CHAPTER FOUR: MACROFAUNAL COMMUNITIES: SURFACE-ACTIVE MACROFAUNA ASSOCIATED WITH WRACK DEPOSITS

Abstract

Wrack deposits provide potential food, shelter and breeding sites for marine and terrestrial invertebrate macrofauna and can support communities with high diversity, abundance and biomass. Macrofauna may also play important roles in the fragmentation, decomposition and incorporation of wrack into the beach and nearshore ecosystem. In this chapter I sampled surface-active macrofauna using pit-fall traps set overnight and assessed abundance, species richness and community structure of sandy-beach macrofaunal communities. Two studies were carried out.

In Study 1, I sampled the macrofauna that occurred at various positions on the beach face, specifically investigating occurrence with respect to wrack deposits. Sampling was conducted in 6 positions on the beach; three positions within the driftline (DL, in bare sand, among wrack and under wrack), above the DL (in bare sand and among wrack) and below the DL (in bare sand but not among wrack since none was present). A total of 6607 individuals from 20 species were captured, with the beach pill bug *Actaecia pallida* comprising 76% of the total abundance. The abundance and species richness of fauna differed significantly among positions, with communities in the DL having the most abundant and diverse fauna. Multivariate analyses indicated that positions within the DL (in bare sand, among wrack and under wrack) had similar macrofaunal communities that shared the same species and/or had similar abundances.

The aim of Study 2 was to determine whether macrofaunal communities utilising wrack deposits differed temporally (i.e. seasonally) and/or spatially (i.e. between beaches). I sampled the macrofaunal communities that occurred on 4 local South Australian sandy beaches (Robinson Point, Moana, Aldinga and Normanville) in each of four seasons over a one-year period. The sampling effort was designed to capture the widest representation of macrofaunal communities (i.e. as many of the

species occurring on the beach as possible), based on the results of Study 1. Pit-fall trapping was thus carried out within the DL in bare sand and under wrack and yielded 5961 individuals, comprising 2 marine and 60 terrestrial species. On average, 47 (± 4) individuals and 5.9 (± 0.2) species were captured in each quadrat (i.e. in two pit-fall traps within a $1m^2$ area). Five species each accounted for over 5% of the total individuals: a seaweed fly Coelopidae sp. 1; the sandhopper amphipod *Talorchestia quadrimana*; a mite Acarina sp. 1; the beach pill-bug *A. pallida*; and the weevil *Aphela phalenoides*. Macrofaunal communities (abundance, species richness and overall community structure) were variable in time (visits) and space (beaches and positions), as indicated by 3-way Analysis of Variance and multivariate analyses.

The macrofauna encountered in this study were diverse, with detritivores and predators present. The presence of predators and the dominance of terrestrial species in these wrack deposits suggest that the wrack had been present for a reasonably long time. The wrack deposits sampled in this study thus support multiple trophic levels and provide a basis for a food web spanning both marine and terrestrial habitats. Within the DL, macrofaunal abundances were higher and a different macrofaunal community was present, compared with outside the DL. Within the driftline itself, there were few differences between bare sand and wrack-covered areas, suggesting that the entire driftline area is equally important as a habitat and food resource. The driftline thus provides an area of beach with concentrated resources, which in turn concentrates a distinct macrofaunal community.

Introduction

Wrack deposits provide potential food, shelter and breeding sites for marine and terrestrial invertebrate macrofauna and can support communities with high diversity (Griffiths & Stenton-Dozey 1981; Lavoie 1985), abundance (Ochieng & Erftemeijer 1999; Dugan *et al.* 2003) and biomass (Koop & Griffiths 1982). Wrack provides the basis of a trophic web involving many trophic levels; macrofauna may consume the wrack itself, or the meiofaunal communities associated with wrack, or may be the first of higher-order predators. Wrack-associated macrofauna may also provide food sources for shore-birds, and when wrack is washed into the swash and nearshore zone, may provide prey for fish and larger subtidal invertebrates. The fragmentation

and abrasion caused by herbivorous and detritivorous species can also assist in the decomposition of wrack (Robertson & Mann 1980). Macrofauna thus play important roles in the fragmentation, decomposition and incorporation of wrack into the beach and nearshore ecosystem.

Like wrack deposits, the associated macrofaunal assemblages are variable in time and space. Following deposition of wrack, successional changes may occur in the species composition and abundance of the associated macrofauna (Rodil *et al.* 2008). Herbivorous amphipods, dipterans and coleopterans rapidly colonise wrack deposits within just one to two days (Griffiths & Stenton-Dozey 1981; Koop & Griffiths 1982; Inglis 1989; Jedrzejczak 2002a; Colombini & Chelazzi 2003) but, as wrack dries and ages and prey become available, there may be a shift towards terrestrial (Lavoie 1985) and predatory (Colombini *et al.* 2000) taxa. Seasonality in the recruitment, reproduction and activity of macrofauna, and their tolerances to environmental conditions (e.g. temperature) may also result in longer-scale temporal shifts in macrofaunal communities. The spatial distribution of wrack on the beach may also affect the macrofauna that colonise the deposits. Wrack deposits in the mid and low shore are more likely to be colonised by marine taxa, whereas high-shore deposits may be dominated by terrestrial insects and their larvae (Egglishaw 1965). Large wrack deposits have also been shown to support higher abundances and different macrofaunal communities compared to small deposits (Egglishaw 1965; Griffiths & Stenton-Dozey 1981). There is also evidence to suggest that increases in macrofaunal diversity and abundance occur at the level of the current driftline (Koop & Griffiths 1982), rather than occurring over the entire beach face. Finally, the type of wrack (e.g. algal vs. seagrass material) may influence the associated macrofaunal community. The majority of studies indicate that consumption of seagrass wrack by macrofauna is minimal (Robertson & Mann 1980; Jedrzejczak 2002a) but the consumption of algal wrack may be considerable (e.g. between 60 and 80% of kelp wrack on South African beaches is consumed by amphipods and dipteran larvae within 14 days after deposition, Griffiths & Stenton-Dozey 1981). Thus, to characterise the macrofaunal communitues associated with wrack deposits is a complex task, requiring consideration of temporal and spatial variability.

There were three aims of the first study (hereafter Study 1), which also served as an

overall pilot study. First, I wanted to sample the macrofauna (i.e. abundance, species richness and community structure) that occurred at various positions on the beach face, specifically investigating occurrence with respect to wrack deposits. Second, I wished to determine the appropriate number of replicates and sub-samples that should be used in a second study (Study 2). Finally, I aimed to determine where on the beach sampling should be carried out in Study 2 so that the maximum number of species and most distinct communities could be sampled with least effort. The aim of Study 2 was to determine whether macrofaunal communities utilising wrack deposits differed temporally (i.e. seasonally) and/or spatially (i.e. between beaches). I repeatedly sampled the macrofaunal communities that occurred on 4 local South Australian sandy beaches (Figure 4.1). The sampling effort was designed to capture the widest representation of macrofaunal communities (i.e. as many of the species occurring on the beach as possible), based on the results of Study 1. Sampling was conducted once in each season over one year, and beaches were selected to encompass a range of wrack covers/volumes and types.

Methods

These studies used pit-fall trapping to sample the macrofaunal communities. Pit-fall trapping differs from coring, another method often used to sample macrofauna, in that it samples surface-active macrofauna over a set period of time (in this case overnight), rather than being a snap shot of what is present at any given moment. Pit-fall trapping is also a more effective method for sampling nocturnal species than coring. Pit-fall trapping can be more efficient than coring and sieving sediment samples; it is less time consuming and yields fewer null samples (Langley 2006; pers. obs.).

Study 1: Pilot study and sampling of beach levels

A pilot study was carried out at Robinson Point beach (Figure 4.1) on February 6th – 7th, 2007. Sampling was conducted in 6 Positions on the beach. Three Positions within the drifline (DL) were sampled; DL Wrack (DL W, traps placed adjacent to wrack patches), DL Bare sand (DL B, less than 5% wrack in surrounding 1m^2), and DL Under wrack (DL U, traps positioned under wrack patches) (Figure 4.2). Two

Positions, above the DL (ADL B) and below the DL (BDL B) were also sampled with less than 5% wrack cover. The ADL and BDL were randomly selected distances above (approximately 4-5m) and below (approximately 5-6m) the DL, respectively. Targeted sampling of wrack patches away from the DL was also carried out. Ideally, this would have included sampling wrack patches both below and above the DL but due to the very sparse wrack cover below the DL, only above-DL wrack patches could be sampled; these samples targeted Wrack patches (ADL W) (Figure 4.2). Four replicates (quadrats) were sampled for each Position and three pit-fall traps (sub-samples) were used per quadrat. Pit-fall traps were positioned haphazardly within the quadrat, at least 30cm apart, and according tothe wrack cover as described above. A total of 72 pit-fall traps were deployed and a total of 24 quadrats were sampled.

Study 2: Main study: 4 beaches sampled in 4 seasons

The sampling regime was designed to investigate seasonal differences in the faunal communities associated with wrack and any differences between beaches with varying wrack cover and composition. Sampling was conducted on 4 occasions; once in each season (autumn, winter, spring and summer). Sampling was timed so that the driftline (and hence the pit-fall traps) would not be inundated overnight and thus, in general, sampling was carried out when high tides occurred in the late afternoon or evening. The dates of sampling were 22nd – 24th May (autumn), 9th – 11th July (winter), 8th October (spring) and 17th December (summer) of 2007. Four beaches along the southern metropolitan and upper Fleurieu Peninisula were sampled; Robinson Point, Moana, Aldinga and Normanville (Figure 4.1). The beaches were chosen so that they were in reasonable proximity to one another so that differences due to geographical location could be minimised.

