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One species of seagrass cannot act as a surrogate for others in relation to providing habitat for other taxa

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ABSTRACT: Epibiotic assemblages provide an important source of primary and secondary production in seagrass habitats. Surrogates for biodiversity, such as broad-scale habitat types, have been used in selecting marine park boundaries and zones. As a preliminary test of one assumption of surrogacy that in effect treats all seagrass species as equal, the epibiotic assemblages of pairs of seagrass species, including the regionally rare *Posidonia coriacea*, were sampled between homogeneous or heterospecific patches at 3 separate locations in South Australia. Three seagrass species, each with distinct morphology, had distinguishable epifaunal assemblages. Free-living epifauna showed clear selection between seagrass species with movement likely over small scales within heterospecific patches, but no such distinction was shown when the same seagrass species pair was separated rather than intermingled. Epiphytic sessile species showed less well-defined specificity among seagrass species, but there were still significant differences in epiphytic species richness. The results of this preliminary study suggest that marine conservation planning needs to consider seagrass habitat on a species-by-species basis, including how they are arranged within localised patches.

KEY WORDS: *Amphibolis antarctica* · Epifauna · Epiphyte · Field surveys · Marine conservation planning · *Posidonia coriacea* · *P. sinuosa* · South Australia

INTRODUCTION

There is much interest in conserving marine biodiversity, but knowledge of species distributions critical to marine reserve planning is limited by a fundamental lack of data, time and funds. Thus, habitat surrogates, defined as easily measured features with distributions better known than those of their component species (Rodrigues & Brooks 2007, Hirst 2008), have been proposed to overcome a lack of complete knowledge of species diversity. Representing habitat-level diversity in reserves is thought likely to also capture other levels of biodiversity. The range of habitats considered as surrogates for selecting marine reserves includes seagrass meadows, which are recognised as both economically and environmentally important (e.g. McArthur & Boland 2006).

Seagrasses influence environments of coastal ecosystems (Hemminga & Duarte 2000), acting as ecosystem engineers (Jones et al. 1994) or foundation species by providing habitat for other organisms (Hughes et al. 2009). Seagrasses also provide an important source of primary production (Hemminga & Duarte 2000) that influences coastal food web structure. Seagrass habitat can be quite diverse, harbouring multiple levels of biodiversity, which goes on to enhance productivity and stability of seagrass ecosystems (Duffy 2006). Unfortunately, seagrass ecosystems suffer from increasing anthropogenic impacts (Waycott et al. 2009), and their key ecological

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processes (including carbon sequestration, nutrient cycling, sediment stabilisation and providing trophic links to other habitats) are under decline globally (Orth et al. 2006), requiring protection through the implementation of representative marine reserves.

One common design principle in reserve planning strives for the comprehensive inclusion of distinct biotic assemblages. Such assemblages could be associated with particular or unusual species of seagrass, such as *Posidonia coriacea* Kuo & Cambridge, one of the species used in this study. *P. coriacea* belongs to the *P. ostenfeldii* group, 1 of 2 subgeneric groups within the genus *Posidonia* (Gobert et al. 2006), defined by strong vertical growth, thus forming isolated patches rather than continuous meadows (Gobert et al. 2006, Bryars et al. 2008). *P. coriacea* is a relatively rare seagrass species, endemic to the southern coastline of Australia (Vanderklift & Lavery 2000), including patchy populations along the Fleurieu Peninsula of South Australia. It has long (up to 120 cm), tough leaves, which grow in dense clumps (Gobert et al. 2006). Published literature on *P. coriacea* comes mainly from Western Australia, with only a few studies focusing on the epiphytic macroalgal assemblages associated with *P. coriacea* (Vanderklift & Lavery 2000, Lavery & Vanderklift 2002). *P. sinuosa* Cambridge & Kuo has shorter, finer leaves, and grows in matting aggregations. The temperate Australian endemic seagrass *Amphibolis antarctica* (Labill) Sonder & Asch. ex Asch. grows in dense matting aggregations, with its tough wiry stems ending in numerous terminal leaf clusters.

Various other organisms associate with seagrass plants. Some of these organisms utilise seagrass by attaching themselves to the hard substrate provided by leaves or stems. These epiphytes can include numerous taxa, such as algae, bryozoans, spirorbids and other sessile polychaetes, sponges, hydroids and forams. Epiphytes provide an important source of primary production, sediment production and nitrogen and nutrient cycling (Borowitzka et al. 2006) but can vary depending on a variety of factors, including abiotic (e.g. light attenuation, nutrient loads, wave energy, temperature, hydrodynamics and the substrate for attachment) and biotic (e.g. grazing pressure and propagule supply) variables (Bryars et al. 2008). Free-living epifauna also associate with seagrass and can be classified as motile animals living above the sediment but within the complex leaf and stem structure (Raz-Guzman & Grizzle 2001). They are an important source of secondary production, especially as prey for organisms like fish higher in the food web.

