have affected any comparison between fauna in the surf zone and offshore.

I found much small-scale variation in the fauna associated with drifting macrophytes in surf-zone wrack accumulations (Chapters 2-3) and further offshore (Chapter 5). The constant movement of drifting macrophytes through space and time along the drift pathway into beach surf zones, along with multiple environmental changes such as hydrodynamic forces, coming into contact with the benthos, or nearshore turbulence may contribute to the variation observed. In the surf zone, it appears that beach morphologies may also have some influence on the fauna (Chapter 3) and this highlights the notion that beach-system effects might extend into the nearshore environment (Defeo and McLachlan 2005; Neves et al. 2007; Manning et al. 2013; Carcedo et al. 2014), and so should be considered in future ecological investigations of sandy beaches.

Drifting macrophytes as food sources

The results presented in Chapters 2 and 3 showed that there were high abundances and taxonomic diversity of macroinvertebrates and fishes associated with wrack accumulations in the surf zones of sandy beaches. Those patterns, along with similar results in other studies (Hyndes and Lavery 2005; Crawley et al. 2006), give some support to the idea that wrack accumulations may be an important food resource for nearshore fauna. My study of fish gut contents and carbon and nitrogen stable isotopes in Chapter 4 identified some trophic levels that were associated with wrack accumulations in surf zones of sandy beaches. However, other macroinvertebrates, such as sphaeromatid isopods, may be assimilating carbon from unknown sources that were not investigated in Chapter 4, such as microphytobenthos or particulate organic matter, which has been identified in other studies around mangroves (Bouillon et al. 2002; Vaslet et al. 2012) and on sandy beaches (Colombini et al. 2011).

My finding of the rapid colonisation by fish to artificial or de-faunated seagrass in Chapter 5 gives further evidence of the attractiveness of drifting macrophytes as habitat, rather than as food. Also, the lack of evidence of carbon assimilation in the fish from potential food items also found in the wrack in Chapter 4 suggests that the species of fish that I studied may be foraging over a wide area outside of wrack accumulations for more preferable and nutritious food resources in subtidal habitats nearby (e.g. seagrass meadows). Such foraging behaviour across multiple habitats has also been identified in studies of juvenile fish in mangroves and seagrass meadows (Nagelkerken and Van der Velde 2004;

Vaslet 2012). Foraging for more nutritious food resources would suggest that wrack accumulations may be selected for habitat quality over food availability, which is important for young fish that need to hide from large predators. Crawley and Hyndes (2005) found that fish were mainly feeding on polychaetes and copepods in Western Australian surf-zone wrack accumulations and their stable isotope ratios indicated that they could be assimilating nitrogen from polychaetes. That study provides some evidence that polychaetes may be a missing food item (and hence trophic level) in my study and it would be useful to target benthic organisms in further research to confirm that connection. My study was planned to investigate the trophic pathway directly involved within wrack accumulations in surf zones so other potential habitats, which may have consisted of nutrient rich sources of food (i.e. benthic polychaetes), were not sampled.

The range in stable isotope ratios for all taxa and the site-to-site variation that I observed in Chapter 4 were similar to those found in other studies of wrack accumulations (Crawley et al. 2009), sandy beaches (Colombini et al. 2011) and mangroves (Vaslet 2012). Large variation in carbon and nitrogen stable isotope ratios is particularly problematic for detached macrophytes that are under various stages of decomposition due to fluctuation in isotope signatures with microbial activity (Fellerhoff et al. 2013). Therefore, I suggest that there is a need for further establishment of baselines for isotopic ranges of detached seagrasses and macroalgae as they.

Establishing baselines in extremely patchy habitats

In Chapter 2, a pilot study was implemented to examine the inherent variability in faunal abundances and macrophyte volumes found in surf-zone wrack accumulations. The patchiness of drifting macrophytes and wrack accumulations through space and time is a typical example of the inherent variability (*sensu* Andrew and Mapstone 1987) that is often observed in nature. I successfully quantified the variability in faunal abundances and wrack volumes and so was able to identify an optimal sub-sampling regime and number of replicate samples to be used in the study undertaken in Chapter 3. Patchiness in wrack accumulations was identified in , Chapter 2 , with large ranges in total volumes at some sites, for example ranges of 0.3 to 28 L at the one site of Semaphore. Such large ranges in wrack volumes were also identified in Chapter 3, for example ranges of 1 to 34 L at Long Beach South during one sampling event. Had I not implemented the pilot study approach in Chapter 2 before decisions for sampling were made in Chapter 3, then the data obtained may have been erroneous, leading to Type II statistical error (Andrew and Mapstone 1987, Fairweather 1991, Zuur et al. 2010). Similarly, Downes et al. (2011) used pilot investigations to estimate optimal sample sizes in very patchy leaf-litter habitats in freshwater streams to reduce the effects of Type II error. However, this tendency to under-sampling in highly patchy environments is a problem that is possibly more commonly encountered in ecological studies than is routinely recognised, especially in extremely patchy environments such as wrack accumulations.

A multi-factorial and nested (mixed model) design was used in the Chapter 3 study to investigate the possible influence of weather events on wrack accumulations and associated flora and fauna. A similarly complex experimental design was used in the Chapter 5 study, which was important for capturing small-scale effects in time and space. If such complex designs are not implemented then the importance of the main factors of interest may have been misinterpreted as a result of confounding with small-scale unrelated effects.

Investigation of trophic pathways in Chapter 4 successfully established baselines in the trophic levels associated with wrack accumulations in the surf zone of sandy beaches. Exploration of the raw stable isotope data, rather than the more commonly-used technique of so-called mixing models, was important for establishing and understanding variability in the data. Post (2002) highlighted the importance of establishing baselines of consumer stable isotope signatures to capture the natural spatial and temporal variability of complex trophic webs before more definitive trophic positions can be established. Coarse ranges for fractionation in carbon and nitrogen stable isotope values to delineate trophic levels were useful for examining the possible pathways between consumers and potential food sources, which may have been overlooked with the more commonly-used, fine-range (average) values (Vander Zanden and Rasmussen 2001; Vanderklift and Ponsard 2003; Crawley et al. 2007).

2. Key areas for future research

I propose that the next phase of research focusing on drifting macrophytes should focus on the movement and colonisation by fauna along the entire drift pathway, from detachment through to deposition on beaches, at both the sea surface and seafloor. Manipulative experimental studies should be designed to identify the drift dynamics of different volumes over different weather and hydrodynamic regimes. Tracking of drifting macrophytes at greater distances from shore and over longer timeframes of weeks to months would provide a greater understanding of wrack movement (*sensu* Hobday 2000c; Komatsu et al. 2007). For example, it may identify the relative likelihoods of sinking versus arrival on shorelines or identify the magnitude of multiple pulses of wrack arrival over days or weeks. The colonisation of drifting macrophytes by fish and macroinvertebrates over days or weeks, with comparison to tethered macrophytes at different depths, would also provide a better understanding of the sources of colonising fauna (Ingolfsson 1998; Kenyon et al. 1999). Future studies in surf zones also need to examine different beach morphologies and incorporate changes in those morphologies over time to identify the extent to which they influence wrack accumulations and associated fauna (Defeo and McLachlan 2005; Neves et al. 2007; Manning et al. 2013; Carcedo et al. 2014).

Future investigations of trophic pathways in wrack accumulations in the surf zone, within drifting macrophytes and with benthic habitats along the drift pathway would also be useful to determine the connectivity and production of the nearshore ecosystem. The variation in carbon and nitrogen stable isotope values should also be investigated further (Vander Zanden and Rasmussen 2001; Vanderklift and Ponsard 2003; Crawley et al. 2007), particularly relative to decomposition in macrophytes (Lehmann et al. 2002). Such investigations will lead to better-defined baselines, which will then help to establish more definitive trophic pathways (Post 2002).

Further studies that focus on a multiple-stage approach to the movement of drifting macrophytes and faunal associations along more sections of the drift pathway would also provide essential information of the connectivity amongst nearshore habitats and the role that detached macrophytes play as habitat and within the production of nearshore ecosystems.

3. Management implications

The empirical field-based research in this thesis (Chapters 2-5) provides greater understanding of the ecological function of drifting macrophytes arriving into and accumulating as wrack in sandy-beach surf zones. Sandy beaches, particularly those close to metropolitan centres, are popular public spaces that are regularly used for multiple recreational purposes and are particularly important for tourism (Kirkman and Kendrick 1997). In many regions, particularly in southern Australia, the practice of cleaning wrack from beaches is used to address the public view that wrack piling up on beaches or in surf zones in large volumes is a nuisance for beach users (Kirkman and Kendrick 1997; Fairweather and Henry 2003; Malm et al. 2004). There are also regions such as the South-East of South Australia where wrack is harvested from sandy beaches for fertilisers and other products (i.e. 50-110 tonnes for algae and 3000 tonnes for seagrass per year; Kirkman and

Kendrick 1997, PIRSA 2007). The cleaning of wrack and harvesting from beaches may affect the ecology of the beach itself and into the surf zone, such as the immediate reduction of epifauna and fish abundances (Lavery et al. 1999). So far, hardly any thought is given to the ecological role of wrack on beaches or in the surf zone with regard to beach management practices such as beach cleaning. Nordstrom et al. (2000) highlighted the importance of evaluating the fauna on beaches that have wrack removal programs in place, for future restoration of dunes and beaches in developed areas.

My research builds on the previous evidence highlighting the use of wrack as habitat, its nursery function and its importance as a driver of nearshore production (McLachlan et al. 1985; Colombini and Chelazzi 2003; Coupland and McDonald 2008; Christie et al. 2009; Colombini et al. 2009; Cowles et al. 2009; Dugan et al. 2011). The dominance of small sizes of fish as juvenile representatives of various species that were captured throughout all studies in this thesis highlights the nursery role of wrack found in surf zones. Wrack in the surf zone is not only important for juvenile recreationally- and commercially-important fish species but also for species that have close affinity to attached macrophytes, including syngnathids or pipefishes (which are protected in South Australia) and clinids or weedfishes (Lenanton et al. 1982; Robertson and Lenanton 1984; Lenanton and Caputi 1989; Colombini and Chelazzi 2003; Crawley et al. 2006). This provides more evidence of the ecological links between wrack accumulations in the surf zone and other benthic habitats nearby. Therefore, I suggest that further wrack-cleaning programs need to consider the possibilities of limiting beach cleaning to certain times of the year when fish recruitment does not occur and numbers of juveniles utilising surf-zone wrack are low.

My study of macrophytes drifting near to the shore and in the surf zone identified the lack of predictability associated with macrophytes arriving into surf zones from distances further away from shore (≥1.5 km). Macrophytes that detach close to shore (≤0.5 km) are more likely to drift ashore in the immediate vicinity or on to beaches close by within a day (Chapter 5). There may be a number of days before drifting macrophytes arrive from elsewhere (i.e. across greater distances from shore or other locations) after detachment from the seafloor during large swells, one-off storm events (i.e. rougher than Beaufort 8), or seasonal senescence. It is therefore important for local councils and governments to understand that the first arrival of drifting macrophytes on shorelines after a large one-off storm, swell, or seasonal senescence event, could be followed by multiple pulses in the days or weeks following such events, which is suggested by the tidal oscillation patterns observed in Chapter 5.