Sampling was conducted within the driftline, DL, in two positions based on the amount of wrack present within a 1m^2 quadrat. These were Bare sand (B) and Under wrack (U). For the U Position, surface wrack was carefully removed, the trap was positioned and the wrack was replaced to cover the trap opening. Four replicate quadrats were sampled for each position and two pit-fall traps (sub-samples) were used per quadrat. Thus, 8 quadrats were sampled on each beach, and the total *n* for

this study was 128 quadrats (4 Seasons x 4 Beaches x 2 Positions x 4 replicate quadrats).

Field methods

On each beach, the overall percent wrack cover was estimated using the photopoint method (see Chapter 2). Replicates consisted of a $1m^2$ quadrat, inside which the wrack cover was estimated and the pit-fall traps were placed. In Study 1, 3 pit-fall traps were placed in each quadrat but in Study 2 this was reduced to 2 pit-fall traps per quadrat. Quadrats were placed on the sand during the initial set-up of the traps and were removed immediately to allow access by fauna. Quadrats were positioned haphazardly, at least 3m apart, within each beach level. For the Under wrack position, surface wrack was carefully removed, the trap was positioned and the wrack was replaced to cover the opening of the trap.

The pit-fall traps, constructed from PVC pipe, were 10 cm in diameter and 20 cm in height. A plastic container was fitted snugly into the bottom to collect fauna. Traps were positioned so that the upper rim was flush with the sediment and the surrounding sediments were left as intact as possible. Upon collection, the contents of each pit-fall trap were quickly emptied into a pre-labelled zip-lock bag, or if the traps had become wet (due to overnight rain, not inundation by the tide), the entire trap was placed in the bag.

Pit-fall traps were set out in the evening and were retrieved the following morning, as close as possible to dusk and dawn, respectively. Due to changes in day/night length between seasons, trapping time did vary between seasons but was relatively consistent between beaches for each season. Overall, trapping time varied between 12 and 16 hours. Thus, the trapping effort can be standardised as ‘overnight’ or standardised by the number of trapping hours. Abundance data were analysed using both of these measures. Due to logistical reasons, 2 beaches (randomly selected) were sampled on each evening. Sampling of all 4 beaches was carried out within a maximum of 3 nights to minimise bias between beaches due to temporal variation such as changes in tide times and/or range.

Laboratory methods

The contents of each pit-fall trap were returned to the laboratory and frozen to facilitate processing (because live fauna escape too easily) before being rinsed over a 500um mesh sieve. The fauna retained on the sieve were then identified to the lowest possible taxonomic unit and counted. Sub-samples (# of pit-fall traps/quadrat, i.e. 3 traps in Study 1, and 2 traps in Study 2) were pooled to calculate the total number of individuals (abundance) and number of species (species richness) per quadrat. For Study 2, abundance was also calculated as a rate per hour of trapping (individuals per hour), since trapping time differed between beaches and visit. Since not all taxa could be identified to species, the level of taxonomic classification varies. Larvae were particularly difficult to assign to species and thus where larvae and adults that could potentially be the same species occurred, these were counted separately for the purposes of species richness counts.

Statistical data analysis

Univariate analyses

Univariate analyses were carried out using SYSTAT v.11. For Analysis of Variance and regression, assumptions were checked by inspection of histograms and scatterplots of the residuals. Data were transformed ($\sqrt{}$ or 4^{th} root) as appropriate.

Multivariate analyses

Data were standardised because the actual area/volume of beach sampled by a pit-fall trap may differ between traps or between macrofaunal species. In addition, the trapping time was not identical between beaches and/or seasons (see above). Analyses were performed on standardised data without transformation and on standardised data with a 4^{th} root transformation, which lessens the influence of the most abundant species. Fourth-root-transformed data showed more apparent and consistent patterns than the un-transformed data and gave better separation of groups and thus only the 4^{th} root-transformed data are presented here. Two-dimensional MDS plots were produced using Bray-Curtis similarities. Analysis of similarity (ANOSIM), with 999 permutations, was performed to assess any differences in taxonomic composition and relative abundances among the groups (i.e. factors of Positions, Visits or Beaches). Similarity percentages (SIMPER) analyses were run to determine within-group similarities and between-groups dissimilarities. A high value

of percentage similarity within groups indicates group cohesion and a high dissimilarity between groups indicates distinct communities, for which indicator taxa were also identified using SIMPER analyses. A taxon may be considered a consistent indicator if their ratio of dissimilarity to standard deviation is equal to or greater than 1 (Clarke & Warwick 1994). Multivariate analyses were run using PRIMER v.5 software.

Study 1

Univariate analyses

A one-way Analysis of Variance (ANOVA) was used to determine whether the abundance and species richness of macrofauna differed between Positions. Position was a fixed factor with 6 levels, BDL B, ADL B, ADL W, DL B, DL W and DL U (Figure 4.2). Analyses were conducted on abundance and species richness with the three sub-samples pooled for each quadrat. Analysis of CoVariance (ANCOVA) was used to determine whether the covariate of % wrack cover in each quadrat could explain any additional variance in the abundance and species richness of the fauna. Percent wrack cover (log [x + 1]-transformed) was used as the covariate.

Power analyses were run on abundance and species richness data. To determine the appropriate number of sub-samples (pit-fall traps) in each quadrat, power analyses were run using a 2-way ANOVA for Position and Quadrat (nested in Position) was run with pit-fall traps as the replicates. I also ran power analyses to determine the appropriate number of quadrats per Position. A one-way ANOVA with Position was used as the model, with quadrats as the replicates. Power analyses were run using both 2 and 3 sub-samples per quadrat.

Multivariate analyses

A two-dimensional MDS plot was constructed. One-way ANOSIM was performed to assess any differences in taxonomic composition and relative abundances among the Positions. SIMPER analysis was run to determine within-group similarities (i.e. within each Position) and between-groups dissimilarities (i.e. among Positions).

Study 2

Two traps were excluded from the analyses due to excessive disturbance around the traps (probably due to a dog digging around the traps). These traps were from Moana beach during the May sampling event and were from one quadrat positioned in the Bare sand. Thus, this quadrat was omitted from the analyses and the sample size was only 127 quadrats.

Univariate analyses

A 3-way ANOVA was used to determine whether there were significant differences in the abundance and species richness of macrofauna. Species richness of common species (i.e. excluding species that were encountered only once or twice) and abundance standardised for the number of trapping hours (individuals per hour) were also analysed. The three factors were Visit, Beach and Position. Visit (4 levels) and Beach (4 levels) were considered random factors and Position was a fixed factor with 2 levels (B vs. U). ANCOVA was used to determine whether the covariate of % wrack cover in each quadrat (√-transformed) could explain any additional variance in the abundance or species richness.

Multivariate analyses

A two-dimensional MDS plot was constructed. A set of three, two-way crossed ANOSIM tests were performed to identify differences in taxonomic composition and relative abundances among Positions, Visits and Beaches. The tests were: Visit x Position; Beach x Position; and Visit x Beach. SIMPER analyses were run to determine within-group similarities and between-groups dissimilarities for each factor. Data were also analysed using the aggregate function in PRIMER to aggregate species data to Order. A 2-D MDS was constructed and the same analyses were performed on this data set. The RELATE routine in PRIMER was used to assess relationships between the multivariate patterns from the data at the species level and at the Order level. MVDISP was used to assess multivariate dispersion of groups of samples (i.e. for each Position).

A composite 'factor', including information on Visit, Beach and Position was constructed to allow some estimate of the combined effects of all three factors simultaneously. This yielded 32 combinations of Visit, Beach and Position. A one-

way ANOSIM and SIMPER were then used to determine whether the faunal communities differed among the groups.

The BIO-ENV procedure in PRIMER was used to match environmental data to the macrofaunal communities. The environmental data included wrack cover at 3 scales (within the $1m^2$ quadrat i.e. in the immediate vicinity, DL % cover and whole beach % wrack cover), position of the DL on the beach (distance from base of the first dune to the DL, the width of DL and the total beach width) and wrack composition (% algal wrack). Only wrack cover within the $1m^2$ quadrat is at the scale of quadrats. All other environmental data is for each visit to each beach (i.e. applies to both B and U Positions), and thus some values are repeated. The BIO-ENV procedure was run on standardised, log (x+1)-transformed data using the Spearman rank correlation method, and a maximum of 5 variables were included at any one time.

Results

Study 1

Descriptive findings

A total of 6607 individuals, comprising 20 species, were captured in the 72 pit-fall traps that were deployed and retrieved (Table 4.1). This was, on average, 92 (± 9 se) individuals and 4.8 (± 0.2) species per trap. Every trap had a minimum of three individuals with up to a maximum of 303 individuals per trap. Species richness ranged between 1 and 9 species per trap. Of the 20 species captured, 6 occurred only once (singletons) and 2 occurred only twice (doubletons). The remaining 12 species accounted for over 99% of the total abundance. The 20 species identified comprised members of 9 Orders. Coleoptera accounted for the largest number of species (7 species) but only contributed 5% of the total abundance (355 individuals). The beach pill bug *Actaecia pallida* accounted for 76% (5010 individuals) of the total abundance and the talitrid amphipod *Talorchestia quadrimana* accounted for 17% (1126 individuals) of the total abundance (Table 4.1). Each of these species were the only members of their Orders found (Isopoda and Amphipoda, respectively) (Table 4.1). The remaining 18 species thus contributed only 7% of the total abundance (471 individuals).

The three sub-samples were pooled for each quadrat yielding abundances of between 42 and 676 individuals and species richnesses of between 2 and 9 species per quadrat. There were, on average, 275 (± 42) individuals and 6.7 (± 0.4) species per quadrat. The ADL Position had the lowest mean abundance (73 ± 7 individuals) whilst the highest mean abundance of 544 individuals (± 50) occurred in the DL B Position (Figure 4.3a). The BDL B Position had the lowest mean species richness (2.8 ± 0.3 species), compared with the highest mean species richness of 8 species (± 0.4) for both the DL W and DL U Positions (Figure 4.3b).

