CHAPTER 5: IMPACTS OF VEHICLES ON WRACK AND THE WRACK-ASSOCIATED MACROFAUNA

1. Introduction

Macroinvertebrates perform an important functional role on sandy beaches, reincorporating energy from stranded organic matter back into the food web, thus making it available to higher trophic levels (McLachlan & Brown 2006). Monitoring of beach macroinvertebrate communities can and has been used as a tool to assess human impacts (Colombini *et al.* 2003). Beach macrofaunal populations and communities have been shown to respond negatively, with reduced abundances and diversity, to different levels or gradients of human impact (Barros 2001; Lercari & Defeo 2003). Beach macrofaunal abundance, biomass, species richness, diversity and evenness all reduced with increased proximity to a freshwater drain, in direct response to salinity gradients (Lercari & Defeo 2003). Likewise, ghost crabs (*Ocypode cordimana*) showed decreased burrow occurrence (implying reduced crab abundances) on urban compared to non-urban beaches (Barros 2001), but it must be considered also that burrow counts can be biased by short-term trampling effects, with crabs able to reconstruct collapsed burrows that may be missed in surveys (Lucrezi *et al.* 2009). Beach macrofauna can be negatively impacted by other human activities such as intense trampling (Moffett *et al.* 1998), beach nourishment or coastal armouring (Dugan *et al.* 2008; Fanini *et al.* 2009), bivalve harvesting (Brazerio & Defeo 1999) and recreational off-road vehicle use (e.g. Godfrey & Godfrey 1981; van der Merwe & van der Merwe 1991; Schlacher *et al.* 2008c).

Studies on the impacts of vehicles on beach macrofaunal organisms are almost entirely limited to experimental investigations of susceptibility of individuals from various species to crushing when buried or exposed during exposure to (usually experimental) vehicle traffic (Wolcott & Wolcott 1984; van der Merwe & van der Merwe 1991; Schlacher *et al.* 2008b) or population level studies involving abundance comparisons between areas with and without vehicles (Steiner & Leatherman 1981; Wolcott & Wolcott 1984; Moss & McPhee 2006; Foster-Smith *et al.* 2007; Schlacher *et al.* 2007b; 2008b).

The findings of these studies are reviewed in more detail in Chapter 1 of this thesis. Only one study has investigated the impact of vehicles on macrofauna at the community level (Schlacher *et al.* 2008c). These authors compared the macrofaunal communities of beaches with and without vehicles in south-east Queensland, Australia, and found that there were substantial impacts of vehicles on beach macroinvertebrates, with communities from beaches with vehicles having reduced abundance, diversity and altered community structure, relative to beaches without vehicles (Schlacher *et al.* 2008c).

Impacts on the drift-line habitat

Wrack is an important resource for macrofauna on temperate beaches, providing food and shelter to organisms (Kirkman & Kendrick 1997; Ince *et al.* 2007), and the drift line on temperate beaches usually represents a peak in macrofaunal abundance and diversity (McLachlan & Brown 2006). As vehicles pass over the wrack drift-line, shearing forces from the turning wheels break-up and crush the accumulation, reducing wrack patch sizes and increasing desiccation of sediment and drift-line material (Leatherman & Godfrey 1979; Zaremba *et al.* 1979; Godfrey & Godfrey 1981). Bacterial populations in the back shore and wrack drift-line investigated for vehicle impacts were highly variable, making it difficult to define such impacts directly, so Zaremba *et al.* (1979) used decomposition of wrack material as a proxy for microbial abundance between treatment groups. Wrack decomposition was reduced after a 12-week trial in 10- and 100-pass treatment plots (22.7% & 22.9% decomposed, respectively) relative to vehicle-free controls (27.3% decomposed); however, there was no difference between the two levels of treatment (Zaremba *et al.* 1979). Thus, even low intensities of vehicle exposure seem sufficient to significantly impact microbial communities and reduce decomposition rates of beach wrack. The impacts of vehicles on the macrofauna living or foraging within drift-line accumulations are unknown. It is possible that both the sediment desiccation and the reduction in wrack patch sizes negatively affect macrofaunal communities. Wrack patch size was shown to affect macrofaunal abundance on exposed sandy beaches, with smaller patches ($0.09m^2$; 1kg±50g wet weight) having lower abundance and species richness than medium ($0.25m^2$;

3kg±50g wet weight) or large (0.49m^2; 5kg±50g wet weight) patches on the same beach (Olabarria *et al.* 2007).

The beaches in the temperate southern Adelaide metropolitan region lack the populations of burrowing beach crabs seen on tropical and sub-tropical sandy beaches. They also lack populations of the beach clams (i.e. *Donax deltoides*) that are found on other Australian sandy beaches, a species known to be susceptible to crushing by vehicles (Schlacher *et al.* 2007b). Populations of smaller bivalves (e.g. *Paphies elongata*), predatory gastropods (e.g. *Polinices conicus*) and some beach worms are seen in the swash zone when exposed at low-tide (pers. obs.); however, this area is rarely used by vehicles due to the hazards of driving through the swash (pers. obs.). Wrack drift-lines are prominent features on the beaches in the study area, and tend to occur in the areas of the beach most used intensively by vehicles for driving and parking (i.e. the mid-shore and mid- to high-shore transition point; see Chapter 2). Little is known about the impacts of vehicles on the wrack-associated macrofaunal communities of temperate sandy beaches but it is likely that, at least on the beaches in the study region, these communities are most at risk from vehicle impacts due to the overlap of habitat and vehicle usage zones (*sensu* Schlacher & Thompson 2007; 2008).

Thus, the main aim of this study was to investigate vehicle effects on wrack and the wrack-associated macrofaunal communities (i.e. abundance, species richness, community structure; see Chapter 1; Figure 1.5) of the beaches in the study region, by using a series of between- and within-beach comparisons of univariate and multivariate data. Specifically, this chapter will investigate vehicle effects on:

- Wrack deposition and composition, and if these are related to patterns in macrofaunal abundance and species richness;
- Macrofaunal occurrence, abundance, species richness, community structure and variability;
- Species typifying or defining any similarities or differences, respectively, among macrofaunal communities between- or within-beaches exposed to different types of vehicle access; and

- Recovery of macrofaunal populations after vehicle removal from a section of the beach.

For this study, the overall effects of vehicles, rather than the potential mechanisms of impact (i.e. crushing, loss of habitat, etc.) on macrofauna were of interest, so impacts were investigated at the community scale (i.e. in terms of total abundance, species richness and community structure). It must be noted that vehicle closures on Aldinga Bay, that is the permanent closure at Aldinga Bollards and the seasonal closure at Silver Sands, were found to be ineffective at reducing vehicle traffic relative to the open section, Sellicks (see Chapter 2).

2. Methods

Study sites and design

The macrofaunal communities on each of the nine main study beaches (see Chapter 1 Figure 1.3) were quantified as part of the regular sampling trips using the transect study design described in Chapter 1. All study beaches regularly featured a prominent wrack drift line. Because of this potential concentration of organisms (in terms of both abundance and diversity) on the intertidal beach face, the drift line was targeted for macrofaunal sampling, and thus only the wrack-associated benthic macroinfaunal (i.e. living in/on top of the sand) organisms have been sampled. During the first sampling occasion, the two closure sections at Aldinga were sampled as one beach section, with two replicate transects conducted in the seasonal closure and one inside the bollards, resulting in reduced sample sizes during mid-winter year 1 and for overall year 1 within-beaches comparisons at Aldinga Bay, compared to years 2 and 3.

Macrofaunal sampling

For the purposes of this study, macrofauna are described as all multicellular invertebrate animals that are retained on a 500µm sieve. Macrofaunal sampling was conducted at the level of cover type (i.e. bare sand versus wrack-covered patches of the drift-line) because the drift line on the study beaches were not continuous bands of wrack material, but instead patches of wrack scattered in bands of variable width interspersed with areas of bare sand (e.g. Figure 5.1). Because of this habitat heterogeneity, both wrack-covered and bare sand patches of the drift line were deliberately sampled for each transect (as described in Chapter 1), and contrasted. Three sediment cores (diameter 11cm; depth 15cm; total sample volume 1425.5cm^3) were collected haphazardly from under wrack patches and also from bare sand areas within the drift line, usually within 20m distance either side of the transect (on rare occasions when drift material was very sparse it was necessary to move further away from the transect line to locate wrack patches, but never more than 50m). Beginning with the mid-winter sampling occasion in 2006, the percent cover of wrack over the core was also estimated. A 0.25m^2 quadrat was laid on the sand surrounding core location immediately prior to coring and the percentage of the area within the quadrat covered with wrack was estimated by eye (for both wrack and bare sand patches), based on reference photos of known percent cover (McDonald *et al.* 1990). Cores were sieved *in situ* in seawater using a 500µm mesh sieve and any macrofaunal organisms retained were bagged and transported on ice back to the laboratory, where they were sorted live then preserved in 70% ethanol. All organisms were counted and identified (using a dissection microscope, 40x magnification) to species level where possible (general identification texts: Edgar 2000; Gooderham & Tsyrlin 2003; Gowlett-Holmes 2008; specific texts for: crustaceans, Hale 1927-29; insects, Matthews & Queale 1997; spiders, Davies 1986). Adult forms of Diptera (flies) and winged forms of both the Hymenoptera (social insects) and Hemiptera (bugs) were removed from the data set prior to analyses, because it was considered that the occurrence of these organisms in core samples would be sporadic and easily underestimated (i.e. not considered a benthic infaunal organism). Maggots were still included.

Drift material quantification

The occurrence, location, width, percent cover and composition of the drift line were temporally and spatially variable, and hence these were quantified for each beach (composition) or transect (all other drift line variables) to be included as possible covariables for explaining patterns in macrofauna communities. The biomass and percent cover of each wrack patch were not measured, instead the percent cover of the wrack drift line on

Figure 5.1: Photograph of a study transect (solid black line) on Silver Sands beach taken in December 2005 showing where the transect would extend from dune toe at the top of the beach (or another point [e.g. seawall] in the absence of a fore dune) down to the swash zone, and showing how distance to the top of the beach and width of the drift line were measured. Darker irregular patches are wrack deposits.

the beach was measured (see below). The distance of the upper limit of the drift line to the toe of the foredune was recorded and the width of the drift line measured using the transect tape (Figure 5.1). Initially the location and width of the drift line were not recorded accurately for all transects, and these data are only considered reliable for the second and third years of the study. Photopoint methods (McKechnie 2003; McKechnie & Fairweather 2003; Duong 2008) were used to estimate the percent cover of wrack material across the intertidal beach face. For each transect, a series of photographs were taken looking along the beach (e.g. see Figure 5.1) of: 1) the drift line(s) (taken at the level of the drift-line facing along the beach); and 2) the middle of the beach (also facing along the beach). These photos were randomly ordered and then scored twice (to obtain an average estimate) for percent cover of wrack material in random order using reference photos of known percent cover (McDonald *et al.* 1990).

Finally, to investigate the composition of wrack material deposited on the beach face, three samples of wrack (each approx. $2.5 \times 10^{-3} m^3$) were collected per beach (not per transect), transported back to the laboratory on ice and frozen at -20°C for later processing. Once defrosted, samples were soaked in water to permit ease of separation and sorting of the wrack pieces. Wrack pieces were identified to species level where possible (identifications from non-living detached material were impossible for some species, Duong 2008). Fragments were patted dry and then weighed to determine the percentage composition of each species by wet weight. Composition samples were collected for all but the last two sampling occasions (pre- and post-summer of third year), because it became clear that there was little variation between beaches for any given sampling occasion.

Statistical methods

All data were analysed using version 11 of the SYSTAT software package (for univariate analyses) or version 6 of the PRIMER/PERMANOVA+ software package (multivariate statistics). Data were analysed separately for each year of the study, with each ‘year’ containing a mid-winter, pre-summer and post-summer sampling event (Year 1: mid-winter 2005 – post-summer 2006; Year 2: mid-winter 2006 – post-summer 2007; Year 3: mid-winter 2007 – post-summer 2008). Initial investigation of the data indicated that macrofaunal communities on these beaches were highly variable among years of the study, thus the decision was made to analyse years separately to reduce the over-riding effect of this interannual variation.

A complex set of analyses were used to investigate the overall question of this chapter, that is, to determine vehicle impacts on the macrofauna of the beaches sampled in this study. Essentially, these analyses have been broken down into four overriding hypotheses, related to the aims of this chapter stated in the introduction. Specifically, these were 1) that vehicles may somehow alter the deposition or composition or wrack on the beach-face, and/or relationships between macrofauna and wrack; 2) that vehicles may affect the occurrence, abundance, species richness or community composition and/or variability of macrofauna on the beach; 3) that beaches or beach sections with vehicles may be typified by different species than those beaches or beach sections without vehicles; and 4) that recovery of macrofaunal populations on beach sections previously open to vehicles, relative to nearby closed beaches, will be affected by both the type of closure in place and the duration the closure has been established.

1. Potential vehicle effects on macrofaunal associations with wrack

Regression analysis was used to investigate any relationships between macrofaunal abundance or species richness with wrack percent cover of the beach face, distance of the drift line from the top of the beach and width of the drift line. Percent cover of the beach covered by the drift line was compared between beaches open and closed to vehicles using a series of three (i.e. separately for each year of the study) 3-factor, nested, mixed-model ANOVAs with Beaches considered a random factor. The four study sites (Maslin, Port Willunga, Moana and Sellicks), were split into two Beach levels nested within access Type (a fixed factor with 2 levels; Open and Closed to vehicles) and three separate Seasonal sampling occasions (a fixed factor with 3 levels; Mid-Winter, Pre-Summer and Post-Summer). For within-Bays comparisons at Aldinga and Moana, a series of three (i.e. separately for each year of the study and only two for Moana), 2-factor, mixed-model ANOVAs with access Type (a fixed factor with 3 levels; 3 beach sections per

Bay) and three separate Seasonal sampling occasions (a fixed factor with 3 levels; Mid-Winter, Pre-Summer and Post-Summer).

2. Potential vehicle effects on macrofaunal occurrence, abundance, species richness and community structure and variability

Planned statistical analyses of the macrofauna abundance and species richness data included a series of nested mixed-model ANOVAs to compare differences in measured variables between beaches (i.e. open v. closed beaches) and additional mixed-model ANOVAs comparing differences in measured variables between sections of Bays (i.e. Moana and Aldinga Bays; as described for wrack percent cover). However, planned parametric univariate tests (i.e. analysis of variance) on macrofauna data were not possible due to the large number of null samples (i.e. cores with zero fauna), resulting in highly-skewed distributions that could not be normalised with mathematical transformations. Thus, differences in the frequency of occurrence of null samples between vehicle access types (between beaches = 2 levels; within bays = 3 levels) and core cover types (2 levels) for each of the nine seasonal sampling occasions were tested using a series of contingency tables (Pearson χ^2 or Fisher tests [for 2x2 tables only] in cases where more than one-fifth of cells contained frequencies less than 5 and thus considered ‘sparse’) to investigate the question, ‘was there a higher frequency of null cores (i.e. a lower occurrence of fauna) on beaches/beach sections open to vehicles compared to closed beaches/beach sections?’

Several multivariate statistical tests were used to investigate vehicle impacts on macrofauna at the community level, using transects as replicate units for each beach. Initial inspection of species abundance data revealed that there were a handful of highly-abundant species in communities on these beaches and many more rare species (i.e. those with relatively much lower abundances). Thus, for all multivariate statistics, raw species abundance data were transformed using a blanket fourth-root transformation (considered to be an intermediate level transformation; Anderson *et al.* 2008) to increase the relative influence of rare versus more abundant species, a measure that is especially important for tests using a Bray-Curtis measure (Clarke & Green 1988; Clarke & Warwick 2001; Anderson *et al.* 2008).

To investigate whether there were community-level differences between or within beaches, macrofaunal community data were analysed using a series of multivariate permutation-based ANOVAs (PERMANOVA) and patterns in the data were investigated visually using multidimensional scaling (MDS) ordination plots. Additionally, discriminate canonical analysis of principal coordinates (CAP) routines (Anderson *et al.* 2008) were used to test the hypothesis that macrofaunal communities were different between beaches either closed or open to vehicles. Both PERMANOVA and CAP routines test the *a priori* hypothesis that there were differences in the macrofaunal communities based on vehicle access to beaches (between-beaches comparisons) or beach sections (within-beaches comparisons) but, CAP (discriminate analysis) actively searches for, and displays, the best *a priori* groupings for a specified factor (i.e. Types, in this case) while PERMANOVA does not. An additional advantage of CAP is that, being a constrained ordination routine, CAP allows for differences in *a priori* groups to be more easily seen than an unconstrained routine such as an MDS, PCO or PCA plot. Because multivariate PERMANOVA does not have the same assumptions as univariate ANOVA (Anderson *et al.* 2008), the problem of skewed distributions was avoided by using this multivariate technique.

In total, four analytical designs were used, two each for between- and within-beach comparisons, with data from each individual trip (n = 9 seasonal sampling trips; but for Moana Bay n = 6) and also each year of study (n = 3 years; Moana Bay n = 2) analysed separately, again to reduce the potential effects of interannual variation. Nine 3-factor, nested mixed-model PERMANOVAs were used to compare differences in community structure between Beaches, a random factor with the four study sites (Maslin, Port Willunga, Moana and Sellicks) split into two Beach levels nested within access Type (a fixed factor with 2 levels; Open versus Closed to vehicles) with two different Covers (a fixed-factor with two levels; bare-sand versus wrack-covered cores) sampled per beach. Data for each year were analysed using three 4-factor nested mixed-model PERMANOVAs by adding the factor of Season (a fixed factor with 3 levels; Mid-Winter, Pre-Summer and Post-Summer). For within-beach comparisons, the nested factor (Beach) was removed from each of these designs to give a series of three (i.e. separately for each season) 2-factor fixed-effects model PERMANOVAs with Types (a fixed-factor with 3 levels; different beach sections) and Cover (a fixed factor with 2 levels; bare-sand versus wrack-covered cores) analysed separately for each seasonal sampling occasion, and a series (i.e. separately for each year) of 3-factor fixed-effects model PERMANOVAs with the additional factor Season (a fixed factor with 3 levels; Mid-Winter, Pre-Summer and Post-Summer).

PERMDISP was used to investigate whether vehicle access to a beach altered the degree of variability (i.e. between samples) of the macrofaunal community, using comparisons either between (i.e. open v closed beaches) or among (i.e. Moana & Aldinga Bay sections) vehicle access Types. Change (either increase or decrease) in the multivariate dispersion in ecological data is a potential indicator for stress in marine communities (Warwick & Clarke 1993; Chapman *et al.* 1995), and thus any differences in variability may indicate some effect of vehicles on the macrofaunal communities of these beaches.

3. Species typifying communities on open versus closed beaches and beach sections

The similarity percentages routine (SIMPER) was used to identify species typifying communities (i.e. those with high contributions to similarities between samples from a site) on the different beaches or types of beaches (i.e. closed versus open beaches), and those that made communities unique from other beaches or types of beach (i.e. those with high contributions to dissimilarity between sites or beach types).

