

**Habitat restoration: early signs and extent of faunal recovery relative to seagrass recovery**

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**Manuscript submission category:** Research paper

**Word count:** 5,781

## **Abstract**

The overall intent of restoration is often not only to restore the habitat *per se*, but to restore the ecosystem services it supplies, and particularly to encourage the return of fauna. Seagrass meadows act as habitat for some of the most diverse and abundant animal life, and as the global loss of seagrass continues, managers have sought to restore lost meadows. We tested how quickly the epifaunal richness, abundances and community composition of experimental restoration plots recovered to that in an adjacent natural seagrass meadow relative to the recovery of seagrass *per se*. Seagrass structure in the restoration plots took three years to become similar to a nearby natural meadow. The recovery of epifaunal richness and total abundance, however, occurred within one year. These results suggest that although recovering habitats may not be structurally similar to undisturbed habitats, they can support similar richness and abundances of epifauna, and thus have greater economic and social value than otherwise might have been expected. Nevertheless, whilst epifaunal richness and total abundance recovered prior to the recovery of seagrass structure, full recovery of seagrass was required before the composition and relative abundances of the epifaunal community matched that of the natural seagrass meadow.

**Key words:** *Amphibolis antarctica*, Ecosystem function, Motile epifauna, Recovery, Seagrass restoration.

## **1. Introduction**

Habitat restoration can help to alleviate habitat loss or re-establish ecosystem structure and function (Elliott *et al.* 2007; Reynolds *et al.* 2013). Often, a primary motivation for habitat restoration is to restore the richness and abundance of fauna associated with the lost habitats

(e.g. Muotka *et al.* 2002; Ruiz-Jaén & Aide 2005). However, restoration success varies, due to the inherent difficulties involved in restoring complex environments (Elliott *et al.* 2007; Irving *et al.* 2010). Further, ecosystems are not stable through time, meaning the “baseline” that should be used for restoration targets is often uncertain. Therefore, setting goals for restoration success based solely on compositional or structural attributes that were characteristic of the system prior to disturbance can be problematic (Hobbs & Harris 2001).

Restoration success is often most reliably assessed by comparing structural and functional attributes of the restoration site to those of a neighbouring undegraded habitat or reference site (Hobbs & Harris 2001; Ruiz-Jaén & Aide 2005; Benayas *et al.* 2009). A general element of structural restoration is the replenishment of plant species which provide the physical structure of an ecosystem (McCay *et al.* 2003). Recovery of structure, however, does not necessarily lead to the return of ecosystem function (Zedler & Lindig-Cisneros 2000). For example, arthropod diversity in restored coastal sage scrub was lower than in undisturbed habitat after 15 years, even though vegetation was structurally similar (Longcore 2003).

In marine systems, seagrass meadows form ecologically and economically important coastal habitats (Short & Wyllie-Echeverria 1996; Beck *et al.* 2001; Duarte 2002; Orth *et al.* 2006). Due to their coastal location, seagrass meadows are highly susceptible to disturbance from natural and anthropogenic sources (Short & Wyllie-Echeverria 1996; Ralph *et al.* 2006), and approximately 29% of the world’s seagrass habitat has been lost (Waycott *et al.* 2009). As a consequence, seagrass restoration has become an element of coastal management, with early research primarily focused on establishing the most effective techniques of transplantation (Van Keulen *et al.* 2003; Bell *et al.* 2008; Cunha *et al.* 2012).

The success of seagrass restoration projects has, however, been limited, with only 30 % of studies reporting success (Fonseca *et al.* 1998), which is thought to be primarily due to poor site selection (Fonseca 2011). Restoration success can be defined by a lack of detectable differences in structure (e.g. shoot density) between recovering treatments and undisturbed treatments. Studies that do report ‘success’, generally do so based on short-term monitoring (<1year), and hence long-term success is often not known (Cunha *et al.* 2012). Increasing the length of restoration monitoring may increase the ability to identify successful restoration. For example, long-term monitoring of seagrass restoration near Tampa Bay, Florida, showed the recovery of seagrass to be slow during the first 3 years, followed by rapid recovery 4-7 years after restoration was implemented (Bell *et al.* 2014). Further, the recovery of ecosystem function rather than structure, is only infrequently used to assess restoration success (e.g. Bell *et al.* 1993; Fonseca *et al.* 1996; Sheridan *et al.* 2003). As functional diversity, being the varying functional characteristics of the organisms residing in an ecosystem, is thought to have the greatest influence on ecosystem function (Tilman *et al.* 1997; Díaz & Cabido 2001), it may provide a measurable index of the restoration of ecosystem function. However, in systems where little is known about the functional characteristics of the organisms present, other measures such as species richness may be used as an indicator (Tilman 2001). For restoration to be successful, restored seagrass patches should persist and recover similar ecosystem function, such as the recovery of fauna due to the provision of habitat, to that of a natural undisturbed seagrass meadow (Fonseca *et al.* 1998).