In this preliminary study, we compared the abundance and diversity of leaf-associated epibiotic assemblages between 2 *Posidonia* species, *P. sinuosa* and *P. coriacea*, and with the locally co-occurring species *Amphibolis antarctica* along the Fleurieu Peninsula, South Australia. This preliminary research is one of only a few studies to examine the whole epibiotic assemblage between seagrasses of inherently different morphologies (Borowitzka et al. 2006). Lavery & Vanderklift (2002) included the epiphytic macroalgae of both *P. coriacea* and *A. griffithii* in such a comparison from Western Australia, whilst the association between algae epiphytes, epifauna and plant material of *P. sinuosa* and *A. griffithii* was studied by Jernakoff & Nielsen (1998). Neither study compared epibiota between different patch arrangements of their respective seagrass species, nor their potential for surrogacy. Thus, we sought to assess the potential of epibiotic surrogacy amongst the seagrasses *P. coriacea*, *P. sinuosa* and *A. antarctica.*

MATERIALS AND METHODS

Site selection and descriptions

Sampling was carried out on 12 November 2008 at 3 locations along South Australia's Fleurieu Peninsula (Fig. 1). Locations were off Maslin Beach (MB: 138° 46′ E, 35° 24′ S), Silver Sands (SS: 138° 43′ E, 35° 30′ S) and Sellicks Beach (SB: 138° 44′ E, 35° 33′ S). Locations were dictated by the spatial arrangement of the seagrasses in nature, with the presence of either mono- or heterospecific patches of *Amphibolis antarctica, Posidonia coriacea* and *P. sinuosa* confirmed by examining underwater video footage held by the state Department of Environment and Natural Resources.

Within each location, 3 sites were randomly selected for sampling. Sites, defined as an area within a diameter of 10 m from an anchoring point, contained numerous patches of seagrass. Patches did not form part of larger beds or clumps but instead appeared as plants separated by bare sand over a large spatial scale. Three patches within each site were randomly sampled.

At SS, *Posidonia sinuosa* and *Amphibolis antarctica* occurred together within 3 heterospecific patches of seagrass, with sites separated by 15 to 35 m. At SB, 3 heterospecific patches of *P. coriacea* and *A. antarctica* were sampled, with sites separated by 17 to 22 m. At MB, *P. coriacea* and *A. antarctica* were geographically separated by an area of bare

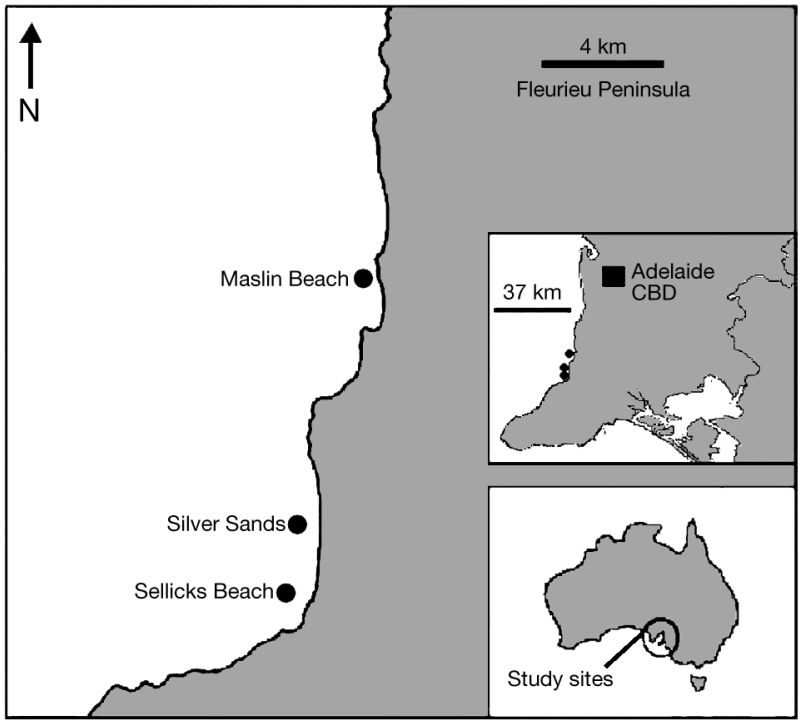

Fig. 1. Sampling locations (off Maslin Beach, Silver Sands, and Sellicks Beach) in relation to the Adelaide Central Business District (CBD), southern Fleurieu Peninsula and the rest of Australia