4. Macrofaunal recovery after vehicle removal from previously open beach sections

To determine if there was any ‘recovery’ of macrofaunal community on the beach sections at Aldinga Bay that had been closed to vehicles at the beginning of the study (i.e. Silver Sands and Aldinga Bollards), the macrofaunal communities of the two closure sections were compared to those of closed beaches (i.e. Maslin and Port Willunga) using SIMPER. Average dissimilarity (with higher values indicating less-similar communities) between Closed beaches and Closure sections was plotted for each sampling occasion under the hypothesis that, if macrofaunal communities could recover on these beach sections after vehicles are removed, then the dissimilarity between closed beaches and beach sections would diminish over time. The underlying assumption of this is that the wrack-associated macrofaunal communities of beaches of the same morphotype, within a relatively spatially-small region and subject to approximately the same disturbances (both human, e.g. urbanisation, and natural, e.g. storms), would be similar but for additional vehicle disturbance at Aldinga Bay. The same procedure was also done for Moana Bay beach sections, which represent approx. 15 years post-closure to vehicles.

Finally, to determine whether the macrofaunal communities from closed-beach sections at Aldinga and Moana Bay identified more closely with closed or open beach macrofaunal communities, these samples were placed onto the canonical axes of the CAP model developed to distinguish macrofaunal communities of closed and open beaches. By doing this, the CAP model developed to compare beaches open and closed to vehicles is used as a hypothesis, specifically that macrofaunal communities belong to one of two types, ‘open’ or exposed to vehicles and ‘closed’ or not exposed to vehicles. Misclassification rates (i.e. samples from closures allocated to open-type macrofaunal communities, or *vice versa*) were then used as a test of this hypothesis. This was done separately for each section and year of sampling at Aldinga Bay to determine if there was a progression from open-type towards closed-type communities over three years of beach closure.

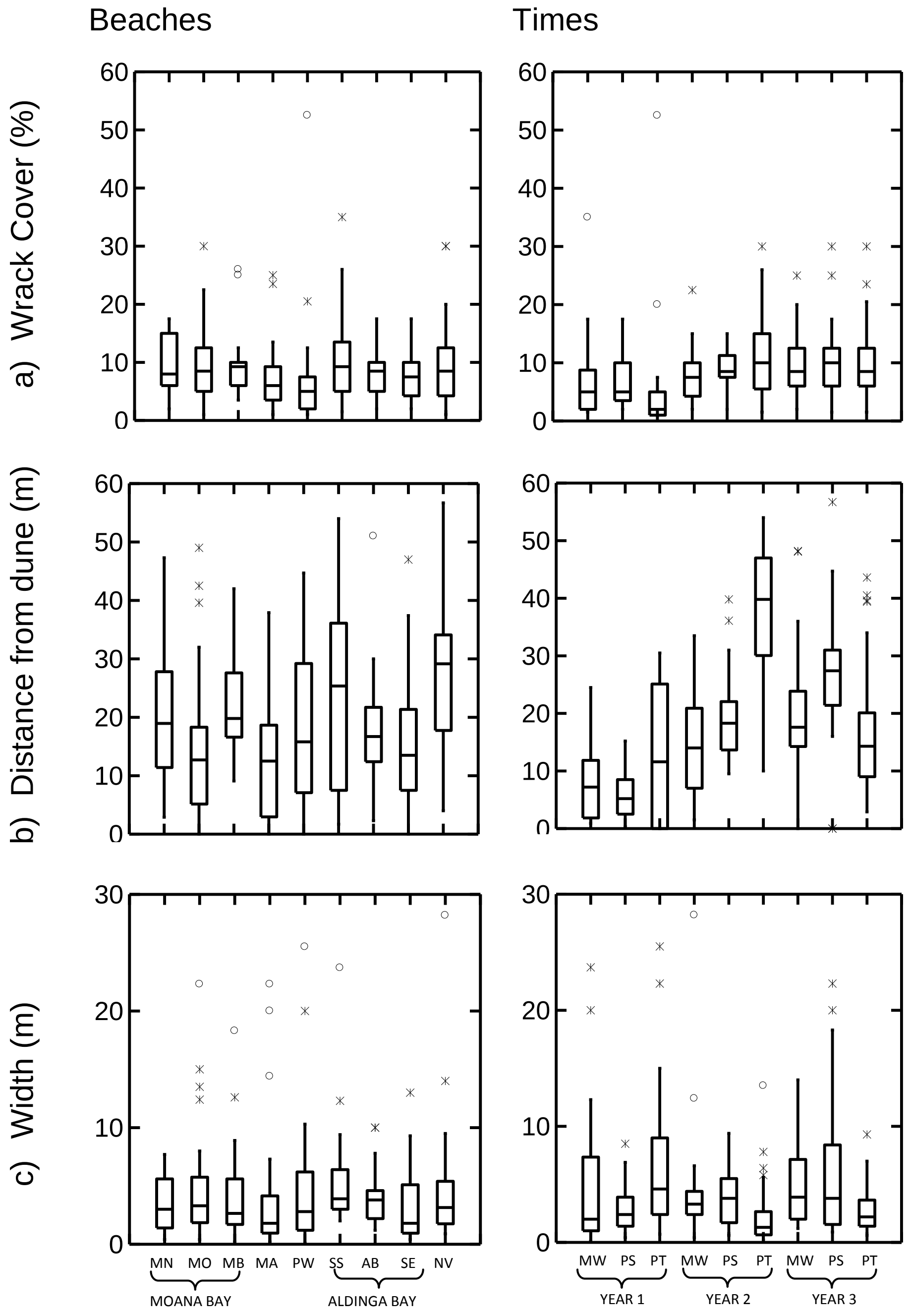
3. Results

1. Potential vehicle effects on macrofaunal associations with wrack

Wrack occurrence and composition

The percent cover, location and width of the wrack drift-line varied greatly in time and space, with no obvious trends among beaches, vehicle access types, seasons or years (Figure 5.2). There was a trend for some unusually large values for these three variables, as indicated by a general trend for positive skew across the box-plots (Figure 5.2). Overall, average wrack percent cover of the total beach was slightly higher at Silver Sands (11.1±1.5%) and Normanville (10.2±1.6%), and slightly lower at Maslin

Figure 5.2: Summary boxplots showing the sample distribution of a) percent wrack cover of the total beach face; b) distance of the driftline from the dune tow; and c) width of the drift line for each site (MN: Moana North; MO: Moana; MB: Moana Bollards; MA: Maslin; PW: Port Willunga; SS: Silver Sands; AB: Aldinga Bollards; SE: Sellicks; NV: Normanville) and sampling occasion (MW: mid-winter; PS: pre-summer; PT: post-summer). The line inside the box is the median value, with the edges of the boxes indicating the range of points in the total distribution 25% above and below the median. The lines extend to extreme values (up to 1.5 the total width of the box), crosses and circles indicate outliers and extreme outliers (Quinn & Keough 2002).



(7.3±1.2%) and Port Willunga (7.8±2.0%), but highly variable between sampling occasions for each beach and season (overall range 1.0 – 52.5%; grand mean = 9.0±0.5%; Figure 5.2).

Both the position and width of the drift line on the beach face was highly variable for different sampling occasions and among study sites (Figure 5.2). The mean distance of the drift line from the top of the beach for each beach and season was compared to the mean location of the transition points between high-, mid- and low-shore zones (see Chapter 3) for that beach on that sampling occasion (data available for years 2-3 only) to determine if there was any pattern in where on each beach that wrack occurred.

Frequently, the drift line occurred in either the high- (20-65% of occasions) or mid-shore (20-60% of occasions) zone of the various beaches, or at the transition point between these two zones (10-35% of occasions; Figure 5.3); in this last case the drift line was most likely deposited by the previous high tide. The drift-line only occurred in the low-shore or the mid- to low-shore transition point at Silver Sands and Aldinga Bollards beach sections at Aldinga Bay and at Normanville beach. Overall, the width and position of the drift-line varied in time and space, indicating a high degree of small-scale temporal and spatial variation among the study sites.

Over the period of this study, wrack on the study beaches was mainly composed of brown algae (e.g. *Sargassum spp.*, *Cystophora spp.*, *Ecklonia radiata, Scaberia agardhii*) and seagrasses (e.g. *Posidonia australis, P. sinuosa, P. coriacea*, *Amphibolis antarctica, A. griffithii*; Figure 5.4). Fragmented wrack (pieces, not whole plants, < 5cm in length) were also often a major component, especially pre-summer (Nov.) 2006. Wrack deposits also contained small amounts of green and red algae, carrion, terrestrial vegetation, rubbish and other debris (e.g. feathers, cuttlebone, shells, rocks etc.; ‘Other’ in Figure 5.4). There was a tendency for a higher percentage of seagrass in samples from post-summer sampling occasions but brown algae dominated samples on other sampling occasions (Figure 5.4). Normanville (and Silver Sands to a lesser degree) also tended to have more seagrass than other sites in the study region (Figure 5.4). Overall, wrack composition on the study beaches varied temporally (i.e. among trips for the same beach) but for any single trip composition of wrack material was reasonably similar among beaches (Figure 5.4). Thus, although the amount

Figure 5.3: Frequency of occurrence (displayed as integers of a possible total of *n* = 6 sampling occasions) of the drift line position in either one of the three beach zones (i.e. H: high-; M: mid-; and L: low-shore) or the transition point between zones (i.e. H-M: high-shore to mid-shore; M-L: mid-shore to low-shore). Beach zones and transition points were measured for the same transects as wrack and macrofauna as part of profile sampling in Chapter 3. Vehicle access types (Access) are indicated as Closed (C), Open (O), Seasonal Closure (S) or Bollarded Closure (B) above the beach names.

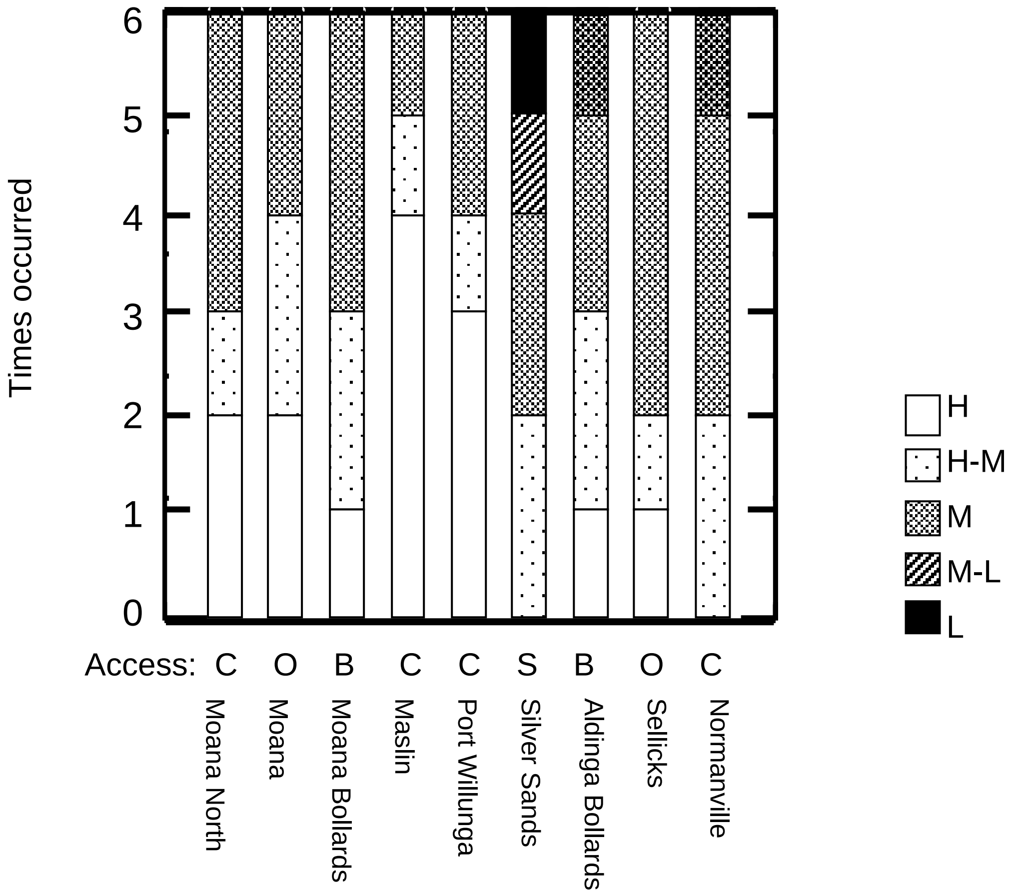
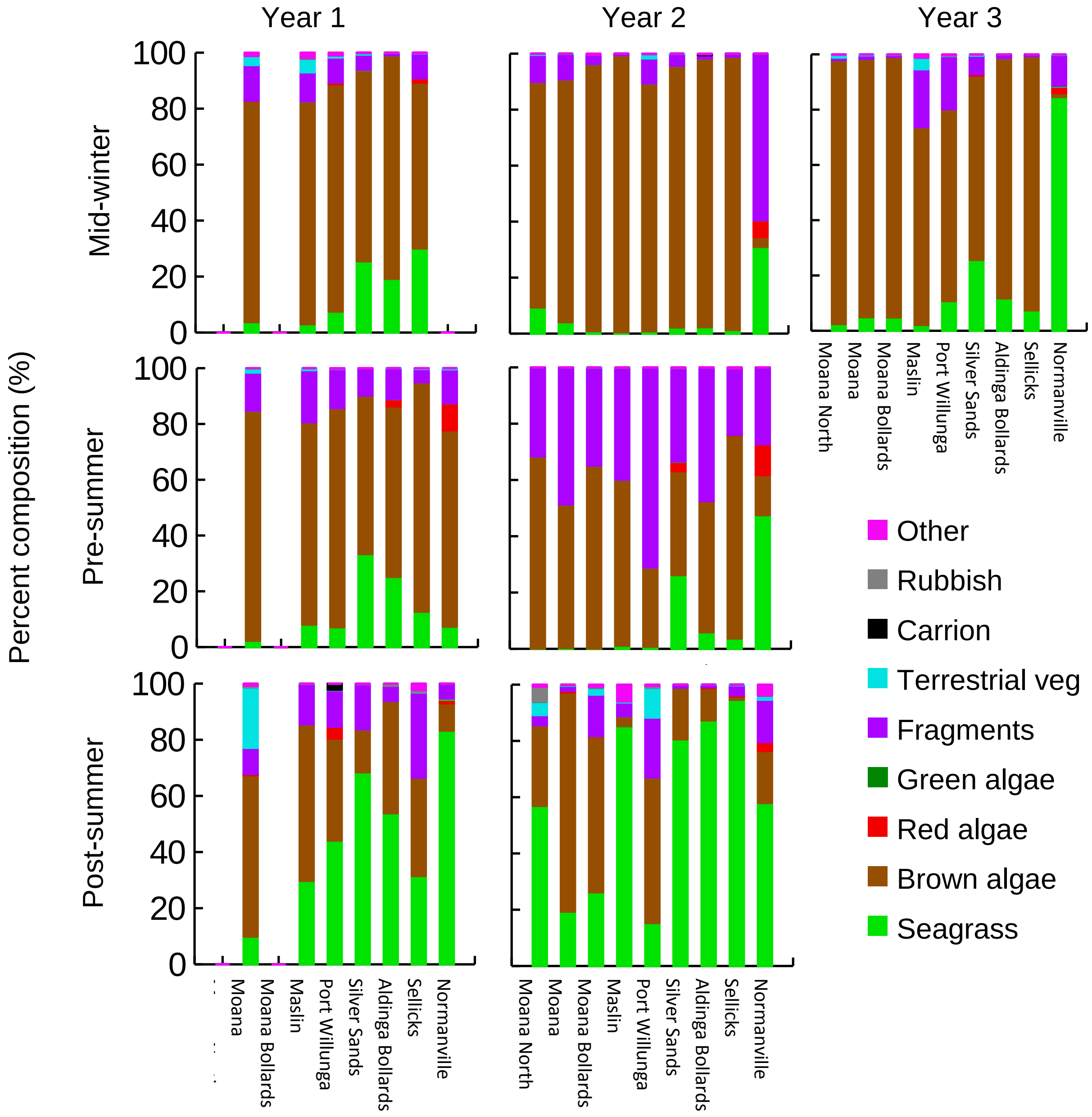


Figure 5.4: Composition of drift-line material. Bars show percentages for groups of different wrack type (including seagrass, various algae, fragments and other items – see Results). Each plot displays results from one sampling occasion (wrack composition was not sampled for the pre- and post-summer occasions of the third year). Bars show beaches (from left to right) in North-South order (see map Figure 1.3). Absence of bars indicates that that beach was not sampled for wrack composition on that occasion (e.g. Moana North, Moana Bollards and Normanville during mid-winter year 1). Wrack composition was not sampled after mid-winter year 3.



of wrack deposited on each study beach and where and how widely it was deposited were specific to particular beaches or beach sections, the composition of wrack among beaches or beach sections at any one time was similar throughout.

Differences in wrack between and within beaches

There were no significant differences in percent wrack cover of the total beach face between beaches open and closed to vehicle access, based on either Beaches (nested in Types), vehicle access Types or Seasons in any year of the study (Table 5.1a). There were significant differences based on Season*access Type interactions for the first ($F_{4,15} = 3.33$; $p < 0.05$) and third ($F_{4,18} = 4.18$; $p < 0.05$) years of the study at Aldinga Bay (Table 5.1b). There were slightly off-set patterns for wrack cover increase and decline on the three sections across the period of the study, with peaks occurring first in the seasonal closure, then the bollarded and open sections, in a north-south directional trend (Figure 5.5a). There were no significant differences or trends for peaks and declines observed for Moana Bay beach sections (Table 5.1a; Figure 5.5b).

Macrofauna and wrack relationships

There was a weak but significant ($r^2 = 0.078$; $p < 0.001$; $n = 255$) positive relationship between the percent wrack cover of the core and total abundance of macrofauna (Figure 5.6). This relationship explained more of the overall pattern when only beaches closed to vehicles were considered ($r^2 = 0.150$; $p < 0.001$; $n = 94$; Figure 5.6) but still explained very little of the observed variation. This relationship was reversed (i.e. negative) but not significant when only open beaches were considered ($r^2 = 0.012$; $p > 0.05$; Figure 5.6).

There were also non-significant tendencies for macrofaunal abundance to decline with increased drift-line width, increased distance of the top of the drift line from the dune toe (i.e. with wrack occurring lower on the shore) and increased percent wrack cover of the beach face Figure 5.7a-c), explaining less than 1% of variation.