Wear *et al.* (2010) developed a novel seagrass restoration technique, using biodegradable hessian (burlap) bags to stabilize the sediment and facilitate the natural recruitment of *Amphibolis antarctica* seedlings, with the overall intention of re-establishing an extensive continuous seagrass meadow, which was present in the area prior to substantial seagrass loss

(> 5,200 ha) (Neverauskas 1987; Nayar *et al.* 2012). This technique has allowed *A. antarctica* seedlings to become established and create new patches (Irving *et al.* 2013), which have persisted for > 5 years (Tanner 2014). *Amphibolis* is a large perennial structure-forming seagrass that grows in similar environments to *Posidonia* (Shepherd & Womersley 1981; Bryars & Rowling 2009). Unlike many other large seagrasses, most of the biomass is above-ground (Paling & McComb 2000), and it has long, wiry vertical stems that support clusters of small leaves (rather similar to a bottlebrush in appearance), rather than long strap-like leaves. It is also unusual in being viviparous, with seedlings released from the parent plant in winter and drifting until they encounter a suitable attachment point (Cambridge 1975; Ducker *et al.* 1977). Attachment is via a comb-like rosette at the base of the seedling that entangles in features such as *Posidonia* root mat (Kirkman 1999; Rivers *et al.* 2011), and it is this feature that allows it to attach readily to hessian bags (Wear *et al.* 2010).

Here, we explicitly seek to estimate the early signs and extent of motile epifaunal recovery relative to seagrass recovery of the series of small-scale experimental seagrass restoration patches described by Tanner (2014). We define motile epifauna as non-sedentary small invertebrates which are directly associated with aboveground seagrass structure. To estimate the early signs and extent of recovery, we compare initially small and expanding patches of restored seagrass to an adjacent continuous natural seagrass meadow. We consider this to be the gold standard for recovery in this situation, as this meadow is well established (hundreds if not thousands of years), large, and not subject to fragmentation, and therefore best reflects the natural situation. Additionally, we tested whether the time scale of epifaunal recovery in these restoration patches matched the time scale of seagrass recovery. If epifaunal recovery occurs before seagrass recovery, then demonstrating this may assist managers by showing early signs of achievement, thus justifying continued investment in restoration.

## 2. Materials and methods

### 2.1. Restoration site and sampling design

Structural recovery and epifaunal use were examined in an experimental seagrass restoration site located just inshore of a large, naturally occurring *A. antarctica* meadow, in approximately 8 m water depth, along the Adelaide metropolitan coast, South Australia (35° 1' S, 138° 18' E). The natural *A. antarctica* meadow consists of a dense continuous canopy, with the edge of the meadow being an abrupt change from dense seagrass to bare sand. The current edge of the natural seagrass meadow marks the margin of seaward retreat of inshore seagrass at this site due to eutrophication (Westphalen *et al.* 2005). In recent years, extensive effort has been invested in improving water quality, allowing a small amount of natural seagrass recovery in deeper waters (Bryars & Neverauskas 2004), and prompted initial studies on restoration.

Restoration trials at this site began in 2007 by deploying hessian bags to promote the recruitment of *A. antarctica* seedlings, which are released from the adjacent natural meadow. Hessian bags (area 0.35 m<sup>2</sup> per bag) were deployed approximately bimonthly, from September 2007 to October 2009 and again from January 2011 to March 2013. On each deployment, ten replicate bags, which represent a restoration plot, were filled with ~ 25 kg of clean play pit sand to anchor them and deployed on sandy substrate, shoreward of and parallel to the natural meadow. Bags were placed end-to-end in a double row by divers ~ 0.5 – 1 m apart, making restoration plots rectangular in shape. Each bimonthly deployment was separated by ~ 2 to 3 m and there was a minimum distance of 10 m between restoration plots deployed in different years. All bags were deployed within 50 m of the natural

meadow, and extended over a distance of ~ 100 m (Fig. S1). The variation in recruitment of *A. antarctica* seedlings with distance from the natural meadow has previously been tested at this site, and bags located within ~ 80 m of the natural meadow effectively recruit *A. antarctica* seedlings (Irving *et al.* 2013). While not formally measured due to the small size of the entire site (~ 2 km between the edge of the seagrass and shoreline, Wear *et al.* 2010) there were no obvious environmental gradients present. Importantly, there was no measurable difference in water depth between the offshore and inshore margin of the restoration site (~ 8 m water depth). In addition, previous measurements showed that seafloor light intensities at this site averaged 15 – 18 % of surface irradiance ( $86.83 \pm 22.71 \mu\text{mol m}^2 \text{s}^{-1}$ ) (Irving *et al.* 2010).