Power analyses

The power analyses to determine the appropriate number of sub-samples (pit-fall traps) in each quadrat indicated that to achieve a power of 80%, 2 sub-sample pit-fall traps per quadrat were required. Power analyses to determine the appropriate number of quadrats per Position indicated that, using 4 replicate quadrats per Position, a power of 79% and 77% was achieved for abundance and species richness, respectively. By increasing the sampling effort to 5 quadrats per Position, power was increased to 91% and 89% for abundance and species richness, respectively. The additional effort required to sample 5 quadrats instead of 4 quadrats in the second study (i.e. 64 traps = 2 traps x 2 Positions x 4 beaches x 4 seasons) was deemed unneccesary, since the power achieved using 4 quadrats was very close to the target 80% (Fairweather 1991). Thus, for Study 2, a sampling regime of 4 quadrats per Position and 2 sub-sample pit-fall traps per quadrat was used.

Univariate analyses

The one-way ANOVA for Position indicated that the abundance and species richness of fauna differed between Positions (Table 4.1, $p < 0.001$ for both abundance and species richness). Tukey's post-hoc tests were used to identify differences among Positions. Positions within the DL had the highest abundances of fauna (Figure 4.3a); the DL B and DL W Positions had significantly higher abundances than any of the other Positions, except for the DL W Position, which was not significantly different to the DL U Position. There were no other significant differences among the other Positions (Table 4.1 and Figure 4.3a). For species richness, the BDL B Position had significantly fewer species than any other Position but there were no differences

among any of the other Positions (Table 4.1 and Figure 4.3b). The covariate (% wrack) was not significant for either abundance or species richness but the main effect of Position remained significant.

Multivariate analyses

The 2-dimensional MDS plot showed reasonably distinct communities based on Position (Figure 4.4). Samples from within the DL (DL B, DL W and DL U) were plotted in a group, although the DL U samples were slightly apart and more spread out than the other DL (B or W) samples (Figure 4.4). Samples from the DL B and DL W plotted closely (Figure 4.4), indicating that these communities were quite similar. Samples from the ADL B and ADL W Positions overlapped somewhat (Figure 4.4), indicating that these communities shared the same species and/or had similar abundances to some extent. Samples for the BDL B Position were plotted away from all other Positions (Figure 4.4), indicating that the BDL B had a different community structure to the other five Positions. The 2-D stress was low (0.12) indicating that the plot was a good 2-dimensional representation of the relationships among the samples (Clarke & Warwick 1994).

The ANOSIM Global *R* value was 0.540 ($p = 0.001$), indicating significantly-different macrofaunal communities among Positions. The BDL B community was significantly different to all other Positions (Table 4.2). In addition, the DL B Position had a different community structure to all of the other Positions except for the DL W Position (Table 4.2). Adding to the evidence provided by the SIMPER analysis that Positions that were physically close were similar, the ADL B and ADL W communities were not distinct and furthermore Positions with similar wrack cover (i.e. DL W, DL U and ADL W) also had similar communities (Table 4.2). Multivariate dispersion was highest for the DL U samples (1.658), supporting the observation that these samples were spread out in the MDS plot (Figure 4.4).

These results were supported by SIMPER analyses. Between-groups dissimilarity was lowest for the DL W and DL B Positions (14%), i.e. these communities had similar species and abundances of those species. The BDL B and DL U Positions had the most distinct communities (between-groups dissimilarity = 40%). Positions that were physically located close together (i.e. within the DL or above the DL) tended to

have lower between-groups dissimilarity than those that were physically far apart. For example, ADL B and ADL W samples had low between-groups dissimilarity (22%) compared to the BDL B and ADL B or ADL W Positions (36%). Samples that were taken from Positions with similar wrack cover (i.e. DL W and ADL W Positions) also tended to be more similar (i.e. between-groups dissimilarity = 20%).

Due to their very high abundances, the beach pill bug *A. pallida* and the sandhopper amphipod *T. quadrimana* consistently contributed the greatest percentages to within-group similarities (between 28 and 58% and 22 and 40%, respectively). Except for the BDL B Position, the weevil *Aphela phalenoides* contributed the third highest percentage to within-groups similarity (13 – 17%). For the significant pair-wise comparisons (identified by ANOSIM), SIMPER was used to identify indicator species (Dissimilarity/SD > 1, Clarke & Warwick 1994) of Position (Table 4.3). Only those species contributing at least 10% to between-groups dissimilarity are included: seven species were identified as indicator taxa in at least one pair-wise comparison; *A. phalenoides*, the beetle, *Symenena amphibia*, an unidentified weevil Curculionidae sp. 1, a beetle Tenebrionidae sp. 1, a spider Lycosidae sp. 1, an ant Formicidae sp. 2, and an earwig Forficulidae sp. 1 (Table 4.3 and Appendix C).

Study 2

Descriptive findings

Of the 254 pit-fall traps that were deployed and retrieved over the total sampling effort, only one trap was devoid of fauna. There were, on average, 23 (± 2) individuals and 4.2 (± 0.1) species per trap. The two sub-samples per quadrat were pooled and thus every quadrat had at least one individual present. A total of 5961 individuals, comprising 62 marine and terrestrial 'species' were collected (Appendix C). Only 2 species are considered to be truly marine, however, the isopod *Cirolana corpulenta* and the crab *Cyclograpsus audouinii*. There were, on average, 47 (± 4) individuals and 5.9 (± 0.2) species per quadrat (*n* =127 quadrats). Species richness ranged between 1 and 14 species per quadrat, and the number of individuals was between 1 and 278 individuals. Of the 62 species recorded, 24 species were considered 'rare'; 18 species occurred only once (singletons) and a further 6 occurred only twice (doubletons). When these rare species were removed from the data set, the

mean (common) species richness was reduced slightly (5.7 ± 0.2 species) and the maximum species richness was 13 species. Of the rare species, 14 occurred in the Wrack quadrats, 9 occurred in the Bare sand quadrats and one species (a doubleton) occurred once in each Position. Thus, of the 66 species, 38 species were considered 'common', and these accounted for over 99% of the individuals. Five species each accounted for over 5% of the total individuals: a seaweed fly Coelopidae sp. 1 (24%); the sandhopper amphipod *Talorchestia quadrimana* (21%); a mite Acarina sp. 1 (19%); the beach pill-bug *Actaecia pallida* (12%); and the weevil *Aphela phalenoides* sp. 1 (9%).

The 62 species represented 18 orders. The Coleoptera (beetles) had the highest species richness (22 species) and contributed 14% of the abundance. The Diptera (true flies) contributed 10 species and the largest proportion of the abundance (28%). Araneae and Hymenoptera contributed 6 and 5 species, respectively, but abundances were low for these Orders (only 55 and 16 individuals, respectively, i.e. less than 1% each). The Isopoda contributed only 3 species but one of these, *A. pallida*, accounted for 12% of the abundance. The Order Amphipoda contributed only 1 species, *T. quadrimana*, but that species accounted for 21% of the abundance. Similarly, the Acarina (mites) had only 2 species, one of which contributed only 1 individual. The other species of Acarina (sp. 1) was quite an abundant species (1144 individuals = 19% of the abundance). The remaining Orders contributed only 1 or 2 species and had low abundances. Four 'species' of larvae were included in the 62 species.

The mean abundance and species richness were higher for the Under wrack position than for the Bare sand position (Figure 4.5 and Figure 4.6). Quadrats in the Under wrack Position had, on average, 52 (± 6) individuals and 7.0 (± 0.3) species, whereas the Bare sand quadrats had a mean of 42 (± 5) individuals and 4.7 (± 0.2) species. Abundance was highest in July (66 ± 11 individuals, Figure 4.5a) and species richness was highest in October (7.5 ± 0.5 species) (Figure 4.5b). Both abundance and species richness were lowest in December (18 ± 2 individuals and 4.8 ± 0.3 species) (Figure 4.5). Normanville had the highest abundance and species richness of any beach (61 ± 11 individuals and 6.4 ± 0.4 species) (Figure 4.6). Moana had the lowest abundance (29 ± 5 individuals, Figure 4.6a) whilst Aldinga had the lowest species richness (5.5 ± 0.5 species) (Figure 4.6b).

Overall, mean wrack cover per quadrat was 30% (± 3) and ranged between 0.5% and 98%. The Bare sand Position quadrats had much lower wrack cover (7 ± 1%) than the Under wrack Position quadrats (52 ± 3%) but there was an overlap in the ranges of % coverage (0.5 – 35% and 5 – 98% for B and U, respectively). Mean wrack cover did not vary greatly between Beaches and ranged between 28 and 33%. There was a slightly greater range in mean wrack cover for each Visit (24 - 36%), with the lowest and highest covers occurring in December and July, respectively.

Univariate analyses

There was a significant, 3-way interaction between Visit, Beach and Position for the abundance ($p < 0.001$), species richness ($p = 0.003$), common species richness ($p = 0.009$) and abundance standardised by the number of trapping hours ($p < 0.001$) (Figures 4.5 and 4.6, Table 4.5). This significant interaction subsumes all other significant effects. The interaction involves the random factors Visit and Beach and thus no further interpretation is required (Underwood 1997).

Percent wrack cover (per quadrat, √- transformed) was used as a covariate in the 3-way ANCOVA. The covariate was not significant for abundance or abundance standardised by the number of trapping hours, and the 3-way interaction remained significant. The significance of the 2-way interactions and main effects did not change. For species richness and common species richness the covariate % wrack cover was significant ($p = 0.007$ and $p = 0.009$, respectively) but the 3-way interaction remained significant ($p = 0.001$ and $p = 0.003$, respectively). For species richness, the interaction of visit and beach became significant ($p = 0.031$) but the significance of the other interactions and main effects did not change. The significance of the 2-way interactions and main effects did not change for the common species richness. In each of these analyses, the significant 3-way interaction subsumes all other interactions and main effects.