Table 5.1: Results of ANOVAs a) between beach comparisons for open v. closed beaches using three separate (i.e. for each year of the study) 3-factor mixed-model ANOVAs on percent cover of wrack on the beach face (4th-root transformed); within beach comparisons at b) Aldinga and c) Moana using three (two for Moana) separate 2-factor orthogonal ANOVAs on percent cover of wrack on the beach face (4th root transformed). Significance values (bold text) are indicated with asterisk (p values: * < 0.05; ** < 0.01; *** < 0.001). No asterisk = NS. df1 and df2 indicate numerator and denominator degrees of freedom, respectively.

a) Open v Closed beaches

			YEAR 1 (N =36)		**YEAR 2 (N = 35) †**		**YEAR 3 (N = 36)**	
Source	**d.f.1**	**d.f.2**	**MS**	***F*-ratio**	**MS**	***F*-ratio**	**MS**	***F*-ratio**
Type	1	2	0.14	0.61	0.17	6.42	0.07	0.30
Season	2	4	0.13	1.15	0.01	0.15	0.02	0.22
Type*Season	2	4	0.06	0.58	0.00	0.07	0.16	2.24
Beach(Type)	2	24	0.23	2.11	0.03	0.42	0.24	2.63
Season*Beach(Type)	4	24	0.11	1.00	0.05	0.72	0.07	0.79
error	24		0.11		0.06		0.09	

† error d.f. = 23

b) Aldinga Bay beach sections

		YEAR 1 (N = 24) †		**YEAR 2 (N = 27)**		**YEAR 3 (N = 27)**	
Source	**d.f.**	**MS**	***F*-ratio**	**MS**	***F*-ratio**	**MS**	***F*-ratio**
Type	2	0.24	**5.23***	0.03	0.34	0.02	0.70
Season	2	0.32	**6.98****	0.13	1.72	0.02	0.64
Type*Season	4	0.15	**3.33***	0.07	0.86	0.14	**4.18***
error	18	0.05		0.08		0.03	

† error d.f. = 15

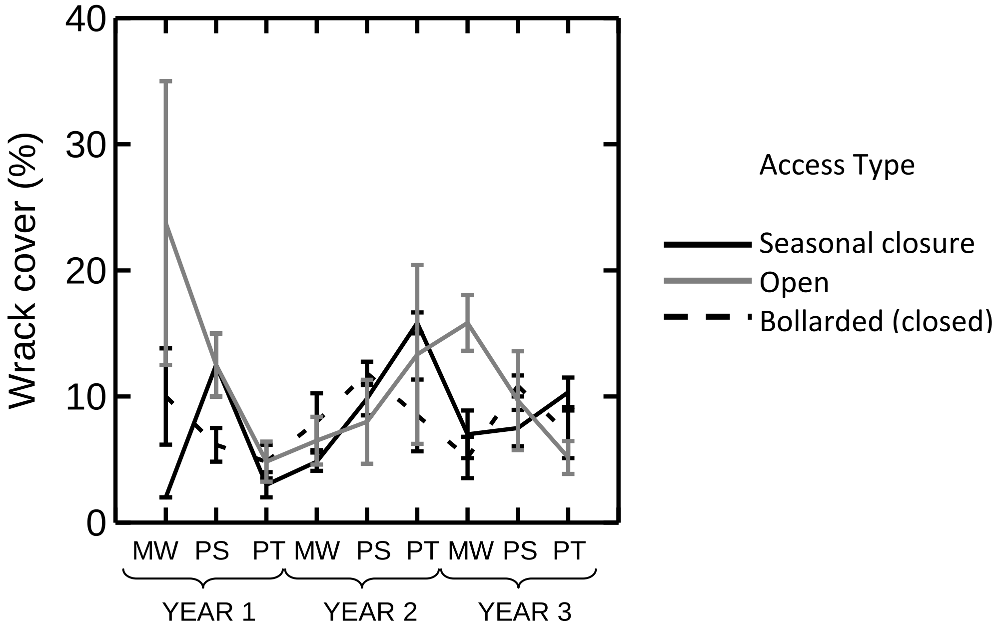
c) Moana Bay beach sections

		YEAR 2 (N = 27)		**YEAR 3 (N = 26)**	
Source	**d.f.**	**MS**	***F*-ratio**	**MS**	***F*-ratio†**
Type	2	0.09	0.99	0.03	0.40
Season	2	0.01	0.11	0.04	0.54
Type*Season	4	0.11	1.15	0.04	0.60
error	18	0.09		0.07	

† error d.f. = 17

Figure 5.5: Mean percent wrack cover (+SE) across the total beach face for each seasonal sampling occasion (MW: mid-winter; PS: pre-summer; PT: post-summer) and year of the study for each beach section at a) Aldinga Bay; and b) Moana Bay.

a)



b)

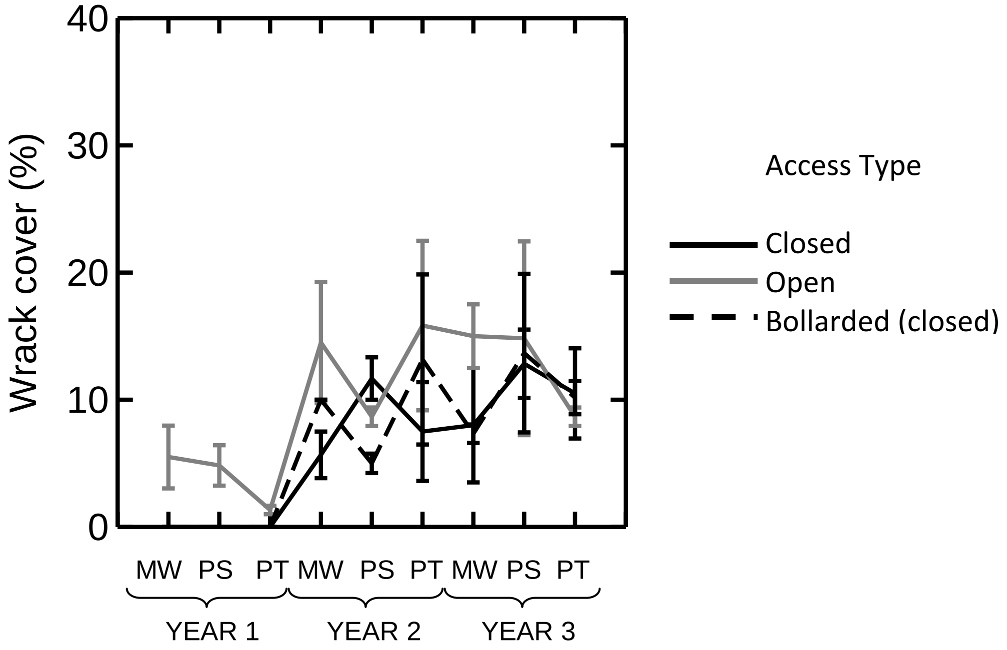
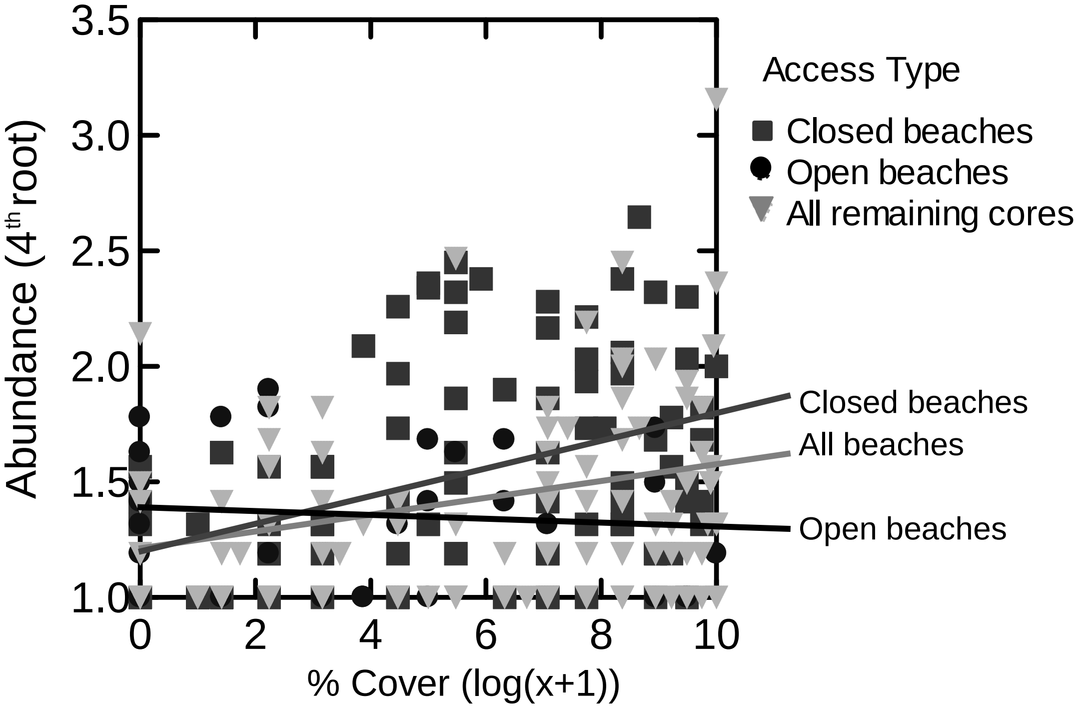


Figure 5.6: Scatterplot showing relationship between average macrofaunal abundance (MFA; 4th-root transformed) per core, only including cores where abundance > 0 (n = 255 of a total 953 cores contained fauna when null cores [i.e. cores containing no macrofauna] were excluded) and the percent cover of wrack over the core (%Cover; log(x+1) transformed). Null cores were excluded because the inclusion of null cores (which formed the bulk of samples) weakened relationships between wrack-cover and macrofaunal abundance. The light grey line represents the relationship between these two variables for all cores (i.e. all cores from open, closed, bollarded and seasonal closures, collected either under wrack or from bare sand patches, combined), the dark grey line represents the relationship for cores from closed beaches only (dark grey squares; n = 94) and the black line represents the relationship for cores from open beaches only (black circles; n = 32). Data were transformed to approximate normality where required.

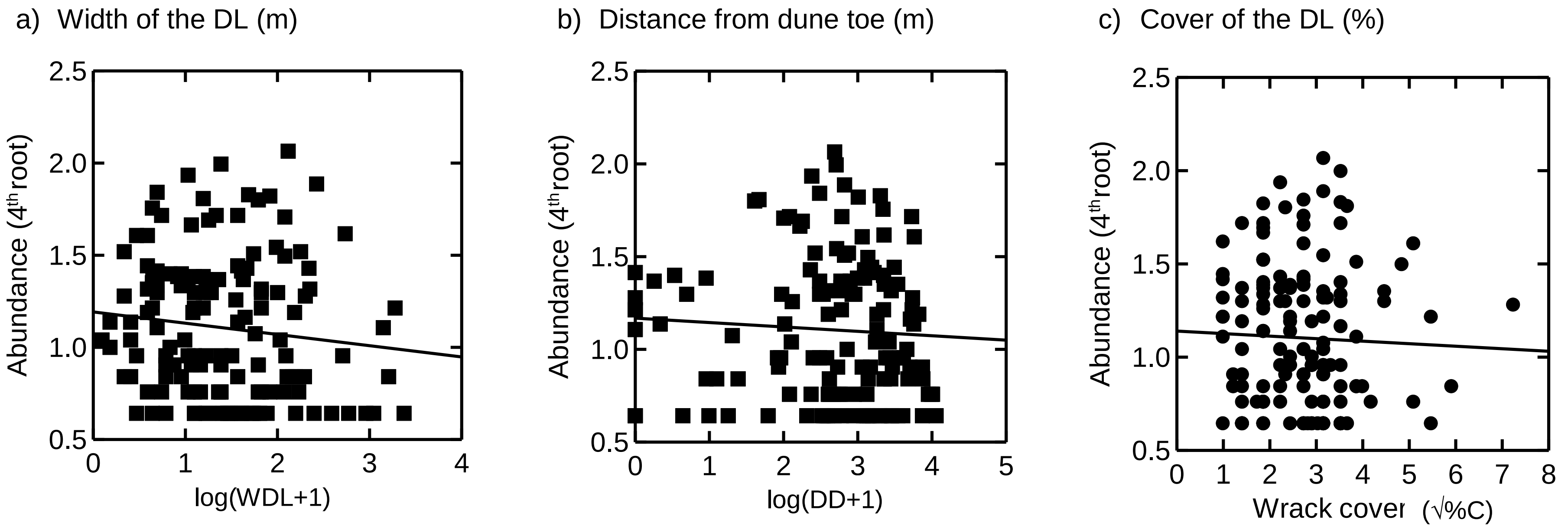


All **$\sqrt[4]{MFA} = 1.204 + 0.035 * \sqrt{(\%C)}$; $r^2 = 0.078$; $p < 0.001$**

Closed **$\sqrt[4]{MFA} = 1.197 + 0.057 * \sqrt{(\%C)}$; $r^2 = 0.150$; $p < 0.001$**

Open $\sqrt[4]{MFA} = 1.371 - 0.010 * \sqrt{(\%C)}$; $r^2 = 0.012$; $p > 0.050$ NS

Figure 5.7: Scatterplots showing relationship between total macrofaunal abundance (MFA; 4th root transformed) per transect, only including transects where abundance > 0 (*n* = 142 of a total 219 transects) and a) the width (WDL measured in metres; log(x+1) transformed) of the drift line; b) the distance (DD measured in metres; log(x+1) transformed) of the drift line below the toe of the foredune/top of the beach; and c) the percent cover of the drift line (Wrack cover (√%C); square root (x+1) transformed). All were non-significant. Data were transformed to approximate normality where required.



$^{4}\surd$ MFA = 1.192 – 0.061*log(WDL+1); r^2 = 0.013; $p > 0.05$

$^{4}\surd$ MFA = 1.168 – 0.024*log(WDL+1); r^2 = 0.004; $p > 0.05$

$^{4}\surd$ MFA = 1.140 – 0.014*√ (%C+1); r^2 = 0.001; $p > 0.05$

2. Potential vehicle effects on macrofaunal occurrence, abundance, species richness and community structure and variability

Macrofaunal abundance and species richness

In total 2,163 macroscopic animals representing 58 distinct species were collected across 1314 cores (Table 5.2). Amphipods were the most abundant group of organism, representing 53% of all organisms collected, while insects were the most diverse group, making up 48% of all species. Species with high abundances (i.e. the most commonly encountered species), such as the amphipod *Talorchestia quadrimana* (Dana), the isopod *Ataecia pallida* (Nicolls & Barnes), the rove beetle *Cafius australis* (Redtenbacher) and the weevil *Aphela phalerioides* (Pascoe), were more abundant on closed beaches and/or beach sections than on open beaches (Table 5.2). Average total abundance (across all sampling occasions, beaches and cover types)was lower on average in year 3 (1.19±0.2/core) than in years 1 (2.00±0.3/core) or 2 (2.19±0.3/core). There were no apparent patterns for macrofaunal abundance across seasons or years (Figure 5.8a). In general, mean abundance was greater for cores collected from under wrack (n = 657 cores; 2.96 ±0.29 organisms per core) than bare sand patches (n = 657 cores; 0.58 ±0.09 organisms per core) within the drift line for all seasons and most beaches (Figure 5.8). Overall mean abundance and species richness for wrack-covered cores was higher at closed beaches (Normanville, Maslin & Port Willunga) and Moana Bay closed-beach sections (Moana North & Moana Bollards) than open beaches (Moana & Sellicks) or closure sections at Aldinga Bay (Silver Sands & Aldinga Bollards; Figure 5.8b).

Differences in faunal occurrence between and within beaches

There was a lower rate of faunal occurrence in cores from open beaches compared to closed beaches. There were few significant differences in the frequency of cores containing fauna from under wrack and bare sand patches on closed versus open beaches (Table 5.3a) but overall there was an association of faunal presence in cores with beach closure and wrack cover, a trend that was consistent (but not often significant) across the three years of sampling and seasonal sampling occasions and for the overall study (Table 5.3a). The frequency of null faunal-core samples between open and

Table 5.2: Macrofaunal species collected across study sites (ordered north – south from left to right; see Chapter 1, Figure 1.3) showing total abundance and rank (top 10 highest abundance) for all sampling occasions (*n* = 9; except Normanville *n* = 8, Moana North and Moana Bollards *n* = 6). Grey shading and formatting indicates summary values for **PHYLA** or ***CLASS*** (dark grey) and **Order** (light grey) groups.

			MOANA BAY					**ALDINGA BAY**			
Species	**Total Abundance**		**Moana North**	**Moana**	**Moana Bollards**	**Port Willunga**	**Maslin**	**Silver Sands**	**Aldinga Bollards**	**Sellicks**	**Normanville**
	Rank	**Ind.**	**Closed**	**Open**	**Bollarded**	**Closed**	**Closed**	**Seasonal**	**Bollarded**	**Open**	**Closed**
ANNELIDA (total)		9	2	1	0	2	4	0	0	0	0
Oligochaete sp. 1		3	0	1	0	2	0	0	0	0	0
Polychaete sp. 1[†]		1	0	0	0	0	1	0	0	0	0
Polychaete sp. 2[†]		1	1	0	0	0	0	0	0	0	0
Polychaete sp. 3[†]		4	1	0	0	0	3	0	0	0	0
SIPUNCULIDA (total)		1	0	0	1	0	0	0	0	0	0
Sipunculid sp. 1		1	0	0	1	0	0	0	0	0	0
MOLLUSCA (total)		7	1	1	1	0	0	3	0	1	0
Paphies elongata		6	0	1	1	0	0	3	0	1	0
Musculista senhousia		1	1	0	0	0	0	0	0	0	0
ARTHROPODA (total)		2146	243	74	191	528	544	32	30	188	316
Unidentified Arthropod 1		6	0	1	5	0	0	0	0	0	0
Springtail sp. 1		1	0	0	0	0	0	0	0	1	0
CRUSTACEA (total)		1349	97	39	55	348	371	6	1	177	255
Cumacean sp. 1		4	0	0	0	0	0	0	0	4	0
Amphipoda (total)		1139	92	35	51	246	339	6	1	173	196
Talorchestia quadrimana	1	997	91	4	25	245	338	6	1	94	193
Chiltonia sp. 1	10	27	1	4	13	1	0	0	0	5	3
Amphithoe flindersi		1	0	0	0	0	1	0	0	0	0
Haustorius sp. 1	6	114	0	27	13	0	0	0	0	74	0
Isopoda (total)		206	5	4	4	102	32	0	0	0	59
Actaecia pallida	3	184	5	2	4	101	26	0	0	0	46
Cirolana corpulenta		22	0	2	0	1	6	0	0	0	13

[†] Polychaetes deteriorated quickly and could not be identified further

Table 5.2: cont.

