RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

PRACTICE AND TECHNICAL ARTICLE

Optimizing the restoration of the threatened seagrass *Posidonia australis*: plant traits influence restoration success

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Restoration is an important activity to assist the recovery of damaged or degraded ecosystems. Accessing healthy donor material can be challenging when restoring threatened ecological communities, but careful selection of donor material may improve the success and cost-effectiveness of restoration projects. We aim to optimize restoration of the threatened seagrass *Posidonia australis* by identifying the traits of donor material that best predict survival and establishment. To avoid collecting donor material from threatened populations, a recent restoration method focuses on using naturally detached fragments of *P. australis* collected from the shoreline, which are stored in outdoor tanks prior to planting. Here, we examine 10 morphological traits of *P. australis* fragments and other variables relating to collection method to identify which traits best predicted survival after replanting. Fragments with more shoots and less dead tissue (necrosis) in their leaves had higher survival 1 year after planting. Fragments that were stored longer in tanks prior to replanting had significantly higher survival rates. These results can refine the selection for donor material used in restoration and optimize the recently developed restoration technique for *P. australis* using beach-cast seagrass material.

Key words: beach-cast seagrass, citizen science, plant morphology, recovery, seagrass conservation, trait ecology

Implications for Practice

- Careful consideration of the traits of naturally detached plant material can improve *Posidonia australis* restoration success.
- Selecting *P. australis* fragments with a high number of shoots (≥3), and low levels of leaf necrosis improves survival after1 year.
- Storing *P. australis* fragments longer in suitable tanks prior to replanting can lead to higher survival rates 1 year after replanting.

Introduction

Human actions are causing extensive loss and degradation of ecosystems worldwide, impacting biodiversity, people and economies (Halpern et al. 2008; Dornelas et al. 2019). Protecting ecosystems from further destruction is key to securing ecosystem services into the future (Jones et al. 2018), but when they become degraded, active restoration can reverse habitat loss and provide effective pathways to a sustainable future (DeFries et al. 2012). Understanding the factors that predict restoration success is crucial to improving the cost-efficiency of restoration efforts, enabling restoration at larger scales. This is a main focus of the "UN Decade on Ecosystem Restoration," which specifically highlights a global need to increase the success of restoration projects (Aronson et al. 2020; United Nations Environment Programme 2021). One factor that can greatly influence restoration success is the quality of the donor material used for restoration (Clark et al. 2012), including morphological and physiological traits, for example, leaf area and photosynthetic rate (Abou Seedo et al. 2018) or size and condition of the transplanted organisms (Pausch et al. 2018).

Author contributions: GF, TMG, AGBP, EAS, JS, GAK, AV conceived and designed the research; GF, TMG, AV collected the data; GF, AGBP, CTC analyzed the data; GF wrote the original draft; GF, TMG, AGBP, CTC, EAS, JS, GAK, AV edited the manuscript.

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doi: 10.1111/rec.13893
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13893/suppinfo

Seagrasses are marine angiosperms that create underwater meadows that support key ecosystem functions and services such as biodiversity, fisheries, and carbon capture (Jackson et al. 2001; Duarte & Krause-Jensen 2017). Seagrasses are among the most human-impacted ecosystems globally (Waycott et al. 2009; Burgos et al. 2017), with their distribution declining due to human factors such as coastal development, climate change, water pollution, and boating activities (Sagerman et al. 2020; Dunic et al. 2021). Active restoration of degraded seagrass meadows is therefore part of conservation efforts in marine ecosystems across the world (van Katwijk et al. 2016; Statton et al. 2018; Orth et al. 2020).

Posidonia australis Hook.f. is a large, perennial, long-lived, and slow-growing seagrass, with high biomass and productivity. It forms dense underwater meadows on soft sediments in marine or estuarine waters of Southern Australia (Larkum et al. 2006). Meadows of *P. australis* in six New South Wales (NSW) estuaries have declined so extensively that they were listed as Endangered in 2010 under the state legislation (*NSW Fisheries Management Act 1994*) with an additional two populations listed as "Endangered Ecological Communities" in 2015 by the Commonwealth of Australia (*Australian Environment Protection and Biodiversity Conservation Act 1999*). Coastal development, increased sedimentation and boating activities are some of the historical and ongoing causes for loss of *P. australis* in NSW estuaries (Department of the Environment and Energy 2018; Glasby & West 2018). Natural recovery of *P. australis* is limited, even with removal of threats, due to the species' slow growth rate (Meehan & West 2000) and low levels of sexual reproduction (Gobert et al. 2007).

