



Seasonal Changes of Surface-Active Beach Invertebrate Assemblages in Southern Central Victoria, Australia

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Abstract

Invertebrates play a critical role in beach ecosystems, and seasonal variation in their occurrence and abundance likely influences food webs. We examine and characterise seasonal patterns in invertebrate activity on a temperate, southern sandy dune and beach ecosystem at Venus Bay, Victoria, Australia. We index invertebrate abundance, diversity and assemblage composition at fixed-site pitfall traps which were deployed in four transects from the lower dunes to the beach. Seasonal differences occurred in assemblage composition (foredunes only), richness and abundance. Insects dominated assemblages in summer, spring and autumn; crustaceans dominated winter assemblages. Morphospecies richness was lowest in winter (139% higher in summer and 169% higher in autumn). Our results contrast with other studies from temperate beaches in that (1) richness was higher on beaches compared to in foredunes across all seasons and (2) abundance differed significantly such that winter abundance was higher than for all other seasons. Possible explanations include the exposed nature of the study foredunes, marine ecological subsidies in the form of beach wrack in winter and/or between-site variations in such factors. Further studies would usefully examine between-beach variation in seasonality in invertebrate activity in foredunes and dunes.

Keywords Dune · Foredune · Pitfall · Sandy shore · Temporal variation · Zonation

Introduction

Coastal ecosystems support distinctly structured food webs, where often sparse vegetation creates low in situ primary productivity (Griffiths et al. 1983; Defeo and McLachlan 2013; Schlacher et al. 2015). On sandy shores, waves and tides deliver (usually) marine subsidies such as detached seagrass and algae ('wrack') (Colombini et al. 2003; Cuttris et al. 2015). Wrack and dune vegetation are a primary food source and refuge for upper beach heterotrophs, including primary and secondary consumers such as amphipods, isopods, beetles and flies (Colombini et al. 2003; Defeo et al. 2009; Dugan et al. 2003; Mellbrand

et al. 2011; Stenton-Dozey and Griffiths 1983). To persist in dynamic and unstable sandy shore habitats, invertebrates exhibit behaviour linked to circadian and/or tidal cycles, cyclic reproductive strategies, the ability to burrow and phenotypical and behavioural plasticity (Brown 1996; Defeo et al. 2009; Dugan and McLachlan 1999; Scapini 2014; Schlacher et al. 2014). Beach-adapted invertebrates recycle nutrients and transform carbon from wrack and dune flora, making energy available to higher trophic levels within the sandy shore food web (Bergamino et al. 2011; Schlacher and Connolly 2009; Quillien et al. 2016). Apex predators, such as shorebirds, consume organisms from these lower trophic pathways (Weston 2007).

Given that invertebrates are often abundant, diverse, have short life cycles and are sensitive to fine-scale environmental fluctuations, research into their diversity, abundance and distribution has potential to contribute to accurate and cost-effective information on beach ecology (Kremen et al. 1993; Ward and Larivière 2004). In Australia, the paucity of studies of invertebrates on sandy beaches is notable in comparison to rocky intertidal shores, where the distribution of macrofauna is relatively well understood

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(McLachlan and Defeo 2017). Available sandy beach invertebrate research has predominantly targeted foreshore and littoral (near shoreline) zone macrofauna, with only a few studies focusing on dune and backshore zones (Chelazzi et al. 2005; Mourglia et al. 2015). Additionally, there is little study of the seasonality of beach/dune invertebrates across these habitats in Australia (Dexter 1979; Haynes and Quinn 1995; Holland and Polgar 1976). Both zonation (dune/backshore) and temporal (seasonal) patterns have been explored in a South American study by Mourglia et al. (2015), who report invertebrate assemblage composition and abundance differences in winter compared to summer, autumn and spring. Mourglia et al. (2015) also found distinct compositional differences between beach and dune habitats during all seasons (Mourglia et al. 2015). There are only two studies that focus on spatial and year-long seasonal patterns from Australian beaches (Dexter 1984; Haynes and Quinn 1995), although neither examine adjacent dunes. These studies found high invertebrate densities in autumn and spring, combined with gradual changes across zones (littoral to backshore) correlating with invertebrate reproductive cycles (Haynes and Quinn 1995; Dexter 1984). Evans-Clay et al. (2020) confirmed that invertebrate assemblage composition differed between dune and backshore zones on an Australian sandy beach. No available study known to us examines seasonal patterns of invertebrates on dune and backshore zones for Australian sandy shores.

Seasonal patterns in invertebrate activity on Australian beaches are likely driven by two main processes. Population cycles of invertebrates related to their reproductive phenology, which is possibly driven at least partly by marine resource subsidies onto beaches, see many species fluctuate seasonally in abundance (Haynes and Quinn 1995; Dexter 1984). Temperature also influences invertebrate activity, especially surface activity, with low temperatures (winter) associated with reduced activity due to physiological constraints, while high temperatures and the risk of desiccation may require the use of refuges away from the sand surface (e.g., the use of burrows) thereby decreasing surface activity (Newell and Branch 1980; Pienkowski 1983; Schoeman et al. 2014). Overall, winter decreases in invertebrate activity appear common on temperate beaches, and foredunes often harbour different invertebrate assemblages (usually with greater species richness and lower abundance) from nearby, adjacent beaches (Evans-Clay et al. 2020), presumably at least partly due to the greater structural complexity in foredunes (topography, rugosity and the presence of some vegetation).