Species	Total Abundance		Moana North	Moana	Moana Bollards	Port Willunga	Maslin	Silver Sands	Aldinga Bollards	Sellicks	Normanville
	Rank	Ind.	Closed	Open	Bollarded	Closed	Closed	Seasonal	Bollarded	Open	Closed
INSECTA (total)		618	32	31	129	154	157	24	29	9	53
Coleoptera (total)		454	23	20	109	110	141	7	7	0	37
Cafius australis	2	189	7	13	67	63	30	1	1	0	7
Aphela phalenoides	4	162	14	0	7	12	95	3	3	0	28
Curculionidae sp. 1		1	0	0	0	0	1	0	0	0	0
Curculionidae sp. 2		1	1	0	0	0	0	0	0	0	0
Trachyscelis ciliaris		23	0	4	2	16	1	0	0	0	0
Scymena amphibia		16	0	0	8	3	2	0	1	0	2
Hyocis bakewelli		5	0	0	0	4	1	0	0	0	0
Lathridiidae sp. 1		4	0	2	0	1	1	0	0	0	0
Lathridiidae sp. 2		1	0	0	0	0	0	0	1	0	0
Halacritus lividus	9	30	0	0	22	1	7	0	0	0	0
Phycosecis litoralis		1	0	0	0	0	1	0	0	0	0
Coccinellidae sp. 1		11	1	1	2	6	0	1	0	0	0
Coccinellidae sp. 2		1	0	0	0	1	0	0	0	0	0
Passalidae sp. 1		9	0	0	1	3	2	2	1	0	0
Hemiptera (total)		33	0	7	4	6	1	3	3	3	6
Cicadellidae sp. 1[†]		22	0	5	1	3	0	3	2	2	6
Naucoridae sp. 1		6	0	2	1	3	0	0	0	0	0
Belostromatidae sp. 1		1	0	0	0	0	0	0	1	0	0
Gardena sp. 1[†]		4	0	0	2	0	1	0	0	1	0
Diptera[†] (total)		111	9	3	15	34	13	11	15	3	8
Chironomidae sp. 1		2	0	0	0	0	0	0	1	1	0
Tethinidae sp. 1	8	40	1	3	0	27	4	1	1	0	3
Tabanidae sp. 1		2	0	0	0	0	0	0	0	1	1
Canacidae sp. 1		1	0	0	1	0	0	0	0	0	0
Chaetocoelopa sydneyensis	7	64	7	0	14	7	9	10	13	0	4
Unidentified Diperan sp.		2	1	0	0	0	0	0	0	1	0

[†] highly motile species, adults omitted from analysis (see text Methods)

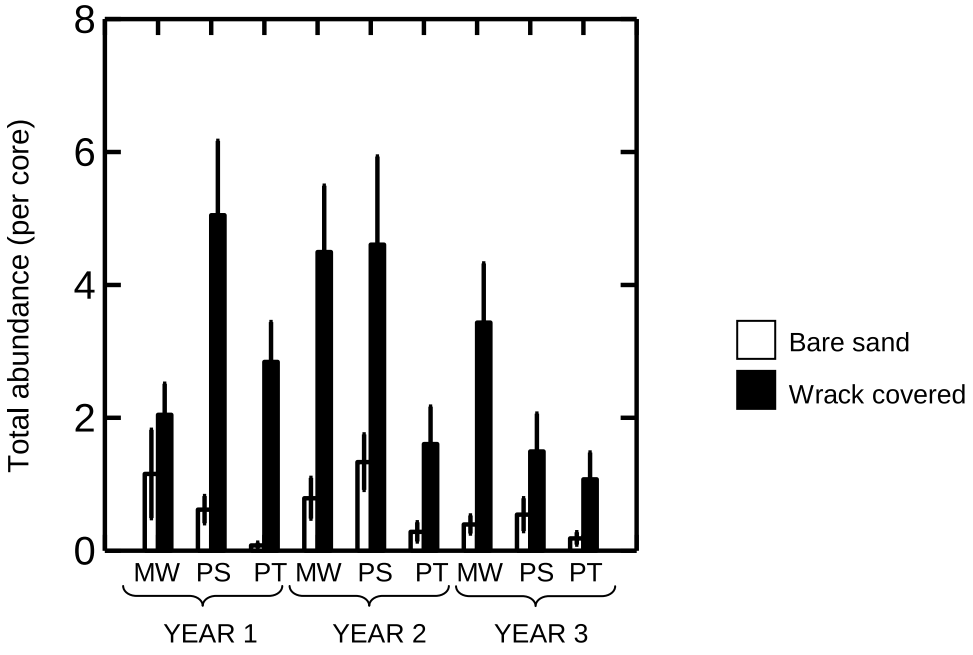
Table 5.2: cont.

Species	**Total Abundance**		**Moana North**	**Moana**	**Moana Bollards**	**Port Willunga**	**Maslin**	**Silver Sands**	**Aldinga Bollards**	**Sellicks**	**Normanville**
	Rank	**Ind.**	**Closed**	**Open**	**Bollarded**	**Closed**	**Closed**	**Seasonal**	**Bollarded**	**Open**	**Closed**
Hymenoptera (total)		20	0	1	1	4	2	3	4	3	2
Formicidae sp. 1		10	0	1	0	4	1	1	3	0	0
Formicidae sp. 2		1	0	0	0	0	0	1	0	0	0
Formicidae sp. 3		1	0	0	0	0	0	0	0	0	1
Formicidae sp. 4		1	0	0	0	0	0	0	0	1	0
Unidentifed wasp sp. 1†		1	0	0	0	0	0	0	0	1	0
Eurytomidae sp. 1†		4	0	0	0	0	1	0	1	1	1
Eurytomidae sp. 2†		1	0	0	0	0	0	1	0	0	0
Apis mellifera†		1	0	0	1	0	0	0	0	0	0
DIPLOPODA (total)		1	0	0	0	0	0	0	0	0	1
Julidae sp. 1		1	0	0	0	0	0	0	0	0	1
ARACHNIDA (total)		9	1	0	0	1	5	1	0	0	1
Thomisidae sp. 1		6	0	0	0	1	4	0	0	0	1
Oxyopidae sp. 1		3	1	0	0	0	1	1	0	0	0
Insect larvae (total)		162	113	3	2	25	11	1	0	1	6
Curculionidae		3	0	0	0	0	3	0	0	0	0
Sciomyzidae	5	118	103	3	2	1	7	0	0	1	1
Blephariceridae		1	0	0	0	0	0	0	0	0	1
Ceratopogonidae		3	0	0	0	0	0	0	0	0	3
Mecoptera		11	0	0	0	10	0	1	0	0	0
Trichoptera sp. 1		22	10	0	0	10	1	0	0	0	1
Trichoptera sp. 2		4	0	0	0	4	0	0	0	0	0
GRAND TOTAL		2163	246	76	193	530	548	35	30	189	316

† highly motile species, adults omitted from analysis (see text Methods)

Figure 5.8: Bar graphs of mean total macrofaunal abundance (log(x+1) transformed; ±SE) under bare sand (unfilled bars) and wrack covered (filled bars) patches of the drift line for a) each sampling occasion (MW: mid-winter; PS: pre-summer; PT: post-summer) averaged across all sites; and b) each site (MN: Moana North; MO: Moana; MB: Moana Bollards; MA: Maslin; PW: Port Willunga; SS: Silver Sands; AB: Aldinga Bollards; SE: Sellicks; NV: Normanville) averaged across all times.

a)



b)

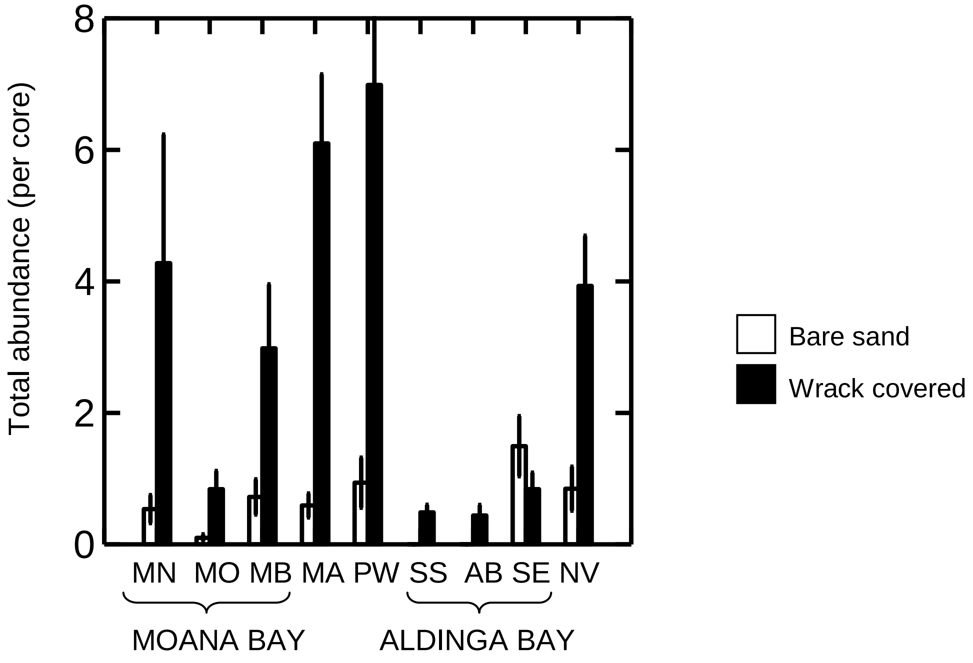


Table 5.3: Summary of results for cross-tabulations testing the association of fauna with wrack-cover and vehicle access types (+ indicates positive association of fauna; - indicates negative association) for a) open v. closed beaches (excluding Normanville); and between vehicle access types b) between-beaches; c) within-beaches at Aldinga Bay and d) Moana Bay. In each case frequencies were tested on each sampling occasion ($n = 9$; $n = 6$ at Moana Bay) and for each year ($n = 3$; $n = 2$ at Moana Bay) and season ($n = 3$) separately. Tables show significant associations of fauna (bold values with level indicated by asterisk: p values: * < 0.05; ** < 0.01; *** < 0.001; not bold = non-significant; blank = no trends observed & no sig. differences) with wrack cover (i.e. wrack v. bare sand patches) and vehicle access (part a) or, of fauna with vehicle access only (i.e. across both cover-types; parts b-d). Grey shading indicates that more than $^{1}/_{5}$ of cells were sparse (i.e. no cores with fauna) and computed significance values may be suspect.

a) Two factor cross-tabulation for open v. closed vehicle access types and bare sand v. wrack cover types (detailed output: see Appendix 5.1)

Season	Year 1	Year 2	Year 3	Overall
Mid-winter	+ wrack - cars	**+ wrack** **- cars ***	+ wrack - cars	**+ wrack** **- cars****
Pre-summer	+ wrack - cars	+ wrack - cars	+ wrack - cars	+ wrack - cars
Post-summer	+ wrack - cars	+ wrack - cars	+ wrack - cars	+ wrack - cars
Overall	+ wrack - cars	**+ wrack** **- cars***	+ wrack - cars	+ wrack - cars

b) Open v. closed beaches across cover types (detailed output: see Appendix 5.2)

Season	Year 1	Year 2	Year 3	Overall
Mid-winter			**- cars***	- cars
Pre-summer	**- cars*****	**- cars*****		**- cars*****
Post-summer	**- cars*****	**- cars*****	**- cars*****	**- cars*****
Overall	**- cars*****	**- cars*****	**- cars*****	**- cars*****

c) Aldinga Bay beach sections across cover types (detailed output: see Appendix 5.3)

Season	Year 1	Year 2	Year 3	Overall
Mid-winter	**+ cars***	**+ cars*****	No fauna found	**+ cars*****
Pre-summer			**+ cars***	
Post-summer				- cars
Overall	+ cars		+ cars	**+ cars****

d) Moana Bay beach sections across cover types (detailed output: see Appendix 5.4)

Season	Year 2	Year 3	Overall
Mid-winter	**- cars*****	+ cars	
Pre-summer	**- cars*****	**- cars*****	**- cars*****
Post-summer	**- cars***		**- cars*****
Overall	**- cars*****		**- cars***

closed beaches (i.e. regardless of core cover type) varied between years and seasons but, overall, there was a strong association for increased faunal occurrence with beach closure across years and seasons and for the overall study (Table 5.3b), indicating sparser faunal assemblages (i.e. more null cores) on beaches open to vehicles compared to closed beaches.

For the within-bays comparisons at Aldinga, low rates of faunal occurrence in core samples resulted in many sparse cells in contingency tables and thus few reliable significant differences. Interestingly, there was often a positive association of faunal occurrence with vehicle presence in the open section at Aldinga Bay, a trend that was usually significant when it occurred (Table 5.3c). Sampling occasions when there were significant positive associations of fauna with vehicle access (Table 5.3c) corresponded closely with times of peak abundance in the open section at Aldinga (Figure 5.9a) that occurred immediately prior to peak vehicle usage times (see Chapter 2; Figure 2.4). Differences between Moana Bay access sections were inconsistent between the two years for which there were data for all three sections of this beach, and, like Aldinga Bay, tests also suffered from low frequencies of occurrence of fauna in cores. In general there was a negative association between faunal occurrence and vehicle presence on a beach section, which was especially clear in year 2 (Table 5.3d). There was one positive association between fauna and vehicles at Moana (mid-winter year 3) but this was the only observed trend that was non-significant (Table 5.3d). There was a complete absence of fauna in cores from the open section (i.e. a negative association between fauna and vehicles) for three of the six sampling occasions (mid-winter year 2 and post-summer years 2 and 3) that resulted in potentially suspect significant differences (i.e. sparse cells; Table 5.3d). This result does, however, support the overall trend for a lack of fauna on the open section of this beach, especially during the sampling occasion (post-summer) immediately following the peak usage time on this beach (see Chapter 2; Figure 2.4). In general, it appears that faunal occurrence is low and faunal assemblages are sparse across both Bays, regardless of vehicle access to individual sections.

Figure 5.9: Mean abundance (±SE) for each sampling occasion (MW: mid-winter; PS: pre-summer; PT: post-summer) and year of the study (*n* = 3) for bare-sand and wrack-covered cores separately for a) beach sections at Aldinga Bay; b) beach sections at Moana Bay; and c) closed beaches. Note the different scales of the y-axis for each of a-c. X- and y-axes are consistent across all six plots.

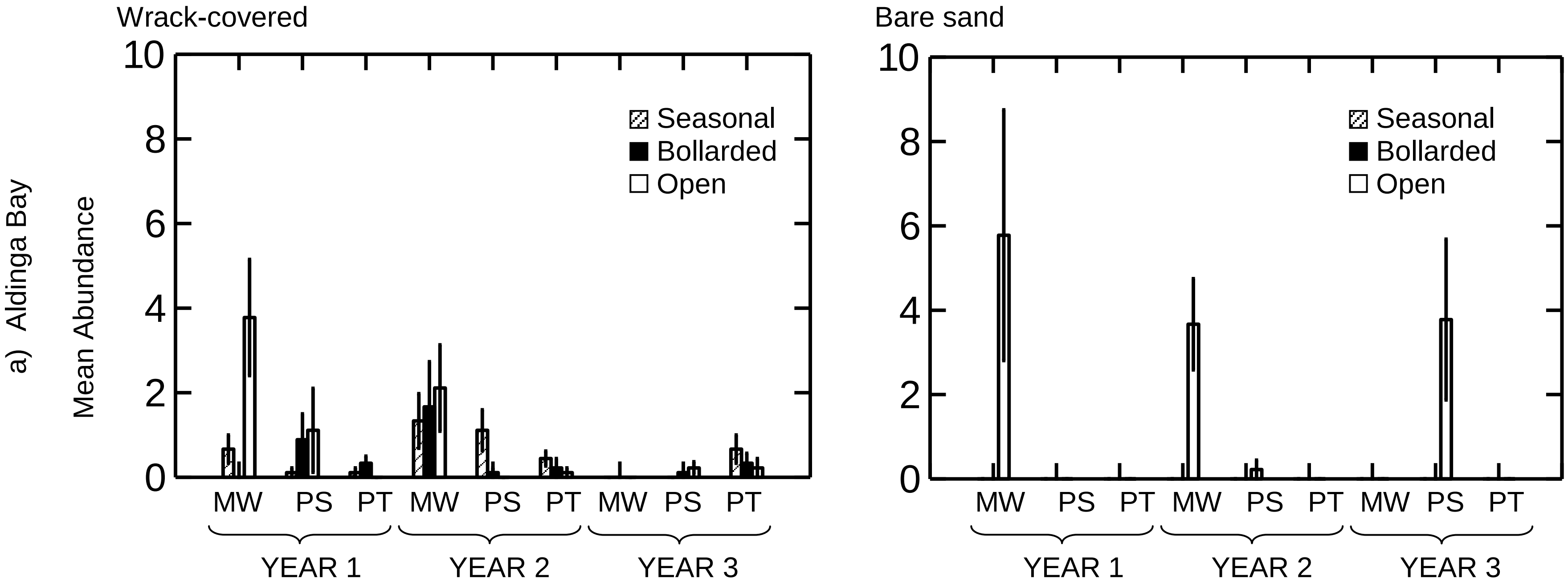
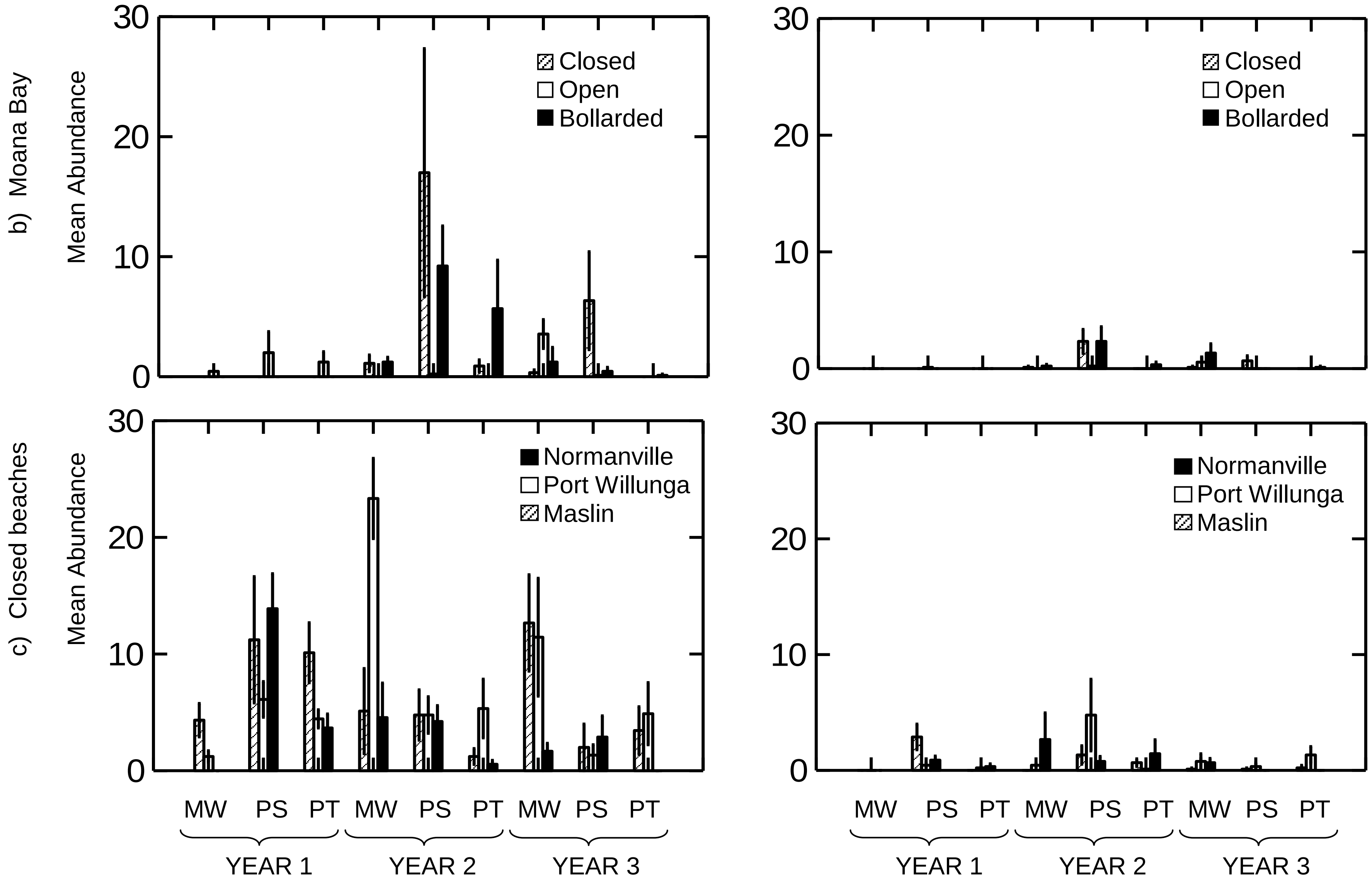


Figure 5.9: cont.