sand, measuring approximately 100 m wide. On either side of this bare sand, 3 sites separated by between 30 and 100 m were chosen, and within each site, 3 monospecific patches contained either *P. coriacea* or *A. antarctica*. Thus, the pairs of seagrass species at each location were either intermingled (SS, SB) or separate (MB).

Sampling

Due to the rarity, potential slow re-growth and unknown recovery time of *Posidonia coriacea* (Edgar 2001), it was imperative that the least destructive sampling be used (rather than uprooting whole plants). Thus, the number of samples was reduced to be just 2 replicates per species per patch to reduce disturbance and only the canopy assemblages associated with the distal portion of leaves were studied (thereby minimising loss of seagrass biomass). Sampling bags (polyethylene zip-lock bags measuring 25 × 30 cm) were used to cover a distal portion of plants, where the opening of the bag was shut, and then all seagrass held within was separated from the rooted plant with scissors before being zip locked. Entire samples were sieved through 500 µm mesh immediately after collection to remove excess water before freezing. Samples were stored on ice before being placed in a −20°C freezer the day following collection. Two control samples (i.e. bags of the nearby water column only) were taken directly opposite each seagrass species, for every patch at SB. These procedural control samples contained no epifauna, and so were subsequently omitted from the comparison.

Processing of epifauna and epiphytes

In the laboratory, each sample was thawed and washed through a 500 µm sieve before the retained contents were identified and counted for estimating abundance and diversity of all macroscopic mobile epifauna.

To sample species presence and the relative abundance of epiphytes, stem and leaves were treated as 2 separate but matched strata for the seagrass *Amphibolis antarctica*. Each sample bag therefore yielded a matched sample of free-living epifauna and of epiphytes attached to leaves.

Following Bramwell & Woelkerling (1984), who found no difference in the epiphytic crustose coralline assemblage between sides of the leaves in *Amphibolis antarctica*, epiphyte presence and abundance was calculated from the total count of each occurrence on both sides. The concave leaf morphology found on one side of *Posidonia sinuosa* may have an impact on its epiphytic assemblage (Trautman & Borowitzka 1999), but for the purpose of this study, no differentiation between sides was made for either *Posidonia* species.

Two levels of sub-sampling were carried out due to the sheer number and volume of epiphytes on the leaves of seagrass, which would have been extremely time consuming to count and identify. All seagrass was emptied onto a sorting tray, and 5 leaves were chosen at random from each bag of *Posidonia coriacea* and *P. sinuosa* (Kendrick & Lavery 2001). A 10 cm sub-section was cut from the middle of each leaf. Five leaf clusters of *Amphibolis antarctica* were randomly chosen per bag of *A. antarctica*. Because different-aged leaf surfaces can contain different epiphytic assemblages (Bramwell & Woelkerling 1984), numerous leaves from each of the 5 leaf

clusters were removed at random until the total length (end to end) of all leaves equalled at least 10 cm for each leaf cluster. Epiphytes were then identified and counted to determine diversity and abundance.

Biomass of seagrass and epiphytes

To determine epiphytic and seagrass biomasses, epiphytes were physically removed by scraping plant material by holding a razor blade at an angle of roughly 90°, before running it along the leaf's entire length. Earlier washing under a gentle stream of fresh water removed any inorganic material, such as sediment. Further care was taken to avoid the excessive inclusion of plant epidermis in epiphytic scrapings. Once all plant and epiphytic material was separated, they were weighed after drying at 75 to 80°C for 48 h (Kendrick & Lavery 2001).

Functional groups of epiphytes

Due to the time, expense and difficulty involved in the identification of small and abundant epiphytic macroalgae, all epiphytic algae were identified to morphospecies and then further characterised into the functional groups proposed by Steneck & Dethier (1994): the functional groups found included filamentous algae, foliose algae, corticated foliose algae, corticated macrophytes and articulated calcareous algae. Other non-algal epiphytes were encountered which did not fit the definitions proposed by Steneck & Dethier (1994). These were grouped into their own functional group called 'fauna'. This faunal functional group contained a diverse range of species across numerous phyla, including a *Pyura* sp. ascidian (Chordata), *Leucosolenia* sp. sponge (Porifera), *Plumularia* sp. hydroid (Cnidaria), spirorbid worms (Annelida), *Thairopora* sp. and Lichenoporidae (Bryozoa) and Foraminifera. Counts of individual algae and fauna were combined for an estimate of abundance of each functional group.