Understanding the dynamic movement of nearshore drifting macrophytes, their arrival into surf zones, eventual deposition onshore and recycling back-and-forth between the beach and surf zone is crucial for better management of sandy beaches, particularly concerning the process of beach cleaning. Gaining more comprehensive evidence of the faunal association with allochthonous inputs such as wrack moving into surf zones and the connection of multiple habitats is also important for understanding the ecological function of nearshore ecosystems. Such ecological understanding has received no attention compared to the terrestrial usage of allochthonous inputs on beaches (i.e. birds using wrack as nesting sites) in previous beach management programs, particularly in southern Australia.

4. Conclusion

The overall aims of this thesis were to investigate the role that drifting macrophytes and wrack accumulations play as habitat and food resources for fish and macroinvertebrates, and the movement dynamics of drifting macrophytes in nearshore ecosystems. I designed this research as a series of studies to establish optimal sampling methods to be used for investigations of weather conditions, identify regional differences in wrack composition and trophic pathways within wrack accumulations in sandy-beach surf zones in southern Australia. Storm events had little influence on the volume of wrack or on the associated faunal assemblages in surf zones but clear regional differences in both were identified. The complex trajectories of drifting macrophytes at further distances from shore also showed that the movement and accumulation of detached macrophytes in the surf zone is unpredictable.

Drifting macrophytes and wrack accumulations are habitats that are extremely patchy in space and time (i.e. ranges of 1 to 34 L wrack volume at Long Beach South on one occasion) and it is not surprising that the associated trophic pathways are also complex, as I found in my study. The inherent natural variation involved with extremely patchy habitats such as drifting macrophytes require thorough examination of the methodology used to capture the true ecological patterns involved (Andrew and Mapstone 1987). The pilot study approach was essential in my thesis, so that precise datasets could be obtained to help explain the biological and ecological function of nearshore processes.

The next phase of research in Australia and elsewhere in the world should focus on an integrated approach that encompasses multiple aspects of the source-to-sink drift pathway, rather than treating stages of the drift pathway as separate entities. Designing studies in this way would address some of the larger questions that need answering to provide better understanding of the ecological connection between particular stages of the drift pathway. Therefore, future research questions need to be based around further investigations of the origin, long-term movement, and final resting place of detached macrophytes in coastal ecosystems. Information obtained from such investigations would be important for future coastal management of disparate places that are actually linked via the drift pathway would better illustrate the continuous biological and ecological connections along the entire drift pathway.

My thesis focused on wrack accumulations in the nearshore surf zone and the drift pathway of recently-detached macrophytes close to shore to address the paucity of information in southern Australia (Figure 6.1). This research was the first to establish precise sampling protocols of wrack accumulations and investigate the composition of multispecies wrack accumulations after multiple storms and calm periods across multiple regions. Also, to my knowledge, there are no previous baseline investigations of the trophic pathways associated with semi-permanent wrack accumulations, especially with varying wrack compositions, anywhere. Lastly, all previous tracking studies of drifting macrophytes have focused on large macroalgae along open ocean coastlines (e.g. Harrold and Lisin 1989; Kingsford 1995; Hobday 2000c; Komatsu et al. 2007) and so my study (Chapter 5) is the first investigation of drifting seagrass in more sheltered coastal regions.

The set of studies in this thesis adds to the scientific knowledge of drifting macrophytes moving into and accumulating as wrack in surf zones and the associated faunal interactions along the drift pathway. This information also highlights the use of drifting macrophytes and wrack accumulations as habitat for juvenile fish and macroinvertebrates and the ecological function they provide to the productivity of nearshore zones. Therefore, the consideration and inclusion of wrack accumulations and their ecological function is essential in future coastal management programs.

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Appendix 2

Table A2.1: List of macrophyte taxa and other categorical groups found in wrack from seine net hauls taken in beach surf zones during August – September 2011 along the metropolitan Adelaide coastline. Numbers shown are total volumes (L) hauled, '<' indicates volumes < 0.01 L and blank cells indicate zero counts. Unid. = unidentified.

				Site					
Phylum or category	Taxonomic group	Genus	Species/category	Brighton	Glenelg	Henley	Semaphore	Largs Bay	Total Volume (L)
Chlorophyta	Unid.	Unid.	small mixed fragments	0.01	<	<	0.16	<	0.17
	Caulerpaceae	*Caulerpa*	*brownii*				<	<	<
	Ulvaceae	Ulva	spp.	<	<	<	0.01	<	0.02
Rhodophyta	Unid.	Unid.	small mixed fragments	0.43	1.24	0.36	1.33	0.07	3.44
	Corallinaceae	Unid.	spp.	0.17	0.03	<			0.19
	Dicranemataceae	*Dicranema*	sp.1		0.77				0.77
Heterokontophyta	Unid.	Unid.	Mixed senesced seagrass leaves	1.18	1.61	0.08	0.07	0.01	2.95
	Unid.	Unid.	Seagrass rhizomes	<	0.03	0.11	1.87	0.13	2.15
	Cystoseiraceae	*Caulocystis*	spp.	0.02	0.40				0.42
	Cystoseiraceae	*Cystophora*	spp.	0.06	0.08				0.13
	Cystoseiraceae	*Scaberia*	*aghardii*		0.13				0.13
	Sargassaceae	*Sargassum*	spp.	0.03	0.21				0.24
	Alariaceae	*Ecklonia*	*radiata*	0.36	0.18				0.54
Magnoliophyta	Cymodoceaceae	*Amphibolis*	*antarctica*	0.39	2.42	0.08	0.30	0.07	3.26
	Posidoniaceae	*Posidonia*	*sinuosa* or *angustifolia*	8.16	13.52	14.99	18.62	1.71	56.99
	Zosteraceae	*Zostera*	spp.	<	0.01	0.01	0.66	0.03	0.71
	Hydrocharitaceae	*Halophila*	spp.		<	<	<		<
Decomposing macrophyte fragments	Unid.	Unid.	Unid.	0.01	0.02	0.03	0.01	<	0.06
Other									

Porifera	Unid.	Unid.	Unid.	0.01	0.01	<			0.02
Bryozoa	Unid.	Unid.	Unid.	<	0.01	<	0.01	<	0.03
Terrestrial plant matter	Unid.	Unid.	Unid.	<	<	<		<	0.01
Litter (Anthropogenic)	Unid.	Unid.	Unid.	0.04	<	<			0.04
Animal fragments	Unid.	Unid.	Unid.	0.02	0.02	0.05	0.04	0.02	0.14
			Total volume (L)	10.89	20.67	15.72	23.08	2.04	72.40
			Number of species or categories	19	22	15	13	13	23

Table A2.2: List of macroinvertebrate taxa and their total numbers (pooled across all hauls) found in wrack from seine net hauls taken in beach surf zones during August – September 2011 along the metropolitan Adelaide coastline. Blank cells mean zero counts.Unid. = unidentified.

Phylum	Taxonomic group	Family	Genus	Species	Site					Overall abundance
					Brighton	Glenelg	Henley Beach	Semaphore	Largs Bay	
Nematoda	Unid.	Unid.	Unid.	sp.1		1				1
Annelida	Polychaeta	Unid.	Unid.	sp.1	2			1		3
	Polychaeta	Eunicidae	Unid.	sp.1	1	1		2		4
	Polychaeta	Orbiniidae	Unid.	sp.2	1					1
	Polychaeta	Nereididae	Unid.	sp.1	1	6		2		9
	Polychaeta	Phyllodocidae	Unid.	sp.1	2	2	1	1	1	7
	Polychaeta	Syllidae	Unid.	sp.1	1					1
	Polychaeta	Sabellidae	Unid.	sp.1	1	5		1		7
	Polychaeta	Serpulidae	Unid.	sp.1		2		1		3
Arthropoda	Pycnogonida	Callipallenidae	*Propallene*	sp.1	4	24	1	14	2	45
	Acarina	Halacaridae	Unid.	sp.1	4	7		3	2	16
	Calanoida	Unid.	Unid.	sp.1		1		9	1	11
	Harpacticoida	Peltidiidae	Unid.	sp.1	4	2			1	7
	Ostracoda	Unid.	Unid.	sp.1	8	7		5	1	21
	Ostracoda	Unid.	Unid.	sp.2	1					1
	Ostracoda	Unid.	Unid.	sp.3	1					1
	Ostracoda	Unid.	Unid.	sp.4	1					1
	Ostracoda	Unid.	Unid.	sp.5				1		1
	Cumacea	Bodotriidae	Unid.	sp.1	5	1		1		7
	Tanaidacea	Tanaidae	Unid.	sp.1	6	4	1	1	2	14
	Isopoda	Anthuridae	Unid.	sp.1	3	3				6
	Isopoda	Chaeteliidae	Unid.	sp.1	1					1
	Isopoda	Cirolanidae	Unid.	sp.1	1					1

	Isopoda	Idoteidae	*Euidotea*	sp.1	2	2		8		12
	Isopoda	Limnoriidae	Unid.	sp.1	2	9	2	3		16
	Isopoda	Paranthuridae	Unid.	sp.1	2	3			2	7
	Isopoda	Sphaeromatidae	*Exosphaeroma*	sp.1	48	25	3	20		96
	Isopoda	Sphaeromatidae	*Dynamenella*	sp.2				2		2
	Isopoda	Sphaeromatidae	Unid.	sp.3			1			1
	Amphipoda	Caprellidae	*Caprella*	sp.1	2	5	2	74	1	84
	Amphipoda	Dexaminidae	*Atylus*	sp.1	11	6	2	3		22
	Amphipoda	Hyalidae	Unid.	sp.1				1		1
	Amphipoda	Hyalidae	*Allorchestes*	*compressa*	3x10^3	3x10^3	102	1x10^3	310	9x10^3
Arthropoda	Amphipoda	Phliantidae	Unid.	sp.1		3				3
	Gammaridea	Unid.	Unid.	sp.1				2		2
	Gammaridea	Unid.	Unid.	sp.2					1	1
	Mysidacea	Unid.	Unid.	sp.3	2	1		3		6
	Decapoda	Crab megalopa	Unid.	spp.	4	1		5	2	12
	Decapoda	Crangonidae	Unid.	sp.1				4	1	5
	Decapoda	Hippolytidae	Unid.	sp.1				3		3
	Decapoda	Hymenosomatidae	Unid.	sp.1	1			8		9
	Decapoda	Majiidae	Unid.	sp.1	1			1	2	4
	Decapoda	Palaemonidae	Unid.	sp.1				2		2
Mollusca	Polyplacophora	Ischnochitonidae	*Ischnochiton*	sp.1		1				1
	Gastropoda	Columbellidae	*Anachis*	*atkinsoni*	2	3		1		6
	Gastropoda	Columbellidae	Unid.	sp.1		1				1
	Gastropoda	Naticidae	*Polinices*	*conicus*	10	1		10		21
	Gastropoda	Eatoniellidae	*Eatoniella*	sp.1	4	1				5
	Gastropoda	Littorinidae	Unid.	sp.1	2	1	1		1	5
	Gastropoda	Ranellidae	Unid.	sp.1	1	1				2
	Gastropoda	Cerithiidae	Unid.	sp.1	2					2

Gastropoda	Mitridae	Unid.	sp.1	1					1
Gastropoda	Lottiidae	Unid.	sp.1	1	1	2			4
Gastropoda	Phasianellidae	*Phasianella*	*australis*	3		1	1	1	6
Gastropoda	Trochidae	*Cantharidella*	*balteata*	2	7	1			10
Gastropoda	Turbinidae	*Turbo*	*undulatus*	3	1		1		5
Bivalvia	Mytilidae	*Brachidontes*	*erosus*	11	14	1			26
Bivalvia	Mesodesmatidae	*Paphies*	*elongata*		1		6		7
		Total catch		$3x10^3$	$3x10^3$	121	$2x10^3$	331	$1x10^4$
		Number of species		42	36	14	34	16	58

Table A2.3: List of fish and their total numbers (pooled across all hauls) found in wrack from seine net hauls taken in beach surf zones during August – September 2011 along the metropolitan Adelaide coastline. Blank cells mean zero counts.