Differences in macrofaunal community structure and variability between beaches

There were some differences detected by PERMANOVA for macrofaunal communities between beaches open and closed to vehicles; however, these were related to small scale spatial differences among beaches rather than an effect of vehicles. The three separate years of the study produced very different sets of multivariate PERMANOVA results for macrofauna community composition between beaches open and closed to vehicles (Table 5.4a), with small-scale spatial variation evident among the four beaches combined with Cover and Season effects in year 1, only Cover effects in year 2, and Type, Cover and Season effects in year 3 (Table 5.4a). Significant differences in the macrofaunal communities among the four individual beaches (i.e. a significant Beach(Type) factor or interaction term) were consistent for all three years overall and on most seasonal sampling occasions (except post-summer for year 2, for which there were no significant factors or interactions; Table 5.4a). However, although there was consistency among sampling occasions for differences among Beaches (nested in Types), there was no corresponding consistency in the MDS patterns generated by species assemblages (Figures 5.10-5.12). For example, in year 1, the MDS for data from the mid-winter sampling occasion showed that most cores from Port Willunga and Moana were void of fauna, thus clumping away in the MDS ordination plot from cores collected at Sellicks and Maslin Beaches that had faunal communities that were broadly distinct from each other (Beach(Type); Pseudo-$F_{2, 64} = 8.71$; $p < 0.001$; Table 5.4a; Figure 5.10a) but, in the same year, a different pattern is observed for the post-summer seasons, with Sellicks cores being devoid of fauna for the post-summer sampling occasion (Beach(Type) Pseudo-$F_{2, 64} = 2.51$, $p < 0.05$, Table 5.4a, Figure 5.10c). Small-scale spatial variation (i.e. differences among beaches) combined with temporal variation (i.e. differences among Seasons sampling occasions) was observed when the data from all three seasons of the first year were analysed together, with a significant Season*Beach(Type) interaction (Pseudo-$F_{4, 192} = 3.89$, $p < 0.001$, Table 5.4a). Core Cover type (i.e. wrack or bare sand) was occasionally significant, either outright (e.g. overall year 1; Cover Pseudo-$F_{1, 2} = 3.89$, $p < 0.01$; also post-summer year 1; Table 5.4a) or

Table 5.4: Results of PERMANOVA tests between a) open and closed beaches as well as within b) Aldinga (dark grey shading: no fauna ∴ no variance between samples and so calculations not possible) and c) Moana Bay (black shading – negative SS and so Pseudo-*F* can't be calculated; Anderson *et al.* 2008) beach sections. Light grey shading indicates that that factor was not applicable for the particular PERMANOVA test (e.g. there is no Season term for tests of just one season). Significance values are indicated with asterisk (*p* values: * < 0.05; ** < 0.01; *** < 0.001). Blank = NS. Seasons are mid-winter (MW), pre-summer (PS) and post-summer (PT).

a) Open v. Closed beaches

	Year 1				Year 2				Year 3			
Source	MW	PS	PT	ALL	MW	PS	PT	ALL	MW	PS	PT	ALL
Season (S)	░	░	░	*	░	░	░		░	░	░	
Type (T)												
Cover (C)			*	**				*	**			
Beach(Type) (B(T))	***	***	*	***	***	***		***	***	*	*	*
S*T	░	░	░		░	░	░		░	░	░	
S*C	░	░	░	*	░	░	░		░	░	░	*
T*C					*			*	*			
B(T)*S	░	░	░	***	░	░	░	***	░	░	░	***
B(T)*C					**			**		*		
S*T*C	░	░	░		░	░	░		░	░	░	*
B(T)*S*C	░	░	░		░	░	░		░	░	░	

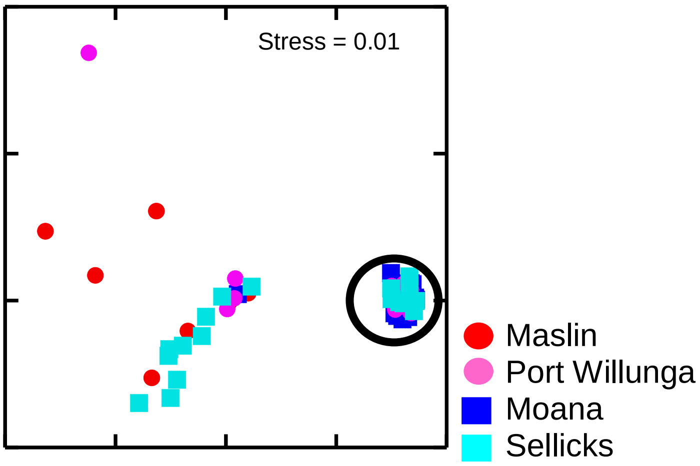
b) Aldinga Bay beach sections only

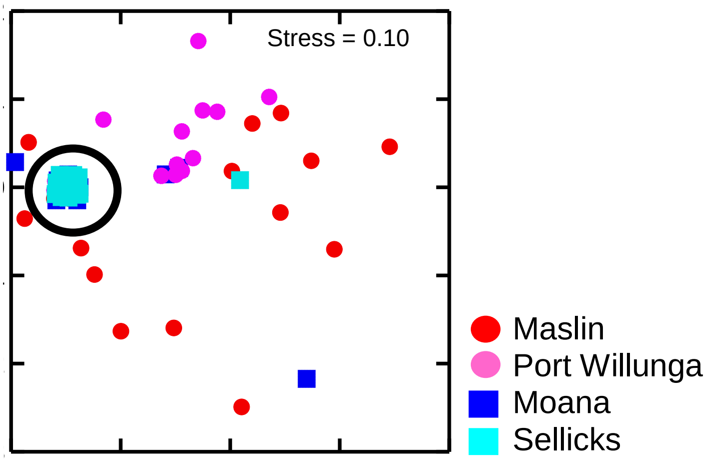
	Year 1				Year 2				Year 3			
	MW	PS	PT	ALL	MW	PS	PT	ALL	MW	PS	PT	ALL
Season (S)	░	░	░	***	░	░	░	***	░	░	░	***
Type (T)	*			**	***			***	▓	**	*	**
Cover (C)		*							▓	**		**
S*T	░	░	░	**	░	░	░	***	░	░	░	***
S*C	░	░	░		░	░	░	*	░	░	░	***
T*C									▓	**		**
S*T*C	░	░	░		░	░	░	*	░	░	░	***

c) Moana Bay beach sections only

	Year 2				Year 3			
	MW	PS	PT	ALL	MW	PS	PT	ALL
Season (S)	░	░	░	***	░	░	░	***
Type (T)	***	***	*	***	*	*		*
Cover (C)		*	***	***			█	*
S*T	░	░	░	***	░	░	░	***
S*C	░	░	░		░	░	░	*
T*C				**			█	
S*T*C	░	░	░		░	░	░	*

Figure 5.10: Multidimensional scaling (MDS) ordination plots displaying relative similarities in macrofaunal communities between cores collected from Open (Moana & Sellicks) and Closed (Port Willunga & Maslin) beaches for each season of the first year of the study. Black rings encapsulate those samples with zero fauna.


a) Mid-Winter


b) Pre-Summer

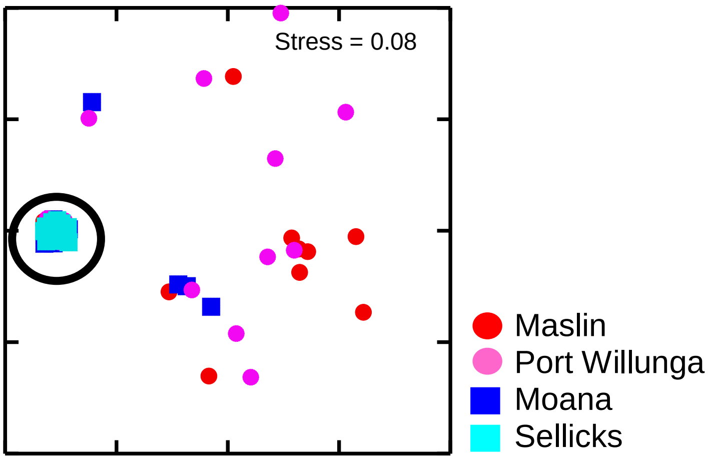
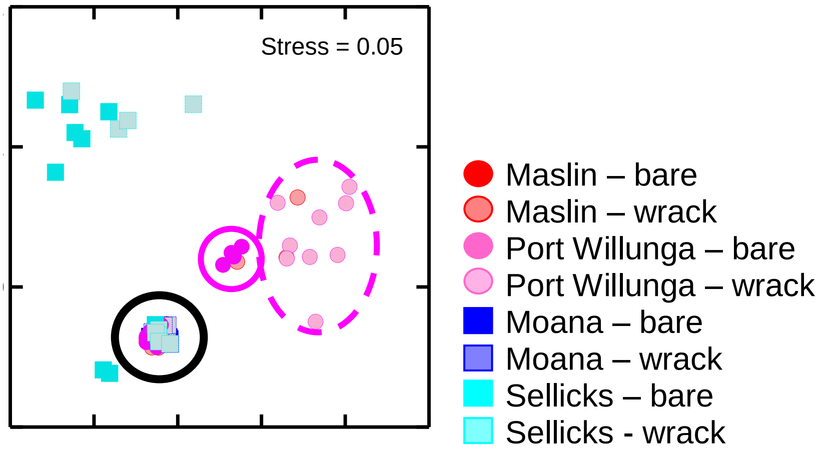
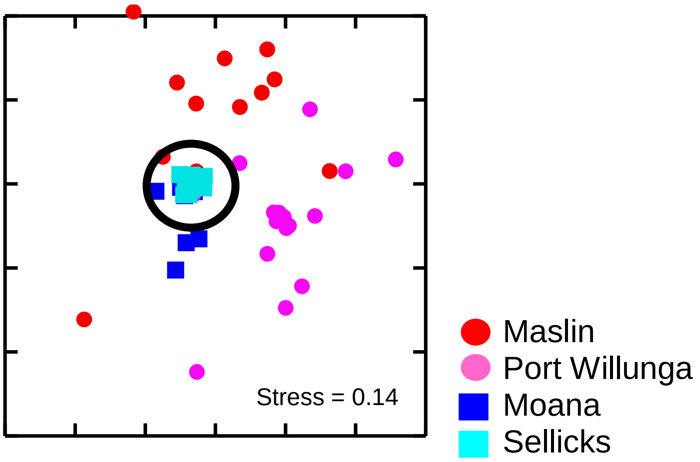

c) Post-Summer

Figure 5.11: MDS plots displaying relative similarities in macrofaunal communities between cores collected from Open (Moana & Sellicks) and Closed (Port Willunga & Maslin) beaches for each season of the second year of the study. Black rings encapsulate those samples with zero fauna. Mid-winter MDS plot shows separation of cores containing fauna from wrack-covered (dashed pink ring) versus bare-sand (solid pink ring) patches from Port Willunga.

a) Mid-Winter



b) Pre-Summer



c) Post-Summer

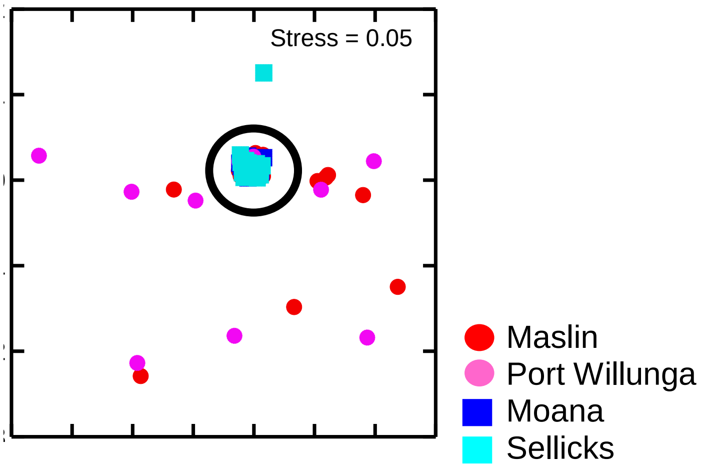
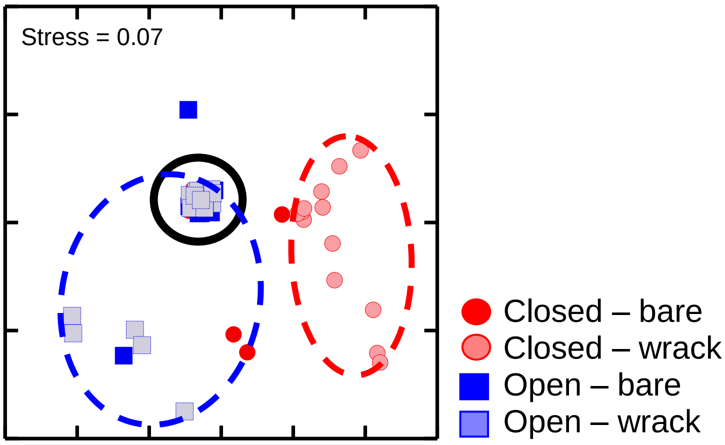
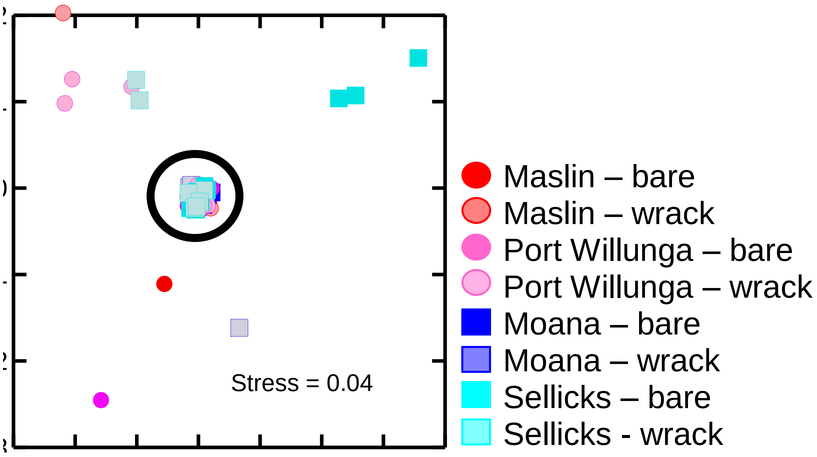


Figure 5.12: MDS plots displaying relative similarities in macrofaunal communities between cores collected from Open (Moana & Sellicks) and Closed (Port Willunga & Maslin) beaches for each season of the third year of the study. Black rings encapsulate those samples with zero fauna. Mid-winter MDS plot shows separation of cores containing fauna from wrack-covered patches from Open (blue dashed ring) apart from Closed (red dashed ring) beaches.

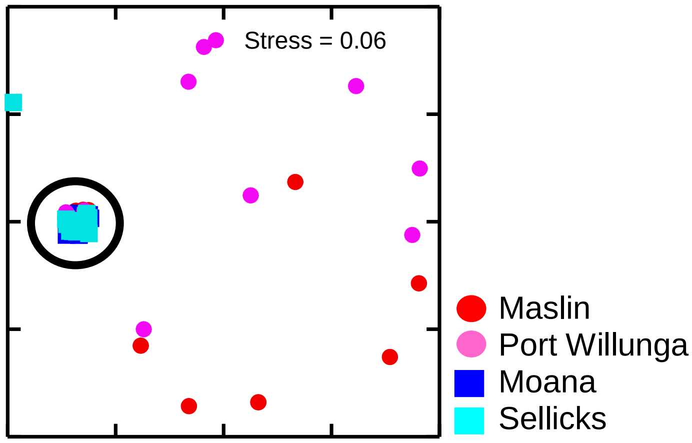
a) Mid-Winter



b) Pre-Summer



c) Post-Summer



combined with some degree of small-scale spatial variation (e.g. mid-winter year 2; Beach(Type)* Cover, Pseudo-$F_{2, 64}$ = 4.13, $p < 0.01$; also overall year 2 and mid-winter year 3; Table 5.4a). The MDS plot for the mid-winter sampling occasion of year 2 shows this trend clearly with samples from wrack-patches on Port Willunga beach grouping apart from bare sand samples (Figure 5.11a). There were no significant differences in the macrofaunal communities of open and closed beaches based solely on Type effects but, in year 3, there was some interaction terms involving Type (Table 5.4a). There was a significant interaction effect of Type*Cover for the mid-winter (Pseudo-$F_{1, 2}$ = 6.53; $p < 0.05$) sampling occasion (Table 5.4a) and overall a significant Type*Cover*Season interaction term (Pseudo-$F_{2, 4}$ = 2.97; $p < 0.05$) for year 3. The MDS plot for mid-winter year 3 shows a clear separation of samples with fauna collected from under wrack-patches on open and closed beaches (Figure 5.12a).

With the exception of the mid-winter sampling occasions of years 1 and 2 and the pre-summer occasion of year 3, there was a significantly higher dispersion of macrofaunal samples (i.e. greater variability) on beaches closed to vehicles relative to open ones for all seasons and years of the study detected by PERMDISP analysis (Table 5.5a). The seasonal occasions for which this was not true (i.e. MW1, MW2 & PS3) were all times when abundances at Sellicks Beach were relatively high compared with other sampling occasions (Figure 5.9a). Otherwise, the reduced variability of faunal communities on open beaches most likely reflected the reduced abundance and species richness of organisms on these beaches (Table 5.5), with fewer organisms and also species most likely being the reason for reduced variability.