We used a space-for-time substitution approach (also known as a chronosequence) to establish the time scale for the recovery of the restoration site. Space-for-time substitution (SFT) has long been used in ecology, particularly as a standard method for looking at successional theory, where time-scales are generally sufficiently long that standard replicated experimental designs are not feasible (Pickett 1989). This technique has allowed us to assess the time scale and extent of epifaunal recovery by taking a series of samples from restoration plots of known ages, representing a “single snapshot” of succession, instead of sampling the one site multiple times. *A. antarctica* samples with associated epifauna were collected from three restoration plots of known ages (based on year and month of bag deployment), 1 year (July 2011 deployment), 3 years (February 2009 deployment) and 5 years (September 2007 deployment). Seagrass within the 1 year old restoration plot was still constrained within the boundaries of the bags, whereas vegetative expansion of seagrass had occurred within the 3 year old (~ 10 cm from the bags) and 5 year old (coalescence between bags) restoration plots (J Tanner, per obs). *A. antarctica* samples were also collected from two plots within the

adjacent natural meadow, the edge (defined as within 0.5 m of the abrupt boundary that divides seagrass and bare sand) and the interior (~ 20 m into the natural meadow,  $n = 5$  per site). Restoration samples were collected from the centre of five randomly selected bags from each of the three restoration plots (1 year, 3 years and 5 years), while a 20 cm x 20 cm quadrat was haphazardly thrown five times and a sample was taken from the centre of the quadrat for the natural meadow (the quadrat was rethrown if it did not land within 0.5 m of the edge for edge samples). Samples were collected from the centre of the bag in order to keep the sampling methods consistent across the restoration plots. All samples were collected in July 2012, using a 9.0 cm internal diameter (area of 64 cm<sup>2</sup>) PVC corer attached to a fine mesh bag (mesh size 0.5 mm). This sampling method targets small invertebrates which are directly associated with aboveground seagrass and does not sample fish or larger invertebrates. The corer was carefully placed over the seagrass, flush with the sediment surface. The seagrass was then cut at the substrate surface using a serrated knife and the mesh bag was tied closed to prevent the escape of motile epifauna. Samples were then drained into the mesh bag and preserved in 10% formalin solution until sorted.

## 2.2. Response variables

All samples were sieved using a 1 mm mesh screen and sorted under magnification in the laboratory. Motile epifauna were removed, counted and identified to the highest taxonomic resolution possible, for most taxa family, except for some rare or poorly known taxa which could only be reliably identified to phylum or class. In addition, the seagrass structure itself was quantified as aboveground seagrass biomass (g dry weight of stems, branches and leaves [DW] m<sup>-2</sup>), stem length (cm) and density (no. m<sup>-2</sup>), leaf cluster density (no. m<sup>-2</sup>) and stem and leaf epiphyte biomass (g dry weight [DW] m<sup>-2</sup>). *A. antarctica* has wiry stems and branches

that are topped by clusters of 5-10 leaves ~5 cm long (Ducker *et al.* 1977). Stem length was measured from the base of the stem to the top of the most distal leaf cluster. All epiphytes were carefully scraped from the seagrass using a scalpel blade. Epiphytes and epiphyte-free seagrass were then placed in separate pre-weighed aluminium foil trays and dried to a constant weight at 60° C for 72 hours.

### 2.3. Data analysis

To establish whether the physical structure and epifaunal composition of *A. antarctica* varied between the restoration plots of known ages and the natural meadow, one-way permutational multivariate analyses of variances (PERMANOVA), followed by pairwise tests, were used. Euclidean distance was used for the physical structure analysis, while the Bray-Curtis similarity measure was used with fourth root transformed data for the epifaunal composition. When the PERMANOVA was significant ( $p < 0.05$ ), separate univariate analyses using Euclidean distance, followed by pairwise tests, were run on each of the individual seagrass structural variables. Univariate analyses were also used to determine whether epifaunal richness and abundance varied between the restoration plots and the natural meadow. Epifauna were then grouped into the three most abundant classes (amphipods, gastropods and polychaetes) and analyzed similarly. All multivariate and univariate analyses were carried out in PRIMER (version 6) with the PERMANOVA + add-on (PRIMER-E Ltd, Plymouth).