Sandy shores host food webs which support a diversity of facultative and obligate beach species, and feature invertebrate and vertebrate predators and prey. Shorebirds can be considered apex predators in these systems (Butler et al. 2020; Cuttriss et al. 2015; Ehmke et al. 2016). For example,

the eastern hooded plover, *Thinornis cucullatus cucullatus* (nationally threatened), is a beach obligate foraging almost exclusively on beach/dune-living invertebrates such as amphipods, isopods and beetles (Weston 2007). Hooded plovers select nesting sites with a higher prey abundance (Cuttriss et al. 2015). A unique seasonal phenological overlap between moult and breeding in this species, which sees no moult or breeding in winter, has led to the hypothesis that a winter restriction exists in food supply for shorebirds living year-round on southern Australian beaches (Rogers et al. 2014). Recent data showing seasonal differences in foraging efficiency (Butler et al. 2020) and variation in winter site occupancy (Barker et al. 2022; Weston et al. 2009) also suggest that higher energetic demands or reduced efficacy of foraging, and a restricted spatial distribution of prey resources, may occur during winter. The ‘winter food restriction hypothesis’ remains untested but suggests there may be a seasonal pattern in invertebrate prey, with a possible drop in abundance or activity in winter.

This study examines whether invertebrate assemblages, abundance and richness change seasonally on a sandy beach and foredune system in Southern Central Victoria, Australia, as provided, for example, by Mourglia et al. (2015) in South America. This is the first study examining seasonal richness across beach and dune habitats in sandy temperate Australian coasts. We tentatively predict that winter will represent a period of relatively few invertebrates, and that foredunes will harbour a greater diversity of invertebrates than the beach due to greater structural complexity in foredunes. While we do not aim to understand the drivers of seasonal changes in the activity of invertebrates, some inference of these may be possible based on nature of the patterns. Such characterisation of any seasonal variation also provides indications of any winter restriction in food supply which might be experienced by resident obligate sandy shore vertebrates.

Materials and Methods

Sampling was undertaken at the southwest-facing ‘Beach Number 5’, Venus Bay, southern Victoria, Australia (38°40′40″S; 145°46′57″E), typical of ocean coasts in the area and harbouring few visitors and limited trampling (Schlacher et al. 2016). The oceanic bay experiences a Mediterranean climate, with warm to hot summers and cooler, wetter winters. The beach is characterised by a wide and low sandy beach (median sand grain size, 0.20–0.26 mm; Schlacher et al. 2016) which transitions to vegetated dunes (up to 1 km wide and 50 m high) and is a known breeding and non-breeding site for hooded plovers (footprints were detected during this study; M. Weston pers. obs.). A handful of other species are known to breed along this coast (pied oystercatcher, *Haematopus longirostris*; red-capped plover

Charadrius ruficapillus; masked lapwing *Vanellus miles*), and some migratory shorebirds also occur here, mostly spring to autumn (e.g., sanderling *Calidris alba*) although double-banded plovers *Charadrius bicinctus* use the study beach in winter (M. Weston pers. obs.).

Sampling

Pitfall traps sample surface-active invertebrates on sand where hooded plovers forage (Butler et al. 2020; Cuttriss et al. 2015), are time and cost-effective, and represent a standard sampling technique for terrestrial invertebrates around the world (Brown and Matthews 2016; Fanini and Lowry 2016). Pitfall traps measure invertebrate surface activity (Lang 2000), and for the purposes of interpretation, we assume this is positively related to relative abundance (as experienced by surface-feeding shorebirds), and we therefore use this as an index of abundance (see Fanini and Lowry 2016).

Pitfall traps (300 ml plastic drinking cups; diameter at top and bottom, 80 and 50 mm, respectively; depth, 110 mm; filled with 5 cm of non-toxic 50% propylene glycol; Fig. S1) were deployed for a 24-h period (mean = 23.96 h, SE = 0.01 h), starting mid-morning and retrieved in the same order in which they were deployed, to standardise sampling effort which encompassed all stages of the tide and day/night cycle. We aimed to deploy traps monthly from July 2018 to October 2019, but weather, trap failure due to inundation or filling with sand and logistics meant sampling were somewhat more sporadic (median days between sampling = 31, min = 11, max = 52). We used fixed trap locations which can risk depleting local invertebrate populations; however, the abundance of invertebrates and dynamism of the substrata

meant this possibility was trivial. Sand temperature may influence invertebrate activity (Newell and Branch 1980; Pienkowski 1983; Schoeman et al. 2014) but was highly colinear with time of year, so is not considered further (Fig. S2).

Pitfall traps were deployed systematically in four separate and fixed straight line transects, that were > 25 m apart to ensure independence (Fig. 1). Two transects were placed east of the Beach 5 access point, and the other two were to the west (Fig. 1). Transects were placed in fixed locations (relative to a fixed marker placed at the landward end of the transect), so that the placement of the transects (and traps) remained consistent through time. Each transect consisted of eight pitfall traps placed in a straight line, perpendicular to the water's edge, at 2-m intervals (Fig. 1). In this nested design, pitfall traps within transects were not independent of each other, but transects were considered independent (Checon 2018).

Transects were perpendicular to the water's edge, capturing the ecological gradient from the upper beach and into the foredune. 'Beach' was defined as the area above the last observable high tide mark and below the seaward margin of the 'foredune' (where dune vegetation started or a sharp change in cross section occurred, whichever was lower). Because pitfall traps are prone to flooding, they could be placed no lower than the upper beach above the last high tide mark. Five traps were placed in the foredune; the other three traps were placed on the beach (Fig. 1). All traps were placed in fixed geographical positions over time; however, trap designations of foredune or beach changed for some trap locations due to the beach's continuously changing structure and erosion of the foredune. This non-random nested design ensured that invertebrates caught in the traps were