CAP results generally supported the findings of the PERMANOVA techniques, with a low strength of the association between patterns in the macrofaunal community structure and the vehicle presence/absence hypotheses seen for all years of both between- (e.g. see Figure 5.13a) and within-beaches comparisons (not shown). There was no distinct or unequivocal visual separation of open or closed beaches into groups based on vehicle access Types on CAP plots, with only a slight off-set in values along the x-axis (Figure 5.13a) but, although the size of the relationship was

Table 5.5: Summary of PERMDISP mean deviations (based on Bray-Curtis similarity) from centroids (i.e. with larger values equating to a wider dispersion of samples and thus greater variability in the macrofaunal community) for a) open versus closed beaches (*n* = 36 per Type per season for $F_{1, 70}$; *n* = 108 per Type per year for $F_{1, 214}$); and within Bays (*n* = 18 per Type per season for $F_{2, 51}$; *n* = 54 per Type per year for $F_{2,159}$) at b) Aldinga; and c) Moana. Significance values are indicated with bold text and asterisks (*p* (permutations-based) values: * < 0.05; ** < 0.01; *** < 0.001). Blank = NS. Seasons are mid-winter: MW; pre-summer: PS; and post-summer: PT.

a) Open v. Closed beaches

	Year 1				Year 2				Year 3			
Source	MW	**PS*****	**PT*****	**ALL*****	MW	**PS*****	**PT*****	**ALL*****	**MW***	PS	**PT*****	**ALL*****
Open	18.2 ±1.4	**A: 10.2 ±2.6**	**A: 6.6 ±1.7**	**A: 12.1 ±1.3**	21.7 ±1.9	**A: 5.4 ±1.6**	**1.8 ±0.9**	**10.5 ±1.3**	**15.6 ±2.5**	10.5 ±2.3	**1.8 ±0.9**	**9.4 ±1.3**
Closed	19.5 ±1.9	**B: 35.5 ±1.9**	**B: 31.3 ±1.5**	**B: 30.6 ±1.3**	25.1 ±1.5	**B: 34.8 ±2.0**	**24.5 ±2.4**	**29.3 ±1.3**	**26.5 ±1.7**	10.2 ±2.1	**23.5 ±2.2**	**21.2 ±1.4**

b) Aldinga Bay beach sections

	Year 1				Year 2				Year 3			
Source	**MW†*****	PS	PT	**ALL‡****	**MW*****	PS	PT	**ALL*****	MW	**PS*****	PT	ALL
Seasonal	**A: 13.0 ±2.3**	3.5 ±1.6	3.5 ±1.6	**A: 5.4 ±1.4**	**A: 8.5 ±3.3**	5.7 ±2.2	10.9 ±2.4	**A: 7.5 ±1.7**	No fauna	**A: 2.9 e^{-12} ±1.8 e^{-12}**	9.3 ±2.0	3.5 ±0.9
Bollarded	**B: 5.3 ±0**	10.6 ±3.4	3.5 ±1.6	**A: 5.7 ±1.8**	**B: 1.9 e^{-15} ±0**	3.5 ±1.6	3.9 ±1.8	**B: 2.1 ±0.9**		**B: 3.5 ±1.6**	5.7 ±2.2	2.7 ±1.0
Open	**C: 21.8 ±1.1**	5.9 ±2.8	4.9 e^{-15}± 2.2 e^{-15}	**B: 14.6 ±1.5**	**C: 27.8 ±1.3**	1.4 e^{-31} ±0	3.5 ±1.6	**C: 16.8 ±1.9**		**C: 17.3 ±3.2**	3.5 ±1.6	7.3 ±1.7

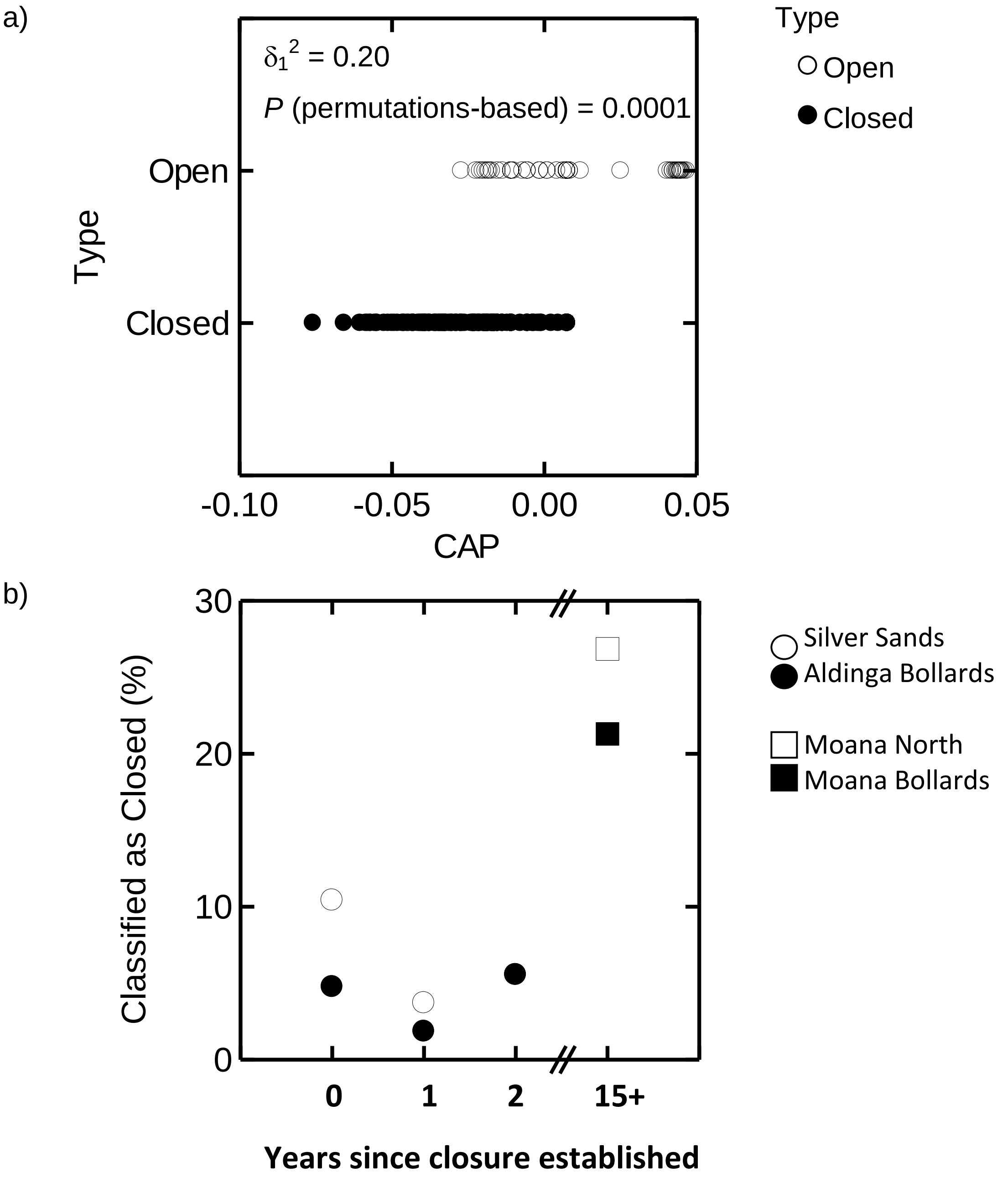
† reduced sample size: *n* = 12 seasonal; 6 bollarded; 18 open per Type; d.f.$_1$ = 2, d.f.$_2$ = 33

‡ reduced sample size: *n* = 48 seasonal; 42 bollarded; 54 open per Type; d.f.$_1$ = 2, d.f.$_2$ = 141

c) Moana Bay beach sections

	Year 2				Year 3			
Source	**MW*****	**PS*****	**PT****	**ALL*****	MW	**PS****	**PT*****	ALL
Closed	**A: 12.0 ±3.0**	**A: 33.2 ±2.4**	**A: 12.7 ±3.4**	**A: 24.8 ±1.9**	9.3 ±3.1	**A: 22.3 ±3.1**	**A: 22.2 e^{-16} ±0**	11.3 ±2.0
Open	**B: 1.3 e^{-15} ±0**	**B: 10.1 ±2.8**	**B: 2.3 e^{-13} ±5.2 e^{-14}**	**B: 3.7 ±1.1**	25.3 ±2.8	**B: 3.5 ±1.6**	**A: 22.2 e^{-16} ±0**	11.6 ±2.0
Bollarded	**A: 18.7 ±1.7**	**A: 29.8 ±1.7**	**A: 22.5 ±4.1**	**A: 26.8 ±2.0**	16.7 ±3.6	**B: 7.2 ±2.2**	**B: 6.6 ±2.0**	9.1 ±1.9

Figure 5.13: a) Constrained ordination canonical analysis of principle coordinates (CAP) plot and test results for the discriminant analysis testing the hypothesis that macrofaunal communities were different between beaches either closed or open to vehicles. Data from all years and seasons were tested together (*n* = 648) and the analysis minimised misclassification error (total misclassification error = 31.5%) using 6 PCA axes (*m* = 6). This model explained 99.3% of the total variation in the relationship between macrofaunal communities of closed versus open beaches; and b) scatterplot showing the percentage of samples collected from closure sections on both Aldinga and Moana Bay that were allocated correctly (using the model shown in part a) to 'closed' beach type macrofaunal communities by number of years each section has been closed to vehicles by CAP routine (i.e. can between-beach patterns predict what happens within beaches?).



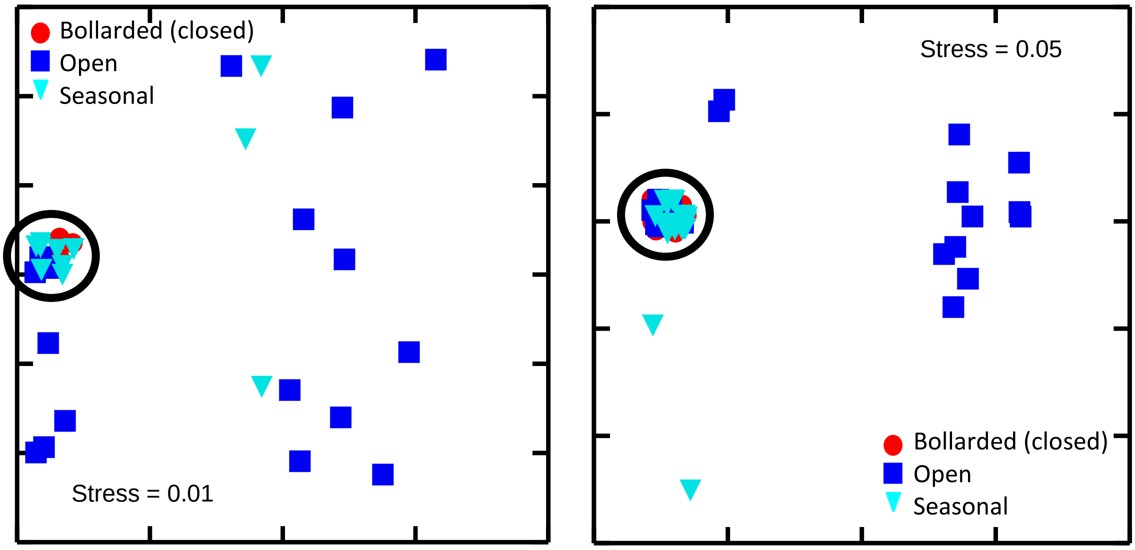
small (i.e. $\delta_1^2 = 0.20$), there was a significant difference between centroid location detected by CAP (Figure 5.13a). The misclassification errors were typically reasonably low for comparisons between open and closed beaches (overall misclassification error = 31.5%) but, misclassification rates of open beach samples (misclassification error = 8.0%) were much lower than closed beaches (misclassification error = 44.9%; Figure 5.13a).

Differences in macrofaunal communities within beaches

Comparisons of macrofaunal communities within Aldinga and Moana Bay Beaches were hampered by low abundances of organisms. Like comparisons between beaches, patterns observed within beaches with sections open and closed to vehicles appeared to be related to small-scale spatial differences rather than an effect of vehicles. Aldinga Bay beach sections recorded very little fauna across all sections, seasons, years & cover types, and, for four of the nine seasonal sampling occasions, there were no fauna on at least one section of the beach (i.e. see Figure 5.9a). On one of these occasions (mid-winter year 3), the complete absence of macrofaunal communities from all sections made analysis impossible (Table 5.4b). The absence of faunal communities on these sections was not restricted to one section of the beach, with each closure and the open section recording no fauna on two sampling occasions over the three year study (Figure 5.9a). The paucity of faunal communities at Aldinga Bay, including the complete absence of a faunal community on any section for one sampling occasion, while fauna were still recorded on nearby closed beaches (Figure 5.9c), indicates that something specific to Aldinga Bay (possibly, but not conclusively, vehicle presence on any part of the beach), was negatively affecting these organisms. Low abundances throughout Aldinga Bay for most sampling occasions made those results variable and inconsistent among seasons and years of the study (Table 5.4). Significant Cover effects were detected for the pre-summer occasion of year 1 (Pseudo-$F_{1,\,48} = 1.75$; $p < 0.05$; Table 5.4b), when fauna was absent from all bare-sand patches but present in all wrack-patches sampled in all three sections (Figure 5.9a). There were differences in macrofaunal communities between vehicle access Types for the mid-winter sampling occasions of the first (Pseudo-$F_{2,\,30} = 4.88$; $p < 0.05$) and second (Pseudo-$F_{2,\,48} = 13.81$; $p < 0.001$) years of the study, and significant Type*Cover interaction effect (Pseudo-$F_{2,\,48}$ = 3.19; $p < 0.01$) for the pre-summer sampling occasion of year 3 (Table 5.4b). Again these sampling occasions corresponded to times of peak abundance in bare-sand patches at Sellicks Beach (Figure 5.9a). MDS plots of similarities among macrofaunal cores showed the samples from Sellicks (open section), that had fauna, grouped apart from cores from closed sections (which had little or no fauna), with an additional separation between bare-sand and wrack-covered cores for pre-summer year 3 (Figure 5.14a-c). There were also differences between Types for the post-summer occasion of the third year (Pseudo-$F_{2,\,48}$ = 1.85; $p < 0.05$; Table 5.4b) but there were few fauna found across all sections (Figure 5.9a) and no apparent pattern based on vehicle access (Figure 5.14d) was seen; thus any differences likely reflect small-scale spatial variation in macrofaunal communities along the Bay. Significant differences among the three Seasonal sampling occasions were detected by PERMANOVA for each year of the overall study (Table 5.4b), with a significant effect of the interaction between Season*Type*Cover for the second (Pseudo-$F_{4,\,144}$ = 2.07; $p < 0.05$) and third years (Pseudo-$F_{4,\,144}$ = 2.71; $p < 0.001$) of the study, but only for Season*Type of the first year (Pseudo-$F_{4,\,126}$ = 3.84; $p < 0.01$; Table 5.4b). These differences again reflect the peak abundances at Sellicks Beach that occur for one season of each year (Figure 5.9a), with greater abundance in bare-sand relative to wrack-covered patches being significant only in years 2 and 3 (Table 5.4b).

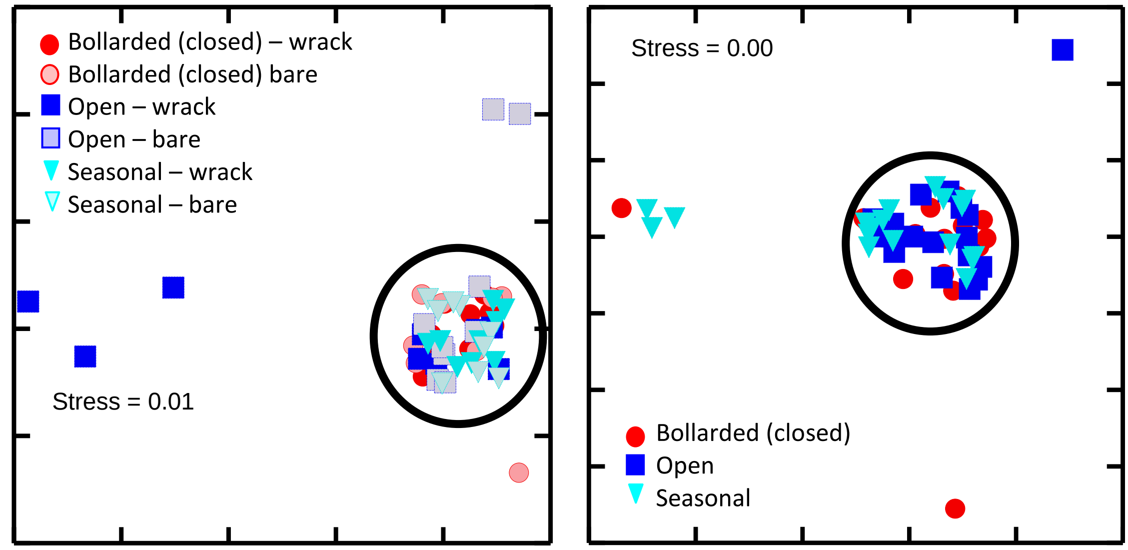
There were few significant differences in the degree of dispersion among samples from Aldinga Bay sections (Table 5.5b), but when significant differences did occur (i.e. mid-winter years 1 and 2, pre-summer year 3; Table 5.5b), dispersion was always greatest on the open beach section, the opposite trend to that seen for between-beaches comparisons (Table 5.5a). Again these are the seasonal sampling occasions for which there were peaks in macrofaunal abundance in the open section of Aldinga Bay but low abundances in both closure sections (Figure 5.9a). Many samples without fauna would result in high similarity among samples and low variability (Figure 5.14), thus resulting in greater variability in the open section where fauna was found. For two of these occasions (mid-winter years 1 and 2) dispersion was greatest on the open section, mid-ranging for the seasonal

Figure 5.14: a) – c) Representative MDS ordination plots displaying relative similarities in macrofaunal communities between cores collected from different type sections at Aldinga Bay for three sampling occasions when peaks in faunal abundance were recorded in the open section (Sellicks); and d) one plot representing MDS plots generated for all other seasons and years which all had stress of 0 with no greatly differing trends or groupings. Black rings encapsulate those samples with zero fauna. During the pre-summer of year 3 (part c) there was a separation of samples collected from wrack-covered versus bare sand patches on the open section of Aldinga Bay, shown by filled versus unfilled points.



a) Mid-winter year 1

b) Mid-winter year 2



c) Pre-summer year 3

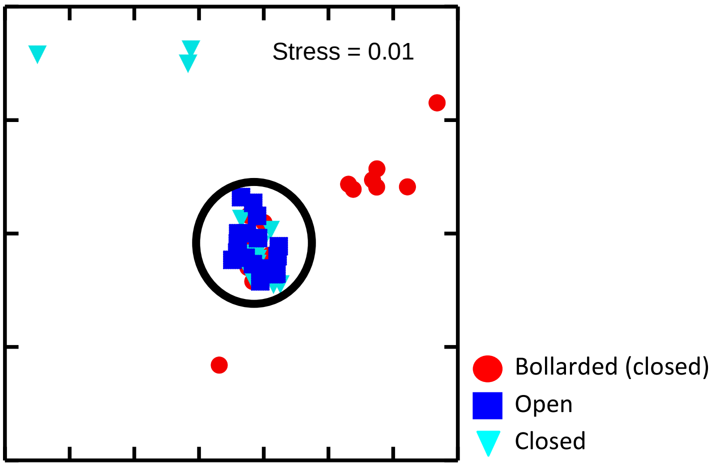
d) Post-summer year 3

section, where vehicles are permitted for only part of the year (but not at the time of sampling), and lowest in the permanently-closed, bollarded section of Aldinga Bay beach (Table 5.5b). On the final occasion (pre-summer year 3) there were no fauna recorded on the seasonal section (Figure 5.9a), and so naturally dispersion of replicate samples on that section of beach was minimal (Table 5.5b). These results could be interpreted as a pattern of increasing variability in the macrofaunal community as vehicle usage becomes more frequent (i.e. the sequence never – sometimes – always); however, abundance data again indicated that this was actually due to the sparser faunal communities in closure sections at these times (Figure 5.9a).

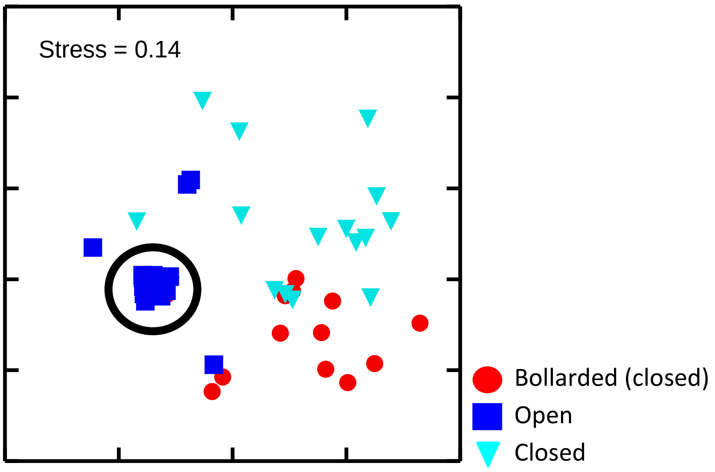
Moana Bay beach sections also recorded low abundance and diversity of fauna. Macrofauna were frequently absent from at least one section at Moana Bay over the two years that this entire Bay was sampled (i.e. often, but not always, the open section; Figure 5.9b). There were significant differences among sections (i.e. across access Types) for five of the six Seasonal sampling occasions for which Moana Bay was sampled, with analysis not possible for the final sampling occasion (post-summer year 3; Table 5.4c) because only two samples collected across the whole of Moana Bay for that occasion contained fauna, resulting in a highly semi-metric geometric system and thus negative SS and pseudo-*F* (Anderson *et al.* 2008). Consistently, most if not all samples from the open section at Moana contained no or very few fauna, and so tended to group around a point representing a hypothetical ‘community’ without fauna in MDS plots from closed beach sections (Figure 5.15). There were also significant differences between Cover types for the pre- (Pseudo-$F_{1, 48}$ = 2.61; $p < 0.05$) and post-summer (Pseudo-$F_{1, 48}$ = 4.60; $p < 0.001$) sampling occasions of the first year of sampling at Moana (Year 2: Table 5.4c). In the first year Moana Bay was sampled (year 2 of the overall study), there was a significant Type*Cover interaction (Pseudo-$F_{2, 144}$ = 3.35; $p < 0.01$) that was not seen for the individual sampling occasions for which there were significant effects of both Type and Cover but no interaction of these two (Table 5.4c). In the second year, although Cover effects were not significant for any individual sampling occasion, there was a significant Type*Cover*Season interaction effect

Figure 5.15: Representative MDS plots displaying relative similarities in macrofaunal communities between cores collected at Moana Bay for the a) mid-winter; b) pre-summer; and c) post-summer seasonal sampling occasions in year 2. Conventions as for Figure 5.12.