## 3. Results

The physical structure of *A. antarctica* differed between the restoration plots and the natural meadow (PERMANOVA:  $F_{4, 20} = 4.534$ ,  $p = 0.005$ ), with pairwise tests showing the structure of the 1 year old restoration plot being different to the older restoration plots (3 and 5 years

old) and the natural meadow (edge and interior). The older plots did not differ from the natural meadow. Patch age had a clear effect on above-ground biomass, leaf cluster density, stem epiphytic biomass and leaf epiphytic biomass (Table 1 a, d, e and f, Fig. 1 a, d, e and f), with 1 year old plots having significantly lower values than all other restoration plots and the natural meadow. Stem length was significantly shorter in the restoration plots (1 year, 3 years and 5 years) than the natural meadow (edge and interior) (Table 1 b and Fig. 1 b). Stem length also differed significantly within the natural meadow; seagrass in the interior of the meadow was significantly shorter than at the edge of the natural meadow. There was no difference in stem density between the three restoration plots and the natural meadow (Table 1 c and Fig. 1 c).

Epifaunal composition differed significantly between plots (PERMANOVA:  $F_{4,20} = 1.70$ ,  $p = 0.002$ ), with pairwise tests showing the 1 year old plot to be different to the older restoration plots (3 and 5 years old) and the natural meadow (edge and interior). Epifaunal composition in the 3 and 5 year old restoration plots did not differ from the natural meadow. There was no difference in epifaunal richness between the three restoration plots of known ages (1, 3 and 5 years old) and the natural meadow (Fig. 2 a, PERMANOVA:  $F_{4,20} = 2.509$ ,  $p = 0.07$ ). Total epifaunal abundance differed significantly between the restoration plots (Fig. 2 b, PERMANOVA:  $F_{4,20} = 3.09$ ,  $p = 0.034$ ), which was due to a lower abundance in the 1 year old plot than the 5 year old plot. However, there was no difference in epifaunal abundance between any of the three restoration plots and the natural meadow (Fig. 2 b). There was no difference in gastropod and amphipod abundance between the restoration plots and natural meadow (Fig. 3 a, b, PERMANOVA:  $F_{4,20} = 1.93$ ,  $p = 0.139$  and  $F_{4,20} = 1.30$ ,  $p = 0.296$ , respectively), however, polychaete abundance was lower in the 1 year old plot

than the 5 year old plot and the interior of the natural meadow (Fig. 3 c, PERMANOVA:  $F_{4,20} = 2.175, p = 0.039$ ).

#### **4. Discussion**

The overall goal of restoration is often not only to restore the habitat *per se*, but to restore the ecosystem services it supplies, and particularly to encourage the return of fauna. Here, we show that epifaunal richness and abundances were comparable to a natural meadow after one year, even though the seagrass structure had not fully recovered. However, epifaunal composition did not recover until the seagrass had fully recovered after 3 to 5 years. These results show that although recovering habitats may not look structurally similar to undisturbed habitats, they can in at least some circumstances support a similar richness and abundance of fauna. However, full recovery of seagrass was required before the taxonomic composition of the epifauna matched that of the natural seagrass meadow.

The rapid recovery of small invertebrate abundance before the recovery of seagrass structure in restored plots most likely reflects the greater proportional abundance of early successional species, which rapidly colonize new habitat patches due to the provision of physical structure. As restored seagrass patches are often isolated from natural meadows (Sheridan 2004), they provide structure which can attract actively dispersing fauna, such as amphipods, in what can be an otherwise un-vegetated environment. Such rapid colonization of fauna due to the provision of structure has also been observed with the transplantation of other seagrass species (e.g. Fonseca *et al.* 1996; Bell *et al.* 1993). For example, a 1.9 year old restored seagrass meadow in Galveston Bay, Texas had similar abundance and composition of fishes and shrimps to an adjacent natural seagrass meadow, and had greater faunal abundances than

a nearby unvegetated habitat (Fonseca *et al.* 1990). The time scale for the recovery of fauna varies, however, and can exceed 5 years (Sheridan *et al.* 2003; Sheridan 2004). To date, insufficient data is available to determine whether faunal recovery is linear, or whether it responds to thresholds in seagrass structure, as suggested by Fonseca *et al.* (1996), who reported similar faunal abundance between restored and natural seagrass beds, even though shoot density of the restored bed was one third that of the natural meadow.