Recently a new method to restore *P. australis* has been developed using naturally detached fragments collected from the beach (Ferretto et al. 2021). However, beach-cast fragments vary widely in size, condition and timing of arrival on the beach—all of which can influence the potential for survival of a given fragment. This study identifies morphological traits and collection methods which best predict restoration success from naturally detached fragments of the threatened seagrass *P. australis*. We test whether probability of fragment survival was influenced by (a) morphological traits of fragments and/or (b) fragment collection details and storage time. Understanding how these predict fragment survival will improve collection and handling of donor material for restoration efforts of this endangered species.

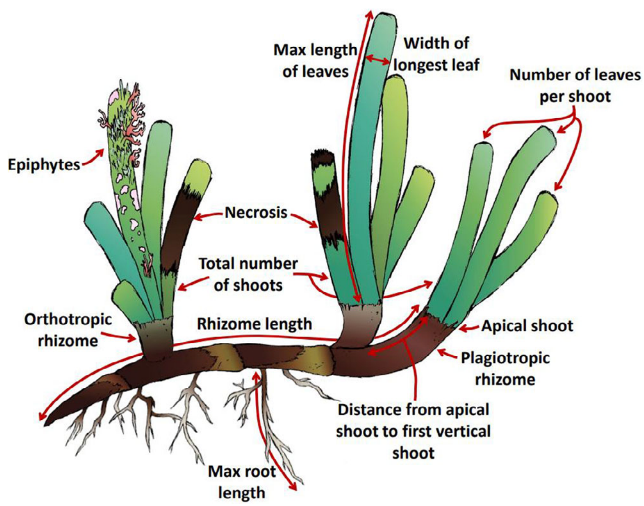

Figure 1. Morphology of *Posidonia australis* fragments. The following morphological traits were tested: epiphyte cover, measured as estimated coverage (%) of epiphytes on leaves; leaf width, width of the longest leaf (cm); maximum leaf length, maximum length of leaves (cm); necrosis, estimate of necrotic tissue on the leaves (%); rhizome length, the length of the rhizome (cm); root length, the maximum length of the roots (cm); total number of shoots, the total number of shoots in a fragment; the distance from apical shoot to first vertical shoot (cm; only for plagiotropic fragments). Rhizome shape corresponds to the growing form: orthotropic rhizomes have vertical growth (mostly to escape sedimentation) while the plagiotropic rhizomes have an apical shoot and grow horizontally (to expand in surrounding environments). Image credit: Zuhairah Dindar.

Collection, Planting, and Monitoring of *P. australis* Fragments

Fragments of *Posidonia australis* were collected from the beaches on the southern side of Port Stephens, an estuary on the mid-north coast of New South Wales (32°43′22.8″S, 152°04′55.4″E, methods detailed in Ferretto et al. 2021). These fragments were naturally detached and washed up by onshore winds (Fig. S1a). Fragments were collected via a citizen science campaign (www.operationposidonia.com), and these collections were augmented by staff from the NSW Department of Primary Industries (DPI) Fisheries. Citizen scientists were asked to collect fragments with one or more shoots connected to the rhizome (Fig. S1a) and to provide collection details (collector, date and location of collection). Fragments were transported to the NSW DPI Port Stephens Fisheries Institute and planted in commercially available building sand in individual boxes (60 × 40 cm) that were suspended 35 cm below the water's surface in large outdoor tanks with flow-through estuarine water (salinity >28 ppt) and receiving natural sunlight (Supplement S1; Fig. S1b). Prior to replanting, fragments were individually tagged and photographed (Fig. S1c). Collection details for each fragment were recorded, including the beach where the fragment was found (collection location) and the collector, when known, with collectors then grouped as DPI staff or volunteer. Morphological traits were quantified for each fragment: growth form (orthotropic/plagiotropic, fragments with an apical shoot were classified as plagiotropic; fragments whose growth form could not be visually classified were classified as "uncertain"), distance from apical to first vegetative shoot, total number of shoots, total number of leaves, maximum length of leaves, width of longest leaf, length of rhizome, maximum length of roots, epiphyte cover, percentage of necrosis on leaves (amount of dead tissue; Fig. 1). Percentage of necrosis and epiphyte cover were visually estimated on a scale 0–100% (using categories of 5%).