Multivariate analyses

The 2-dimensional MDS plot of the 4th root-transformed data showed some separations of samples based on Position but there was overlap between the two

groups (Figure 4.7a). The MDS with symbols plotted by Visit and Position (Figure 4.7b) also showed some separations of Visits, with the December samples plotted further from the other Visits. There was also some separation of samples based on Beach (Figure 4.7c) but there was considerable overlap between the Beaches. The 2-D stress was moderate (0.23) and thus the MDS procedure was repeated several times; on each repeat the same stress value was obtained. The large number of samples (n = 127) was likely responsible for the moderate stress. According to the recommendations of Clarke and Warwick (1994), the conclusions drawn from the MDS plot were cross-checked with a cluster analysis and the use of ANOSIM and SIMPER. Results of these were concurrent and thus the MDS was deemed an adequate representation of the relationships among the samples.

A set of three, two-way crossed ANOSIM tests were performed to identify differences in macrofauanl communities between Positions, Visits and Beaches (Table 4.6). The tests were: Visit x Position; Beach x Position; and Visit x Beach. For each ANOSIM, both factors had significant Global R values (Table 4.6a), indicating that the macrofaunal communities differed between Positions, Visit and Beaches. Examination of the pair-wise differences for the Visits and Beaches when crossed with Position indicated significant differences between Visits and Beaches (Table 4.6a and b). The composite 'factor', including information on Visit, Beach and Position was used as the factor in a one-way ANOSIM. The Global R was large (0.797) and significant (p = 0.001) and of the 496 pairwise comparisons, 465 were significant ($p < 0.05$).

Data were also analysed with the 62 species aggregated into their 18 Orders. The patterns seen were very similar (i.e. similar Global R and pair-wise R values) to those found for the data including all available taxonomic information (Table 4.6b). All Global R values were significant (p = 0.001) and all pair-wise comparisons were also significant. For Positions, within-group similarity increased but between-groups dissimilarity decreased (from 70% for the 66 taxa to 54% for the 18 Orders). The RELATE procedure in PRIMER was used to relationships in the multivariate patterns of the two ordinations. The Rho value was high (0.802) and significant (p = 0.001), indicating that the patterns were very similar.

Four species were classified as indicator species (i.e. had Dissimilarity/SD > 1, Clarke & Warwick 1994 and contributed at least 10% to between-groups dissimilarity) in at least one pair-wise comparison between Positions, Visits and/or Beaches (Table 4.7). These were a seaweed fly Coelopidae sp. 1, a mite Acarina sp. 1, *A. pallida* and *T. quadrimana* (Table 4.7). Coelopidae sp. 1 was the only consistent indicator of Position, with greater abundances occurring Under wrack than in Bare sand (Table 4.7).

The BIO-ENV procedure yielded only low correlations between environmental variables and macrofaunal communities. The highest correlation ($\rho_w = 0.298$) included 5 variables: beach width, DL width, % wrack in the $1m^2$ quadrat, the distance from the dune to the DL, and the % algal wrack. The best single-variable predictor was beach width ($\rho_w = 0.222$), with the inclusion of each additional variable (in the order listed) only slightly increasing the correlation coefficient.

Discussion

The macrofauna encountered in this study were diverse, representing 62 species from 18 Orders in total. On one beach alone (Robinson Pt, Study 1), 20 species were captured in a single sampling event. These results fall in the range reported by previous studies, which have reported species richnesses of between 6 (McLachlan 1985) and 75 (Egglishaw 1965) species of macroinvertebrates associated with wrack deposits (Table 4.8). Previous studies have also found that Coleopterans (beetles) are the most diverse group, contributing over 50% of the species (Griffiths & Stenton-Dozey 1981; Lavoie 1985; Inglis 1989). My results also showed that coleopterans were the most diverse group although they contributed a smaller proportion of the total species richness; only 35% and 33% of the species in Study 1 and Study 2, respectively. The other taxa encountered in this study included similar taxonomic groups to previous studies, including Diptera (true flies), Arachnida (mites and spiders), and Crustacea (amphipods and isopods) (Egglishaw 1965; Inglis 1989; Jedrzejczak 2002; Ince *et al.* 2007).

Although not all fauna were identified to species level, and thus their exact trophic niche is not always known, herbivorous/detritivorous species and predators were

both represented. Predatory taxa such as staphylinid beetles and spiders colonise older wrack deposits, presumably in response to the availability of their prey (Colombini *et al.* 2000), and terrestrial species are known to colonise wrack once it has dried sufficiently (Griffiths & Stenton-Dozey 1981; Lavoie 1985). The presence of predators (e.g. Arachnida and the rove beetles *Cafius* spp.) and the dominance of terrestrial species in these wrack deposits thus suggest that the wrack had been present for a reasonably long time, a result supported by personal observations that the wrack deposits sampled were located in the high shore zone and were relatively old and dry. Only a small number of larval forms and few individuals (4 species and 112 individuals in Study 2) were captured in this study, in contrast to previous work (Egglishaw 1965; Lavoie 1985). This is likely an artefact of the pit-fall trapping method, which samples surface-active fauna rather than fauna which are present in the sediments or wrack itself. Their presence in the pit-fall traps, however, suggests that they are present in these wrack deposits. The wrack deposits sampled in this study thus support multiple trophic levels and provide a basis for a food web spanning both marine and terrestrial habitats.

The most abundant taxa in these studies (Coelopidae sp. 1, *T. quadrimana* and *A. pallida*) have previously been reported as the dominant members of wrack-associated macrofaunal communities. Coelopidae sp. 1 (Diptera) dominated the abundance in Study 2; this result concurs with previous reports that flies are abundant and can dominate macrofaunal communities in wrack deposits (Egglishaw 1965; McAlpine 1991; Blanche 1992). The amphipod *T. quadrimana* was the second-most abundant species in Study 2; again amphipods are well-known macrofauna from wrack accumulations (Griffiths & Stenton-Dozey 1981; McLachlan 1985; Jaramillo *et al.* 2006). The beach pill-bug *A. pallida* dominated the abundance (76%) in Study 1. This isopod was ubiquitous over the entire beach face, suggesting that it is highly mobile, and utilises the whole beach rather than just the wrack deposits.

Macrofaunal abundances were higher within the driftline than away from the driftline. Within the driftline itself, there were few differences between bare sand and wrack-covered areas, suggesting that the entire driftline area is equally important as a habitat and food resource. A possible explanation for this result is that, within the driftline, macrofauna move between patches of wrack and are captured in the bare

sand between wrack patches. Wrack deposits at the driftline also appear to support different macrofaunal communities from wrack deposited away from the driftline. This result concurs with previous studies that the highest macrofaunal biomass occurs at the level of the current driftline (Koop & Griffiths 1982). The driftline is by definition the largest wrack accumulation on the beach and has deeper, larger patches, and higher overall cover (pers. obs). The relatively higher abundance and differing community between wrack in the driftline and away from the driftline may be due to the difference in the sizes of the accumulations. Previous studies of wrack patches of varying size have also found that larger deposits have higher abundances and diversities of macrofauna (Griffiths & Stenton-Dozey 1981; Olabarria *et al.* 2007). Thus, wrack deposits provide an important habitat and food source for macrofauna, and the driftline provides an area of beach with concentrated resources and hence concentrated macrofaunal communities.

The abundance, species richness and overall macrofaunal communities were variable in time (among visits) and space (among beaches and between positions on the beach). Attempts to link environmental variables with macrofaunal community structure produced only weak relationships. Information on beach type (beach width), the size and location of the DL (DL width, % wrack in the $1m^2$ quadrat and the distance from the dune to the DL) and wrack composition (% algal wrack) together explained less than 9% of the variation in community structure. This was probably because the data were produced for each visit to each beach (except % wrack cover in the quadrat), and does not provide additional information relating to Position. Beach width was the best sole predictor, suggesting that beach type (which is linked to beach width) is an important determinant of the macrofaunal community. This supposition is supported by many previous studies on the links between beach type and macrofauna (McLachlan's work and others). Comparison of the results for abundance and abundance standardised by the number of trapping hours indicated that standardising the data had no effect on the results of the analyses. Thus, differences can be attributed to real differences in the abundance of fauna rather than a difference due to trapping time.

Macrofaunal communities are also known to differ due to beach morphological type, sediment characteristics (e.g. grain size, moisture and organic matter content),

proximity to source populations, environmental conditions (e.g. temperature and rainfall) and human disturbances such as urbanisation, recreational activities and pollution. As well as these variables, the type, location, cover, depth, and persistence of wrack deposits may influence the macrofaunal communities present, and the interactions between the wrack and macrofauna which occur. Future investigations of the macrofaunal communities associated with wrack deposits could include experimental manipulations of some of these factors. For example, wrack deposits could be manipulated to change their composition (e.g. algal vs. seagrass wrack, by removing or adding material), size (cover, patch size and depth, by moving wrack into the desired configurations) or location on the beach (high vs. low shore, moving wrack deposits on the beach) and macrofaunal communities could be monitored over a period of weeks to assess both community structure and successional changes. Wrack accumulations should not be ignored in studies of sandy beach macrofauna but should be explicitly incorporated into sampling regimes.

Conclusion

The macrofauna on these SA sandy beaches were diverse, abundant, and variable in both time and space. The macrofauna were dominated by terrestrial rather than marine taxa, and spanned multiple trophic levels, concurring with the results of previous studies. The most abundant taxa were also diverse and included a seaweed fly, amphipod, mite, isopod and a weevil. Macrofaunal abundances were higher in wrack-covered areas of the beach compared to bare sand areas and furthermore the driftline, which is the largest accumulation of wrack on the beach, had different (more abundant and diverse) communities to wrack patches away from the driftline. Within the driftline itself, there were few differences between bare sand and wrack-covered areas, suggesting that the entire driftline area is important as a habitat and food resource. Thus, wrack deposits provide an important habitat and food source for macrofauna, and the driftline provides an area of beach with concentrated resources, which in turn concentrates a distinct macrofaunal community.