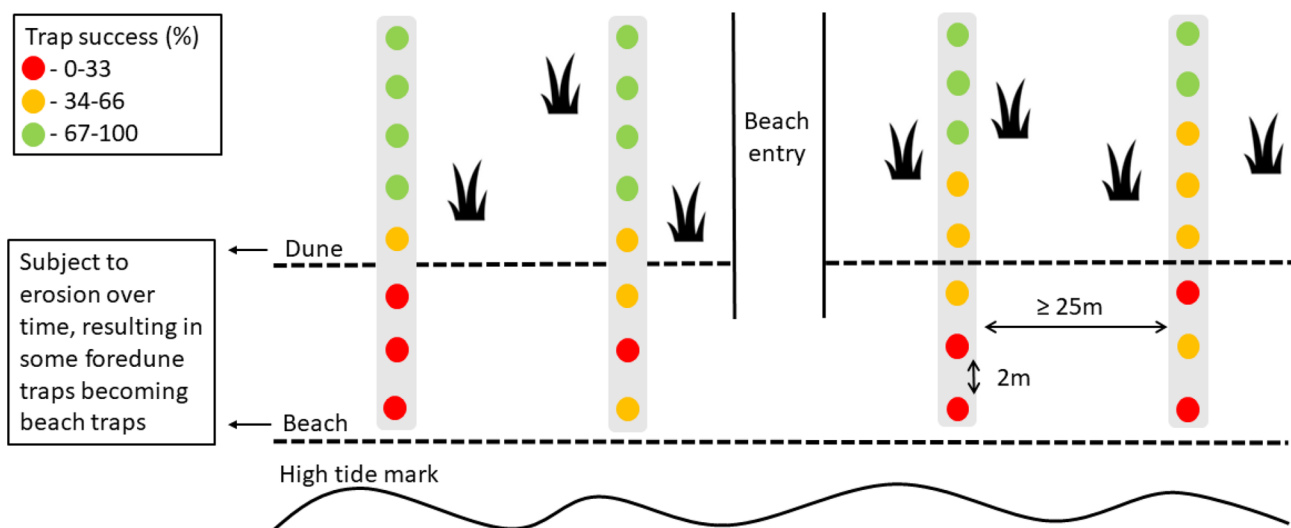


Fig. 1 Configuration of pitfall traps deployed across beach and dune habitats. Circles represent pitfall traps, and colours represent percentage of deployments that were successful (i.e., not flooded or filled with sand)

systematically measured across this ecological gradient to capture zonation patterns.

Trap contents were transferred to labelled falcon tubes with ethanol added for longer-term preservation. During this transfer invertebrates were separated from sand in the trap through density separation, effectively washing the lighter invertebrates from the heavier sand. The contents of each sample were sorted in ethanol under a binocular microscope. All invertebrates in each sample were identified to morphospecies, and the number of each morphospecies recorded (Fig. S3). Springtails (Collembola) were not counted, as they were considered to be too small to represent hooded plover food.

Statistical Analysis

To investigate whether invertebrate assemblages, abundance and richness changed seasonally across the beach-foredune gradient, we conducted multivariate analyses for assemblages and univariate generalised linear mixed models (GLMMs) for richness and individual species abundances (per trap deployment). We use a circular time function for assemblage analyses; however, we also used a categorical time factor (i.e., Austral seasons: winter, June–August; spring, September–November; summer, December–February; autumn, March–May) for univariate analyses for ease of interpretation and comparison with published research.

Assemblage Composition

Invertebrate assemblages were examined using multivariate analyses in PRIMER-e (version 7; PRIMER-e: Plymouth, 2015). To avoid analysis becoming dominated by taxa with high abundances, trap-level counts of morphotaxa were fourth root transformed. To account for habitat (beach or dune) nested within transects, samples from different pit-fall traps in each transect, within each habitat (foredune or beach), were averaged for each sampling date (there were occasions when no beach samples were collected due to all beach traps being flooded; see Fig. 1). The averaged data was used to create a resemblance matrix based on the zero-adjusted Bray–Curtis resemblance measure.

To analyse time of year, we converted date to a cyclic factor. Days since the preceding January 1 were converted to x and y coordinates of a circular time function whereby $x = 1 * \sin(\text{days passed since January 1})$ and $y = 1 * -\cos(\text{days passed since January 1})$ (Clarke and Gorley 2015). These coordinates were used to generate a Euclidean resemblance matrix which represented the similarity of each sampling date to all other sampling dates.

To examine whether assemblage composition varied seasonally, while accounting for habitat nested within

transect, we used PRIMER's RELATE routine to test among sample relationships between the averaged assemblage composition matrix and the time matrix (Clarke and Gorley 2015). RELATE examines whether correlations exist between two matrices, and so this analysis tests for a seasonal signal in assemblage composition, accounting for habitat (and transect of sampling was accounted for by pooling data). To clarify habitat-specific patterns, we also ran RELATE separately for beach and dune. Patterns in assemblages were visualised using non-metric multidimensional scaling (nMDS). For presentation, two-dimensional MDS are presented, even when stress (a standard measure of goodness of fit) > 0.19 , but in each case, separation was also evident in the three-dimensional solutions.

Richness and Abundance

Generalised linear mixed models (GLMMs) were used to test for seasonal and habitat differences for species richness (number of species per trap), abundance (number of individuals of all taxa captured per trap) and the abundances of individual morphospecies. Correlation between species richness and abundance was modest in terms of magnitude ($r_{\text{Spearman}} = 0.317$, $p < 0.001$). Models featured a fixed effect of habitat and season with a random effect of transect, to account for lack of independence of samples within each transect. Models were run with a negative binomial distribution, as Poisson models were found to be overdispersed. Models were validated through visual assessment of residual values versus fitted values and residuals compared to each variable in the model. All analysis was conducted in 'lme4' (Bates et al. 2015) in R, version 4.3.0 (R Core Team 2013).

GLMMs failed to converge for individual taxon models of abundance (zero inflation and rank deficiency [insufficient data across factor level combinations]), so chi-squared contingency table tests of independence examined differences in abundance of all taxa between habitats and seasons.