Fragments were randomly allocated in groups of 24 and planted in a fragmented *P. australis* meadow in Shoal Bay, Port Stephens. All plantings took place in old boat mooring scars where the traditional moorings had been removed (Fig. S1d), with two scars revegetated in January 2019 and two in June 2019. Six plots were established in each of the 4 scars (3 with stabilizing mats made of natural biodegradable fiber and 3 without), with each plot having 24 fragments distributed in 4 rows of 6 fragments, as described by Ferretto et al. (2021). Fragments with orthotropic rhizomes were secured with 150-mm long starch-based pegs (GreenStake™) with biodegradable budding tape (Ryset Australia), while plagiotropic rhizomes were secured with either 150-mm-long metal Weed Mat Pins (Whites Outdoor) for fragments planted in January or 200-mm-long bamboo pegs for those planted in June. The plots were monitored by SCUBA divers every 2 months for 12 months, recording whether each fragment was alive or dead (including lost).

Statistical Analysis

Separate generalized linear mixed models with binomial distribution were used to test for the effects of *Posidonia australis* fragments collection details (month of collection, location of collection, collector, and duration [in months] of storage before planting) or morphological traits at the time of planting (seven independent continuous trait variables; Fig. 2) on the survival of fragments. The models were fitted using the R function *glmmTMB* and included plot as a random effect. For the collection details, statistical inference for predictor variables was also obtained from likelihood ratio tests using the *anova* function (Table S1).

For the morphological traits, planting month (January or June) was analyzed separately. We opted to fit two separate models—one for each planting month—rather than a model with planting month as a random factor as there are only 2 months and random factors with fewer than five levels can lead to biased parameter estimation (Bolker et al. 2009; Harrison et al. 2018). Model residual checks were performed using the package DHARMa (Hartig 2017). Predictors were standardized using the function *rescale* in the package arm (Gelman et al. 2018) and log-transformed, if required. We investigated correlation among morphological traits using the R function *ggpairs* in the package GGally (Schloerke et al. 2018) and *ggcorplot* in ggplot2 (Wickham 2016) before modeling. We used a cutoff of $r > 0.5$ to exclude one of the two correlated variables (total number of leaves was removed due to high correlation with total number of shoots; $r = 0.76$) and correlations with $r > 0.4$ and < 0.5 were classified as important. All traits represent competing models, with no a priori expectations as to specific traits that would influence survival. Therefore, we used averaged regression coefficients across many competing models (Dormann et al. 2018). All possible subsets of models (i.e. possible trait combinations, Table S3) were ranked with Akaike Information Criterion corrected (AICc) for small sample sizes and we averaged regression coefficients over models with ΔAIC <4. The functions *dredge* and *model.avg* in the R package MuMIn (Barton 2015) were used to perform a model averaging analysis. R^2 was obtained with the function r.*squaredGLMM* in the R package MuMIn. "Growth form" (orthotropic/plagiotropic, categorical variable) and "distance from apical shoot to first vertical shoot" (only applicable to plagiotropic fragments) were analyzed separately with additional GLMMs with the same structure described above (Tables S4 & S5). All statistical analyses were conducted using the software R (version 4.0.5; R Core Team 2020).

Results

Effect of Collection Date and Storage

A total of 569 *Posidonia australis* fragments were included in this study, with 56% (n = 320) collected by "Operation