			Site					Overall abundance
Family	Genus	Species	Brighton	Glenelg	Henley Beach	Semaphore	Largs Bay	
Arripidae	*Arripis*	*georgianus*				1		1
Atherinidae	*Leptatherina*	*presbyteroides*	29	1			76	106
Clupeidae	*Sprattus*	*novaehollandiae*		2				2
Leptoscopidae	*Leseurina*	*platycephala*	19	35	5	8	7	74
Mugilidae	*Aldrichetta*	*forsteri*	10	44	77	56	46	233
Platycephalidae	*Platycephalus*	*speculator*	2	1		17	6	26
Rhombosoleidae	*Ammotretis*	*rostratus*		1	1	3	6	11
Sillaginidae	*Sillago*	*schomburgkii*	1		3	1		5
Syngnathidae	*Stigmatopora*	*nigra*	1					1
Syngnathidae	*Vanacampus*	*vercoi*			1			1
Tetraodontidae	*Contusus*	*brevicaudus*	34	13		15	26	88
Tetraodontidae	*Tectractenos*	*glaber*			10			10
Tetrarogidae	*Centropogon*	*latifrons*				6		6
		Total catch	96	97	97	107	167	564
		Number of species	7	7	6	8	6	13

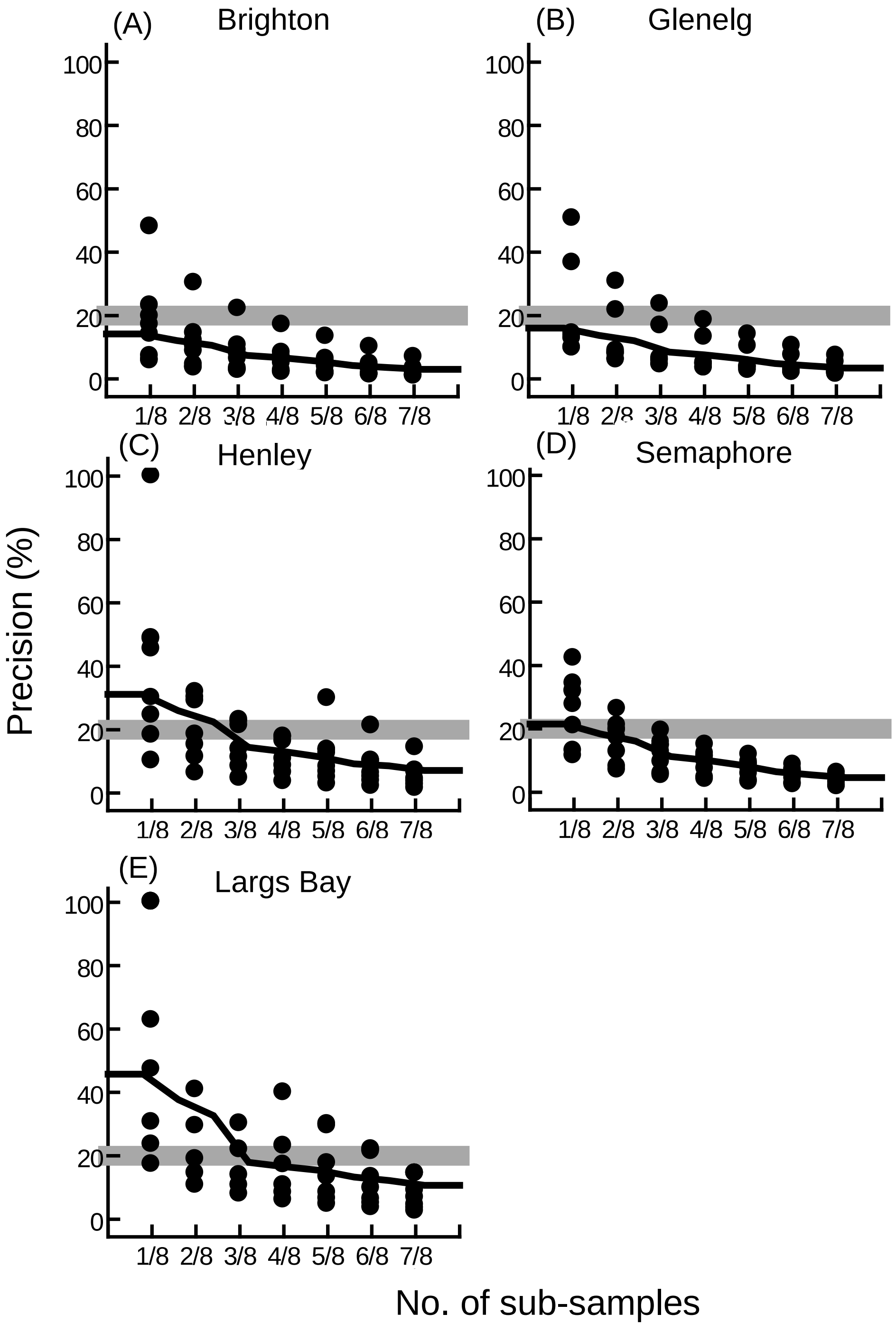

Fig.A2.1: Sub-sampling: Precisions (as % of the mean) for algae volumes with an increase in sub-sample fraction at each of the five sites sampled during 2011. The black smoother line indicates the mean of the precision values. The grey line highlights the pre-determined acceptable (i.e. ≤20 % of the mean) precision cut-off score used to establish the most precise number of sub-samples for future studies of wrack and faunal assemblages in the surf zone of sandy beaches.

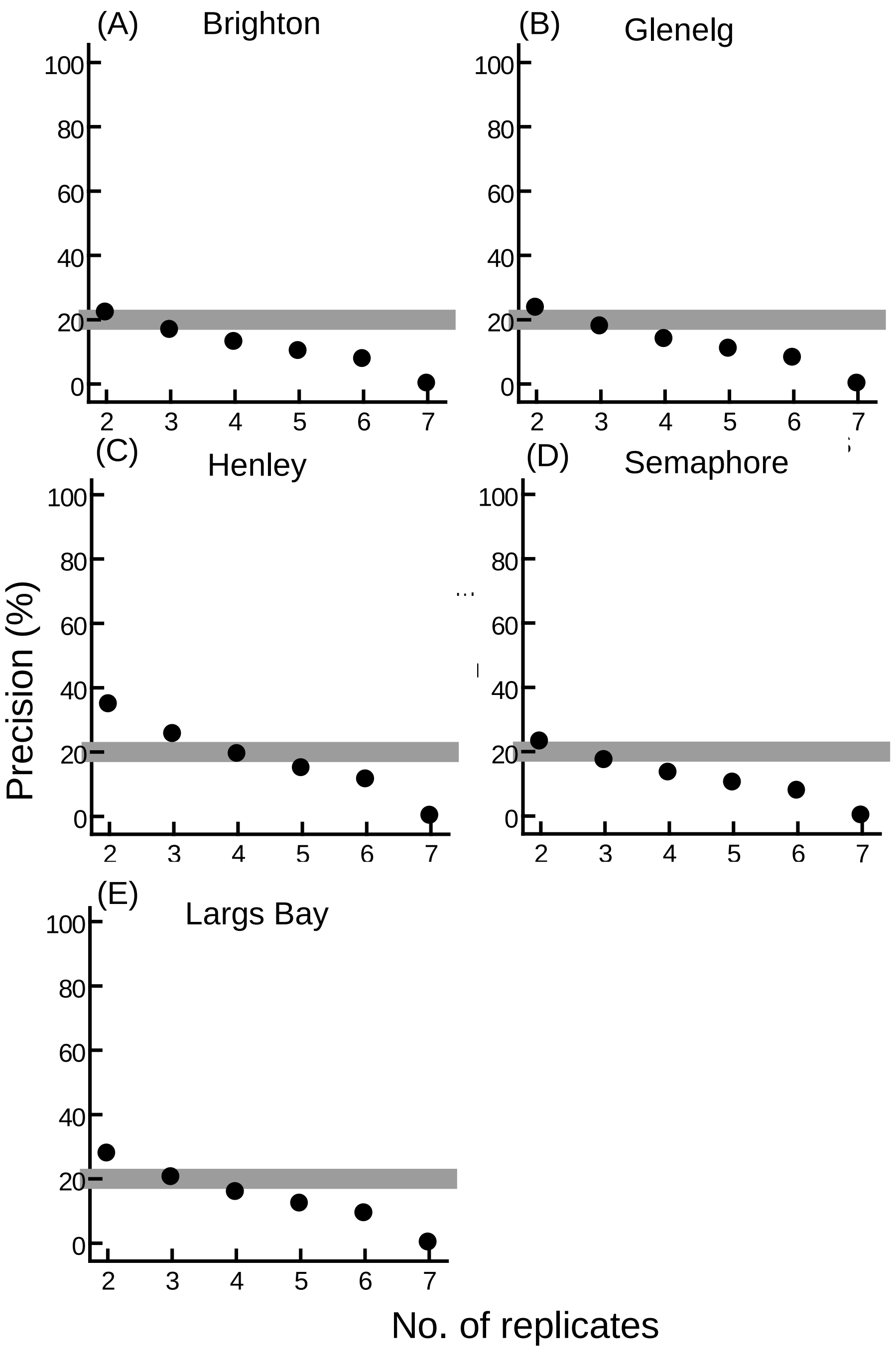

Fig.A2.2: Replication: Precisions (as % of the mean) for algae volumes with an increase in replicate number at each of the five sites sampled during 2011. The black smoother line indicates the mean of the precision values. The grey line highlights the pre-determined acceptable (i.e. ≤20 % of the mean) precision cut-off score used to establish the most precise number of replicate seine net hauls for future studies of wrack and faunal assemblages in the surf zone of sandy beaches.