List of Figures

Figure 4.7. Study 2: 2-dimensional MDS plots of the macrofaunal communities found on the 4 study beaches on 4 sampling occasions. Symbols: Open = bare sand, black = under wrack. a) by Position only, b) by Visit and Position. Circle = December, square = July, triangle = May, diamond = October and c) by Beach and Position. Circle = Aldinga, square = Moana, triangle = Normanville, diamond = Robinson Point. Plots were produced using 4^{th} root-transformed data and Bray-Curtis similarities. 2-D stress was 0.23.

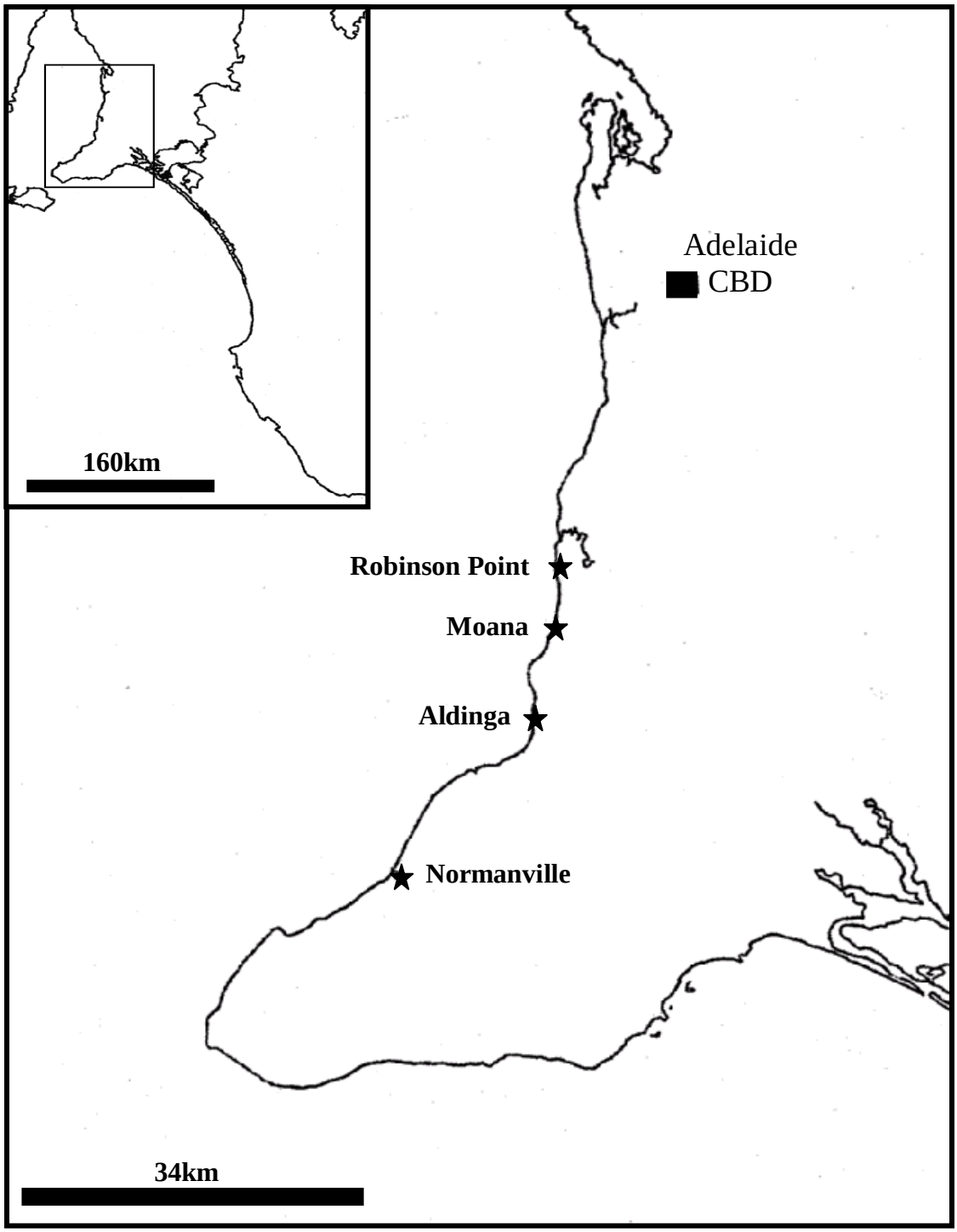

Adelaide
CBD
160km
Robinson Point
Moana
Aldinga
Normanville
34km

Figure 4.1

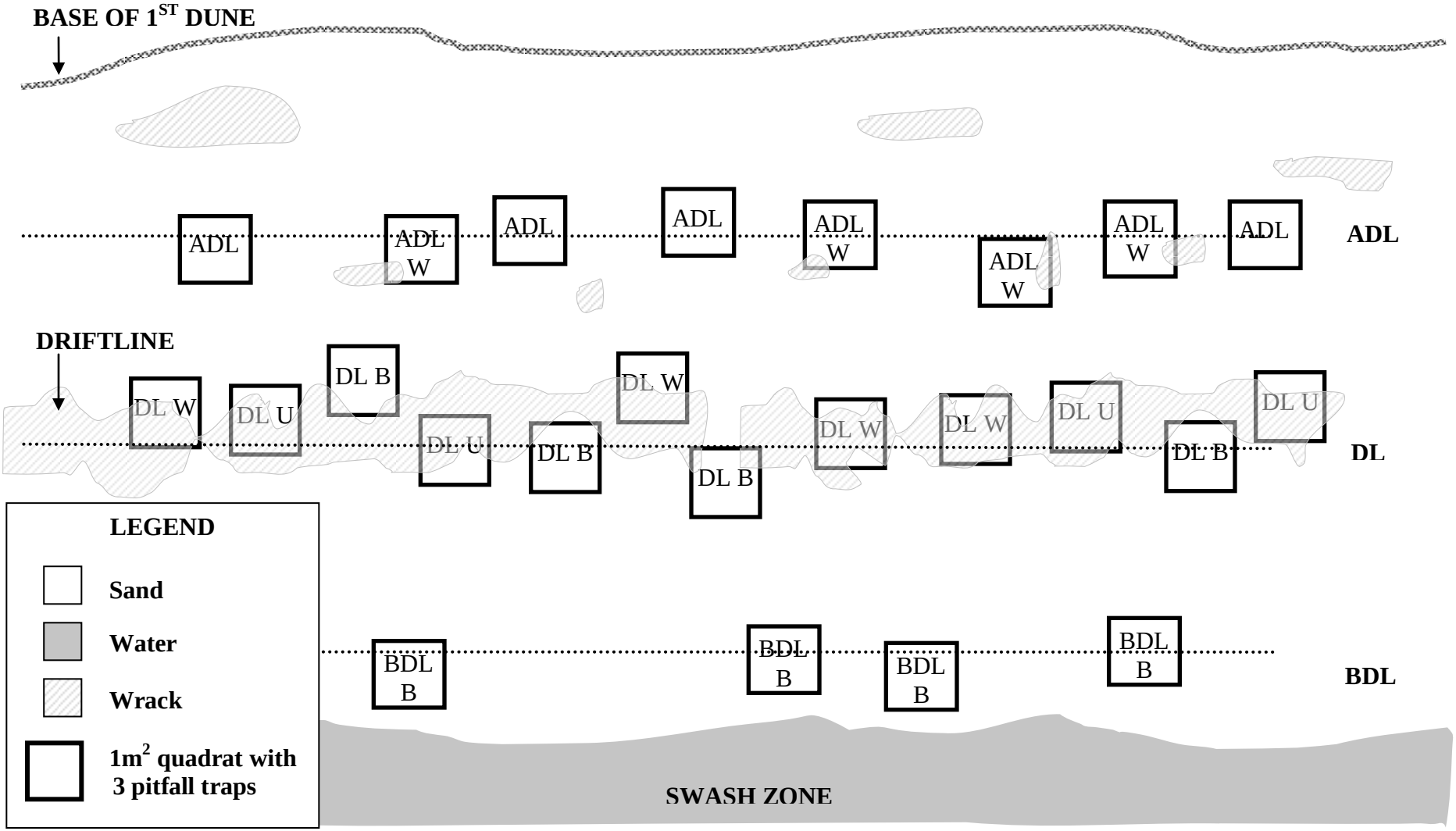
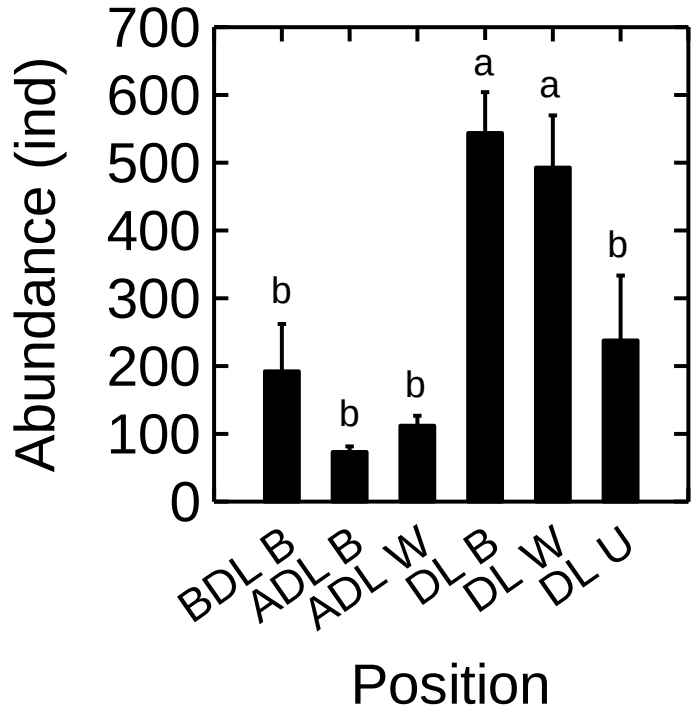