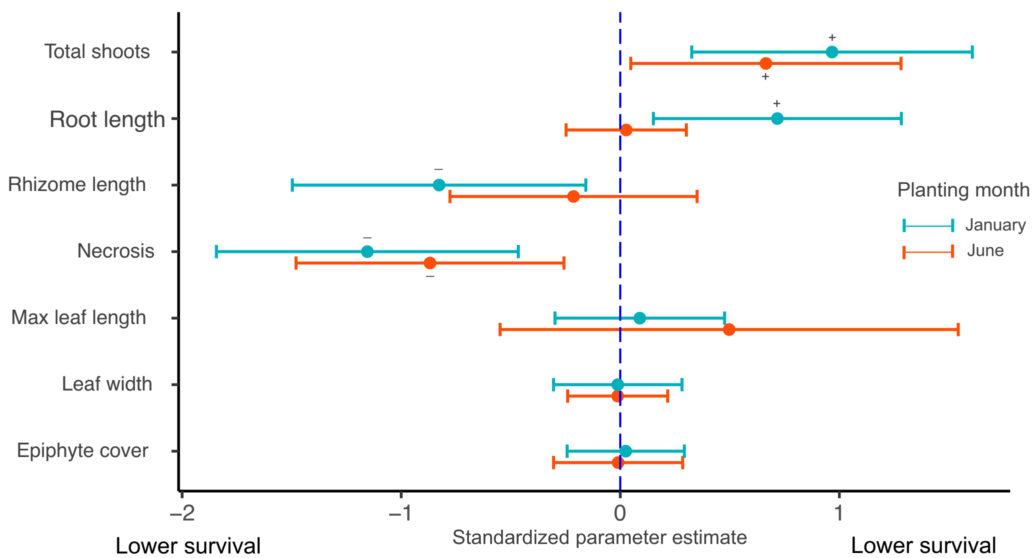

Figure 2. Model averaged coefficients (standardized parameter estimate) that measure the effect of seven morphological traits on survival for fragments planted in January (light blue) and June (red). Values >0 have a positive effect on survival. Values marked with the signs + or − have a significantly positive or negative effect on survival, respectively. Data are means of parameter estimates ±95% CI.

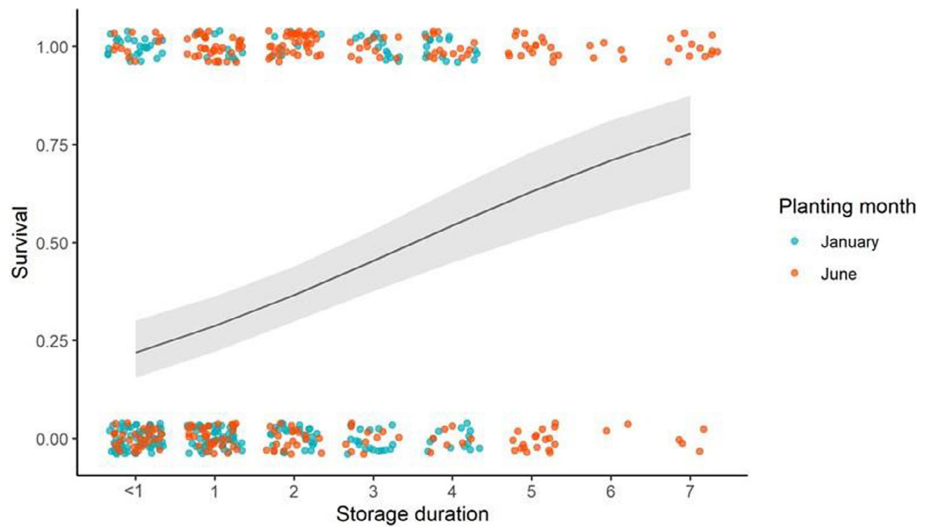

Figure 3. The effect of storage duration (number of months spent in tank before planting) on the survival of fragments after 12 months. Each point represents a fragment, with the transparent points jittered to avoid overplotting and colored by planting month. Fragments planted in January were not kept beyond 4 months. Only fragments with recorded month of collection were included in these plots. When survival is 1, fragments survived, when survival is 0 fragments died. The fitted line and shaded area represent the prediction of survival and 95% CI from model A.

Posidonia" volunteers, 27% ($n = 152$) by DPI Fisheries staff and 17% ($n = 97$) with no record of the collector's identity. Survival of planted fragments did not differ according to who collected the fragments ($p = 0.995$) or by collection location ($p = 0.831$; Table S1). The number of fragments collected varied during the year and fragment survival varied among months of collection ($p < 0.01$; Fig. S2; Table S1). The duration of fragment storage prior to planting varied between 2 weeks and 7 months, with most fragments (68%, $n = 346$) stored between 2 weeks and 2 months. Increased storage times were associated with increased fragment survival in the field ($p < 0.001$; Figs. 3 & 4; Table S1). Fragments stored in tanks for 6 or 7 months (4.5%, $n = 23$) before being planted in June had a high rate of survival (86%), while June fragments stored less than a month in tanks had a low average survival rate (36%). Fragment storage time also affected the January planting: only 28% of fragments stored less than 3 months survived 12 months after being planted, whereas 55% of January fragments stored for 4 months survived. Fragments planted in January were not stored beyond 4 months.