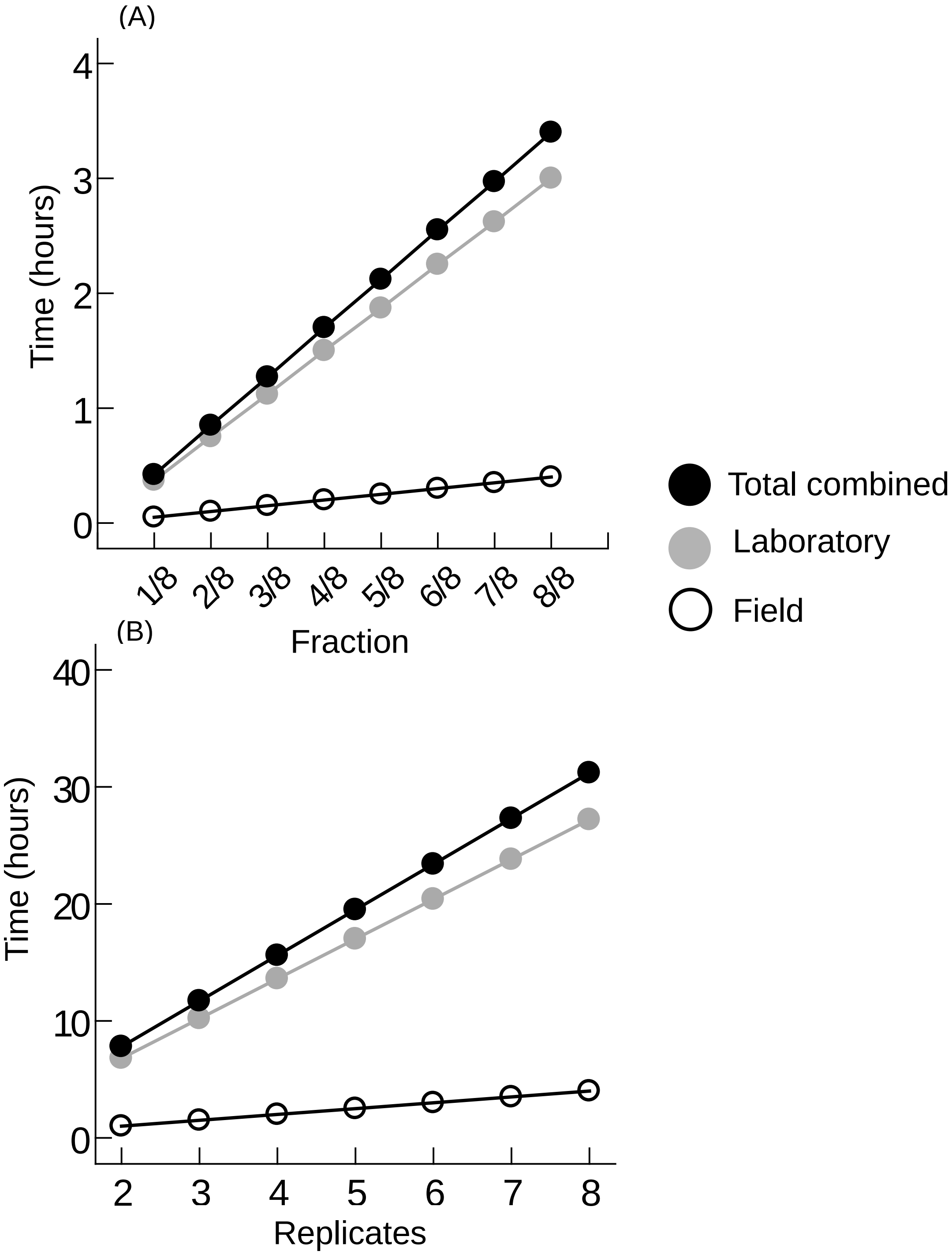

Fig. A2.3: Approximate times taken in hours for total combined processing of samples and field and laboratory components separately for (A) sub-sample fractions and (B) replicate seine-net samples.

Appendix 3

Table A3.1: Results summary of four-factor univariate PERMANOVAs for wrack total volume, total species richness and all major macrophyte groups. Analyses were based on untransformed data using Euclidean distance similarity matrices. $p > 0.05$ (blank cell); $p < 0.05$ (*); $p < 0.01$ (**); $p < 0.001$ (***); NA = not applicable from main test results.

Source	Species richness	Total volume	Green algae	Red algae	Brown algae	Kelp	Seagrass	Fragments	Other
Weather				*		*			
Region	*	*		*	**	*	**		**
Event (We)	**								
Site (Re)			**						
We x Re									
We x Si (Re)									
Re x Ev (We)	**								
Ev (We) x Si (Re)	**	***	*	***	***	**	***	***	***
Wind speed (co-var)									
Wind speed effect on design							Site (Re) *	Site (Re) *	
Pair-wise test term for sig. Region effects	MA ≠ FP ** MA ≠ SE **	MA ≠ SE *	NA	MA ≠ SE *	MA ≠ FP ** MA ≠ SE *	MA ≠ SE *	MA ≠ FP ** MA ≠ SE **	NA	MA ≠ FP * MA ≠ SE **

Table A3.2: Results summary of four-factor multivariate PERMANOVAs for wrack, macroinvertebrate and fish assemblages. Analyses were based on untransformed wrack, cube-root transformed macroinvertebrate or cube-root transformed fish data using Bray-Curtis similarity matrices. $p > 0.05$ (blank cell); $p < 0.05$ (*); $p < 0.01$ (**); $p < 0.001$ (***); NA = not applicable for category tested.

Source	Wrack	Macroinvertebrates	Fish
Weather			
Region	**	**	
Event (We)		***	***
Site (Re)	**	***	***
We x Re			
We x Si (Re)			
Re x Ev (We)		***	**
Ev (We) x Si (Re)	***	***	***
Wind speed (co-var)			
Wind speed effect on design	Event (We) *		
Wrack volume (co-var)	NA	***	***
Wrack volume effect on design	NA		Region *
	NA		
Macroinvertebrates (co-var)	NA	NA	*
Macroinvertebrates effect on design	NA	NA	
Pair-wise test term	MA ≠ FP *	MA ≠ FP *	
for sig. Region effects	MA ≠ SE **	MA ≠ SE **	

Multivariate statistical tests of the full experimental design

Wrack assemblages, when analysed as a multivariate dataset, did not differ among Weather states but were significantly different among Regions and Sites, with a significant interaction between Events and Sites (Table B). Pairwise tests of wrack assemblages for Region revealed significant differences between MA and both of the other two regions (Table B), which was consistent with the univariate results presented above. There were no significant differences between the two Weather states for macroinvertebrate assemblages (Table B). However, for macroinvertebrate assemblages, there were significant differences between Regions, Events and Sites, and significant interactions between Region by Event plus Event by Site (Table B). Pairwise tests identified that the Region differences were between MA and both of the other two regions (Table B), which was also consistent with the univariate results presented above. Fish assemblages were not significantly different between the two weather levels (Table B). However, there were significant differences in the fish assemblages between Events and Sites and significant interactions between Region by Event plus Event by Site (Table B), which was also consistent with the univariate results presented above.

Table A3.3: Results summary of four-factor univariate PERMANOVAs for macroinvertebrate total abundance, total species richness and the eight most common taxonomic groups. Analyses were based on cube-root transformed data using Euclidean distance similarity matrices. *p* > 0.05 (blank cell); *p* < 0.05 (*); *p* < 0.01 (**); *p* < 0.001 (***); NA = not applicable from main test results.

Source	Species richness	Total abundance	Polychaeta	Copepoda	Ostracoda	Isopoda	Amphipoda	Decapoda	Gastropoda	Bivalvia
Weather										
Region	*	*		*		**	*			
Event (We)				*		*		***	***	
Site (Re)	*				*	*			*	
We x Re										
We x Si (Re)										
Re x Ev (We)								***		
Ev (We) x Si (Re)	***	*		***	*		***		***	***
Wind speed (co-var)										
Wind speed effect on design					Region *		Weather *	We x Si (Re) *		Site (Re) ** We x Si (Re) *
Wrack volume (co-var)								**		
Wrack volume effect on design							Weather *	Site (Re) *		
Pair-wise test term for sig. Region effects	MA ≠ SE *	MA ≠ SE **	NA	MA ≠ FP * MA ≠ SE *	MA ≠ SE *	MA ≠ SE ***	MA ≠ SE ***	NA	NA	NA

Table A3.4: Results summary of four-factor univariate PERMANOVAs for fish total abundance, total species richness and the six most common species. Analyses were based on cube-root transformed data using Euclidean distance similarity matrices. $p > 0.05$ (blank cell); $p < 0.05$ (*); $p < 0.01$ (**); $p < 0.001$ (***).

Source	Species richness	Total abundance	*A. forsteri*	*A. truttaceus*	*C. brevicaudus*	*L. platycephalus*	*L. presbyteroides*	*T. glaber*
Weather								
Region								
Event (We)		**					*	
Site (Re)	**			*			***	**
We x Re								
We x Si (Re)								
Re x Ev (We)		**		**				
Ev (We) x Si (Re)	*		*		*	***		*
Wind speed (co-var)								
Wind speed effect on design								
Wrack volume (co-var)		**						
Wrack volume effect on design								
Macroinvertebrates (co-var)								
Macroinvertebrates effect on design		Ev (We) x Si (Re) **		Ev (We) x Si (Re) **	Event (We) *			Region *
Pair-wise test term for sig. Region effects								MA ≠ FP *

Table A3.5: List of total volumes (L per haul) for macrophyte taxa and other categorical groups found in wrack from seine net hauls taken in beach surf zones for storm and calm weather events (Storm, S; Calm, C) and all regions: Metropolitan Adelaide, MA; Fleurieu Peninsula (FP) and South-East (SE). Blank cells = zero counts. Unid. = unidentified specimen.