Results

A total of 24,363 invertebrates (283 morphospecies) were captured and counted. Overall, 208 trap deployments were successful (86 beach samples, 206 foredune samples); 182 trap deployments (38.5%) failed to capture invertebrates due to flooding, filling with sand or human interference. The most prevalent taxa included isopods *Actaecia* spp. (43.0% of captured individuals), followed by amphipods *Notorchestia* spp. (11.0%), the beetle *Mecynotarsus leai* (Anthicidae 8.0%) and the beetle *Phycosecis litoralis* (Phycosecidae 7.7%).

Seasonality of Invertebrate Assemblage Composition

Time as a cyclic factor tended to be associated with the composition of invertebrate assemblages, averaged across samples with habitat specified as a factor (RELATE, $\rho=0.089$, $P=0.08$). Separate analyses indicated changes of assemblage composition with time occurred in dunes ($\rho=0.161$, $P=0.020$) but not beaches ($\rho=0.018$, $P=0.322$). However, the nMDS plot indicated distinct patterns in invertebrate composition between winter, summer, autumn and spring, more pronounced for dunes than beaches, but nevertheless evident for beaches (Figs. 2 and 3). The high failure rate of traps on the beach (Fig. 1) meant data were limited compared to those available for dunes. Assemblage composition of averaged samples was most similar during winter months, displayed by the tightly grouped points on the nMDS (Fig. 2) in comparison to the more loosely grouped points in summer, spring and autumn months, which displayed greater compositional variation (Fig. 2). The most dissimilar invertebrate assemblage composition occurred between summer and winter, occurring at opposite ends of the nMDS space (Fig. 2). Seven morphotaxa were highly

correlated with these seasonal patterns (i.e. r_{Pearson} exceeded 0.5) (Fig. 2). Crustaceans (*Actaecia* spp. and *Notorchestia* spp.) dominated during winter months and were most abundant in beach habitats (Fig. 2). Insects were positively correlated primarily with summer months and slightly in autumn and spring. Phycosecid beetles (*Phycosecis litoralis*) (adults and larvae) were most abundant in summer and spring in foredunes, whilst the fly *Tethina pallidiseta* was most abundant in summer on beaches (Fig. 2). The beetles *Hyocis bakewelli* (Tenebrionidae) and *Mecynotarsus leai* were both most abundant in summer and autumn in foredunes (Fig. 2).

Seasonality of Species Richness and Relative Abundance

Invertebrate richness was influenced by both season ($F=18.401$, $p<0.001$) and habitat ($F=17.479$, $p<0.001$). Species richness was highest in autumn and spring (13.3 and 12.7 species per trap, respectively; Tukey $p>0.05$) followed by summer (10.9; Tukey $p>0.05$). Winter species richness was lower than all other seasons (7.85; Tukey $p<0.001$ in all comparisons; Fig. 4). Species richness was greater in beach compared to foredune habitats (beach = 12.9 species;

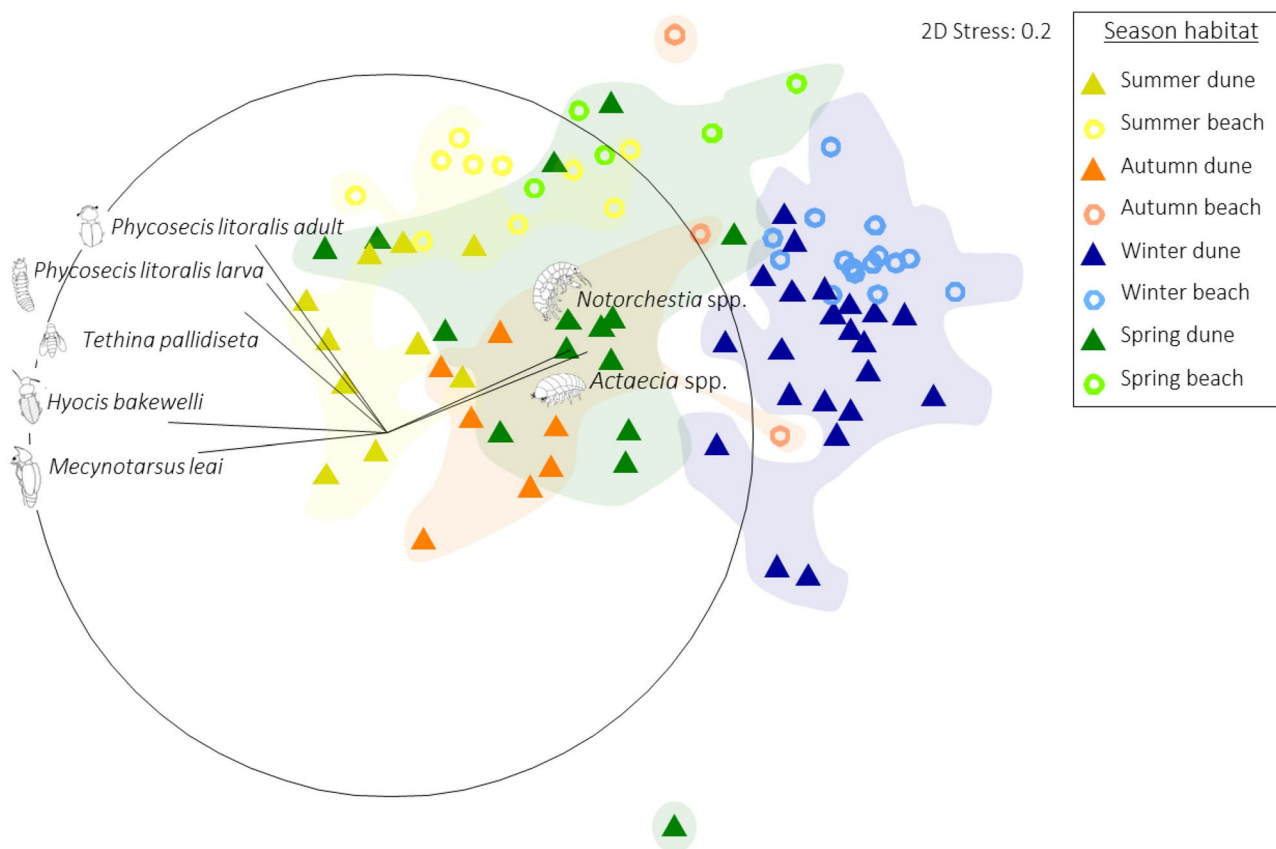


Fig. 2 Non-metric multidimensional scaling plot based on zero-inflated Bray–Curtis similarity resemblance matrix based on fourth root transformed abundance data. Coloured points represent a sample

averaged across pitfall traps for foredune (solid triangles) and beach (open circles) within a transect. Black vectors display morphotaxa with correlations >0.5