Morphological Traits that Best Predict Planting Success

Overall, the variance explained by our full model was 20% in January and 70% in June ($R^2_{\text{January}} = 0.2$; $R^2_{\text{June}} = 0.7$). Leaf necrosis was the most important predictor of survival for fragments planted in January and in June ($p < 0.01$; Figs. 2 & 5A, 5C, 4). Increased necrosis was associated with decreased survival in both months. The number of shoots per fragment was the second most important predictor for both planting months (Fig. 2) and showed a strong positive relationship with survival ($p < 0.01$; Fig. 4, 5B & 5D); however, beach-cast fragments generally had low numbers of shoots (average $= 1.93 \pm 0.04$ cm; Table S2; Fig. S3). Length of rhizome was negatively related to survival for January plantings ($p < 0.05$; Fig. 2), but not for June plantings. The survival of fragments planted in January was positively related to the maximum length of roots ($p < 0.05$; Fig. 2) and negatively related to distance from apical to first vertical shoot ($p < 0.05$; Table S5). No association was detected between survival and the other measured traits (maximum length of leaves, width of longest leaf, epiphyte cover, orthotropic/plagiotropic growth form, root length in June and distance from apical to first vertical shoot in June). Some fragment traits differed between the two planting months (Supplement S2; Table S2; Fig. S3). Two morphological traits were correlated to storage time (negatively for necrosis and positively for root length; Figs. S4).

Discussion

We demonstrate that trait selection of naturally detached plant material and storage duration before planting can improve restoration success. Selecting *Posidonia australis* fragments with a higher number of shoots and low levels of leaf necrosis can significantly improve survival after 1 year. Fragments with longer roots and reduced rhizome length had increased survival when planted in January (austral summer). Fragments that spent longer in tanks prior to planting also had higher rates of survival. These results suggest that selecting beach-cast material with more shoots and less leaf necrosis can enhance restoration success and improve the cost-efficiency of *P. australis* restoration. The greatest losses of *P. australis* transplants happen during the first 3–6 months (Statton et al. 2020), however, longer-term monitoring (2+ years) will determine whether survival at 1 year is indicative of long-term restoration success in boat mooring scars.

a. Timing of beach-cast fragment collections and storage

- Collect fragments whenever they are available, although fragment collection throughout the year varies depending on the weather (storm events) and collectors' availability.
- When possible, store (i.e. by planting) fragments in suitable tanks prior to restoration as this will stockpile fragments, enable fragments recovery, and naturally select the healthiest fragments that are more likely to survive once replanted. Suitable storage tanks would have flow through water, natural light, temperature control to avoid excessive heat and constant maintenance (e.g. remove excessive epiphyte growth).

b. Choosing donor material based on traits (at collection stage or after storage before planting)

- Consider the traits of naturally detached plant material: targeting fragments with a high number of shoots (≥3), and minimal (or no) leaf necrosis can improve survival after 1 year. This rapid selection can be done visually at the point of collection, as part of a volunteering training.
- When large beach-cast fragments are not available, more research may be needed to improve restoration with fragments with a single shoot (securing fragments with a single shoot is more time consuming than planting multiple shoot fragments).

c. Timing of planting and restoration sites

- Planting during autumn/ winter may be preferable as marine plants can be sensitive to heat and because plants are less actively growing.
- Avoid planting in sites with high sediment movement, or consider using methods to reduce sediment movement (e.g. using stabilising natural fibre mats).

Figure 4. Guidelines for improved restoration of the seagrass *Posidonia australis* (this study and Ferretto et al. 2021). These steps should be considered only after the reasons for seagrass disappearance have been resolved (e.g. swing moorings were removed or replaced with Environmentally Friendly Moorings).

Collection and Storage of Seagrass Prior to Planting

Fragments collected by volunteers were equally as successful for restoration as those collected by DPI staff, showing that help of trained volunteers can be extremely valuable in citizen science projects (Ferretto et al. 2021). It should be noted, however, that we did not record the fragments that died during storage time, which were removed. Fragment collection varied throughout the year due to seasonality in weather events or to variation in the likelihood of community volunteers walking on local beaches and collecting fragments. We found no effect of the location from which fragments were collected, probably because all collection beaches receive naturally detached fragments from the same local meadows within the estuary and fragments were collected and planted within the same estuary.