Epifauna inhabiting *Amphibolis* meadows respond directly to changes in habitat complexity and can be divided into two groups: leaf-associated, being fauna that respond directly to the presence of seagrass leaves; and epiphyte-associated, being fauna that respond to epiphytic biomass (Edgar & Robertson 1992). In this study, the most prevalent taxa (amphipods, nereidid and nephtyid polychaetes) are known to be associated with the epiphytic algae that they consume, or to consume faunal species that are associated with epiphytic algae (Fauchald & Jumars 1979; Duffy & Hay 2000; Caron *et al.* 2004). Although epiphytes were present throughout the restoration plots and natural meadow, epiphyte biomass was significantly lower in the 1 year old restoration plot. As expected based on this low epiphyte biomass, polychaetes were relatively less abundant in the 1 year old restoration plot. Unexpectedly, amphipod abundance was similar in the 1 year old restoration plot to that in the natural meadow, and so this group does not appear to be responding to total epiphyte biomass.

Patterns of colonization may also reflect the mobility of fauna (Virnstein & Curran 1986; Russell *et al.* 2005). Relatively motile fauna such as amphipods can actively select habitat that provides increased refuge from predators and food resources (Stoner 1980; Bell & Westoby 1986). Amphipod movement can be further enhanced through passive dispersal via

tidal currents (Virnstein & Curran 1986), and they are therefore good dispersers with early opportunity for colonization of restoration plots, explaining their high relative abundance in the 1 year old plot.

The proximity of restored seagrass patches to the natural meadow may influence faunal abundance (Sheridan *et al.* 2003), with restored patches close to natural meadows having a greater probability of attracting or entraining dispersing fauna. Importantly, the closer habitats are to each other, the more likely, motile organisms are to encounter them in their daily movements (Russell *et al.* 2005), lowering the likelihood of dispersal related mortality, such as encountering a predator. Furthermore, in seagrass beds, hydrodynamic conditions change with distance from the habitat edge, with flow rate decreasing towards the habitat interior (Fonseca *et al.* 1982), resulting in the accumulation of fauna along the seagrass edge (Bologna & Heck 1999; Tanner 2005). It is likely that the small sizes of the restoration plots sampled here mean that they are made up entirely of patch edge. These influences would actually bias our study away from finding recovery, as we would expect that at some stage as plots get smaller and more isolated, the epifaunal composition would change as a result of those factors alone. Although this study found no natural edge effects, small restoration plots may more rapidly accumulate fauna, as the increased amount of habitat edge relative to the plot size may increase the relative encounter rates of fauna dispersing passively (Boström *et al.* 2006).

In the majority of systems that we study, the life spans of the plants and animals exceed that of several generations of scientific careers, which means that progress in testing recovery theory is challenging. Seagrass systems, therefore, open an opportunity to test these ideas because the structure and function (in terms of recovery of composition and relative

abundance of epifauna) of these systems often return relatively quickly after restoration commences (e.g. Fonseca *et al.* 1996; Sheridan 2004). Whilst epifauna recovered to similar levels as the natural patch, further work is required in order to determine the composition and abundance of fish species using the restoration plots as habitat for shelter or foraging activity. Nevertheless, this study demonstrates that the recovery of restored patches can be remarkably quick, with epifaunal richness and abundance taking as little as one year and seagrass structure and epifaunal composition taking three years to resemble adjacent natural systems. Further trials are now being undertaken in order to assess the potential use of hessian bags for the restoration of seagrass species that have different life history strategies to *Amphibolis*.

Restoration of this site began as a trial of new techniques to facilitate the natural recruitment of *A. antarctica* seedlings, with the overall intention of re-establishing an extensive continuous seagrass meadow (see Irving *et al.* 2010; Wear *et al.* 2010; Irving *et al.* 2013; Tanner 2014). As a result, restoration plots are replicated temporally rather than spatially. Although this design has enabled us to quantify the recovery of epifaunal inhabitants and seagrass structure over time, it has resulted in a sampling design that was unavoidably pseudo-replicated. This is typical of many such space-for-time substitutions, which are often used to study ecological processes that occur on time scales that are too long to be amenable to the application of properly replicated experiments (Pickett 1989). However, due to the small size of the entire restoration site, we consider that the sampling design had no influence on the interpretation of the results, as there were no obvious environmental gradients present that could affect the recruitment of seagrass or epifauna. Furthermore, more detailed analysis of data on stem length and density on all 240 bags deployed during the study (Tanner 2014) confirms our results for these two variables. The seemingly logical progression in our results

from 1 to 3 to 5 year old restoration plots also suggests that these results are robust against this pseudo-replication.