Data analysis

In order to test the difference in epibiotic communities between seagrass species, each location was analysed separately, due to different pairs of seagrass species being found within each (although *Amphibolis* was found at each location) and the different arrangements of either hetero- or monospecific patches. In each case, comparing assemblages across the pair of seagrass species was the prime factor of interest, but the effects of site-to-site or patch-to-patch variation were not allowed to confound that interpretation (by estimating their effects also). SS and SB had the same experimental design, but the 2 locations differed as *Posidonia sinuosa* or *P. coriacea,* respectively, was the second species in the pair. The design for SS and SB was treated as a 3-factor mixed-model analysis of variance (ANOVA). The 3 factors included Sites (considered as a random factor), Species (treated as fixed) and Patches nested within Sites (random).

MB had a different, 3-factor hierarchical or nested design, where sites were separate and contained only 1 of the 2 species, either *Posidonia coriacea* or *Amphibolis antarctica*. Factors used in the design for MB included Species (fixed), Sites nested within Species (random) and Patches nested within Sites, which were nested within Species (random). SYSTAT v.11 software was used for ANOVA and to graphically represent raw or transformed univariate data for richness and abundance.

All multivariate analysis was carried out using PRIMER v.6 and PERMANOVA+ software (Clarke & Gorley 2006, Anderson et al. 2008). Multi-dimensional scaling (MDS) ordination plots were used to represent the assemblage composition and relative abundances of all replicate samples per seagrass species. Sample points close together in 2D ordination space are similar in terms of their species and abundances, whereas points far apart share few epibiota in common. Replicate samples lacking any epibiota were removed from further analysis. Permutational MANOVA (PERMANOVA, Anderson et al. 2008) was used to test the simultaneous response of epibiota to factors in the same statistical designs as outlined above for each location. Similarity percentage (SIMPER) analysis (Clarke & Gorley 2006) was used to determine the most consistent contributions of indicator species to the total average dissimilarity between seagrass species.

RESULTS

Epifauna

A total of 86 species of motile epifauna in 4 phyla were recorded during this study. Of the phyla, Arthropoda was the most diverse, with a total of 51 species. The second-most diverse phylum was Mol-

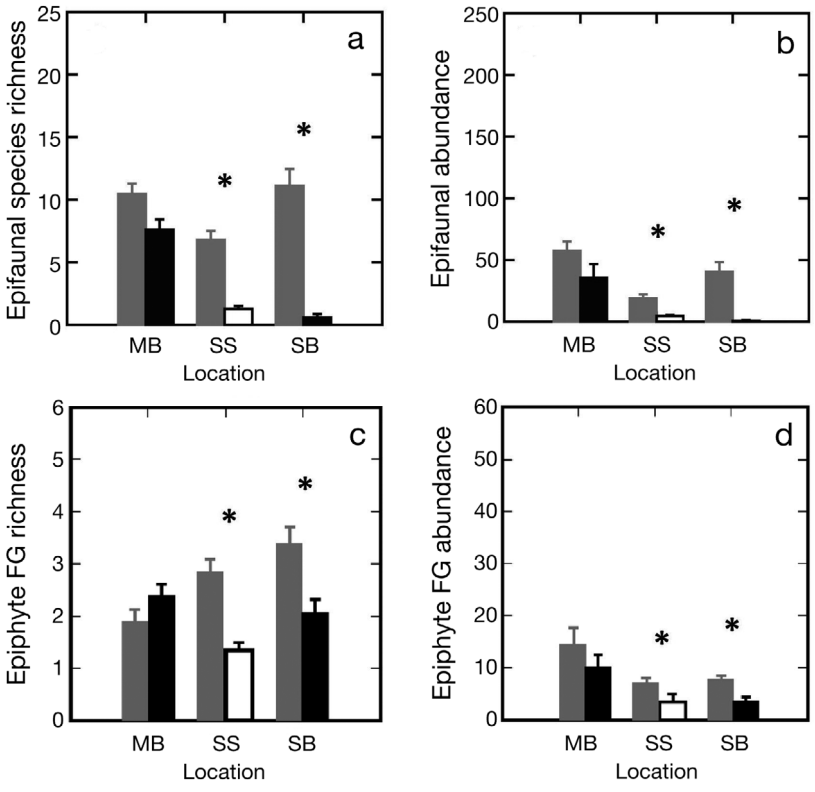

Fig. 2. *Amphibolis antarctica* (grey), *Posidonia coriacea* (black), and *P. sinuosa* (white). Untransformed mean (+SE) for epifaunal (a) species richness, (b) abundance, (c) functional group (FG) richness and (d) FG abundance across all locations for each species. MB: Maslin Beach, SS: Silver Sands, SB: Sellicks Beach. The *y*-axis shows the range of the raw data per sample. *Statistical significance ($p < 0.05$) between seagrass species pairs