We show that beach-cast fragments stored for a longer time in tanks prior to planting were more likely to survive after 1 year. This supports Balestri et al. (2011), who also demonstrated the benefits of a storage phase for beach-cast *Posidonia* spp. fragments prior to replanting. The storing of beach-cast fragments likely has a screening effect, naturally selecting the healthiest fragments that are more likely to survive once replanted, and/or gives fragments time to recover (i.e. grow new leaves and longer roots). Although there may be an opportunity to optimize future survival based on storage times, storage was also advantageous for stockpiling sufficient fragments to schedule cost-efficient planting events that involve costly resources such as SCUBA diving and boating. Thus, investing in seagrass nurseries could assist not just propagation but also storage of wild material (van Katwijk et al. 2021).

Selecting Fragment Traits to Optimize Restoration Success

Fragments with low leaf necrosis were most likely to survive after replanting, therefore selecting fragments in good condition can enhance restoration success. Warmer water and air temperature in January 2019 might at least partially explain the higher levels of necrosis for the fragments planted in January compared to those planted in June, with January 2019 being the hottest month on record in Australia (Hague 2021). Evidence of increasing levels of necrosis due to heat has also been found in *Posidonia oceanica* (Ontoria et al. 2019).

Fragments with a higher number of initial shoots were more likely to survive after planting, yet it was rare to find naturally detached fragments with more than three shoots (only 8% of the beach-collected fragments had >3 shoots). Fragments with a large above-ground component have a larger surface area for photosynthesis, thus ensuring that the basic physiological processes (i.e. cellular division and growth) are maintained immediately following planting (Zimmerman 2007). This supports the theory that increases in shoot numbers of a *P. australis* fragment are positively influenced by initial number of shoots (Bastyan & Cambridge 2008).