To conclude, recovering habitats may not be structurally similar to undisturbed habitats, but they can support similar components of composition (e.g. epifaunal richness and total epifaunal abundance), suggesting that whilst habitats may not appear fully recovered they can act as equivalents for some aspects of richness and abundance. If such faunal recovery occurs before full recovery of the habitat, then the intention of restoring the function of the lost habitat may assist managers by showing early signs of achievement of pressing goals towards full habitat recovery *per se*.

### **Acknowledgements**

We thank I. Moody, A. Dobrovolskis and L. Mantilla for their field and laboratory assistance. D. Fotheringham, S. Murray-Jones (South Australian Department for Environment, Water and Natural Resources), T. Flaherty (Adelaide and Mount Lofty Ranges Natural Resources Management Board), and M. Fernandes (SA Water) provided strong support for this work, and assisted with obtaining funds from their organizations. Part of this work was conducted under Australian Research Council (ARC) Linkage Projects to J. S. Quinton (Flinders University), S. Connell and B. Russell, including a Future Fellowship to S. Connell.

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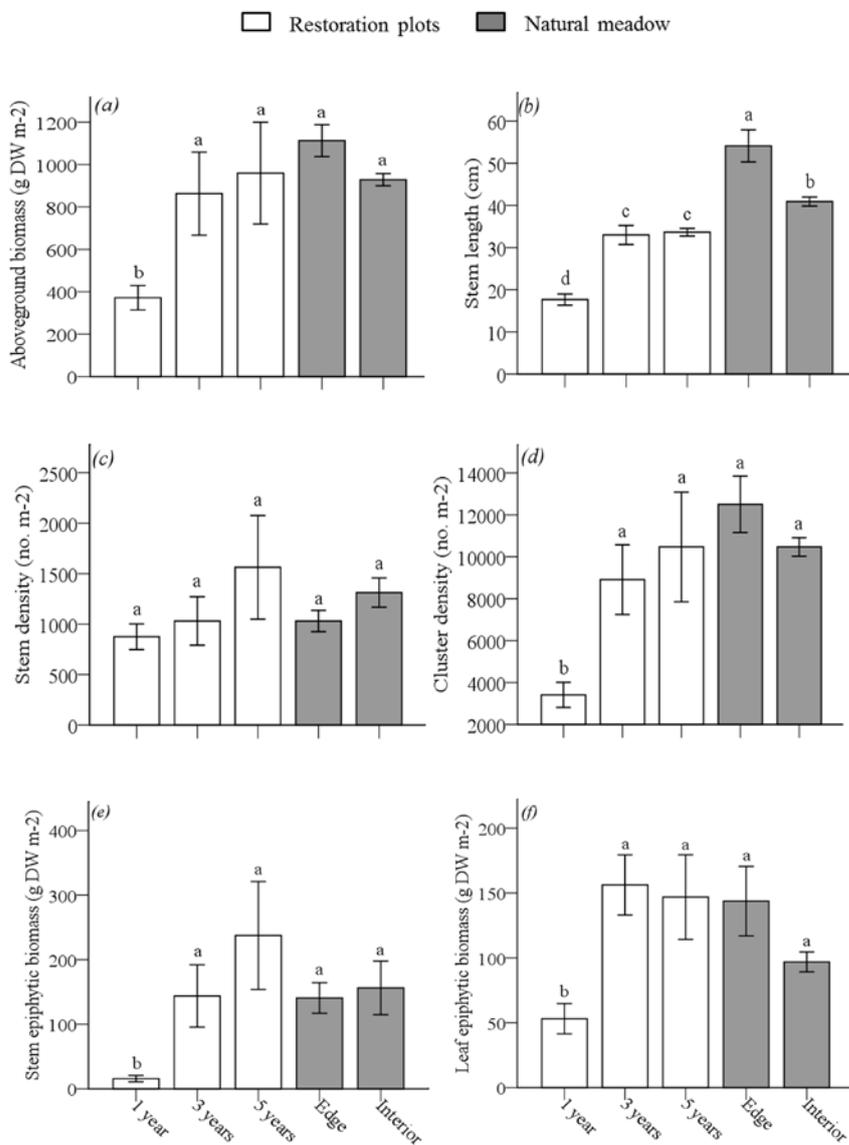
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**Table 1.** The structural characteristics of *A. antarctica* (aboveground biomass, stem length, stem density, leaf clusters, stem epiphytic biomass and leaf epiphytic biomass) as a function of site, as determined by one-factor PERMANOVAs.