lusca, with a total of 26 species, followed by Annelida with 7, and a single contribution from Chordata. Some 54 species were found exclusively on *Amphibolis antarctica*, 7 only on *Posidonia coriacea*, 2 only on *P. sinuosa*, and 23 species were found on all 3 seagrass species. Members of the Polychaeta, Gastropoda, Isopoda and Amphipoda accounted for the majority of species found exclusively on *A. antarctica*. Only a single morphospecies, a copepod from the order Harpacticoida, was recorded across all 3 seagrass species at all locations. At MB, 33 species were unique to *A. antarctica* compared to 11 unique species on *P. coriacea*, whilst 17 species were found on both. At SB, 48 unique species were found on *A. antarctica*, 2 were found solely on *P. coriacea*, and 4 species were found on both. At SS, 26 unique species were found on *A. antarctica*, 5 on *P. sinuosa*, and 4 species were shared by this pair of seagrass species.

Mean epifaunal species richness was high for *Amphibolis antarctica* across all locations, in both mono- and heterospecific patches (Fig. 2a). At SS and SB, both *Posidonia coriacea* and *P. sinuosa* showed significantly lower mean species richness when compared with *A. antarctica* in the same hetero-specific patches. *P. coriacea* in monospecific patches (at MB) had higher species richness than heterospecific patches (at SB). The increase in species richness shown by *P. coriacea* between homogeneous and heterogeneous patches did not apply for *A. antarctica* (Fig. 2a).

Epifaunal abundance data showed a similar trend, where the mean abundance for *Amphibolis antarctica* remained comparatively high across all 3 locations, only decreasing in heterospecific patches at SS (Fig. 2b). The mean epifaunal abundance in heterospecific patches at SS and SB, containing either *Posidonia coriacea* or *P. sinuosa,* showed a significant difference when compared to *A. antarctica*. The monospecific patches of *P. coriacea* sampled at MB showed a large abundance of epifauna (exceeding that found in heterospecific patches of the same species at SB) but were not significantly different from *A. antarctica* at MB.

Multivariate analysis of epifauna

In the MDS plots, the faunal assemblages at MB (Fig. 3a), SS (Fig. 3b) and SB (Fig. 3c) all showed a strong separation when analysed by seagrass species. Both MDS plots for SS and SB had acceptable stress values of 0.07 (Fig. 3b,c), whilst the MDS plot for MB had a higher but still acceptable stress value of 0.13 (Fig. 3a).

SIMPER analysis then revealed the key species most likely to contribute most to dissimilarity between seagrass species. Ten species, including 4 species of Amphipoda, a mitrellid gastropod, a chydorid cladoceran, harpacticoid copepods, an *Apseudomorpha* species, Polyplacophora sp. 1 and an *Electroma* species each contributed consistently (dissimilarity/SD > 1) to the average dissimilarity between the seagrass species at MB. The average dissimilarity between *Posidonia coriacea* and *Amphibolis antarctica* was less than for seagrass pairs at SS and SB but still large (78.8%).