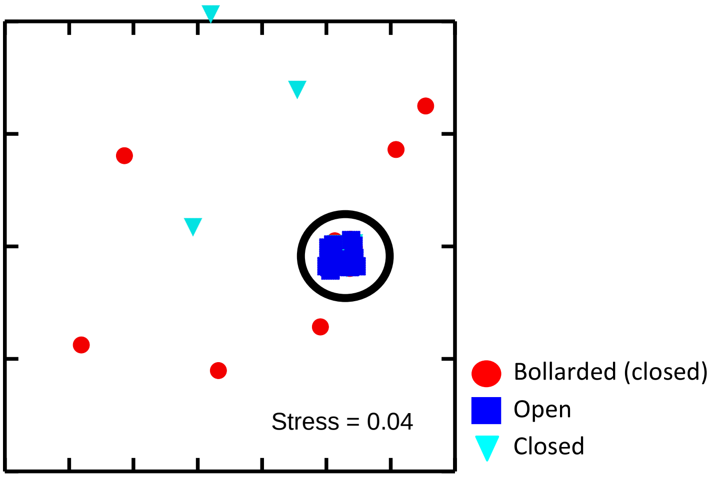
a) Mid-winter Year 2



b) Pre-summer Year 2



c) Post-summer Year 2



(Pseudo-$F_{4, 144}$ = 1.72; $p < 0.05$; Table 5.4c), most likely reflecting patterns of abundance by cover type for the three sections across this year (Figure 5.9b).

Patterns of variability among samples from different sections at Moana Bay were inconsistent between the two years for which there was data from this Bay (Table 5.5c). For the first year, there was a consistent trend across all three seasons and overall (i.e. for the entire year) for decreased variability in macrofaunal communities from the open section relative to the two closed ones (Table 5.5c), reflecting trends seen in the between beaches comparisons (Table 5.5a). Post-hoc tests on these data revealed that the open section was more variable than both closures, which grouped together (Table 5.5c). In year 3, this effect was not seen, with inconsistent patterns among seasons and no overall significant effects (i.e. no significant differences for ALL year 3; Table 5.5c).

3. Species typifying communities on open versus closed beaches and beach sections

SIMPER analysis showed that macrofaunal communities on closed beaches were generally typified by the amphipod *Talorchestia quadrimana*, the isopod *Actaecia pallida* and two beetle species, the predatory rove beetle *Cafius australis* and the weevil, *Aphela phalerioides*. The macrofaunal communities of the individual closed beaches, Maslin and Port Willunga, were generally typified by the same species selected by SIMPER to typify closed beaches (i.e. as above), but larval species of the Order Mecoptera and Trichoptera were also occasionally typical of communities at Maslin Beach but not Port Willunga. The macrofaunal communities on the two closed beaches, Maslin and Port Willunga, although being reasonably dissimilar to each other, were generally more similar to each other than to either open beach (i.e. Moana or Sellicks) or than the two open beaches were to each other for most seasons and years of the study (Table 5.4), indicating that vehicle presence on a beach may alter macrofaunal community structure by increasing the degree of dissimilarity from beaches without vehicles, but with additional intrinsic differences existing between these two open beaches. Communities on open beaches were also typified by *T. quadrimana*, as well as the amphipods *Haustorius* sp., and *Chiltonia* sp.; the latter two species typically being more common in the lower intertidal zone (i.e. mid- and low-shore to the swash; McLachlan & Brown 2006).

The macrofaunal communities of the two individual open beaches, Moana and Sellicks, were typified by the same species as selected by SIMPER for open beaches overall. Communities on open beaches appeared to be quite patchy, with low similarity within-samples from each open beach, and quite unique, with high dissimilarity of samples between the two open beaches for most seasons and all three years of the study (Table 5.6). In addition, open beaches (i.e. both Moana and Sellicks) frequently had no fauna (i.e. all ‘empty’ cells from null cores) or zero similarity (Table 5.6), indicating sparse communities with low abundances and species richness on these beaches. There was high dissimilarity between samples collected on closed versus open beaches for all seasons and across all three years of the study (Table 5.6). In general, macrofaunal communities of beaches either open or closed to vehicles were distinguished by both the presence and/or increased abundance of a number of species on closed beaches relative to open ones (Table 5.7). There were occasional exceptions to this trend, with relatively higher abundance of *T. quadrimana* (mid-winter year 1), *Haustorius sp.* (mid-winter years 2,3; pre-summer year 3; overall year 3) and a cumacean sp. (mid-winter year 2; Table 5.7). The timing of these exceptions again corresponds to times of peak abundances on Sellicks Beach (Figure 5.9a) and sampling occasions for which there was high dissimilarity between open beaches (average dissimilarity 100.00; Table 5.6).

SIMPER analyses of macrofaunal communities at Aldinga Bay indicated that fauna were very sparse and often absent from beach sections regardless of vehicle access (e.g. all sections, mid-winter year 3; Figure 5.9a) and frequently being highly dissimilar between samples within or between sections (Table 5.8). There were no consistent patterns in typifying species for any section based on either vehicle access type or seasonal sampling occasions between years, including the seasonal closure at Silver Sands, which was closed to vehicles during the mid-winter occasion but open for the two summer sampling occasions. The bivalve, *Paphies elongata* (Reeve), typified macrofaunal communities at Silver Sands for the post-summer sampling occasion of year 2, a time when the drift line occurred lower on the

Table 5.6: Average similarity within (bold text with light grey shading) and dissimilarity between (no shading) samples from beaches open (Moana & Sellicks) or closed (Maslin & Port Willunga) to vehicles for each seasonal sampling occasion (MW: mid-winter; PS: pre-summer; PT: post-summer) and overall year (ALL) of the study. Dark shading indicates duplicate cells. Detailed table available in Appendix 5.5.

Year	Season	Beach	Moana	Sellicks	Maslin	Port Willunga
1	MW	Moana	**0.00**			
		Sellicks	94.73	**30.76**		
		Maslin	92.30	71.36	**41.27**	
		Port Willunga	91.92	83.09	73.75	**15.43**
	PS	Moana	**0.00**			
		Sellicks	97.33	**0.00**		
		Maslin	96.89	98.94	**12.93**	
		Port Willunga	93.64	95.92	89.52	**30.43**
	PT	Moana	**9.58**			
		Sellicks	100.00	**Empty†**		
		Maslin	83.47	100.00	**55.14**	
		Port Willunga	87.78	100.00	68.15	**21.74**
	ALL	Moana	**2.48**			
		Sellicks	97.25	**27.19**		
		Maslin	95.59	91.55	**14.51**	
		Port Willunga	93.87	94.48	88.14	**15.53**
2	MW	Moana	**Empty†**			
		Sellicks	100.00	**28.84**		
		Maslin	100.00	98.84	**8.63**	
		Port Willunga	100.00	97.73	84.18	**51.24**
	PS	Moana	**0.00**			
		Sellicks	100.00	**Empty†**		
		Maslin	100.00	100.00	**11.66**	
		Port Willunga	99.22	100.00	95.50	**27.75**
	PT	Moana	**Empty†**			
		Sellicks	100.00	**0.00**		
		Maslin	100.00	100.00	**12.63**	
		Port Willunga	100.00	100.00	90.64	**9.84**
	ALL	Moana	**1.61**			
		Sellicks	100.00	**22.06**		
		Maslin	99.92	99.76	**8.38**	
		Port Willunga	99.52	99.17	92.99	**24.57**
3	MW	Moana	**13.84**			
		Sellicks	100.00	**Empty†**		
		Maslin	100.00	100.00	**27.93**	
		Port Willunga	98.80	100.00	73.93	**25.34**
	PS	Moana	**0.00**			
		Sellicks	100.00	**9.85**		
		Maslin	100.00	97.75	**0.00**	
		Port Willunga	100.00	92.75	95.34	**8.58**
	PT	Moana	**Empty†**			
		Sellicks	100.00	**0.00**		
		Maslin	100.00	100.00	**12.62**	
		Port Willunga	100.00	100.00	94.24	**8.58**
	ALL	Moana	**7.59**			
		Sellicks	100.00	**3.85**		
		Maslin	100.00	99.64	**9.63**	
		Port Willunga	99.61	98.86	91.62	**10.14**

† indicates no samples contained fauna

Table 5.7: Summary of SIMPER analyses of species showing the three species with the highest percent contributions (% cont.) to dissimilarities between beach types (i.e. dissimilarities between beaches open or closed to vehicles) showing trends in relative abundances (4th root transformed) for beaches Open versus those Closed to vehicles (excluding Normanville). Species highlighted by **bold** text were more abundant on open beaches than closed ones for particular seasons or years of the study. Species names have been abbreviated; *Talorchestia quadrimana*: *T. quad*.; *Cafius australis*: *C. australis*; *Actaecia pallida*: *A. pallida*; *Aphela phalerioides*: *A. phal.*; *Haustorius species*: *Haust. sp.*; Cumacean species: Cum. sp.; Tricoptera larvae #1: Tricopt. #1; Polychaete species 3: Polyc. sp. 3.

Year	Season	Species 1	% cont^{n}	Open	v.	Closed	Species 2	% cont^{n}	Open	v.	Closed	Species 3	% cont^{n}	Open	v.	Closed
1	MW	***T. quad.***	**86.42**	**0.47**	**>**	**0.39**	*C. australis*	8.74	0.00	<	0.12	n/a				
	PS	*T. quad.*	35.96	0.10	<	0.60	*A. phal.*	14.37	0.00	<	0.29	*A. pallida*	10.00	0.00	<	0.29
	PT	*C. australis*	39.69	0.10	<	0.52	*A. pallida*	26.17	0.00	<	0.41	*T. quad.*	13.20	0.03	<	0.14
	ALL	*T. quad.*	42.16	0.20	<	0.37	*C. australis*	17.17	0.04	<	0.23	*A. pallida*	11.81	0.00	<	0.23
2	MW	*T. quad.*	49.51	0.03	<	0.77	***Haust.* sp.**	**22.89**	**0.38**	**>**	**0.00**	**Cum. sp.**	**10.48**	**0.11**	**>**	**0.00**
	PS	*T. quad.*	32.65	0.00	<	0.46	*A. pallida*	14.55	0.00	<	0.21	Tricopt. #1	9.91	0.00	<	0.18
	PT	*A. pallida*	38.42	0.00	<	0.25	*C. australis*	21.13	0.00	<	0.18	*A. phal.*	13.24	0.00	<	0.14
	ALL	*T. quad.*	33.14	0.01	<	0.44	*A. pallida*	15.41	0.00	<	0.15	*C. australis*	9.01	0.01	<	0.13
3	MW	*T. quad.*	48.51	0.00	<	0.61	***Haust.* sp.**	**13.33**	**0.24**	**>**	**0.00**	*A. phal.*	12.60	0.00	<	0.21
	PS	*T. quad.*	47.97	0.06	<	0.17	***Haust.* sp.**	**23.86**	**0.15**	**>**	**0.00**	Polyc. sp. 3	8.44	0.00	<	0.04
	PT	*A. phal.*	28.67	0.00	<	0.22	*T. quad.*	27.46	0.00	<	0.18	*A. pallida*	27.11	0.00	<	0.25
	ALL	*T. quad.*	41.83	0.02	<	0.32	*A. phal.*	14.47	0.00	<	0.14	***Haust.* sp.**	**12.10**	**0.13**	**>**	**0.00**

Table 5.8: Average similarity within (bold text with light grey shading) and dissimilarity between (no shading) samples from Aldinga Bay beach sections each with different vehicle access for each seasonal sampling occasion (MW: mid-winter; PS: pre-summer; PT: post-summer) and overall year (ALL) of the study. Dark shading indicates duplicate cells. Detailed output for similarities among samples (listing species with high contributions to similarities) available as Appendix 5.6.

Year	Season		Seasonal	Bollarded	Open
1	MW	Seasonal	**23.56**		
		Bollarded	100.00	**Empty†**	
		Open	78.19	100.00	**30.76**
	PS	Seasonal	**0.00**		
		Bollarded	100.00	**2.67**	
		Open	100.00	100.00	**0.00**
	PT	Seasonal	**0.00**		
		Bollarded	100.00	**0.00**	
		Open	100.00	100.00	**Empty†**
	ALL	Seasonal	**4.42**		
		Bollarded	100.00	**0.80**	
		Open	87.73	100.00	**8.62**
2	MW	Seasonal	**0.00**		
		Bollarded	100.00	**Empty†**	
		Open	99.69	100.00	**28.84**
	PS	Seasonal	**0.00**		
		Bollarded	100.00	**0.00**	
		Open	100.00	100.00	**Empty†**
	PT	Seasonal	**11.54**		
		Bollarded	100.00	**0.00**	
		Open	92.68	100.00	**0.00**
	ALL	Seasonal	**2.34**		
		Bollarded	100.00	**0.00**	
		Open	99.04	100.00	**22.06**
3	MW	Seasonal	**Empty†**		
		Bollarded	Empty	**Empty†**	
		Open	Empty	Empty†	**Empty†**
	PS	Seasonal	**Empty†**		
		Bollarded	100.00	**0.00**	
		Open	100.00	100.00	**9.85**
	PT	Seasonal	**14.29**		
		Bollarded	92.31	**0.00**	
		Open	100.00	100.00	**0.00**
	ALL	Seasonal	**6.25**		
		Bollarded	97.06	**0.00**	
		Open	100.00	100.00	**3.85**

† no samples contained fauna

beach. Otherwise, macrofaunal communities in closed sections at Aldinga Bay were typified by high-shore species, the amphipod *Talorchestia quadrimana* and the beetle, *Aphela phaleroides*. Assemblages in the open section were rarely typified by any species, but more frequently showed a higher degree of similarity between samples than did either closure section (Table 5.8), specifically during the mid-winter sampling occasions of years 1 and 2 and pre-summer of year 3, again when abundances on the open section were relatively high (Figure 5.9a). The seasonal closure section showed little to no pattern based on vehicle presence on the beach. Instead, faunal communities were sparse and species poor regardless of when vehicles were allowed access to that section.

Like Aldinga Bay, SIMPER analysis indicated that macrofaunal assemblages were frequently highly-dissimilar between samples within or between sections at Moana Bay (Table 5.9). Often, but not always, the assemblages between the two closed sections (i.e. Moana North and Moana Bollards) although highly dissimilar, were more similar to each other than either was to the open section (Table 5.9). The macrofaunal assemblage in the section open to vehicles, at Moana, was rarely typified by any species (only Scimyzidae larvae for year 2 overall and *Haustorius* sp. for mid-winter year 3 and year 3 overall), while closed sections were frequently typified by multiple species indicating more diverse assemblages. Moana North faunal assemblages were typified by the amphipod, *Talorchestia quadrimana*, the weevil beetle, *Aphela phalerioides* and larvae of the sciomyzid fly, while at Moana Bollards the crustacean species *T. quadrimana*, *Actaecia pallida*, *Chiltonia sp.* and *Haustorius sp.* were more typical, as well as the beetles, *Cafius australis* and *Trachyscelis ciliaris* (Champion).

5. Macrofaunal recovery after vehicle removal from previously open beach sections

Recovery after vehicle removal

There was no apparent recovery of macrofaunal populations through the brief (~ 3 year) period of the study after vehicle restrictions were put in place at Aldinga Bay (Figure 5.16). The lowest dissimilarity between closed beaches and closure sections at Aldinga Bay was 78.98% in the mid-winter

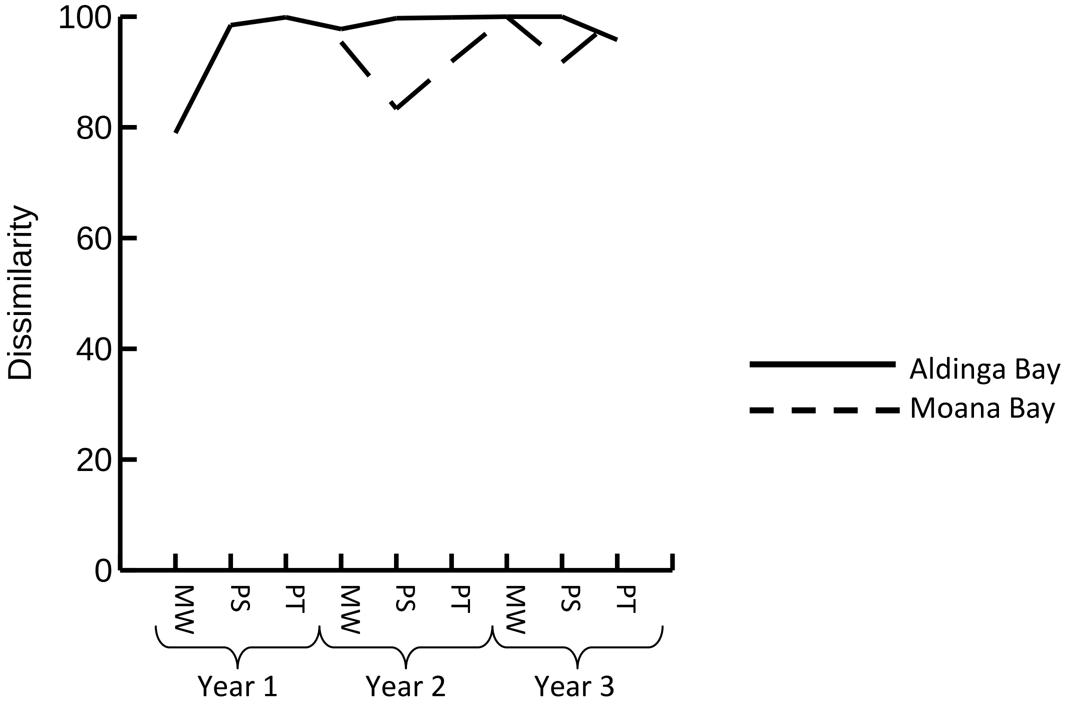
Table 5.9: Average similarity (light grey shading) within and dissimilarity (no shading) between samples from Moana Bay beach sections each with different vehicle access for each seasonal sampling occasion (MW: mid-winter; PS: pre-summer; PT: post-summer) and overall year (ALL) of the study. Dark shading indicates duplicate cells. Detailed output for similarities among samples (listing species with high contributions to similarities) available as Appendix 5.7.