				Region - Weather						
				MA		FP	SE			Total
Phylum or category	Family	Genus	Species/Category	S	C	S	C	S	C	volume (L)
Macrophytes										
Chlorophyta	Unid.	Unid.	Unid. green algae fragments	0.25	0.61	1.51	2.14	6.64	2.24	13.38
	Caulerpaceae	*Caulerpa*	*brownii*				0.40	2.92	1.43	4.75
	Caulerpaceae	*Caulerpa*	*obscura*						0.15	0.15
	Codiaceae	*Codium*	*fragile*			0.60				0.60
	Codiaceae	*Codium*	*pomoides*				0.20			0.20
	Ulvaceae	*Ulva*	spp.			11.33	2.92	0.27		14.52
Rhodophyta	Unid.	Unid.	sp.1			0.30	0.12	0.75	2.77	3.94
	Unid.	Unid.	sp.2					0.60		0.60
	Unid.	Unid.	sp.3					2.19		2.19
	Unid.	Unid.	sp.4					0.20		0.20
	Unid.	Unid.	sp.5				0.50	0.16	0.80	1.46
	Unid.	Unid.	sp.6					0.76	2.87	3.63
	Unid.	Unid.	sp.7			0.20				0.20
	Unid.	Unid.	sp.8			0.60				0.60
	Unid.	Unid.	sp.9					0.99	2.98	3.97
	Unid.	Unid.	sp.10	0.12			0.10	0.13	0.40	0.75
	Unid.	Unid.	sp.11					2.68	0.36	3.04
	Unid.	Unid.	sp.12				0.10			0.10
	Unid.	Unid.	sp.13					0.60	0.63	1.23
	Unid.	Unid.	sp.14					0.20	0.16	0.36
	Unid.	Unid.	sp.15					0.80		0.80
	Unid.	Unid.	sp.16					0.28		0.28
	Unid.	Unid.	sp.17		3.00				0.32	3.32
	Unid.	Unid.	sp.18						0.16	0.16
	Unid.	Unid.	sp.19						0.80	0.80
	Unid.	Unid.	sp.20						0.44	0.44
	Unid.	Unid.	sp.21					0.16	0.20	0.36
	Unid.	Unid.	sp.22						0.12	0.12
	Unid.	Unid.	Unid. red algae	3.70	1.18	9.54	7.56	16.43	28.53	66.94

			fragments							
	Bonnemaisoniaceae	*Asparogopsis*	sp.1			0.56				0.56
	Bonnemaisoniaceae	*Delisea*	*pulchra*					0.80		0.80
	Ceramiaceae	*Ceramium*	sp.1				0.62			0.62
	Rhodomelaceae	*Chondria*	sp.1			0.40				0.40
	Laurencieae	*Laurencia*	sp.1				0.40			0.40
Rhodophyta	Corallinaceae	*Unid.*	spp.	0.62	0.30	1.13	1.27	2.92	0.50	6.74
	Dicranemataceae	*Dicranema*	sp.1			0.24	0.60	0.26		1.10
	Hypneaceae	*Hypnea*	sp.1	0.36		0.64	0.17	0.80		1.97
	Kallymeniaceae	*Callophyllis*	sp.1				0.70	3.56		4.26
	Phacelocarpaceae	*Phacelocarpus*	sp.1			0.30	0.12	0.75	2.77	3.94
	Gracilariaceae	*Gracilaria*	sp.1			0.20				0.20
	Halymeniaceae	*Cryptonemia*	undulata				0.40	13.84	0.25	14.49
	Halymeniaceae	*Thamnoclomium*	dichotomum					0.37	0.50	0.87
	Peysonneliaceae	*Peyssonnelia*	novaehollandiae						0.40	0.40
	Plocamiaceae	*Plocamium*	sp.1			1.13	0.20	14.89		16.22
Heterokontophyta	Unid.	*Unid.*	sp.1					1.44		1.44
	Unid.	*Unid.*	sp.2			0.11				0.11
	Unid.	*Unid.*	sp.3			0.46				0.46
	Unid.	*Unid.*	Unid. brown algae fragments	6.86	1.68	16.94	8.64	45.82	28.29	108.23
	Unid.	*Unid.*	Unid. kelp fragments	0.24		0.36	1.74	14.31	4.85	21.50
	Chordariales	*Cladosiphon*	fillum			0.46				0.46
	Dictyotaceae	*Dictyopteris*	muelleri			2.16	0.40			2.56
	Dictyotaceae	*Zonaria*	angustata						0.16	0.16
	Dictyotaceae	*Zonaria*	spiralis				0.20	0.16	0.60	0.96
	Dictyotaceae	*Zonaria*	sp.1.			0.25				0.25
	Durvillaeaceae	*Durvillaea*	potatorum						0.80	0.80
	Cystoseiraceae	*Acrocarpia*	paniculata					0.20		0.20
	Cystoseiraceae	*Caulocystis*	spp.	0.52	0.60	0.22	1.90	1.34	0.38	4.96
	Cystoseiraceae	*Cystophora*	spp.	0.44	0.14	6.14	9.65	12.86	13.93	43.16
	Cystoseiraceae	*Platythalia*	angustifolia					0.13	0.78	0.91
	Cystoseiraceae	*Platythalia*	quercifolia					0.24		0.24
	Cystoseiraceae	*Scaberia*	aghardii	0.21			1.22			1.43
	Hormosiraceae	*Hormosira*	banksii				0.10	0.22		0.32
	Sargassaceae	*Carpoglossum*	confluens				0.54	0.34	0.40	1.28
	Sargassaceae	*Sargassum*	spp.	0.56	0.55	1.86	4.73	2.54	4.42	14.65

	Seirococcaceae	*Phyllospora*	comosa			0.50	0.30	2.70	1.73	5.23
	Seirococcaceae	*Scytothalia*	doryocarpa			0.50	1.33	0.50		2.33
	Alariaceae	*Ecklonia*	radiata	1.49		1.89	3.98	17.66	14.36	39.38
	Lessoniaceae	*Macrocystis*	pyrifera					0.40	0.10	0.50
Heterokontophyta	Cladostephaceae	*Cladostephus*	*spongiosus*			0.20		0.66		0.86
	Stypocaulaceae	*Halopteris*	spp.			0.42		4.10	2.90	7.42
	Sporochnaceae	*Perithalia*	*caudata*					6.97	7.27	14.24
	Sporochnaceae	*Sporochnus*	spp.			0.28				0.28
Magnoliophyta	Unid.	Unid.	Mixed senesced seagrass leaves	0.40		89.33	6.69	38.00	55.86	190.28
	Unid.	Unid.	Seagrass rhizomes	1.57	19.72	0.50	0.19	0.62		22.60
	Cymodoceaceae	*Amphibolis*	*antarctica*	3.26	0.96	8.65	9.45	27.16	1.34	50.82
	Cymodoceaceae	*Amphibolis*	*griffithii*		0.20	0.17	0.53		0.80	1.70
	Posidoniaceae	*Posidonia*	*australis*		0.16		0.20	2.67	2.52	5.55
	Posidoniaceae	*Posidonia*	*coriacea*	0.70	0.12		0.57	1.41	6.28	9.08
	Posidoniaceae	*Posidonia*	*sinuosa* or *angustifolia*	41.96	4.50	27.18	35.64	4.56	0.20	114.04
	Zosteraceae	*Zostera*	spp.	0.16	0.43	0.43	0.38	2.86	0.52	4.77
Magnoliophyta	Hydrocharitaceae	*Halophila*	spp.	0.20	0.60	0.34		0.22		1.36
Fine fragments	Unid.	Unid.	Unid. macrophyte fragments	4.90	0.62	3.78	0.41	26.20	27.27	63.18
Other										
Porifera	Unid.	Unid.	Unid.	0.52	0.10	0.37		1.75	0.33	3.07
Cnidaria	Unid.	Unid.	Unid.					0.76		0.76
Bryozoa	Unid.	Unid.	Unid.			0.24	0.11	0.72	0.86	1.93
Terrestrial plant matter	Unid.	Unid.	Unid.	0.42	0.45	0.40		0.20		1.47
Litter (Anthropogenic)	Unid.	Unid.	Unid.	0.20	0.20	0.20		0.12	13.22	13.94
Animal fragments	Unid.	Unid.	Unid.	0.76	0.23	0.48	0.21	0.62	0.47	2.77
	Total Volume			70.42	36.34	193.50	107.64	295.41	240.39	1×10^3
	Number of species or categories			24	21	44	42	61	50	

Table A3.6: List and total abundances of macroinvertebrate taxa found from seine net hauls taken in beach surf zones for storm and calm weather events (Storm, S; Calm, C) and all regions: Metropolitan Adelaide, MA; Fleurieu Peninsula (FP) and South-East (SE). Blank cells = zero counts.

						Region - Weather						
						MA		FP		SE		Overall
Phylum	Class	Order	Family	Genus	Species	S	C	S	C	S	C	abundance
Platyhelminthes	Turbellaria	Polycladida	Notoplanidae	*Notoplana*	sp.1			393	14	52	368	$1x10^3$
Nemertea	Unid.	Unid.	Unid.	Unid.	sp.1				1		64	65
Annelida	Polychaeta	Unid.	Unid.	Unid.	sp.1	8		5	16			29
	Polychaeta	Eunicida	Eunicidae	Unid.	sp.1	6					16	22
	Polychaeta	Opheliida	Opheliidae	Unid.	sp.1			2				2
	Polychaeta	Phyllodocida	Nereididae	*Nereis*	sp.1	2	25	68	174		4	273
	Polychaeta	Phyllodocida	Phyllodocidae	Unid.	sp.1	4	15	22	2			43
	Polychaeta	Phyllodocida	Phyllodocidae	Unid.	sp.2		2					2
	Polychaeta	Phyllodocida	Syllidae	Unid.	sp.1	4		4	2	16	64	90
	Polychaeta	Sabellida	Sabellidae	Unid.	sp.1	2		72				74
Sipuncula	Phascolosomatidae	Phascolosomatiformes	Phascolosomatidae	Unid.	sp.1					32		32
Arthropoda	Pycnogonida	Pantapoda	Callipallenidae	*Propallene*	sp.1	6	13	156	62	16	32	285
	Arachnida	Acarina	Halacaridae	Unid.	sp.1	4	23	54	13		2	96
	Copepoda	Calanoida	Unid.	Unid.	sp.1	58	29	6				93
	Copepoda	Harpacticoida	Peltidiidae	Unid.	sp.1	$1x10^3$	479	270	1	16	11	$2x10^3$
	Copepoda	Harpacticoida	Peltidiidae	Unid.	sp.2		8			176		184
	Copepoda	Harpacticoida	Unid.	Unid.	sp.3		1		8			9
	Ostracoda	Myodocopida	Unid.	Unid.	sp.1	13	69	6	74	16	32	210
	Ostracoda	Myodocopida	Unid.	Unid.	sp.2			254	65	16	32	367
	Ostracoda	Myodocopida	Unid.	Unid.	sp.3	16		82	9		1	108
	Ostracoda	Myodocopida	Unid.	Unid.	sp.4	6	1					7
	Ostracoda	Myodocopida	Unid.	Unid.	sp.5	28	1	36	1			66
	Malacostraca	Cumacea	Bodotriidae	Unid.	sp.1	34	6	12		16	1	69
	Malacostraca	Tanaidacea	Tanaidae	Unid.	sp.1	1	1	74	48	64	24	212
	Malacostraca	Isopoda	Anthuridae	Unid.	sp.1	2			64		1	67
	Malacostraca	Isopoda	Arcturidae	Unid.	sp.1	6						6
	Malacostraca	Isopoda	Corallanidae	Unid.	sp.1		2	39				41
	Malacostraca	Isopoda	Idoteidae	*Euidotea*	sp.1	6	34	$3x10^3$	$3x10^3$	$8x10^3$	$2x10^3$	$2x10^4$
	Malacostraca	Isopoda	Idoteidae	Unid.	sp.2				4	32		36
	Malacostraca	Isopoda	Idoteidae	*Paridotea*	sp.1				32	32		64
	Malacostraca	Isopoda	Janiridae	Unid.	sp.1		1					1
	Malacostraca	Isopoda	Limnoriidae	Unid.	sp.1	6	2	2		16	1	27