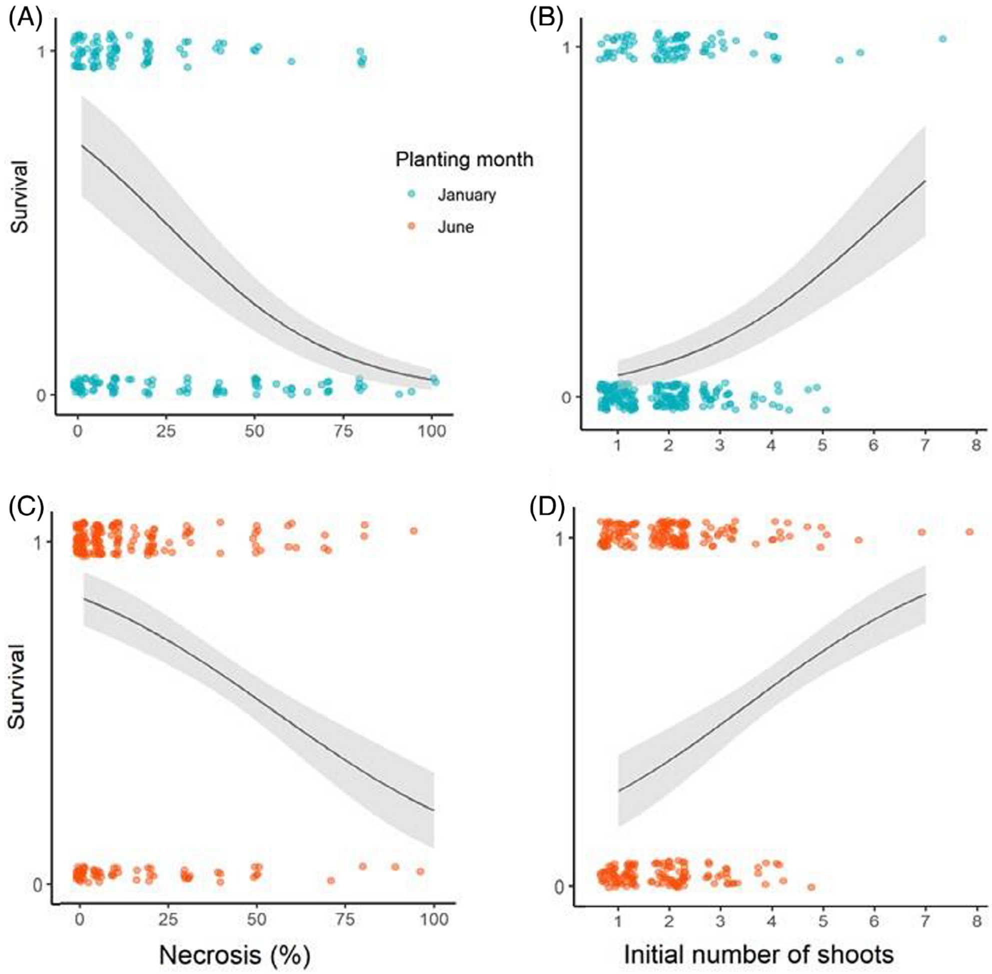

Figure 5. The effect of necrosis in leaves (A,C) and initial number of shoots (B, D) on the survival of fragments after 12 months when planted in January (A, B) and June (C, D). Each point represents a fragment, with the transparent points jittered to avoid overplotting. When survival is 1, fragments survived, when survival is 0 fragments died. The fitted line and shaded area represent the average predicted effect, 95% CI, for each model from the mixed-effects models, averaged over the random levels (i.e. plots) in the model and holding all other predictor variables constant.

The negative relationship between rhizome length and survival for the January planting might be related to respiration demands. Longer rhizomes did not benefit survival, despite their important role in supplying energy and nutrients (Larkum et al. 2006). These longer rhizomes may however have imposed higher respiration demands. If these higher respiration requirements are not compensated by the photosynthetic rate of the above-ground organs (Hemminga 1998) and nutrients in below-ground organs are not distributed to above-ground parts (Hocking et al. 1981), this could cause an imbalance between above-ground productivity and below-ground respiration. Longer roots had a positive effect on survival for the January planting. This is consistent with what is often observed in terrestrial plants (Harrison & LaForgia 2019; Garbowski et al. 2020) but for seagrasses, having roots may be also a disadvantage, exacerbating the negative carbon balance towards the respiration (Hemminga 1998). We found no evidence of an effect of rhizome morphology on restoration success, supporting Balestri et al. (2011). Nevertheless, we acknowledge that visually recognizing growth form is complicated. In addition, fragments can change their growth form (Piazzi et al. 1998; Alagna et al. 2019) depending on the space available, with plagiotropic fragments becoming orthotropic when space is limited (Molenaar et al. 2000), so using beach-cast fragments and storing them in tanks might have interfered with this process.

In conclusion, improving clarity around quality selection and storage time of naturally detached fragments (this study) and considering timing of replanting and local environmental conditions of restoration sites (Ferretto et al. 2021) can assist in optimizing *P. australis* seagrass restoration that uses beach-cast fragments.

Acknowledgments

This research was supported by the NSW Government via the Environmental Trust and NSW Department of Primary Industries. GAK and EAS were supported by an Australian Research Council (DP180100668). The authors are especially grateful to

Graham Housefield for collection and storage of fragments and for ideas for planting methods. For assistance with field work, the authors thank Derrick Cruz, Madelaine Langley, Sophie Powell, Roger Laird, and Gwenael Cadiou. The authors thank Lana Kajlich for the support in the community engagement efforts. Work was carried out under NSW DPI Fisheries Section 37 permit (P13/0007-2.0) and a NSW Marine Parks Permit. The authors also thank all our Operation Posidonia citizen scientists and UNSW volunteers (Clayton Mead, Zuhairah Dindar, Alice McGowan, Rachel Figueroa) for collecting the fragments and helping us measure traits. Open access publishing facilitated by The University of Western Australia, as part of the Wiley - The University of Western Australia agreement via the Council of Australian University Librarians.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Processing of a naturally detached *Posidonia australis* fragment, from collection to planting.
Figure S2. Number of naturally detached *Posidonia australis* fragments collected each month.
Figure S3. Variation of morphological traits of naturally detached fragments prior to planting.
Figure S4. Correlation plot among variables.
Table S1. Output of the model testing the effect of the collection details on fragment survival. Statistical inference for predictor variables was obtained using the ANOVA function. Plot was included as random effect.
Table S2. Value range and median values of the morphological traits of naturally detached fragments prior to planting.
Table S3. Details of the models included in the model selection process.
Table S4. Output of the model testing the effect of growth form on fragment survival.
Table S5. Output of the model testing the effect of "distance from apical to first vegetative shoot".
Supplement S1. Details of collection and storage of *Posidonia australis* fragments
Supplement S2. Differences in morphological traits between fragments planted in January and June.

Coordinating Editor: Susan Bell

Received: 22 September, 2022; First decision: 2 January, 2023; Revised: 25 February, 2023; Accepted: 26 February, 2023