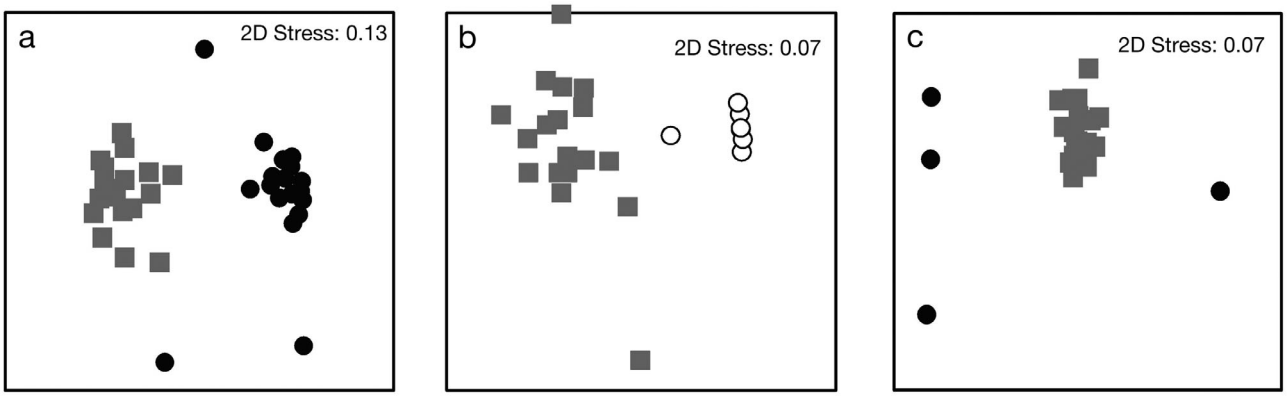

Fig. 3. *Amphibolis antarctica* (grey squares), *Posidonia coriacea* (black circles), and *P. sinuosa* (white circles). Multi-dimensional scaling (MDS) ordination plots of the epifaunal assemblages compared between *A. antarctica* and (a) *P. coriacea* at Maslin Beach (MB), (b) *P. sinuosa* at Silver Sands (SS), and (c) *P. coriacea* at Sellicks Beach (SB). Raw data were standardised and log(x+1) transformed. All 18 samples of *A. antarctica* at each location and *P. coriacea* at MB contained epifauna, whereas *P. sinuosa* at SS had only 6 sample bags with epifauna, and *P. coriacea* at SB gave only 4 replicate bags with epifauna

At SS, 3 main taxa were substantial contributors to the average dissimilarity (89.1%) between the 2 seagrass species: harpacticoid copepods, a tanaid *Apseudomorpha* sp. and the family Chydoridae. Of these 3 main contributors, only harpacticoid copepods were more abundant on *Posidonia sinuosa* compared to *Amphibolis antarctica.*

At SB, the large average dissimilarity (91.3%) between *Posidonia coriacea* and *Amphibolis antarctica* was represented by 4 main contributors. Three of those were also the main contributing species for the dissimilarity at SS (i.e. *Apseudomorpha* sp., harpacticoid copepods and Chydoridae), with Polyplacophora sp. 1 contributing most to the average dissimilarity at SB. Other important contributing species were a limpet *Asteracmea* sp. and a member of the family Mesanthuridae. Of these 6 species, only harpacticoid copepods were more abundant in *P. coriacea* than *A. antarctica*.

PERMANOVA for MB revealed no significant difference between *Amphibolis antarctica* and *Posidonia coriacea*. At SS, PERMANOVA revealed a significant difference in the total assemblage between *P. sinuosa* and *A. antarctica* ($p = 0.001$). At SB, there was a significant difference in the epifaunal assemblage between *P. coriacea* and *A. antarctica* ($p = 0.001$). At SB, the exact effect of species varied from patch to patch ($p = 0.04$) and also amongst patches nested within sites ($p = 0.022$).

There was a strong distinction between the epifaunal assemblage between seagrass species at MB (Fig. 3a), where all replicate samples contained epifauna. The MDS ordination plots of epifaunal assemblages for SS and SB showed a clear distinction between the respective seagrass species (Fig. 3b,c), but these plots did not include any samples that yielded no epifauna. This occurrence metric, in itself, can provide insight into the different assemblages. All samples of *Amphibolis antarctica* at every location yielded some epifauna, as did *Posidonia coriacea* at MB, but a total of 12 and 14 replicate bag samples (out of 18 each) of *P. sinuosa* and *P. coriacea* at SS and SB, respectively, showed a complete lack of epifauna (Fig. 3b,c), demonstrating that the epibiotic assemblages on *Posidonia* spp. were much sparser at SS and SB than at MB. All samples at MB, however, contained epifauna, regardless of seagrass species.

Epiphytes

Epiphytes occurred on all leaves of each species in every sample. Each of the 72 epiphytic algal morphospecies distinguished was classified into the functional groups outlined above; another 19 morphospecies were allocated into the faunal functional group. The most diverse functional group of algae contained 41 species of corticated macrophyte; there were 16 species of foliose algae, 11 species of filamentous algae, 3 species of articulated coralline algae and a single species of corticated macrophyte.