Arthropoda	Malacostraca	Isopoda	Paranthuridae	Unid.	sp.1	4	6	48	52		1	111
	Malacostraca	Isopoda	Sphaeromatidae	Amphoroidea	sp.1			64				64
	Malacostraca	Isopoda	Sphaeromatidae	Exosphaeroma	sp.1	228	24	$1x10^{5}$	$5x10^{4}$	$2x10^{5}$	$1x10^{5}$	$4x10^{5}$
	Malacostraca	Isopoda	Sphaeromatidae	Dynamenella	sp.2	2	1	68	34	16		121
	Malacostraca	Isopoda	Sphaeromatidae	Unid.	sp.3				8	16	248	272
	Malacostraca	Isopoda	Sphaeromatidae	Unid.	sp.4	2						2
	Malacostraca	Isopoda	Sphaeromatidae	Unid.	sp.5			38	22	2		62
	Malacostraca	Isopoda	Sphaeromatidae	Unid.	sp.6					16		16
	Malacostraca	Amphipoda	Caprellidae	Caprella	sp.1	6	15	54	6		19	100
	Malacostraca	Amphipoda	Corophiidae	Unid.	sp.1	16	29	6		32		83
	Malacostraca	Amphipoda	Dexaminidae	Atylus	sp.1		2				288	290
	Malacostraca	Amphipoda	Hyalidae	Unid.	sp.1		2		1		234	237
	Malacostraca	Amphipoda	Hyalidae	Allorchestes	compressa	874	$2x10^{3}$	$7x10^{4}$	$7x10^{4}$	$2x10^{5}$	$3x10^{5}$	$7x10^{5}$
	Malacostraca	Amphipoda	Unid.	Unid.	sp.1			2				2
	Malacostraca	Mysidacea	Unid.	Unid.	sp.1	16	3	16	32			67
	Malacostraca	Decapoda	Crab megalopa	Unid.	spp.	56	39	64	4		2	165
	Malacostraca	Decapoda	Crangonidae	Unid.	sp.1			2				2
	Malacostraca	Decapoda	Diogenidae	Unid.	sp.1					2		2
	Malacostraca	Decapoda	Grapsidae	Unid.	sp.1			2				2
	Malacostraca	Decapoda	Hippolytidae	Unid.	sp.1		2					2
	Malacostraca	Decapoda	Hippolytidae	Latreutus	compressus	2	6					8
	Malacostraca	Decapoda	Hymenosomatidae	Unid.	sp.1	22	27			4		53
	Malacostraca	Decapoda	Majiidae	Unid.	sp.1		9				2	11
	Malacostraca	Decapoda	Majiidae	Naxia	sp.1				1			1
	Malacostraca	Decapoda	Palaemonidae	Unid.	sp.1	2						2
	Malacostraca	Decapoda	Palaemonidae	Unid.	sp.2		4			2		6
	Malacostraca	Decapoda	Portunidae	Nectocarcinus	integrifrons				5			5
	Malacostraca	Decapoda	Portunidae	Ovalipes	australiensis	27	21	4	16	31	11	110
	Malacostraca	Decapoda	Portunidae	Portunus	pelagicus	6	1					7
Mollusca	Polyplacophora	Chitonida	Ischnochitonidae	Ischnochiton	sp.1	38	4	76	4			122
	Polyplacophora	Chitonida	Ischnochitonidae	Ischnochiton	sp.2					2		2
	Gastropoda	Cephalaspidia	Bullidae	Bulla	quoyii	2	3	516				521
	Gastropoda	Hypsogastropoda	Columbellidae	Anachis	atkinsoni	96	22	12				130
	Gastropoda	Hypsogastropoda	Triphoridae	Aclophoropsis	festiva	2						2
	Gastropoda	Hypsogastropoda	Naticidae	Polinices	conicus	$3x10^{3}$	411	394	21	152		$4x10^{3}$

Mollusca	Gastropoda	Littorinomorpha	Anabathridae	Pisinna	sp.1		2			16	128	146
	Gastropoda	Littorinimorpha	Anabathridae	Pisinna	sp.2				88	48		136
	Gastropoda	Littorinomorpha	Eatoniellidae	Eatoniella	sp.1	2	12	124	26	$1x10^3$	213	$2x10^3$
	Gastropoda	Littorinomorpha	Ranellidae	Unid.	sp.1	8						8
	Gastropoda	Mesogastropoda	Cerithiidae	Unid.	sp.1	22	2	42				66
	Gastropoda	Neogastropoda	Muricidae	Dicathais	orbita		2					2
	Gastropoda	Neogastropoda	Nassariidae	Nassarius	sp.1	2						2
	Gastropoda	Patellogastropoda	Lottiidae	Unid.	sp.1	36	1	64	16		1	118
	Gastropoda	Patellogastropoda	Lottiidae	Notoacmea	flammea	4	4	13		64	162	247
	Gastropoda	Pleurobranchomorpha	Pleurobranchidae	Unid.	sp.1			112				112
	Gastropoda	Vetigastropoda	Haliotidae	Haliotis	sp.1	2						2
	Gastropoda	Vetigastropoda	Phasianellidae	Phasianella	australis	334	28	122	26	52	8	570
	Gastropoda	Vetigastropoda	Phasianellidae	Phasianella	ventricosa						264	264
	Gastropoda	Vetigastropoda	Phasianellidae	Phasianella	unknown	$1x10^3$	$3x10^3$	$6x10^3$	364	64		$1x10^4$
	Gastropoda	Vetigastropoda	Trochidae	Austrocochlea	sp.1						1	1
	Gastropoda	Vetigastropoda	Trochidae	Cantharidella	balteata	166	7	12		96	2	283
	Gastropoda	Vetigastropoda	Trochidae	Chlorodiloma	odontis	2		1		2		5
	Gastropoda	Vetigastropoda	Trochidae	Clanculus	sp.1					2		2
	Gastropoda	Vetigastropoda	Trochidae	Clanculus	sp.2		4	4				8
	Gastropoda	Vetigastropoda	Trochidae	Phasionotrochus	sp. 1	4						4
	Gastropoda	Vetigastropoda	Trochidae	Phasionotrochus	eximinus					4	3	7
	Gastropoda	Vetigastropoda	Trochidae	Phasionotrochus	iridontes	16						16
	Gastropoda	Vetigastropoda	Trochidae	Phasionotrochus	rutilus						1	1
	Gastropoda	Vetigastropoda	Trochidae	Prothalotia	lehmani		2			92	15	109
	Gastropoda	Vetigastropoda	Trochidae	Thalotia	chlorostoma	5		1		2		8
	Gastropoda	Vetigastropoda	Turbinidae	Turbo	undulatus	22	8	12	32	124	8	206
	Cephalopoda	Idiosepiida	Idiosepiidae	Idiosepius	notoides					2		2
	Bivalvia	Mytiloida	Mytilidae	Brachidontes	erosus	64	18	469	282	24	288	$1x10^3$
	Bivalvia	Pectinoida	Pectinidae	Unid.	sp.1	2						2
	Bivalvia	Pterioidea	Vulsellidae	Electroma	georgiana	6						6
	Bivalvia	Veneroida	Donacidae	Donax	deltoides			14				14
Mollusca	Bivalvia	Veneroida	Mesodesmatidae	Paphies	elongata			$2x10^3$	137	192	129	$2x10^3$
	Bivalvia	Veneroida	Mesodesmatidae	Unid.	sp.1	18	12			32		62
Echinodermata	Echinoidea	Camarodonta	Temnopleuridae	Unid.	sp.1					2		2

Total catch	8x10^3	6x10^3	2x10^5	1x10^5	4x10^5	4x10^5	1x10^6
Number of species	58	53	53	42	45	40	

Table A3.7: Total abundances of fish species found from seine net hauls taken in beach surf zones for storm and calm weather events (Storm, S; Calm, C) and all regions: Metropolitan Adelaide, MA; Fleurieu Peninsula (FP) and South-East (SE).

			Region								
			MA		FP		SE		Overall	Fished = F	Mean standard length (cm)
Family	Genus	Species	S	C	S	C	S	C	abundance	Protected = P	(Range)
Arripidae	*Arripis*	*georgianus*	0	0	3	17	2	8	30	F	9.1 (7.8-11.0)
Arripidae	*Arripis*	*truttaceus*	2	0	39	4	81	93	219	F	9.8 (1.7-17.4)
Atherinidae	*Leptatherina*	*presbyteroides*	1	4	$1x10^3$	772	0	0	$2x10^3$		3.0 (1.7-6.0)
Clinidae	*Cristiceps*	*australis*	4	0	3	14	1	0	22		5.2 (1.9-8.8)
Clinidae	*Heteroclinus*	spp.	0	0	1	1	226	14	242		5.6 (3.4-14.0)
Clupeidae	*Spratteloides*	*robustus*	0	2	33	0	0	0	35		2.9 (2.3-3.5)
Clupeidae	*Sprattus*	*novaehollandiae*	10	0	0	0	0	0	10		1.8 (1.3-2.0)
Diodontidae	*Diodon*	*nicthemerus*	0	0	1	0	0	0	1		7.8
Enoplosidae	*Enoplosus*	*armatus*	1	2	36	59	7	0	105		2.9 (1.6-6.2)
Gobiesocidae	*Cochleoceps*	*spatula*	2	1	0	0	0	0	3		3.8 (3.5-4.0)
Gobiesocidae	*Parvicrepis*	sp.1	0	0	0	1	0	0	1		2.3
Hemiramphidae	*Hyporamphus*	*melanochir*	0	0	3	7	1	3	14	F	9.4 (3.4-18.5)
Leptoscopidae	*Leseurina*	*platycephala*	26	6	16	3	68	88	207		4.1 (1.5-8.7)
Monocanthidae	*Brachaluteres*	*jacksonianus*	1	0	0	0	0	0	1		1.5
Monocanthidae	*Scobinichthys*	*granulatus*	0	0	2	1	2	0	5	F	1.6 (0.9-3.8)
Mugilidae	*Aldrichetta*	*forsteri*	12	7	89	11	84	108	311	F	8.6 (2.1-27.0)
Odacidae	*Neodax*	*balteatus*	0	0	1	12	0	0	13		6.7 (3.1-8.5)
Odacidae	*Siphonagnathus*	*attenatus*	0	0	1	0	0	0	1		6.3
Platycephalidae	*Platycephalus*	*speculator*	10	32	2	7	0	0	51	F	7.0 (2.8-37.0)
Plotosidae	*Cnidoglanis*	*macrocephalus*	5	1	144	6	0	1	157	F	5.2 (2.6-45.0)
Rhombosoleidae	*Ammotretis*	*elongatus*	3	5	1	0	0	0	9	F	9.4 (7.3-11.5)
Rhombosoleidae	*Ammotretis*	*rostratus*	16	10	4	2	1	4	37	F	8.9 (6.0-21.0)
Rhombosoleidae	*Rhombosolea*	*tapirina*	2	0	0	1	0	0	3	F	12.6 (9.7-15.0)
Sillaginidae	*Sillago*	*schomburgkii*	1	3	0	9	0	0	13	F	3.6 (1.7-6.8)
Sparidae	*Acanthopagrus*	*butcheri*	0	0	3	0	0	0	3	F	7.4 (3.0-13.5)
Syngnathidae	*Histiogamphelus*	*briggsii*	0	1	8	2	0	1	12	P	13.9 (6.7-20.5)
Syngnathidae	*Histiogamphelus*	*cristatus*	0	0	0	5	0	0	5	P	8.0 (5.1-12.2)