Year	Season		Closed	Open	Bollarded
2	MW	Closed	**1.93**		
		Open	100.00	**Empty†**	
		Bollarded	100.00	100.00	**19.43**
	PS	Closed	**25.55**		
		Open	98.52	**0.00**	
		Bollarded	81.29	98.70	**25.85**
	PT	Closed	**4.29**		
		Open	100.00	**6.21**	
		Bollarded	96.09	100.00	**Empty†**
	ALL	Closed	**16.43**		
		Open	98.86	**1.61**	
		Bollarded	91.26	98.94	**15.98**
3	MW	Closed	**0.00**		
		Open	99.09	**13.84**	
		Bollarded	99.44	95.60	**2.58**
	PS	Closed	**8.78**		
		Open	100.00	**0.00**	
		Bollarded	91.36	100.00	**5.76**
	PT	Closed	**Empty†**		
		Open	Empty†	**Empty†**	
		Bollarded	100.00	100.00	**0.000**
	ALL	Closed	**3.96**		
		Open	99.22	**7.59**	
		Bollarded	96.82	96.91	**2.95**

† no samples contained fauna

Figure 5.16: Average dissimilarity for each sampling occasion between the macrofaunal communities of closed beaches (Maslin or Port Willunga) and closure sections at Aldinga (Silver Sands and Aldinga Bollards) or Moana (Moana North and Moana Bollards) Bays.

a)



of year 1, after which point Aldinga Bay closure macrofaunal communities became highly dissimilar to those from closed beaches, indicating that recovery of these macrofaunal communities towards community structures observed on nearby closed beaches did not occur in the three years following the partial or complete closure of these sections of beach to vehicles. Likewise, recovery following the establishment of vehicle closures at least 15 years prior to sampling was not observed at Moana. Macrofaunal communities within closures at Moana Bay were also highly dissimilar from those of nearby closed beaches (Figure 5.16), with some temporal variation among seasons and years. This result was also supported by the CAP routine, with only a small percentage (i.e. < 11%; Figure 5.13b) of samples from the closed-beach sections at Aldinga Bay (i.e. Silver Sands and Aldinga Bollards) identifying with macrofaunal communities from closed beaches (Figure 5.13b). This percentage did not increase with increasing time closed to vehicles (Figure 5.13b). Closure sections on Moana Bay more closely identified with closed beach macrofaunal communities, with 23% and 29% of samples from Moana Bollards and Moana North, respectively, being allocated to closed-type communities (Figure 5.13b) but, even after at least 15 years of vehicle exclusion, macrofaunal communities in closure sections at Moana more closely identified with those from open beaches (i.e. >70% classed ‘open’). For this CAP model, 45.1% of closed beaches were correctly classified, an accuracy that was greater than that for either Bay.

4. Discussion

The occurrence, composition and percent cover of the wrack resource was highly variable in time and space, at multiple spatial scales (i.e. across the whole beach for photopoint, drift-line patchiness and core cover). These trends were most likely the result of small-scale spatial variation in the distribution of an ephemeral resource (i.e. wrack; Columbini & Chelazzi 2003) occurring along a bay, as was expected. Wrack was similar in composition among beaches for each sampling occasion, indicating that wrack on these beaches came from a common source across the spatial scale of this study (i.e. the study region). Thus wrack on these beaches appears to be an ephemeral resource, with small-scale spatial and temporal variation in composition and cover but was generally similar among beaches for each sampling occasion. Thus it is not likely that any differences among macrofaunal communities on these beaches are related to differences in the wrack resource availability or composition.).

Macrofauna tended to be associated with wrack patches in the drift-line (i.e. there was a higher faunal occurrence in wrack patches versus bare sand). Macrofauna also showed weak trends for declining abundance with increasing wrack cover on the largest spatial scale (i.e. percent cover of the beach face and width of the drift line). These results indicate that wrack may have a concentrating effect on wrack-associated macrofauna; as the wrack resource became spatially spread (i.e. across a wider drift-line), macrofauna became more dispersed but there were still similar numbers between wrack patches. This study was not designed to capture all seasonal variation in wrack percent cover on the study beaches, only to relate wrack accumulation characteristics when sampled to macrofaunal populations across beaches and beach sections with different vehicle access types, thus no generalised conclusions regarding wrack occurrence and macrofaunal relationships can be made from this data. A thorough investigation of the patterns of wrack occurrence and macrofaunal utilisation of the wrack resource on sandy beaches across South Australia, including a number of the beaches sampled in my study, can be found in Duong (2008).

Overall, these data, analysed from a number of different angles, show one clear trend that wrack-associated macrofauna were generally not found on beaches where vehicle access was permitted. There were lower rates of wrack-associated macrofaunal occurrence (i.e. SIMPER and contingency table results), lower macrofaunal abundances and altered community composition (i.e. PERMANOVA, PERMDISP [i.e. reduced variability on open beaches because of fewer fauna], CAP and MDS plots) on beaches with vehicles compared to closed beaches, even though the amount and composition of wrack did not vary among beaches based on vehicle access types. The absence or near absence of macrofaunal communities from beaches with vehicles, relative to nearby beaches without vehicles has also been observed on off-road vehicle impacted beaches in California, North America (Dugan *et al*. 2009) and Queensland, Australia (Schlacher *et al.* 2008c). Reduced abundance of beach crab species have also been reported on beaches with vehicles relative to beaches without vehicles (Steiner & Leatherman 1981; Moss & McPhee 2006; Foster-Smith *et al.* 2007; Schlacher *et al.* 2007b). These results are also in line with predictions made prior to commencement of the study (see Chapter 1; Figure 1.5).

Besides vehicle access to the beaches I sampled, the beaches in this study are relatively similar, with similar physical environments (i.e. see results of Chapter 3) and subject to the same regional disturbances, both natural (i.e. storm events) and anthropogenic (e.g. urbanisation), thus the differences in vehicle access among the study beaches may be negatively affecting wrack-associated macrofauna. Alternatively, the quality of the wrack resource on open beaches may be poorer than nearby closed beaches, and hence less suitable habitat. These results are in line with those of Schlacher *et al.* (2008c), who found substantial impacts on vehicles on beach macroinvertebrates (not just wrack-associated macrofauna), with reduced macrofaunal abundance, diversity and altered community structure of organisms on beaches with vehicles relative to those without vehicles. These effects of vehicles on macrofauna were found to vary among zones of the beach, with greater effects observed in the high- and mid-shore, and no differences between the low-shore zone between impacted and reference beaches (Schlacher *et al.* 2008c). Effects of vehicles on the macrofauna of different zones on the beach were not investigated in my study. However, differences in the intensity of vehicle use among the high-, mid- and low-shore zones of beaches sampled in my study (see Chapter 2) suggest that there is potential for similar differences in vehicle effects on macrofauna among beach zones on these temperate beaches. This potential vehicle impact on macrofauna could be investigated with a survey type study similar to that designed to contrast sediment variables among zones in this thesis (Chapter 3).

Sellicks Beach appears to defy the trend on open beaches for reduced macrofaunal abundance during the mid-winter sampling occasions of years one and two and in the pre-summer sampling occasion of year 3. SIMPER results indicated that there was an increase in abundance of amphipods, including *Haustorius* sp. (see Appendix Table 5.5). Further investigation revealed that these increases in abundance did not appear to be related to any measured wrack variable (i.e. composition, amount, location or drift-line width) and similarly-timed increases were not observed on any other study beach (i.e. see Figure 5.8). There are many potential explanations for the observed increase in abundance; for example, storm events may have deposited fresh wrack on the beach just prior to sampling, including any swash organisms that may have been caught amongst the wrack material. There was one major storm event immediately prior to a peak in macrofaunal abundance for the pre-summer of year 3, with no weather data available prior to the mid-winter sampling occasion of year 1 and only some weather data prior to mid-winter year 2 (see Appendix 1.4), so storms may have been a contributing factor to the observed increases. Alternatively, these times may have represented annual recruitment events for these species (see Appendix Table 5.5) or breeding times. Regardless of how the peaks in abundance arose, they quickly diminished, and so there was no lasting colonisation of the wrack resource on the open beach, Sellicks. An increase in *Haustorid* amphipods on this beach open to vehicles year-round was surprising; a closely related amphipod species, *Urohaustorius* sp., was found to decrease rather than increase in abundance on vehicle-impacted beaches in Queensland (Schlacher *et al.* 2008c). Such discrepancies highlight the importance of investigating effects of potential anthropogenic impacts (such as vehicles) on beaches locally, as closely related species may show vastly different responses to effects.

Multi-dimensional scaling (MDS) plots showed that cores collected from open beaches did often group apart from those collected on closed beaches despite PERMANOVA results indicating no significant differences based on vehicle access types. There were also, however, a large number of samples clumped together that contained no fauna (hence classed by PRIMER as 100% similar, although the complete similarity of samples with no fauna is meaningless in biological terms). Often, this clump would contain all the samples from one open beach, with only a few samples that contained one or two invertebrates from the second open beach scattered around it (e.g. see Figure 5.12b). This resulted in apparently ‘dissimilar’ communities between beaches, even though the ecological significance of ‘almost no’ versus ‘possibly no’ macrofauna may be negligible. Interestingly, when the results from all three years are compared (i.e. see Figure 5.10-5.12) there was a pattern for an increasing number of samples from open beaches to have no fauna (i.e. be plotted within the black ring) after the season of peak vehicle usage (i.e. before the post-summer sampling occasion; see Figure 5.8, 5.10c, 5.11c and 5.12c). This result indicates that macrofauna do in fact occur on open beaches when vehicle traffic is at a minimum (i.e. around the time of the mid-winter sampling occasion; see Chapter 2) but that these communities are unable to persist as vehicle traffic intensifies over the summer peak usage period.

The key difference in species typifying macrofaunal communities from beach open versus those closed to vehicles was the absence (or near absence) of three typically high-shore species, the isopod *Actaecia pallida* and the beetles *Cafius australis* and *Aphela phalerioides* on beaches open to vehicles (Table 5.2; also see Appendix Table 5.5). The isopod, *A. pallida*, and the rove beetle, *C. australis*, were occasionally recorded at Moana, but in lower abundances than the two closed beaches (i.e. Maslin & Port Willunga) or the bollarded closure in Moana Bay (Moana Bollards; Table 5.2), while the weevil, *A. phalerioides*, was never recorded on the open section at either Moana or Aldinga Bays (Table 5.2). Likewise, decreased abundance of the isopod species, *Pseudolana concinna* and insects was observed in the high-shore zone of vehicle-impacted beaches in Queensland, Australia (Schlacher *et al.* 2008c). These results together suggest a particular susceptibility of terrestrial and semi-terrestrial species in particular to vehicle traffic. Equally, however, the absence or near absence of the two beetle species from beaches I sampled may also be related to differences in the back-shore habitat among beaches. There are no dunes backing the beach at Aldinga Bay, with only small foredunes at the top of the beach at Silver Sands and Aldinga Bollards (the dune system has been developed into housing), and a cobble bank forms the high-shore and back-beach at Sellicks. Thus the absence of beetles from Aldinga Bay could be explained by either the presence of vehicles or a lack of suitable back-shore habitat. Dune systems back the beach at the Moana and Moana Bollards sections at Moana Bay, but not Moana North. The abundance of *C. australis* in Moana Bollards (closed section) was higher than any other beach or beach section sampled, but this species was nearly absent from the open section at Moana Bay, Moana Beach, and the northern closure, Moana North (Table 5.2). Thus it seems that the absence of vehicles, as well as a well-developed dune system, may be important factors in wrack-associated macrofaunal occurrence on a beach or beach section.

Interestingly, putatively closed sections on otherwise-open beaches at Aldinga and Moana Bays did not act as refugia for macrofauna, with no increase in abundance or species richness and no difference in overall community structure based on access types among the different sections of both Bays. These results suggest that the effect of vehicles may not be limited to those sections permitting vehicle access. Additionally, MDS plots for macrofaunal communities at Aldinga and Moana Bays displayed very low stress values, with 6 of the 9 plots generated for Aldinga and one plot from Moana Bay having zero stress. Inspection of all plots for both Bays (not shown here) revealed a general pattern of a large number of samples without fauna with a few points scattered around that main clump representing cores that contained a few organisms (e.g. see Figure 5.14a). Because the species identity of these few organisms differed between samples, these scattered points are often relatively widely spaced (i.e. samples represent ‘different’ low-abundance and species-poor communities). Low stress values indicate little effort was required to group samples in these plots, suggesting that these plots depict minimal scatter around a ‘common’ point, in this case samples containing no fauna, effectively producing plots ‘zoomed-in’ on this single point.

There was also no apparent recovery of macrofaunal populations in closure sections either immediately following beach closure to vehicles (i.e. at Aldinga Bay) or after at least 15 years of complete vehicle exclusion (i.e. Moana Bay) when data were tested with both SIMPER and CAP routines. Although some recovery of wrack-associated macrofaunal communities was observed six months after establishing closure areas on beaches previously open to vehicles in California, North America, there were still differences between recovering macrofaunal populations and those of nearby reference beaches (Dugan *et al.* 2009). However, the results of this thesis indicate that recovery of macrofaunal populations after vehicle exclusion from a previously impacted area is impeded by some factor. It is possible that vehicle restrictions at Aldinga Bay are not adequate to protect macrofauna. Winter closures at Silver Sands are not effective (i.e. see Chapter 2) and this whole beach may be considered more like an open beach than one with a closure regime. Also, the bollarded closure is spatially small, although reasonably effective at preventing vehicle access (see Chapter 2). Both these closures are also newly established and, at the completion of my sampling, had only been in effect for a little over three years. Moana Bay closures, however, should have been more effective if vehicles were the cause of depauperate macrofaunal communities. More of this beach is closed to vehicles than is open and the closures at Moana have been in effect for well over a decade. The northern, closed section of this beach is backed by a seawall and carpark, and has been mechanically cleaned at least once during the study period, and any one of these additional factors may also have negatively affected all beach macrofauna. However, the southern, bollarded closure at Moana is backed by a dune system and is never mechanically cleaned but this section also displays a depauperate macrofaunal community.

These results together suggests that macrofaunal communities in Bays with sections open to vehicles were generally sparse and lacked diversity, regardless of vehicle presence on a particular section, and again indicate that vehicles may impact fauna outside of the zone of vehicle disturbance (i.e. the beach sections open to vehicles). It is possible that vehicle impacts observed in the closure sections are an artefact persisting from usage prior to vehicle removal, and populations have never been able to recover. Equally, the observed result could be due to some other aspect of Moana and Aldinga Bays, specifically a spatial effect of unknown origin rather than one due to vehicles. Without data pre-dating vehicle usage of Aldinga and Moana Bays, it is impossible to know whether these beaches have always had depauperate fauna or if the low macrofaunal abundances observed on both Bays are a beach-wide effect of vehicles, either historical or current.

The question of how vehicles could potentially negatively impact macrofaunal populations with which they have no direct contact (i.e. in closed sections on open beaches) is perplexing. It has been posed that, to affect macrofaunal populations, vehicles must use the same part of the beach that is habitat for those organisms (Schlacher & Thompson 2007). However, these results show that vehicle impacts may be imposed on macrofaunal populations that are notionally protected from direct vehicle activity by spatial (e.g. permanently-bollarded closures) or temporal (i.e. seasonal bans) closures. It is possible that closures on beaches with sections open to vehicles are ineffective at reducing levels of vehicle activity. This theory is supported by vehicle usage data (i.e. see Chapter 2) at Aldinga Bay, but not Moana Bay, where closure sections are highly effective at reducing vehicle usage of the bollarded and northern closure sections. Alternatively, beaches suitable for the driving of vehicles (i.e. wide, flat beaches with firm sands) may be unsuitable for wrack-associated macrofauna. This alternative is not supported by the widely-held theory that beach macrofauna respond to gradients in the physical environment of the beach, with increased abundance and diversity towards the Dissipative extreme (Defeo & McLachlan 2005; McLachlan & Dorvlo 2005; also see Chapter 1). Although the beaches in the study region are low-tide terrace (Intermediate) morphotypes, and thus towards the Reflective extreme of the gradient, they are all characterised by a low-shore Dissipative beach that should be highly suitable habitat for macrofaunal organisms. Another explanation for depauperate fauna across the whole of both Aldinga and Moana Bays may be that populations of wrack-associated macrofauna are highly mobile, and able to move around the whole beach. High mobility would be an advantage to any macrofaunal animal that utilises a highly ephemeral resource, such as wrack (Colombini & Chelazzi 2003). If this were the case, populations of macrofaunal organisms may be subjected to heavy traffic when they move into the open sections of these beaches, that is, mobility of these organisms is too great to allow the different sections to be considered as separate entities. Vehicle activity may attract avian predators, such as gulls (e.g. *Larus novaehollandiae*, commonly seen on the study beaches, personal observation) that may forage in both closed and open sections, increasing predation and hence reducing abundance. Increased chemical pollution (e.g. hydrocarbons) of sediments due to vehicle activity may have affected macrofaunal populations on open beaches. Sampling for hydrocarbons was not undertaken due to funding and expertise constraints. All the beaches sampled in this study are likely to be subjected to potentially contaminated stormwater runoff from roads, car parks and drains or creeks, regardless of vehicle activity. Finally, it may be also possible that vehicles are able to disturb ecological processes and links beyond the zone of actual physical disturbance, possibly via the disruption of food chains, thus having an indirect negative impact on beach macrofaunal communities. To my knowledge, no indirect mechanisms for disturbance of macrofaunal communities caused by vehicles have yet been identified or investigated.

Again, there is a high degree of spatial and temporal variability in the macrofaunal communities of the study beaches; for example, there was a trend for fewer macrofauna in samples of the third year across all tests. Significant spatial and temporal variability has been reported for other studies investigating vehicle impacts on macrofauna communities (see Schlacher *et al.* 2008c). But, unlike the physical environment of the beach (i.e. see Chapter 3), there still appears to be some influence of vehicles on macrofauna. Thus this study shows that there is a degree of inter-annual variation in macrofaunal abundance on the study beaches and community structure, regardless of vehicle access, highlighting the importance of long-term, large spatial-scale investigations.

5. Conclusion

This chapter has shown that the presence of vehicles on a beach may negatively affect macrofaunal occurrence, with reduced macrofaunal frequency of occurrence and also reduce abundances observed on open beaches relative to closed beaches. There was also some indication of negative effects of vehicles on beach macrofauna community structure, but not variability, and there was no indication that vehicles alter wrack deposition or composition. Macrofauna was also found to be increasingly absent from core samples throughout the year (i.e. from mid-winter to pre- and finally post-summer, when there was a very low rate of faunal occurrence on open beaches) as vehicle activity on open beaches intensified (see Chapter 2). These results are in line with predictions and expectations from Chapter 1(see Figure 1.5). However, closed-sections on open beaches did not act as refugia for wrack-associated macrofauna, with depauperate macrofaunal communities recorded across both Bays with sections open to vehicles, the opposite trend to what was expected (see Chapter 1, Figure 1.5).

Vehicles appear to have a negative effect on the wrack-associated macrofauna that is not mitigated by seasonal or permanent long- or short-term closures. The beaches permitting vehicle access within the study region have reduced wrack-associated macrofaunal occurrence and altered community structures relative to nearby beaches without vehicles, despite general consistency in the wrack resource among the beaches for a given time. Vehicle closure sections on open beaches do not seem to benefit the macrofauna by providing refugia or allowing recovery of populations, and vehicle impacts are seemingly felt by macrofaunal organisms beyond the area of direct impact; however, the mechanisms behind this apparent impact remain unknown.