Mean epiphytic functional group richness was higher on *Amphibolis antarctica* across all locations with monospecific patches, compared to either *Posidonia sinuosa* or *P. coriacea* (Fig. 2c). However, in heterospecific patches at MB, epiphytic functional group richness was higher on *P. coriacea* (Fig. 2c). Monospecific patches of *A. antarctica* showed the

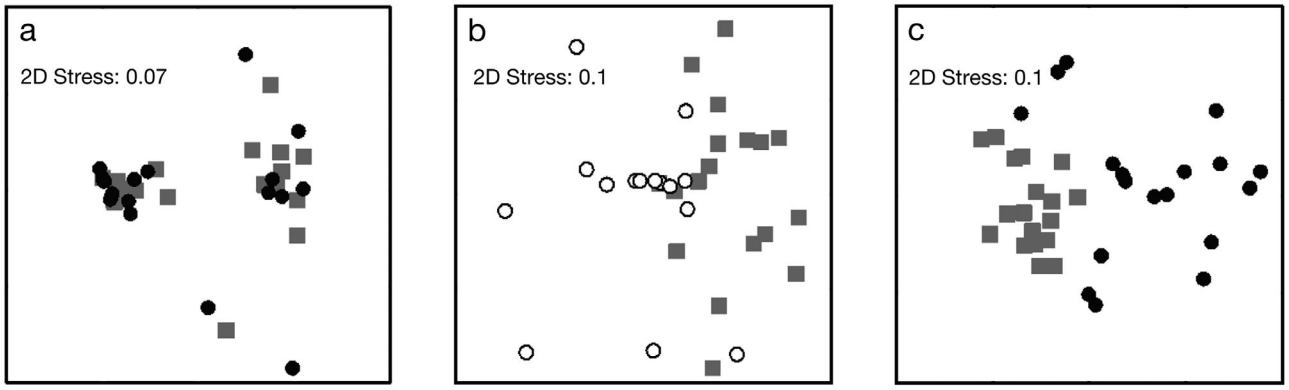

Fig. 4. *Amphibolis antarctica* (grey squares), *Posidonia coriacea* (black circles), and *P. sinuosa* (white circles). Multi-dimensional scaling (MDS) ordination plots of the epiphytic assemblages compared between *A. antarctica* and (a) *P. coriacea* at Maslin Beach, (b) *P. sinuosa* at Silver Sands, and (c) *P. coriacea* at Sellicks Beach. Raw data were standardised and log(x+1) transformed. All replicate bag samples contained epiphytes (n = 18 per seagrass species per location)

highest mean epiphyte abundance across all locations (Fig. 2d), with significantly more than on *Posidonia coriacea* at SB and more than on *P. sinuosa* at SS. At MB, *A. antarctica* had higher mean epiphytic abundance, but this was not significantly different from the abundance of epiphytes on *P. coriacea*.

Multivariate analysis of epiphytes

The MDS analyses showed no separation of the epiphytic assemblages of MB (Fig. 4a) or SS (Fig. 4b) between the pairs of seagrass species at those locations. For SB (Fig. 4c), the MDS showed a moderate separation of the epiphytic assemblages when grouped by seagrass species. The MDS plots for all sites had acceptable stress values of either 0.07 (MB) or 0.1 (SS, SB).

SIMPER analysis revealed 3 main functional groups that contributed to the average dissimilarity (57.5%) between the 2 seagrass species found at MB, *Posidonia coriacea* and *Amphibolis antarctica*: corticated macrophytes, fauna and filamentous algae. Of these 3, only corticated macrophytes showed greater occurrence on *A. antarctica*.

At SS, SIMPER analysis revealed that 2 functional groups contributed consistently to the average dissimilarity (32.4%) between *Posidonia sinuosa* and *Amphibolis antarctica*: foliose algae and corticated macrophytes. Both functional groups were more abundant on *A. antarctica* than on *P. sinuosa*.

At SB, 3 functional groups contributed to the average dissimilarity (43.0%) between seagrass species. Of the 3 functional groups, *Posidonia coriacea* had more filamentous algae, whereas foliose algae and corticated macrophytes were more abundant on *Amphibolis antarctica.*

At MB, PERMANOVA (with Monte Carlo testing) revealed that epiphytic functional groups varied among sites and patches, p(MC) = 0.003 and p(MC) = 0.02, respectively, but not between *Posidonia coriacea* and *Amphibolis antarctica*. PERMANOVA for SS revealed no significant difference for any interaction, including between patches, sites and the 2 seagrass species, *P. sinuosa* and *A. antarctica*. At SB, there was a significant difference between *P. coriacea* and *A. antarctica* (p = 0.0215), but the exact effect varied from patch to patch, due to a significant interaction of patches with species (p = 0.032).