BASE OF 1ST DUNE
ADL
ADL W
ADL
ADL
ADL W
ADL W
ADL W
ADL
ADL
DRIFTLINE
DL W
DL U
DL B
DL U
DL B
DL W
DL B
DL W
DL W
DL U
DL B
DL U
DL
LEGEND
Sand
Water
Wrack
1m2 quadrat with 3 pitfall traps
BDL B
BDL B
BDL B
BDL B
BDL
SWASH ZONE

Figure 4.2

a)


Abundance (ind)
700
600
500
400
300
200
100
0
b
b
b
a
a
b
BDL B
ADL B
ADL W
DL B
DL W
DL U
Position

b)

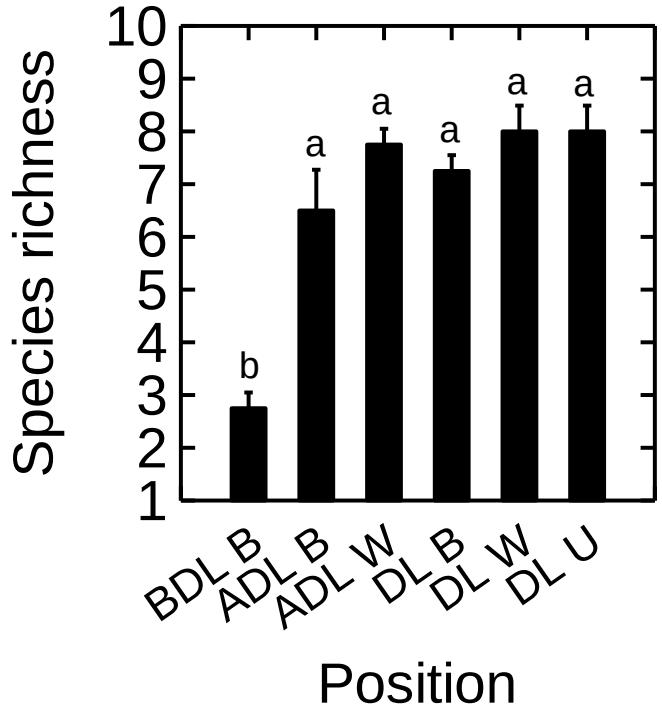

Species richness
10
9
8
7
6
5
4
3
2
1
b
a
a
a
a
a
BDL B
ADL B
ADL W
DL B
DL W
DL U
Position

Figure 4.3

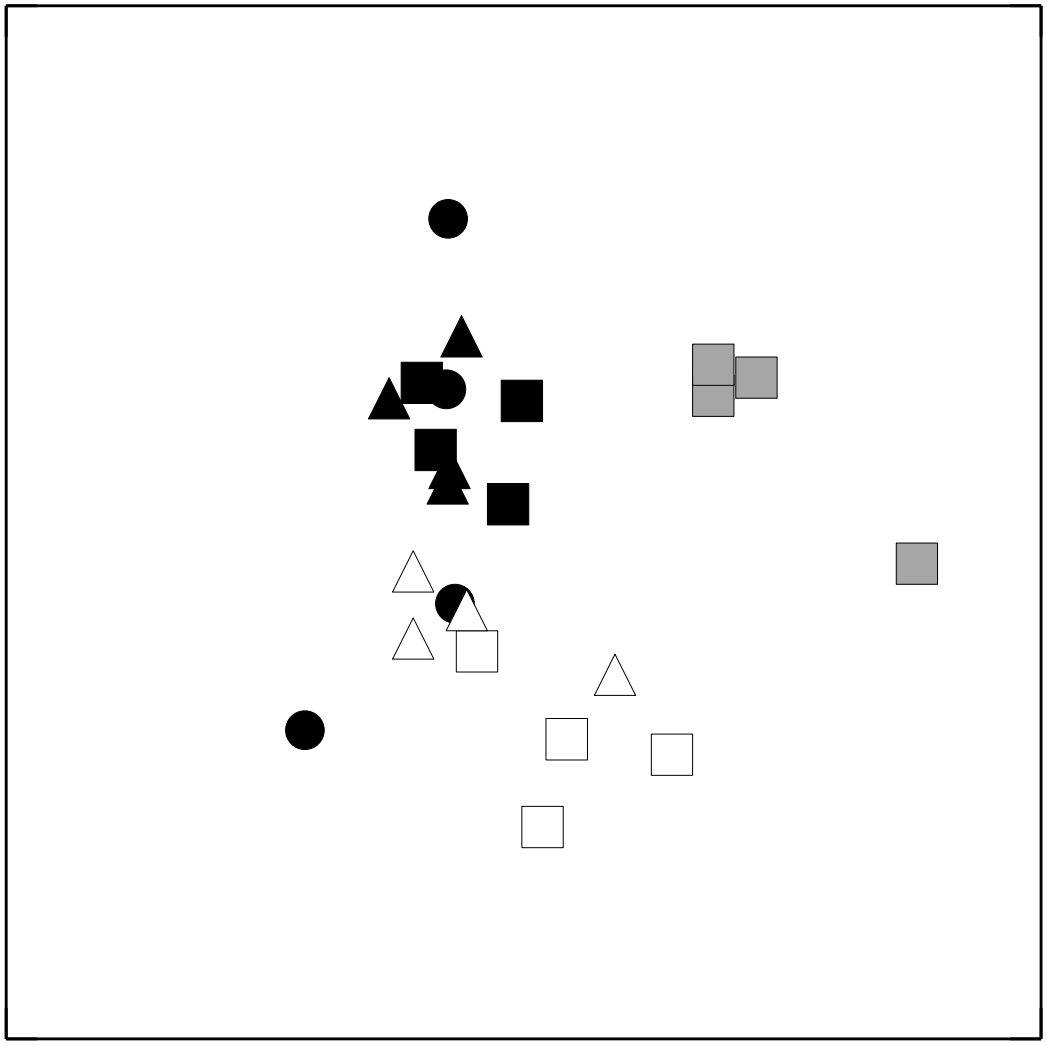
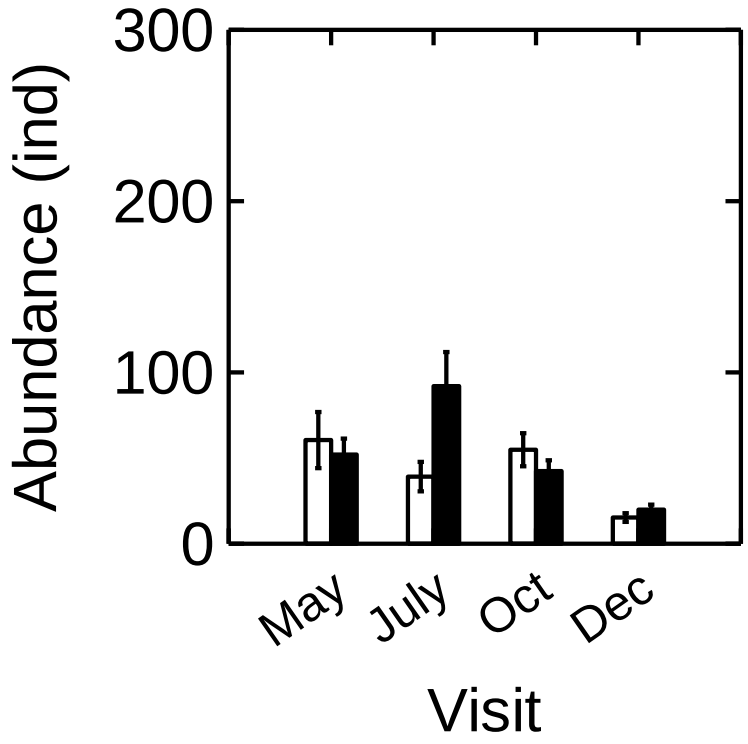


Figure 4.4

a)


300
200
100
0
Abundance (ind)
May
July
Oct
Dec
Visit

b)

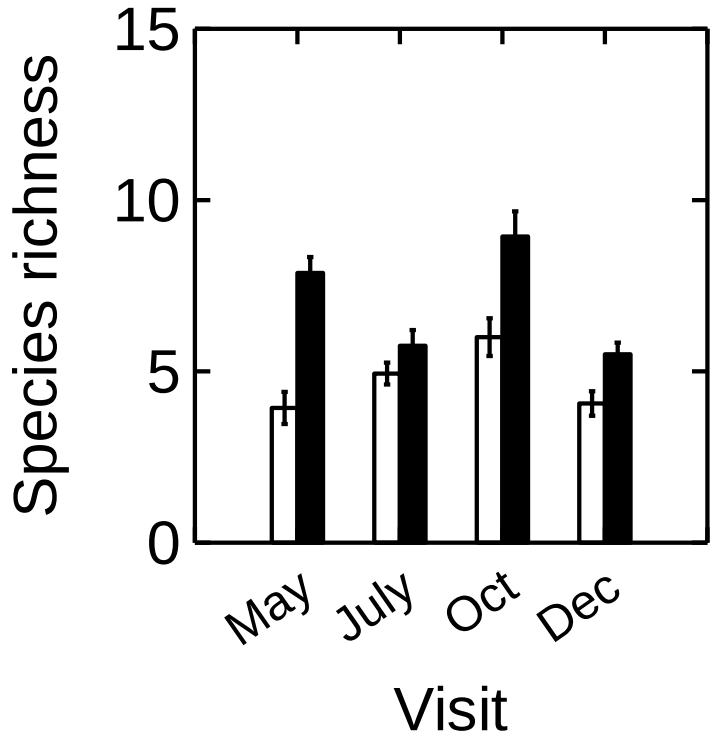
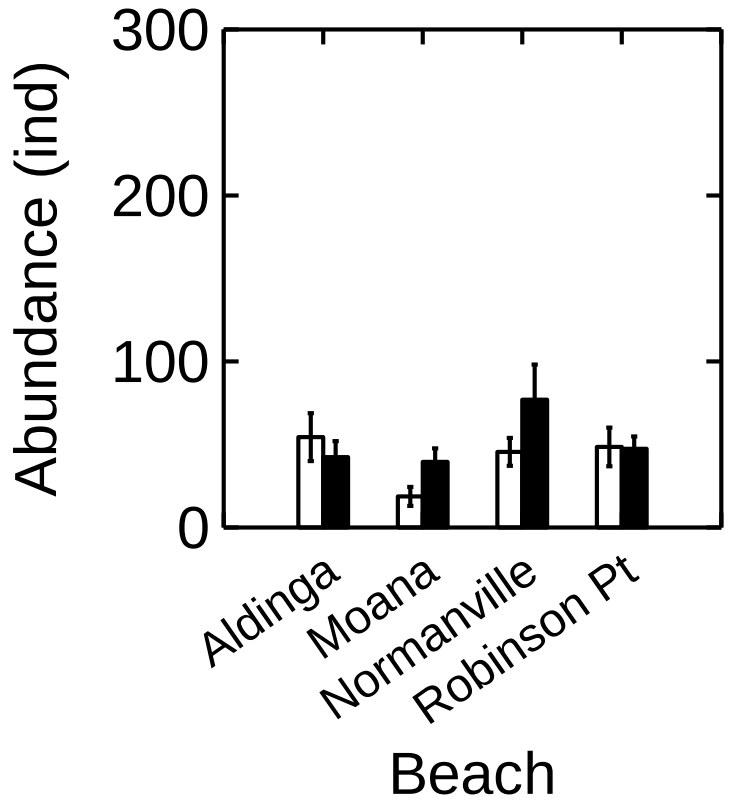