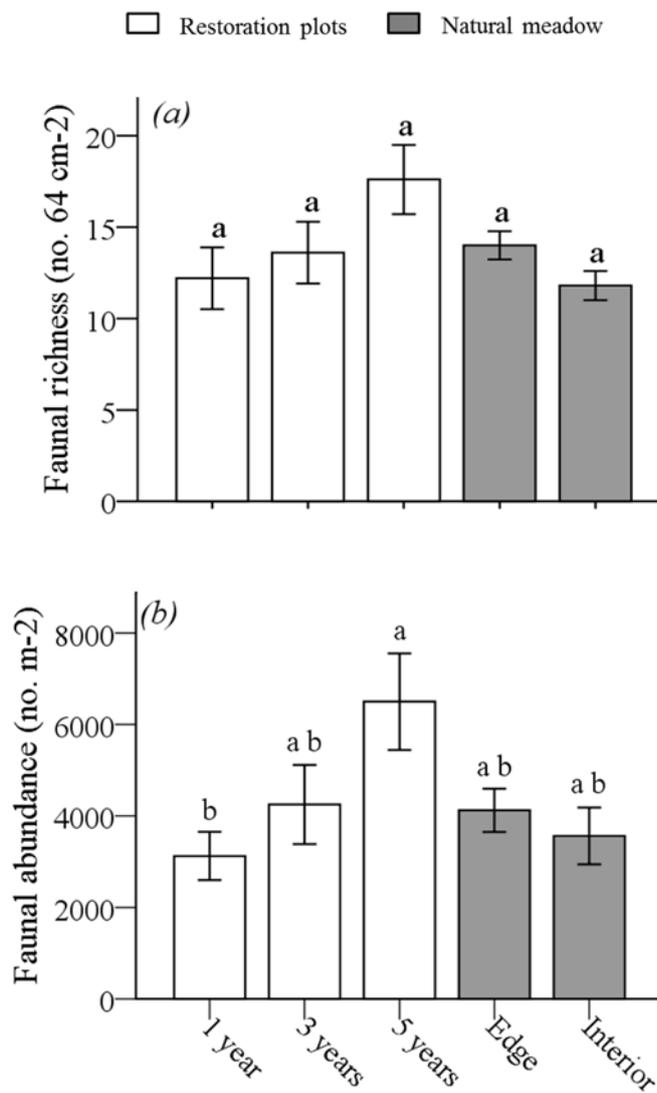
Source	df	MS	<i>F</i>	<i>P</i>
<i>(a) Aboveground biomass</i>				
Site	4	394600	3.732	<b>0.026</b>
Residual	20	105720		
<i>(b) Stem length</i>				
Site	4	878.180	37.224	<b>0.001</b>
Residual	20	23.592		
<i>(c) Stem density</i>				
Site	4	374510	1.013	0.437
Residual	20	369630		
<i>(d) Leaf clusters</i>				
Site	4	59688000	4.984	<b>0.006</b>
Residual	20	11976000		
<i>(e) Stem epiphytic biomass</i>				
Site	4	31558	2.711	<b>0.041</b>
Residual	20	11641		
<i>(f) Leaf epiphytic biomass</i>				
Site	4	9506.8	3.781	<b>0.021</b>
Residual	20	2514.6		

**Fig. 1.** Structural characteristics of *Amphibolis antarctica* at the three restoration plots of known ages: 1 year, 3 years, 5 years and the two natural meadow plots: edge and interior, including (a) aboveground biomass (g DW m<sup>-2</sup>), (b) stem length (cm), (c) stem density (no. m<sup>-2</sup>), (d) leaf cluster density (no. m<sup>-2</sup>), (e) stem epiphytic biomass (g DW m<sup>-2</sup>) and (f) leaf epiphytic biomass (g DW m<sup>-2</sup>). Values are mean ± S.E. (n = 5). Within each panel, plots with the same letter are not significantly different according to pairwise tests.