DISCUSSION

Although our samples of seagrass only covered the distal ends of plant leaves, they yielded a diverse epibiota. Epifaunal species from the phylum Crustacea, including harpacticoid copepods, a chydorid cladoceran and *Apseudomorpha* sp., were found to contribute to observed differences between seagrass species in all 3 locations. The chiton (Polyplacophora) also contributed to observed differences at several locations. Epiphytic functional groups, including corticated macrophytes, foliose algae and filamentous algae, all contributed consistently across sites.

This research demonstrates differences among 3 local seagrass species, *Posidonia coriacea*, *P. sinuosa* and *Amphibolis antarctica,* in regards to their associated epibiotic assemblages. Although this is a preliminary study, which did not include a temporal aspect in its design, these findings also yielded

contrasting patterns between 2 patch arrangements, hetero- and monospecific beds, for 1 pair. More examples of such arrangements should be studied in future.

The design of this study allowed the comparison of epibiota between pairs of the seagrass species, including one contrast of monospecific with heterospecific patches (albeit across different locations but with the same pair of seagrass species). Previous studies of epibiota, like those of MacArthur & Hyndes (2001) and Hyndes et al. (2003), did not encounter heterogeneous patches, and so were confined to comparing monospecific patches of a single species at a time.

Motile epifaunal species showed a clear preference for the structurally complex *Amphibolis antarctica* where it shared patches with the simpler *Posidonia coriacea* (at SB) or *P. sinuosa* (at SS). Epifaunal species richness and abundance in *P. coriacea* fell noticeably when sharing patches with *A. antarctica*. Where segregated, patches of *P. coriacea* showed no significant difference in assemblage from patches of *A. antarctica* at the same location. These results must, however, be interpreted with some level of caution because these patch types themselves occurred in separate locations (MB and SB, respectively). This may suggest that mobile epifauna show habitat selection via movement over small scales within patches but will live in a wide range of seagrasses when choice is limited. Therefore, predicting epifauna requires an understanding of what seagrass species are where, and also how, they are arranged in localised patches.

Structural complexity may not be the only driving factor behind the epifaunal preference towards *Amphibolis antarctica*. Epiphytic assemblages also showed a clear preference for the leaves of *A. antarctica*, which in turn may attract motile epifauna (Edgar 1991, Bologna & Heck 1999, Bostrom & Mattila 1999), e.g. for food, further increasing epibiotic assemblages. However, due to the preliminary and purely descriptive nature of this biological survey, we suggest that further complementary sampling and manipulative experiments (e.g. giving choices to some epibiotic taxa across seagrass species) are needed to elucidate the mechanisms behind such observed differences.

PERMANOVA revealed significantly different epifaunal assemblages between 2 species of seagrass sharing the same patch at SS and SB but not between 2 species when separated into monospecific patches (at MB). The result for MB is surprising, given the strong dissimilarity between the epifaunal assemblages associated with either seagrass species, shown in ordinations. The PERMANOVA test for MB did have only a small number of available permutations (unique permutations = 10 only), meaning that very few unique values of the test statistic were obtained, reducing our ability to make inferences about the p value, even with Monte Carlo testing (Anderson et al. 2008). We would therefore need to increase the number of samples to include more seagrass species, or include more sites to increase the power to detect species differences.

Borowitzka et al. (2006) suggested that epiphyte assemblages can vary significantly across different spatial scales, from tens of metres to between patches. However, Moore & Fairweather (2006) found that mean epiphytic biomass remained relatively homogeneous at a local (<100 m) scale in South Australia (because assemblages were quite variable at all scales). We found that the epiphytic assemblage varied significantly from patch to patch ($p = 0.02$ and 0.032 at MB and SB, respectively) and from site to site ($p = 0.0215$) at MB, representing great small-scale variation.

We therefore conclude that the potential of one seagrass to act as a surrogate for the epibiotic assemblage of another is poor, with each seagrass species showing a high level of specificity of epibiota when found in heterospecific patches. This study is the first to show both effects of species identity and arrangement simultaneously and thus has broad implications for conservation agencies that use broad-scale habitats as surrogates for biodiversity (Rodrigues & Brooks 2007), where more than 1 seagrass species may be present. Marine reserve planning thus needs to consider seagrass habitat on a species-by-species basis, including how each species is arranged within localised patches, to be sure to capture the biodiversity of epibiota underlying such gross habitat patterns.

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