Syngnathidae	*Kaupus*	*costatus*	0	0	0	1	0	0	1	P	7.7
Syngnathidae	*Lissocampus*	*caudalis*	0	3	0	0	0	0	3	P	5.4 (4.6-7.0)
Syngnathidae	*Pugnaso*	*curtirostris*	1	0	8	2	0	0	11	P	8.1 (2.8-15.8)
Syngnathidae	*Stigmatopora*	*argus*	0	0	2	0	0	0	2	P	10.7 (10.1-11.3)
Syngnathidae	*Stigmatopora*	*nigra*	1	8	0	0	0	0	9	P	7.6 (4.1-10.5)
Syngnathidae	*Vanacampus*	*margaritifer*	0	0	0	0	1	0	1	P	12.5
Syngnathidae	*Vanacampus*	*phillipi*	0	0	0	9	0	0	9	P	7.3 (4.9-11.3)
Tetraodontidae	*Contusus*	*brevicaudus*	16	19	8	53	0	2	98		2.7 (1.5-7.3)
Tetraodontidae	*Tectractenos*	*glaber*	3	4	258	107	4	1	377		5.7 (1.4-14.0)
Tetrarogidae	*Centropogon*	*latifrons*	0	0	1	0	0	0	1		0.7
Tetrarogidae	*Gymnapistes*	*marmoratus*	0	0	2	0	0	0	2		2.5 (2.4-2.6)
Urolophidae	*Urolophus*	*gigas*	0	0	0	1	0	0	1		30.5
	Total Catch		117	108	2x10^{3}	1x10^{3}	478	323	4x10^{3}		
	Number of species		19	16	26	25	12	11			

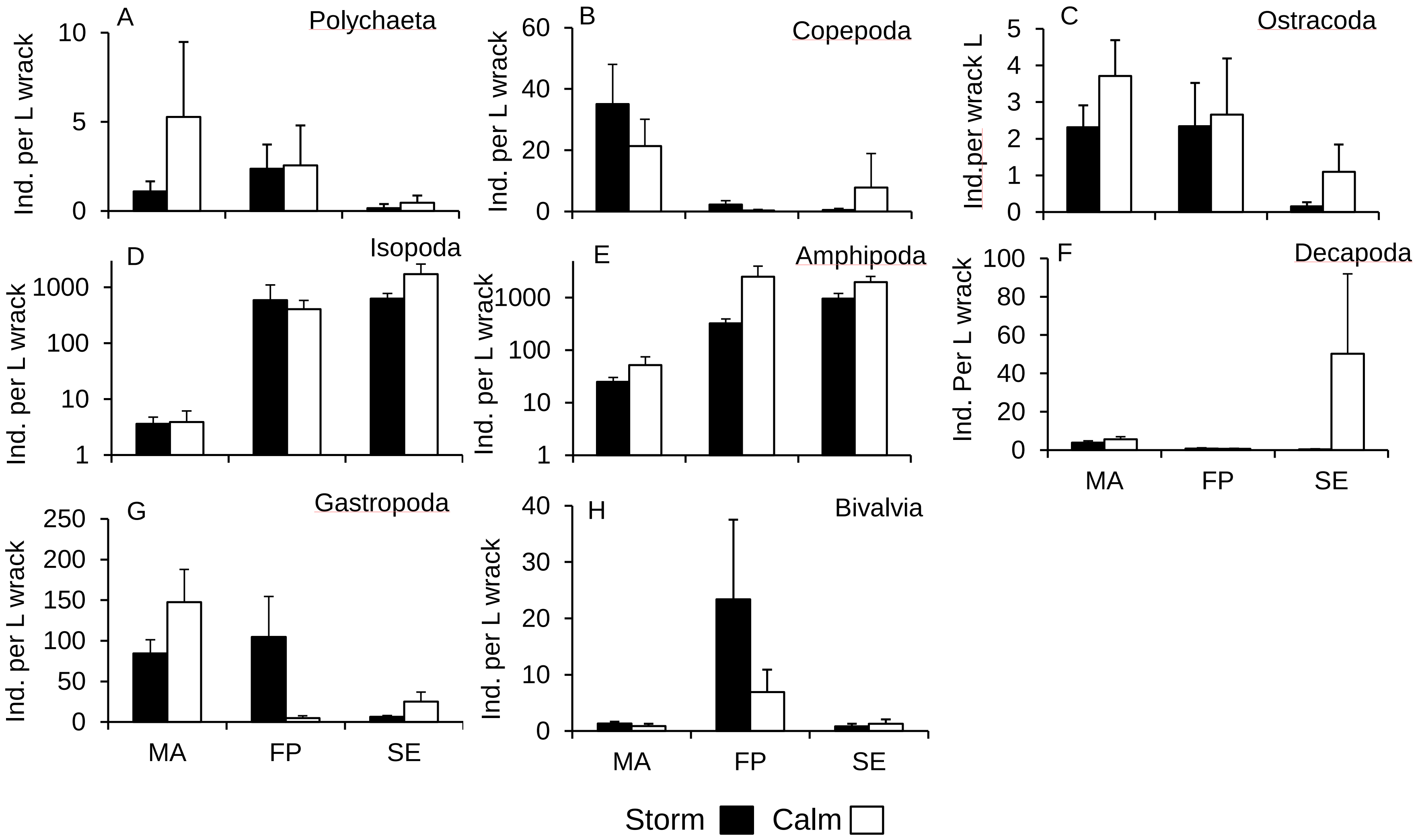

Figure A3.1: Mean (+SE) individual abundances of (A) Polychaetes, (B) Copepods, (C) Ostracods, (D) Isopods, (E) Amphipods, (F) Decapods, (G) Gastropods and (H) Bivalves captured in seine net hauls during storm and calm weather surveys in each of three regions druing 2012. Regions are MA, Metropolitan Adelaide; FP, Fleurieu Peninsula; and SE, South East. Note logarithmic scale on y axis for Isopods and Amphipods. Note the differences in scale on the y-axes across panels.

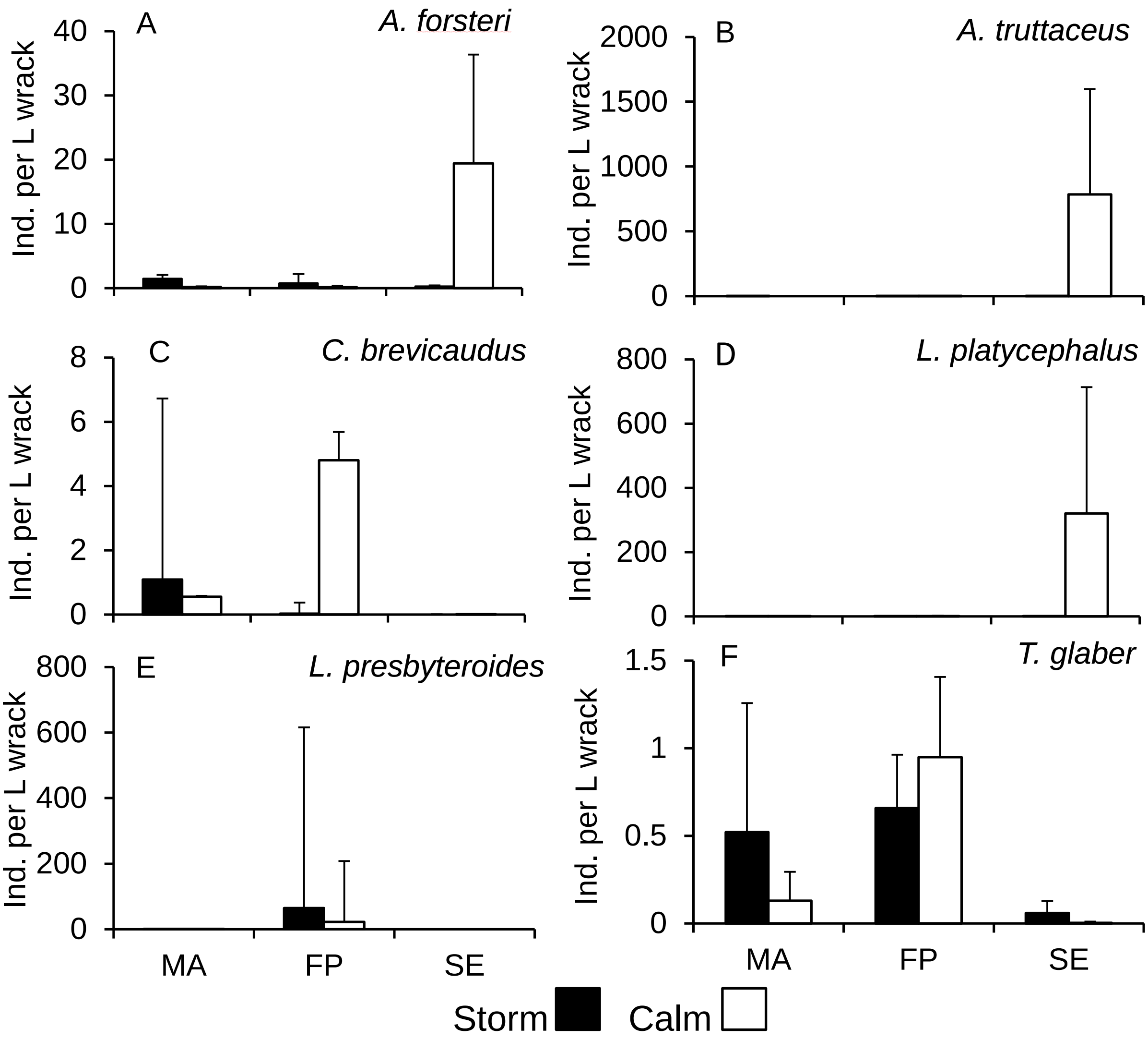

Figure A3.2: Mean (+SE) abundances of (A) *A. forsteri*, (B) *A. truttaceus*, (C) *C. brevicaudus*, (D) *L. platycephalus*, (E) *L. presbyteroides* and (F) *T. glaber* captured in seine net hauls during storm and calm weather surveys in each of three regions druing 2012. Regions are M, Metropolitan Adelaide; FP, Fleurieu Peninsula; and SE, South East. Note the differences in scale on the y-axes across panels.

Appendix 4

Table A4.1: Food items found in the most common fish species captured around wrack accumulations in sandy-beach surf zones at Basham Beach and Long Beach South during March 2013. Percent volume contribution (V %), Frequency of Occurrence Index (FOI %) and Gut Fullness Index (GFI) were calculated and are represented for each item. Standard errors are presented for GFI and V %. Bold values are for most common food items for each set of samples. Blank cells = < 0.1 %.