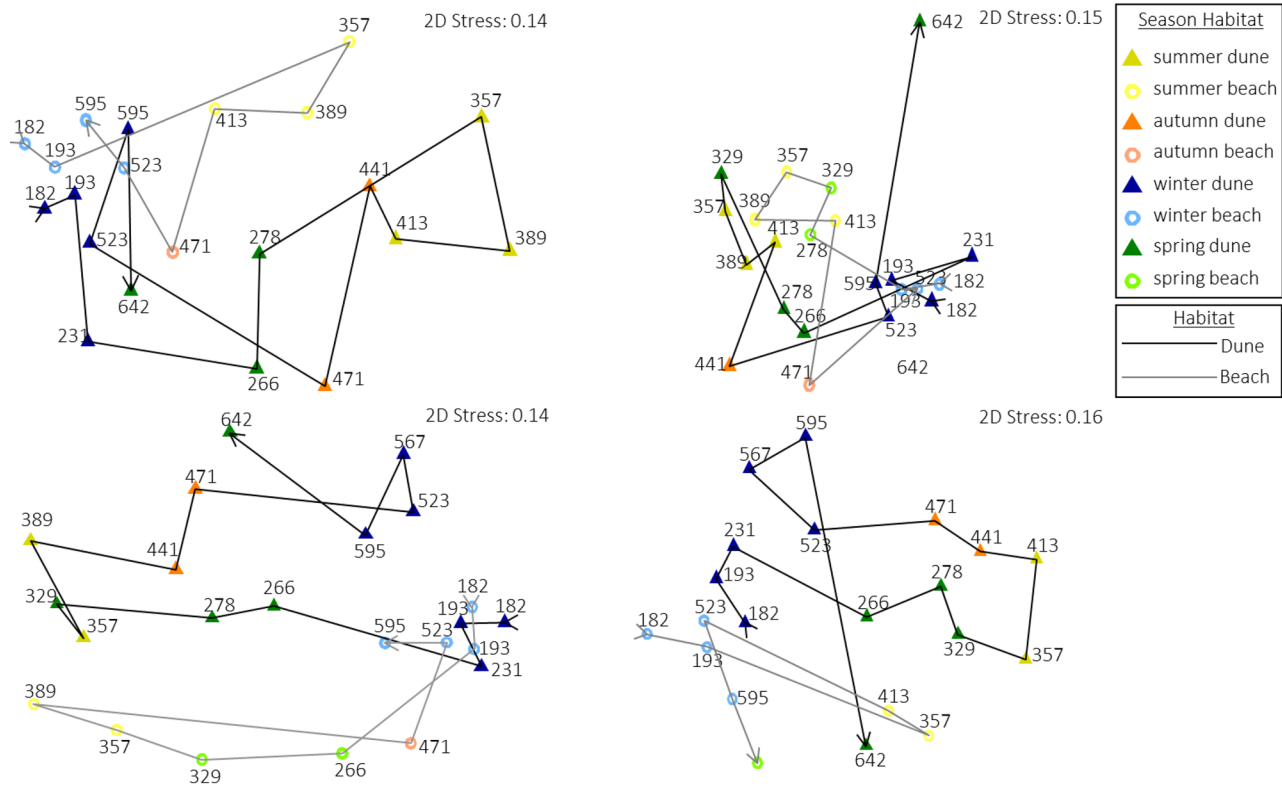


Fig. 3 Assemblage composition change through time for each transect. Four non-metric multidimensional scaling plots based on Bray–Curtis dissimilarity resemblance measures for each transect, with

fourth root transformed abundance data. The beach (grey) and dune (black) lines join each point in order of Julian day (numbers)

foredune = 9.3 species). Invertebrate abundance was influenced by both season ($F = 67.449$, $p < 0.001$) and habitat ($F = 10.140$, $p < 0.001$). Species abundance was greater in winter compared to other seasons (mean = 115.6 individuals per trap Tukey $p < 0.05$) which did not differ from one another: summer (78.3), spring (63.4) and autumn (56.8; Tukey $p > 0.05$; Fig. 4). Abundances were higher on the beach (mean = 113.3) compared to foredune habitats (50.4; Tukey $p < 0.001$).

Individual species responses differed between seasons and habitats. GLMMs were possible for *Notorchestia* spp. and *Actaecia* spp.; however, zero inflation and rank deficiency meant lower abundance species could not be modelled at a trap level. We therefore elected to use chi-squared tests to confirm the strong differences between groups (Fig. 5). *Notorchestia* spp. and *Actaecia* spp. were more abundant on the beach when compared to dune habitats (Tukey $p < 0.05$; mean abundance beach 4.26, 6.05; dune 0.39, 1.99, respectively). *Notorchestia* spp. and *Actaecia* spp. were more abundant in winter (24.36, 80.80, respectively) compared to spring (1.36, 6.06), with limited abundances in summer (0.35, 0.26) and autumn (0.24, 1.14; Fig. 5).