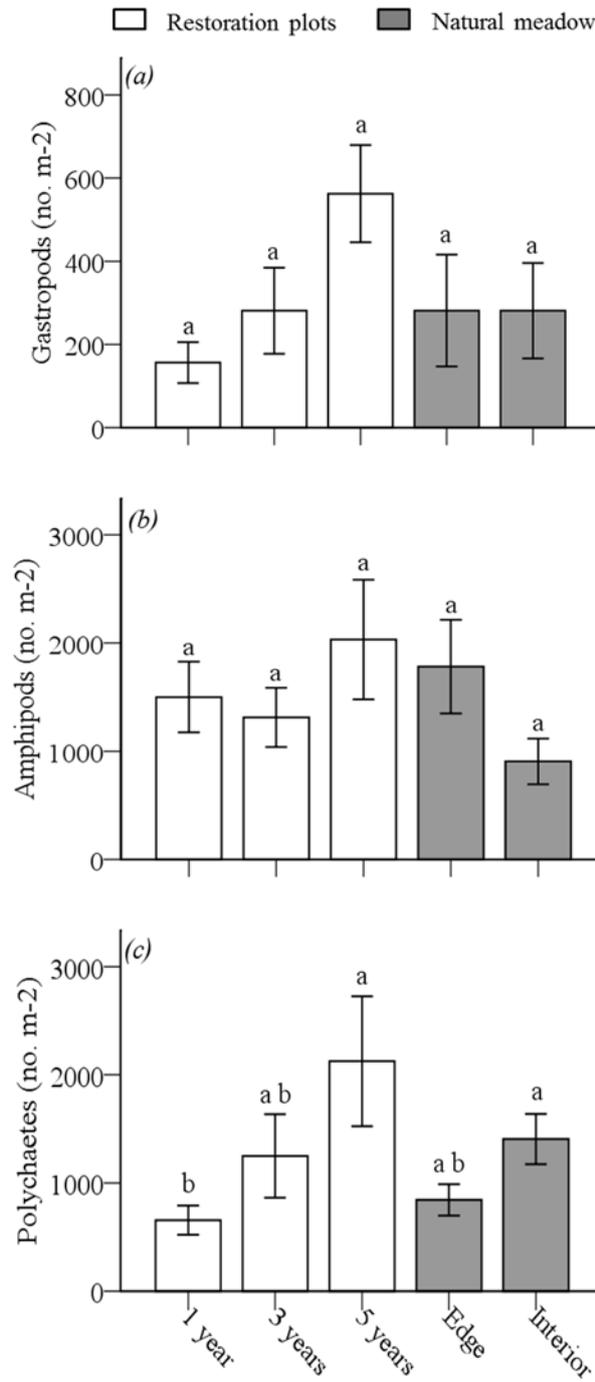


**Fig. 2.** Epifaunal richness (*a*) and epifaunal abundance (*b*) at the three restoration plots of known ages: 1 year, 3 years, 5 years and the two natural meadow plots: edge and interior. Values are mean  $\pm$  S.E. ( $n = 5$ ). Within each panel, plots with the same letter are not significantly different according to pairwise tests.

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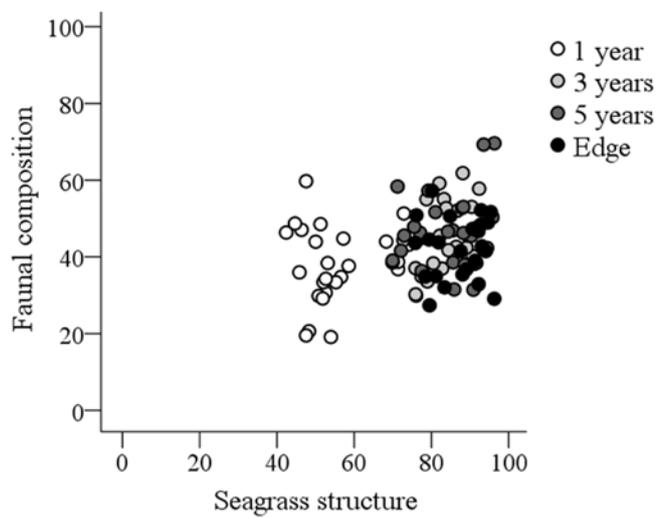


**Fig. 3.** Gastropod abundance (*a*), amphipod abundance (*b*) and polychaete abundance (*c*) at the three restoration plots of known ages: 1 year, 3 years, 5 years and the two natural meadow plots: edge and interior. Values are mean  $\pm$  S.E. ( $n = 5$ ). Within each panel, plots with the same letter are not significantly different according to pairwise tests.



**Graphical abstract.** Scatter plot of Bray-Curtis similarity measures of seagrass structure (x-axis) and epifaunal composition (y-axis) showing the convergence between all replicate samples within the three restoration plots (1, 3 and 5 years) and natural meadow (edge), to the interior of the natural meadow. Similarity coefficient = 100 if two samples are completely similar, 0 if two samples are completely dissimilar.

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**Fig. S1.** Map showing the natural meadow (line), the restoration site (boxes), the date of deployment of each plot and the location of the three restoration plots sampled (yellow boxes). The distance between the natural seagrass meadow and the furthest deployment is < 50 m and the length of the site is ~ 100 m. Please note: the positions of the restoration plots have not been precisely mapped.