	Basham Beach				Long Beach South			
Fish species	*E. armatus*		*T.glaber*		*A. forsteri*		*T. glaber*	
	(*n* = 18)		(*n* = 20)		(*n* = 19)		(*n* = 20)	
Food items	V %	FOI %	V %	FOI %	V %	FOI %	V %	FOI %
Polychaeta			6.8 (± 4.7)	10.0	11.0 (± 5.9)	21.1		
Ostracoda	2.7 (± 1.9)	22.2	1.0 (± 0.9)	10.0				
Harpacticoida Copepoda	0.2 (± 0.2)	5.6						
Isopoda	**32.8** (± 6.7)	**88.9**	19.9 (± 6.8)	40.0			**50.1** (± 7.3)	**95.0**
Amphipoda	4.2 (± 2.5)	27.8	1.8 (± 1.4)	10.0	4.7 (± 4.7)	5.3	4.6 (± 2.0)	45.0
Brachyura	16.8 (± 5.8)	38.9	15.0 (± 6.7)	25.0			28.9 (± 6.8)	70.0
Caridea	5.0 (± 2.6)	22.2						
Gastropoda	1.5 (± 1.2)	11.1	2.6 (± 1.9)	10.0			1.3 (± 0.7)	25.0
Bivalvia	0.7 (± 0.5)	11.1						
Unidentified invertebrate tissue	19.8 (± 6.2)	44.4	**34.2** (± 9.2)	**50.0**	**68.5** (± 9.9)	**78.9**	8.9 (± 5.0)	40.0
Algae			1.2 (± 1.2)	5.0	5.3 (± 5.3)	5.3	1.9 (± 1.0)	35.0
Seagrasses	0.7 (± 0.7)	5.6	2.0 (± 1.2)	20.0			0.3 (± 0.2)	10.0
Unidentified detrital matter	4.3 (± 3.2)	27.8	12.6 (± 5.8)	40.0			3.9 (± 3.3)	20.0
Sand grains	0.2 (± 0.2)	5.6	3.0 (± 1.9)	15.0				
Number of food groups present	11		11		4		8	
GFI (%)	9.4 (± 1.6)		12.1 (± 1.8)		10.0 (± 2.9)		6.9 (± 1.0)	
Empty stomachs (%)	11.1		0		15.7		0	

Appendix 5

Table A5.1: Results from PERMANOVA pairwise tests for the variable cumulative distance travelled between time points for each release distance from shore (km) for all tag types resulting from the significant interaction term of Distance from shore (Dfs) x Tag type x Time point. Significant values are shown as * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$. Blank cells indicate no significant differences ($p > 0.05$).

Release distance	Tide height		Wind speed	
Time groupings	Natural	Artificial	Natural	Artificial
<u>0.25 km</u>				
0.5, 1				
0.5, 1.5				
0.5, 2				
0.5, 4				***
0.5, 6				
1, 1.5				
1, 2				
1, 4				***
1, 6				
1.5, 2				
1.5, 4				***
1.5, 6				
2, 4				***
2, 6				
4, 6		***		
<u>0.5 km</u>				
0.5, 1				
0.5, 1.5				
0.5, 2				
0.5, 4			***	**
0.5, 6			**	***
1, 1.5				
1, 2				
1, 4			**	**
1, 6				
1.5, 2				
1.5, 4				
1.5, 6				
2, 4				
2, 6				

A5.1 Cont’d

Release distance	Tide height		Wind speed	
Time groupings	Natural	Artificial	Natural	Artificial
4, 6				
<u>1.5 km</u>				
0.5, 1.5	*	*		
0.5, 2			*	*
0.5, 4			*	*
0.5, 6	**		*	
1, 1.5				
1, 2				
1, 4			*	
1, 6	***	**	**	*
1.5, 2				
1.5, 4				
1.5, 6	***	***	***	***
2, 4				
2, 6	*	*		
4, 6				
<u>3 km</u>				
0.5, 1				
0.5, 1.5				
0.5, 2	*			
0.5, 4				
0.5, 6	*		*	*
1, 1.5	***	***		
1, 2				
1, 4				
1, 6	*	*		
1.5, 2	***	***		
1.5, 4				
1.5, 6	*			
2, 4				
2, 6				
4, 6				

Table A5.2: Total macroinvertebrate abundances (pooled from *n* = 15, except 3 km *n* = 13) for all taxa captured at all distances from shore for both tag types, natural (NAT) or artificial (ASU) seagrass during tracking experiments in September - December 2013. Blank cells = zero values.

Taxa	Species	Distance from shore x tag type								Grand Total
		0.25		0.5		1.5		3		
		NAT	ASU	NAT	ASU	NAT	ASU	NAT	ASU	
Polychaeta	Ophellidae Sp.1							1		1
Crustacea	Cumacea Sp.1				1					1
	Tanaidae Sp.1			1		3				4
Copepoda	Calanoida Sp.1	3							1	4
	Harpacticoida Sp.1			1		1		1		3
Isopoda	Paranthuridae Sp.1							1		1
	Sphaeromatidae Sp.1					1				1
	Sphaeromatidae Sp.2							1		1
	Sphaeromatidae Sp.3	2								2
Amphipoda	Gammaridea Sp.1	14	3	92	3	11	2	3		155
	Gammaridea Sp.2	1		1		11	5	4		22
Mysida	Mysidae Sp.1					1		1		2
Decapoda	Hippolytidae Sp.1	67	3	7	2	4	1	6		9
	Latreutus sp.1	7		4				2		13
	Crab megalopa	22	8			2				32
Gastropoda	Lottidae Sp.1	1								1
	Trochidae Sp.1					2				2
Cephalopoda	*Idiosepius notoides*	2		3				2	1	8
	Total abundance	119	14	109	33	36	8	22	2	343
	Total species	9	3	7	3	9	3	10	2	18
	Total abundance per distance	133		142		44		24		

Table A5.3: Fish abundances for all species captured at all distances from shore (pooled from $n = 15$, except 3 km $n = 13$) for both tag types, natural (NAT) or artificial (ASU) seagrass during tracking experiments in September - December 2013. Blank cells = zero values.

Fish		Distance from shore x tag type								Grand total
		0.25		0.5		1.5		3		
Family	Species	NAT	ASU	NAT	ASU	NAT	ASU	NAT	ASU	
Arripidae	*Arripis georgianus*				1					1
Carangidae	*Psuedocaranx georgianus*					1				1
Monocanthidae	*Scobinichthys granulatus*	24	3	2	2	18	8	28	6	91
Syngnathidae	*Hippocampus breviceps*		1							1
	Stigmatopora argus		1						1	2
	Total fish	24	5	2	3	19	8	28	7	96
	Total species per distance	1	3	1	2	2	1	1	2	5
	Total abundance per distance	29		5		27		35		

Table A5.4: Total macrophyte volumes (L) for all species captured at all distances from shore (pooled from *n* = 3-10) around *in situ* drifting macrophytes during tracking experiments in September - December 2013. Blank cells = zero values.

		Distance from shore				Grand Total
Phylum	Species	0.25	0.5	1.5	3	
Heterokontophyta	*Caulocystis* sp.1	<0.1	0.3	0.2	0.1	0.6
	Sargassum sp.1	1.0	1.1	0.7	3.8	6.7
	Scaberia aghardii	0.1	<0.1	<0.1	0.2	0.3
Seagrasses	*Amphibolis antarctica*		<0.1	<0.1	<0.1	0.1
	Halophila ovalis			<0.1		<0.1
	Posidonia spp.	0.1	0.7	<0.1	<0.1	0.8
	Zostera spp.		<0.1	0.1		0.1
	Total volume	1.2	1.8	1.1	4.2	8.6
	Total species	4	6	7	5	7

Table A5.5: Macroinvertebrate total abundances (pooled from *n* = 3-10) for all taxa captured at all distances from shore around *in situ* drifting macrophytes during tracking experiments in September - December 2013. Blank cells = zero values.

		Distance from shore				Grand Total
Taxa	Species	0.25	0.5	1.5	3	
Polychaeta	Ophellidae sp.1	1			3	4
	Orbinidae sp.1	1				1
	Phyllodocidae sp.1		4			4
	Syllidae sp.1			3	2	5
	Syllidae sp.2				1	1
	Unid. polychaete sp.1			1	4	5
Arachnid	Acarina sp.1				1	1
	Pycnogonida sp.1		6	3		9
Crustacea	Cumacea sp.1			1		1
	Ostracoda sp.1		1		1	2
	Tanaidae sp.1	2	3		5	10
Copepoda	Calanoid sp.1	1	1			2
	Harpacticoid sp.1			1		1
Isopoda	Asellotta sp.1			3	1	4
	Crabyzos longicaudatus		1			1
	Cymothoidea sp.1		1			1
	Euidotea sp.1	5	14	3	2	24
	Ligiidae sp.1		4			4
	Paridotea sp.1	1		1		2
	Exosphaeroma sp.1	8	8	16	165	197
	Sphaeromatidae sp.1			1	10	11
	Sphaeromatidae sp.2	2	1	1	7	11
Amphipoda	Caprellidae sp.1	4	36	22	6	68
	Gammaridea sp.1	82	1329	239	70	1720
	Gammaridea sp.2	11	93	101	112	317

	Gammaridea sp.3		1	1	1	3
	Gammaridea sp.4			1	3	4
	Gammaridea sp.6		1			1
	Mysida sp.1		2	2		4
	Ochlesidae sp.1		4			4
Decapoda	Hippolytidae sp.1	1285	561	254	2105	4205
	Crab megalopa sp.1	255	7	10	80	352
	Hymenosomatidae sp.1	1	6	4	22	33
	Latreutus compressus	158	201	26	481	866
	Pilumnidae sp.1			1		1
Gastropoda	*Anachis atkinsoni*	1	10	1	2	14
	Cantharidella sp.1	1				1
	Lottidae sp.1					
	Neogastropoda sp.1		1			1
	Phasianella australis			1		1
	Trochidae spp.	2		2	4	8
Bivalvia	*Mimachlamys asperrimus*		1			1
	Mytilidae sp.1	1		1	16	18
Cephalopoda	*Idiosepius notoides*	8	26	26	20	80
	Total species	20	26	27	25	43
	Total abundance	1830	2323	726	3124	8003

Table A5.6: Fish total abundances (pooled from n = 3-10) for all species captured at all distances from shore around in situ drifting macrophytes during the tracking experiments in September - December 2013.

Fish Family	Species	Distance from shore				Grand Total
		0.25	0.5	1.5	3	
Clinidae	*Heteroclinus* spp.	3	1		2	6
Monocanthidae	*Scobinichthys granulatus*	112	66	49	228	455
Syngnathidae	*Hippocampus breviceps*			1	2	3
	Stigmatopora argus	1	1	19	5	26
Tetrarogidae	*Gymnapistes marmoratus*			12	3	15
Tripterygiidae	*Trianectes bucephalus*		2			2
	Total species	3	4	4	5	6
	Total abundance	116	70	81	240	507