Chi-squared tests of independence confirmed species difference in abundance between habitats ($\chi^2 = 1895.5$, $df = 6$,

$p < 0.001$) and seasons ($\chi^2 = 18,879.3$, $df = 18$, $p < 0.001$). *Notorchestia* spp. and *Actaecia* spp. were in higher abundances than expected in winter and in lower abundances than expected in summer and autumn (adjusted residuals, winter = 35.3, 87.1; summer = -27.5, -80.7; autumn = -10.9, -28.5, respectively). *Phycosecis littoralis*, *Hycosis bakewelli* and *P. littoralis* larvae were in higher abundances than expected in summer (49.3, 32.8 and 27.3, respectively; Fig. 5) while *Mecynotarsus leai* was in higher abundances than expected in autumn and summer (54.8, 44.8). All four species of beetle were in lower abundances than expected in winter (-60.1, -39.6, -22.7, -60.8, respectively). *Tethina pallidiseta* was in higher abundances than expected in summer (53.1) and less than expected in winter (-39; Fig. 5).

Discussion

The seasonality in sandy shore invertebrate assemblages which has been reported from studies throughout the world (Carpaneto and Fattorini 2001; Dexter 1984; Maurer et al. 1979) extends to the temperate sandy beach and dune habitats of Southern Central Victoria, Australia. We found

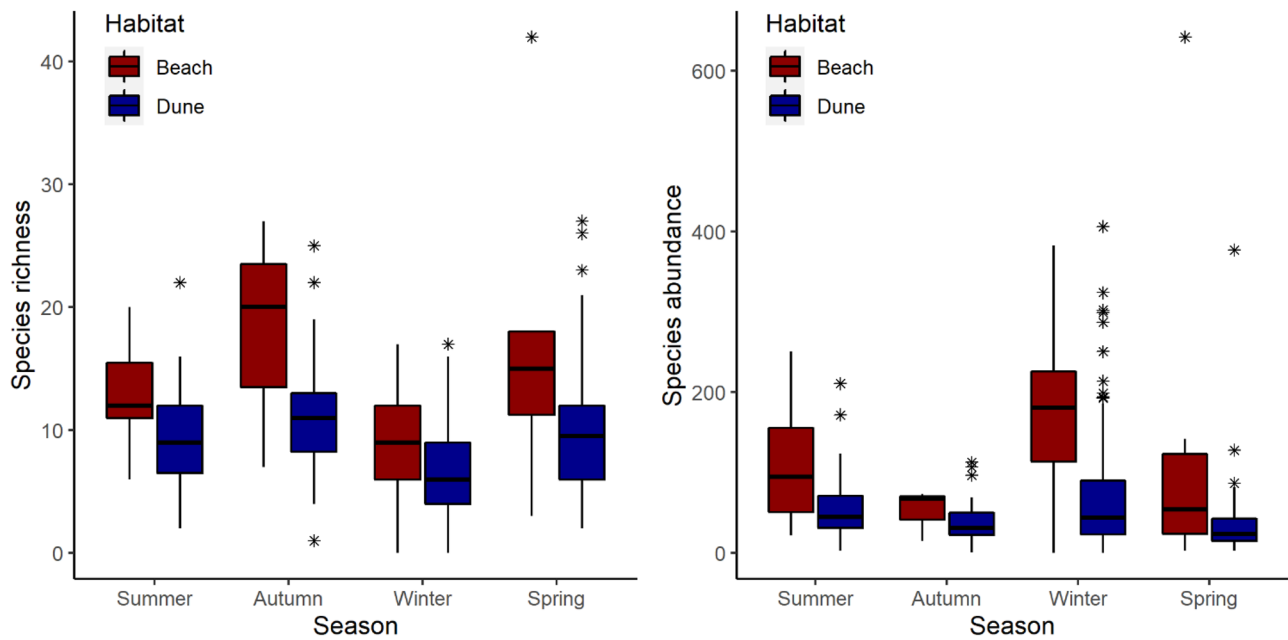


Fig. 4 Species richness per trap deployment (left) and overall abundance per trap deployment (right) by season and habitat (median \pm 2 SD). Red represents beach habitats, and blue represents foredune habitats

distinct assemblages within the two habitats considered and observed increasing diversity in invertebrate assemblages through spring and summer months. Despite a reduced diversity in winter, species abundances were much greater suggesting there is a year-round food resource for predators of invertebrates on sandy shore beaches. However, assemblage composition, richness and relative abundance changed throughout the year.

Seasonal and Spatial Patterns in Invertebrate Assemblage Composition

Assemblage composition of invertebrates showed distinct variation between foredune and beach habitats and between seasons. Habitat structure is a key influence on invertebrate assemblage compositions (Peng et al. 2020). Foredues represent areas of greater topographical and structural complexity compared to beaches, and also support vegetation and even possibly different microclimates compared with beaches. Thus, while our prediction of distinct assemblage differences between foredunes and beaches was borne out, we expected greater species richness in foredunes, which was not evident.

The most dramatic differences in assemblages we report occurred between the colder (winter) and warmer (summer) seasons. Insects (*Phycosecis litoralis* adults and larva, *Hyo-cis bakewelli*, *Mecynotarsus leai* and *Tethina pallidiseta*) were the most abundant species during the warmer times of year, in contrast to winter assemblages, which were

dominated by two crustaceans (*Actaecia* spp. and *Notorchestia* spp.). These changes in assemblage composition are likely be driven by species-specific phenologies, seasonal availability of species-specific resources such as beachcast wrack or activity patterns and the degree to which species are influenced by, or cope with, temperature fluctuations.