15
10
5
0
Species richness
May
July
Oct
Dec
Visit

Figure 4.5

a)


300
200
100
0
Abundance (ind)
Aldinga
Moana
Normanville
Robinson Pt
Beach

b)

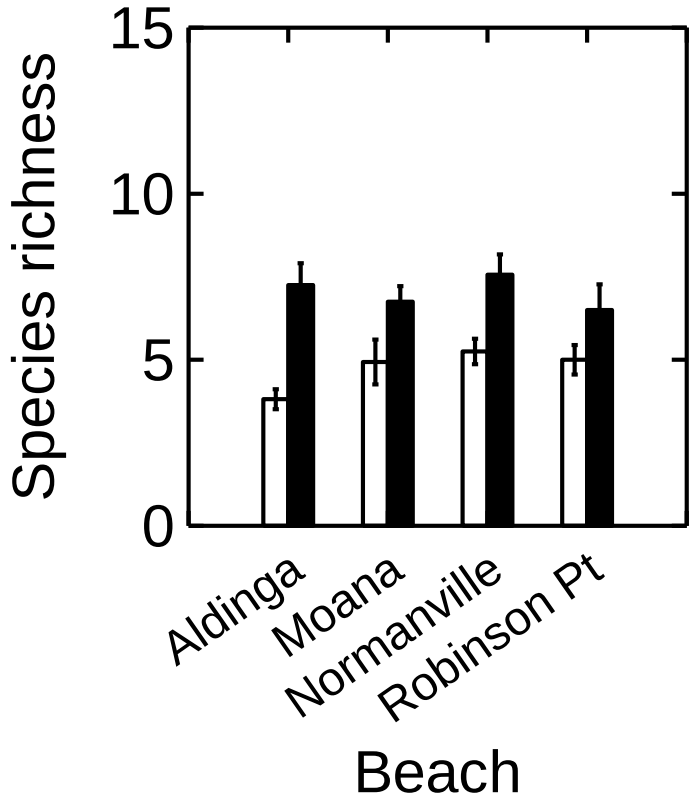
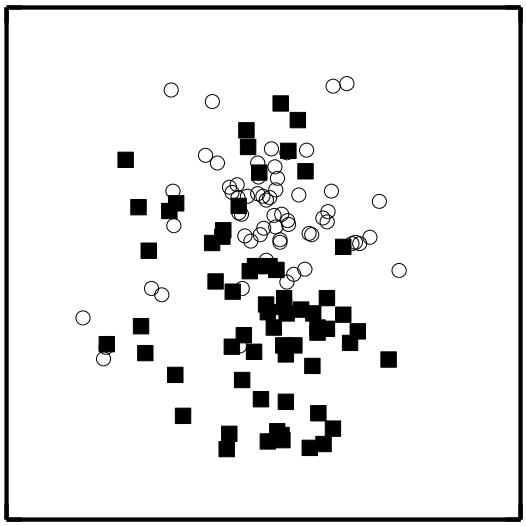
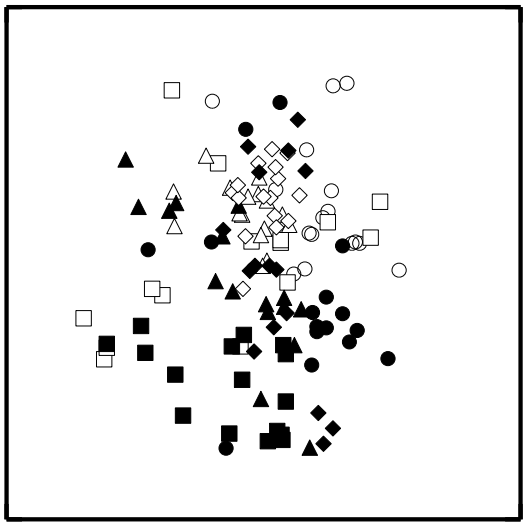

15
10
5
0
Species richness
Aldinga
Moana
Normanville
Robinson Pt
Beach

Figure 4.6

a)



b)



c)

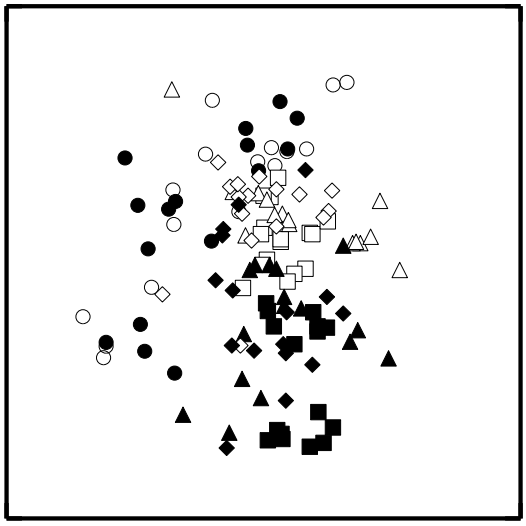


Figure 4.7

Table 4.1. Study 1: Total number of individuals and total species richness for the 9 Orders or macro-invertebrates found at Robinson Pt in the 6 Positions sampled. *n* = 4 quadrats, each with 3 sub-sample pit-fall traps, per Position. BDL = Below the driftline, ADL = Above the driftline, DL = in the driftline. B = Bare sand, W = among wrack and U = under wrack.

Order	**# of species**	**BDL B**	**ADL B**	**ADL W**	**DL B**	**DL W**	**DL U**	**Total individuals**	**% of total**
Isopoda	1	630	166	271	1769	1528	646	5010	75.8
Amphipoda	1	135	75	109	310	340	157	1126	17.0
Coleoptera	7	4	26	44	75	86	120	355	5.4
Grylloblattodea	1	0	11	14	13	7	7	52	0.8
Araneae	3	0	4	5	5	5	5	24	0.4
Hymenoptera	2	0	11	2	3	3	3	22	0.3
Diptera	2	0	0	2	0	0	13	15	0.2
Dermaptera	2	0	0	1	0	1	0	2	< 0.1
Lepidoptera	1	0	0	0	0	1	0	1	< 0.1
Total		769	293	448	2175	1971	951	6607	
# of species	20	3	6	8	6	8	7	9	

Table 4.2. Study 1: Summary of the one-way ANOVA for Position for abundance and species richness. Significant *p*-values are shown in **bold**.

		Abundance (√-transformed)			Species richness(√-transformed)		
Source	df	MS	*F*-ratio	*p*	MS	*F*-ratio	*p*
Position	5	145.474	12.809	< **0.001**	0.825	33.282	< **0.001**
Error	18	11.357			0.025		

Table 4.3. Study 1: ANOSIM Pairwise comparisons 4th root transformed data. In each row the top line is the pair-wise R and the bottom line is the *p*-value. Significant *p*-values are shown in **bold**. BDL = Below the driftline, ADL = Above the driftline, DL = in the driftline. B = Bare sand, W = among wrack and U = under wrack.

	BDL B	ADL B	ADL W	DL B	DL W	DL U
BDL B	-					
ADL B	0.990	-				
	0.029					
ADL W	1.000	0.188	-			
	0.029	0.171				
DL B	0.979	0.708	0.490	-		
	0.029	**0.029**	**0.029**			
DL W	1.000	0.688	0.344	-0.125	-	
	0.029	**0.029**	0.057	0.829		
DL U	0.906	0.500	0.083	0.250	0.146	-
	0.029	**0.029**	0.257	**0.029**	0.171	

Table 4.4. Study 1: Indicator taxa as identified for pairwise comparisons of groups found by SIMPER. Only species contributing over 10% to the dissimilarity and that are consistent indicators (i.e. have Diss/SD > 1) are presented. Only significant ANOSIM pair-wise comparisons are presented. BDL = Below the driftline, ADL = Above the driftline, DL = in the driftline. B = Bare sand, W = among wrack and U = under wrack.