To the best of our knowledge, this is the first study of seasonal variation in invertebrate assemblages in Australian foredune habitats. Previous studies in similar climatic conditions and locations to that of this study considered the intertidal zone (Dexter 1984; Haynes and Quinn 1995). Haynes and Quinn (1995) found amphipod *Talorchestia* cf. *Novaehollandiae* and fly *Chaetocoelopa sydneyensis* to be dominant during summer and winter, compared to isopod *Actaecia thomsoni*, which was only abundant in summer. These results differ to our study which found the isopod *Actaecia* spp. (likely *A. thomsoni*) and the amphipod *Notorchestia* spp. to be most abundant in winter. Differences in results may reflect different sampling techniques (cores, Haynes and Quinn 1995; pitfalls, this study) and zones sampled. We did not sample lower beach zones, zones in which invertebrates are known to vary between seasons elsewhere in the world (Brazeiro and Defeo 1996; Gimenez and Yannicelli 1997; Gonçalves and Marques 2011). The contrasting results from similar Australian southern temperate beach systems suggest that isopods and amphipods may have been present in warmer months below the sand surface, rather than active on the surface, thus reducing capture rates. Invertebrates are thought to be less detectable on the surface during dry periods such as

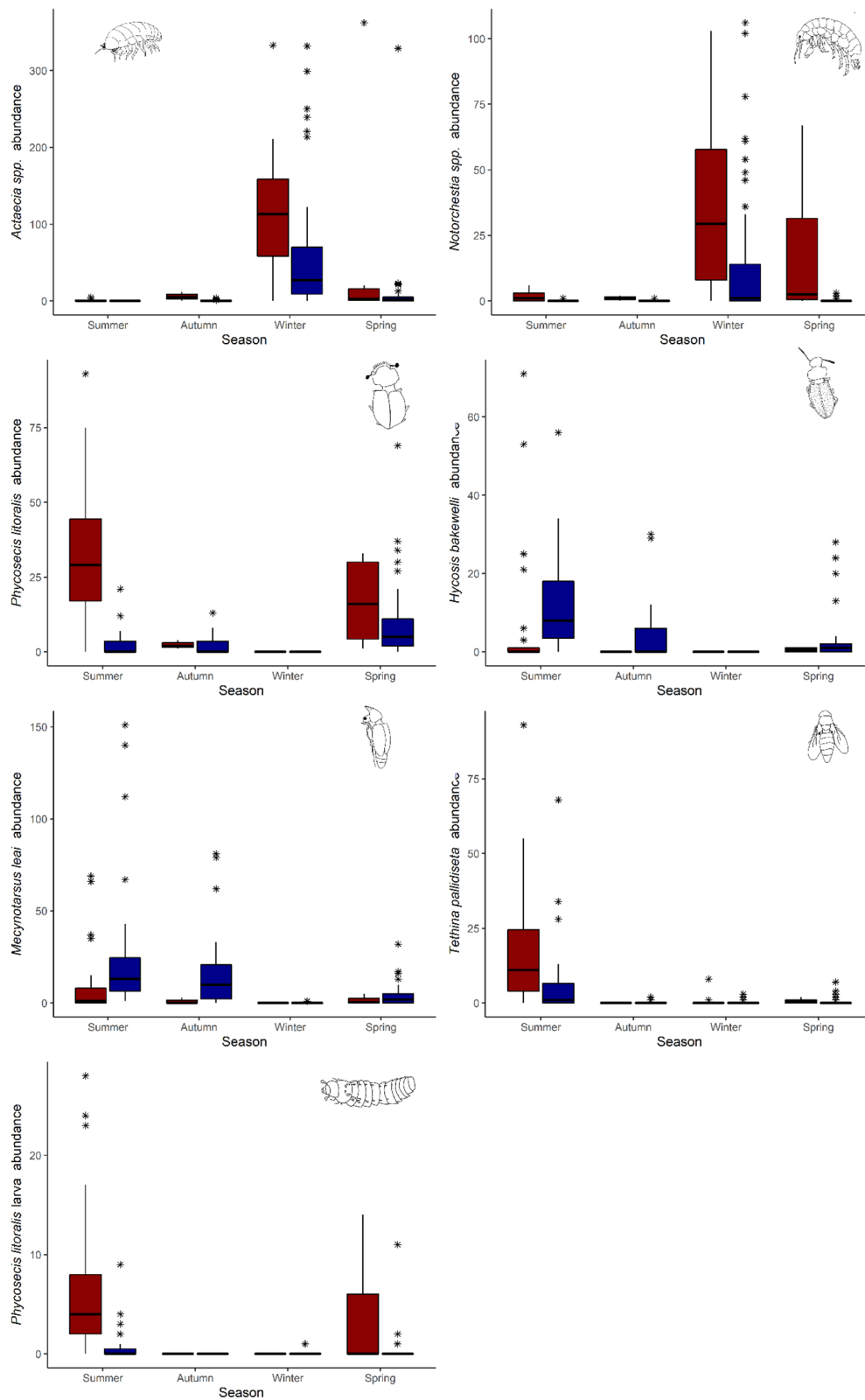


Fig. 5 Mean abundance of morphotaxa which drove seasonal patterns in assemblage composition (i.e., with correlations ≥ 0.5 in Fig. 2). Abundance at both beach (red) and foredune sites (blue) are included (median \pm 2 SD)

summer (Legakis and Adamopoulou 2005) possibly because individuals are more likely to burrow deeper into the sand profile. This is particularly true for crustaceans that cannot control the rate they lose water, thus requiring moist habitats to avoid desiccation (Morritt 1987, 1988; Williams 1995). Thus, it is likely that crustaceans were abundant in the beach system for the duration of this study; however, in summer, they were more likely to burrow in the sand towards the littoral and foreshore zones to escape desiccation. Crustaceans escaping desiccation under the surface of the sand, and remaining inactive, would not have been captured by our pitfall traps (Fanini and Lowry 2016), although our traps remained overnight and for all tide cycles. This study therefore provides information regarding what invertebrates are available as prey to predators on or close to the surface of sandy beaches and dunes (Butler et al. 2020; Weston 2007).

Seasonal and Spatial Patterns of Species Richness and Relative Abundance

Species richness decreased in winter and was seemingly related to the presence of a greater diversity of insects in summer. This is the first study examining seasonal richness across beach and dune habitats in sandy temperate Australian coasts; however, results match previous research from elsewhere (Mourglia et al. 2015). The similarity in seasonal richness trends between the different geographical locations (with different beach morphodynamics) parallels Degli et al. (2021), who found no changes in species richness with contrasting beach morphodynamics (such as sand temperature, grain size, elevation, compaction and moisture), but report significant seasonal changes, independent of morphodynamics.

We found no support for the winter food restriction hypothesis (Rogers et al. 2014) with respect to invertebrate abundance in contrast to Mourglia et al. (2015) who provide evidence for a winter bottleneck in invertebrate abundance. We note that our study site provides breeding and non-breeding habitat for hooded plovers, so may have greater winter food resources than sites which are abandoned in winter (Barker et al. 2022). Our results complement others in Australia where invertebrates remained abundant year-round (Dexter 1984; Haynes and Quinn 1995; Rundio and Lindley 2008), indeed with activity or abundance being highest in winter (this study). This contrasts with studies overseas where invertebrates may be more limited in winter due to climatic differences (i.e., colder winters), or different beach morphodynamics—factors known to affect the abundance of crustaceans, beetles and flies (Degli et al. 2021; Lercari and Defeo 2006; Gimenez and Yannicelli 1997). We note that all studies investigating the variability of invertebrate assemblages between seasons and zones on beaches, such as this study, only sample in one location (rather than multiple

locations), meaning that variation in the nature and extent of seasonal shifts in habitats, and the invertebrates in them, along shorelines effectively remains unknown.

Worldwide, invertebrate richness and abundance are consistently higher in dunes compared to beaches (Barboza et al. 2012; Degli et al. 2021; Defeo and McLauchlan 2011; Haynes and Quinn 1995; Mourglia et al. 2015; Richardson et al. 1999), contrasting the findings of this study, where richness and abundance were higher on beaches compared to foredunes, irrespective of season. Certainly, our foredunes were exposed and erosion-prone. Our findings may be explained by there being fewer beach traps compared to dune traps (beach traps being more prone to failing), with traps that were retrieved more reliably being situated closer to the beach/dune ecotone (this study), where richness and abundance is known to peak (Mourglia et al. 2015). Our beach traps may have been more likely to provide samples (less likely to fail) when better weather prevailed, potentially biasing our sample to some extent. Future research conducted over a larger across-shore gradient may be beneficial in detecting shifts in surface level zonation patterns across seasons.

Mechanisms Driving Seasonal Patterns

This study does not aim to understand the drivers of seasonal changes in the activity of invertebrates, but some are suggested by our results or might influence interpretation. The fact that insects were more abundant and richer in warmer months (this study) is likely related to their ectothermic nature, with temperature influencing population growth, fitness and performance (Abram et al. 2017; Frazier et al. 2006). Sand temperature is suspected to be an influential factor for the activity of epigeal arthropods (Haynes and Quinn 1995; Lastra et al. 2006; Pienkowski 1983); we recorded *Phycoscis littoralis*, *Hyocis bakewelli*, *Mecynotarsus leai* and *Tethina pallidiseta* as more abundant/active during warmer times of year. Brazeiro and Defeo (1996) suggest that annual changes in amphipod zonation are related to temperature fluctuations, as a result of behavioural thermoregulation tactics. Indeed, crustaceans in our study may have shifted in summer to lower zones that we did not sample.

Other factors, correlated with season, may contribute to seasonal patterns in invertebrates. Wrack is associated with increased abundance of amphipods and isopods (Colombini et al. 2003; Gonçalves and Marques 2011; Schlacher et al. 2016). In Victoria, storm swells occur most frequently in winter (McInnes et al. 2003), leading to increased wrack deposition on beaches (Orr et al. 2005). In addition to food, wrack also offers thermal refuge for invertebrates, and such an abundant, thermally stable resource (Ulaski et al. 2023) could explain why invertebrate abundance was highest on beaches, and in winter, both findings which were contrary

to our predictions. While this could drive seasonal patterns in invertebrates, no substantive wrack was noted during any sampling period, but might have conceivably been available between sampling periods (M.A. Weston pers. obs.). Crustaceans display changes in behaviour with rain (which varies seasonally at the study beach), whereby rain can initiate surface activity in buried invertebrates, which rely on moist habitats for osmoregulation (Morritt 1987, 1988). Selectively sampling during periods with no rainfall (to avoid pitfall traps from flooding; this study) may therefore underestimate the activity of crustaceans we recorded during summer.

The Winter Food Restriction Hypothesis and Future Research

We found no compelling evidence for winter food shortages for shorebirds such as hooded plovers, as hypothesised by Rogers et al. (2014), at least for the study beach and foredune. However, a greater diversity of prey was available when plovers moult and breed (Figure S2). However, a series of caveats exist. Shorebirds exhibit complex prey selection which may vary seasonally (Backwell et al. 1998; Colwell and Landrum 1993), and while the current understanding of hooded plover diet suggests the birds take a broad variety of invertebrate prey (Weston 2007), we may not have effectively indexed prey which they prefer across the year. We did not index the food resource on all levels of the beach at which foraging occurs (Butler et al. 2020). We sampled a known winter flocking area, but it is known that some areas are not occupied in winter (Barker et al. 2022; Weston et al. 2009), so seasonal food restrictions may occur in other areas. Future research should examine seasonal patterns across more coastline, across all levels of the beach and dune, and explore any spatial heterogeneity associated with temporal fluctuations.

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Data Availability Data are available upon reasonable request from the corresponding author.

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