Species	**Positions**			**Diss/SD**	**% Contribution**
	BDL B		**ADL B**		
Formicidae sp. 2	0.0	<	2.0	11.3	20.8
Aphela phalenoides	0.8	<	5.3	2.4	19.9
Forficulidae sp. 1	0.0	<	2.8	1.6	18.3
Lycosidae sp. 1	0.0	<	1.0	1.7	13.8
	BDL B		**ADL W**		
Forficulidae sp. 1	0.0	<	3.5	7.0	19.5
Aphela phalenoides	0.8	<	6.0	2.2	15.6
Curculionidae sp. 1	0.3	<	3.0	2.2	14.9
Symenena amphibia	0.0	<	2.0	1.7	13.4
Lycosidae sp. 1	0.0	<	1.0	1.6	11.3
	BDL B		**DL B**		
Forficulidae sp. 1	0.0	<	3.3	9.8	20.3
Aphela phalenoides	0.8	<	12.3	1.6	18.2
Curculionidae sp. 1	0.3	<	5.8	1.9	18.1
Lycosidae sp. 1	0.0	<	1.0	1.6	12.7
	BDL B		**DL W**		
Curculionidae sp. 1	0.3	<	7.0	2.1	17.7
Aphela phalenoides	0.8	<	12.8	1.9	17.4
Forficulidae sp. 1	0.0	<	1.8	5.9	15.6
Lycosidae sp. 1	0.0	<	1.3	15.0	14.4
Symenena amphibia	0.0	<	1.3	1.5	11.5
	BDL B		**DL U**		
Aphela phalenoides	0.8	<	18.8	2.4	18.8
Curculionidae sp. 1	0.3	<	4.3	2.4	13.6
Symenena amphibia	0.0	<	3.8	1.6	13.3
Tenebrionidae sp. 1	0.0	<	2.3	1.6	11.3
Lycosidae sp. 1	0.0	<	1.3	1.5	10.2
Forficulidae sp. 1	0.0	<	1.8	1.6	10.0
	ADL B		**DL B**		
Formicidae sp. 1	2.0	>	0.5	2.7	20.5
Forficulidae sp. 1	2.8	<	3.3	2.9	13.3
Lycosidae sp. 1	1.0	=	1.0	1.8	11.5

Species	Positions			Diss/SD	% Contribution
Curculionidae sp. 1	0.5	<	5.75	1.3	11.5
	ADL B		**DL W**		
Formicidae sp. 1	2.0	>	0.8	2.7	19.6
Forficulidae sp. 1	2.8	>	1.8	3.3	13.7
Symenena amphibia	0.8	<	1.3	1.7	11.9
Curculionidae sp. 1	0.5	<	7.0	1.1	11.5
	ADL B		**DL U**		
Formicidae sp. 2	2.0	>	0.8	1.8	14.4
Symenena amphibia	0.8	<	3.8	1.4	12.9
Tenebrionidae sp. 1	0.0	<	2.3	1.5	12.1
Forficulidae sp. 1	2.8	>	1.8	1.7	11.2
	ADL W		**DL B**		
Symenena amphibia	2.0	>	0.5	1.8	16.2
Lycosidae sp. 1	1.0	=	1.0	1.5	10.9
Formicidae sp. 2	0.5	=	0.5	1.1	10.6
	DL B		**DL U**		
Tenebrionidae sp. 1	0.0	<	2.3	1.5	14.9
Symenena amphibia	0.5	<	3.8	1.6	14.4
Aphela phalenoides	12.3	<	18.8	1.4	10.7

Table 4.5. Study 2: Summary of the three-way ANOVA for Visit, Beach and Position for abundance, species richness, common species richness and abundance standardised by the number of trapping hours. NS = not statistically significant for $\alpha = 0.05$. *p*-values in **bold** indicate significance at $\alpha = 0.05$.

		Abundance (4^{th} root-transformed)			Species richness (√-transformed)			Common species richness (√-transformed)			Abundance standardised by trapping hours (4^{th} root transformed)		
Source	df	MS	*F*-ratio	*p*	MS	*F*-ratio	*p*	MS	*F*-ratio	*p*	MS	*F*-ratio	*p*
Visit	3	2.686	1.840	NS	1.610	7.352	< **0.01**	1.434	5.713	< **0.025**	0.589	1.423	NS
Beach	3	1.312	0.899	NS	0.245	1.119	NS	0.204	0.813	NS	0.286	0.691	NS
Position	1	1.330	undefined		7.332	undefined		6.855	undefined		0.338	undefined	
Visit x Beach	9	1.460	14.904	< **0.001**	0.219	1.919	0.058	0.251	2.428	**0.016**	0.414	15.838	< **0.001**
Visit x Position	3	0.777	1.563	NS	0.771	2.197	NS	0.705	2.564	NS	0.198	1.511	NS
Beach x Position	3	0.393	0.791	NS	0.279	0.795	NS	0.207	0.753	NS	0.102	0.779	NS
Visit x Beach x Position	9	0.497	5.076	< **0.001**	0.351	3.075	**0.003**	0.275	2.656	**0.009**	0.131	5.009	< **0.001**
Error	95	0.098			0.114			0.103			0.026		

Table 4.6. Study 2: Summary of the three, 2-way crossed ANOSIM tests for 4th root-transformed data using a) all 66 species individually and b) data aggregated into their 18 Orders. All Global *R* values were significant ($p = 0.001$).

a) By species

Factor	Global *R*		Factor	Global *R*
Visit	0.411	x	Position	0.379
Beach	0.275	x	Position	0.215
Visit	0.558	x	Beach	0.505

b) By order

Factor	Global *R*		Factor	Global *R*
Visit	0.399	x	Position	0.390
Beach	0.227	x	Position	0.209
Visit	0.562	x	Beach	0.482

Table 4.7. Study 2: ANOSIM pairwise comparisons (4th root transformed data) for a) Visit in the Visit x Position ANOSIM and b) Beach in the Beach x Position. Pairwise comparison for Position are not required since there were only 2 Positions (B vs. U) and thus the Global *R* and *p* values apply. $p = 0.001$ for all pair-wise tests except Robinson Pt vs. Normanville for which $p = 0.003$.

a) Visit x Position

	May	July	October	December
May	-			
July	0.314	-		
October	0.425	0.474	-	
December	0.396	0.570	0.346	-

b) Beach x Position

	Robinson Pt	Moana	Aldinga	Normanville
Robinson Pt	-			
Moana	0.348	-		
Aldinga	0.293	0.253	-	
Normanville	0.106	0.312	0.370	-

Table 4.8. Study 2: Indicator taxa as identified for pairwise comparisons of groups found by SIMPER. Only species contributing over 10% to the dissimilarity and that are consistent indicators (i.e. have Diss/SD > 1) are presented.

Species	Comparison			Diss/SD	% Contribution
	Position				
	B		**U**		
Coelopidae sp. 1	0.3	<	21.7	1.1	10.6
	Visits				
	May		**July**		
Coelopidae sp. 1	4.2	<	36.5	1.1	13.3
Acarina sp. 1	27.5	>	6.3	1.1	13.2
A. pallida	12.5	>	5.4	1.2	11.9
	May		**October**		
T. quadrimana	1.9	<	25.9	1.4	10.7
Acarina sp. 1	27.5	>	2.3	1.1	10.1
	May		**December**		
Acarina sp. 1	27.5	>	0.5	1.2	11.6
A. pallida	12.5	>	2.9	1.1	10.6
	July		**October**		
Coelopidae sp. 1	36.5	>	3.5	1.2	11.5
	July		**December**		
Coelopidae sp. 1	36.5	>	0.0	1.3	12.5
	October		**December**		
(None)					
	Beaches				
	Robinson Pt		**Moana**		
(None)					
	Robinson Pt		**Aldinga**		
Acarina sp. 1	0.44	<	32.2	1.2	13.4
A. pallida	10.81	>	0.3	1.2	10.5
	Robinson Pt		**Normanville**		
A. pallida	10.8	<	11.0	1.2	11.2
T. quadrimana	19.5	>	11.7	1.2	10.0
	Moana		**Aldinga**		
Acarina sp. 1	2.4	<	32.2	1.1	10.2

Species	Comparison			Diss/SD	% Contribution
	Moana		**Normanville**		
A. pallida	0.7	<	11.0	1.6	10.6
	Aldinga		**Normanville**		
A. pallida	0.3	<	11.0	2.0	13.8
Acarina sp. 1	32.2	>	0.75	1.2	11.8

Table 4.9. Summary of number of species and orders, location and other notes from studies of macrofaunal communities associated with wrack deposits. N/A signifies data unavailable.

# of taxa at lowest unit	# of Orders	# of individuals collected	Location	Sampling method used	Notes	Reference
75 species	11	N/A	Durham, England	'Observations & collection'	Sampled wrack deposits of various sizes	Egglishaw 1965
27 species	3	N/A	South Africa	Collected wrack & core from underlying sand	*Ecklonia maxima*, sampling over 30 days	Griffiths & Stenton-Dozey 1981
53 species	12	21227	California, USA	Coring in wrack & sand	Sampling over 80 days to study successional changes	Lavoie 1985
6 species	N/A	N/A	Perth, Western Australia	Coring	2 beaches, one sampling event	McLachlan 1985
22 species	7	1150	Canterbury, New Zealand	Coring & litterbags	*Macrocystis pyrifera*	Inglis 1989
30 species	5	16464	Poland	Litterbags	*Zostera marina*	Jedrzejczak 2002b
53 species	N/A	7360	Spain	Collected wrack & core from underlying sand	Sampled wrack deposits of various sizes	Olabarria *et al.* 2007
60 species	N/A	N/A	California, USA	Coring	15 beaches sampled, 11-37 species/beach	Dugan *et al.* 2003
14 families	9	4751	Western Australia	Collected wrack & core from underlying sand	Sampled fauna in and under wrack	Ince *et al.* 2007
29 species	N/A	7820	Spain	Collected wrack & core from underlying sand	Algal wrack, sampling over 21 days. One beach	Rodil *et al.* 2008
62 species	18	6607	South Australia	Pit-fall trapping	4 repeat sampling (1/season) 4 beaches sampled	This study: Study 1
20 species	9	5961	Robinson Pt, South Australia	Pit-fall trapping	One sampling event	This study: Study 2