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PRACTICE AND TECHNICAL ARTICLE

Investigating transplantation as a mechanism for seagrass restoration in South Africa

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The extent of seagrasses has declined globally, with restoration through transplantation seen as an important tool for reversing population loss, yet restoration studies for African seagrass species are scarce. This study investigated the use of different planting patterns (straight-line, compact, and star) and core sizes (11, 18, and 25 cm Ø) in transplanting ecotypes (intertidal and subtidal) in the predominantly open Knysna and temporarily closed Klein Brak estuaries in South Africa. Cores of the endangered seagrass, *Zostera capensis*, were transplanted in two experimental repeats per ecotype and core size along transects to investigate survival of plants post-transplant. No significant differences were observed among core sizes, patterns, or ecotypes in the Knysna Estuary, but cores with the compact pattern had better survival rates in the Klein Brak Estuary. Holes left by the smallest cores in donor sites recovered faster through sediment deposition compared to larger holes. Our study demonstrated that seagrass restoration in South Africa is challenging due to limited suitable habitats and strong environmental variability in estuarine ecosystems. It is important that careful consideration, including of genomic diversity and population structure, as well as ecological similarity between donor and recipient populations must be made for each restoration site when assessing its restoration potential. Effective "no-take bait zones" and upstream catchment management will be important for protecting potential donor meadows.

Key words: donor and recipient sites, ecotypes, South Africa, temporarily closed estuary, *Zostera capensis*

Implications for Practice

- Estuaries are dynamic in their abiotic and biotic variability and face unique anthropogenic pressures; hence, restoration practices of seagrass meadows will require individualized approaches.
- Smaller-sized cores are likely to be advantageous for future restoration attempts as they least impact donor meadows, with planting arrangements an important consideration for persistence of donor cores.
- There were no differences in survival of transplants between intertidal and subtidal ecotypes at each study site.
- Restoration is an important tool for maintaining seagrass meadows into the future, but its success will depend on identifying and managing anthropogenic stressors, with sites of low impact likely to have increased survival of restored meadows.

Introduction

Concerns around seagrass decline require deeper understanding of impacts experienced by coastal environments (Tan et al. 2020) and ways in which existing and disturbed seagrass beds can be protected and restored (van Katwijk et al. 2016). Seagrass restoration aims to return meadows to pre-existing conditions (i.e. same species composition, abundance, distribution, and ecosystem function), which contrasts with seagrass rehabilitation (Paling et al. 2009). This has led to different types of rehabilitation or restoration projects (Tan et al. 2020), although the distribution of these is skewed toward the northern Hemisphere (e.g. Europe [van Katwijk et al. 2016; Paulo et al. 2019; Unsworth et al. 2019], Indo-Pacific region [Tan et al. 2020], and North America [Orth et al. 2006]).

In South African estuaries which suffer from anthropogenic (e.g. bait digging, pollution) and natural (e.g. extended mouth closures) pressures, *Zostera capensis* occurs as disjunct, fragmented populations (Adams 2016). Considering that the species does not colonize quickly, there is a continued decline of *Z. capensis* in many estuaries (Adams 2016). Apart from Amone-Mabuto et al. (2023), which focused on restoration of *Z. capensis* in Maputo Bay, Mozambique, restoration of this

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regionally endangered seagrass has received little scientific attention. Furthermore, intersite comparisons are lacking, yet such data are critical for estuaries that experience wide variations in their physicochemical parameters.

Within the context of this study, transplantation using cores has proven successful (Matheson et al. 2022), but considerations around core sizes and transplant patterns remain. It has been suggested that the use of larger cores (>15 cm Ø) may improve anchoring properties due to the cohesive bulk of sediment surrounding the transplanted shoots, which also reduces disturbance of the rhizome and associated microbiome (Fonseca 1998; van Keulen et al. 2003). Our study reports on the results of the first monitored, short-term pilot transplanting experiment in South Africa, conducted across two estuarine systems. Specifically, this study focused on two important considerations for restoration, core size and transplant patterns. The aim of this study was to (1) investigate the significant effects of different planting patterns, (2) core sizes on transplant survival, (3) how long resulting holes in donor sites persist, and (4) whether transplanting experiments yield different results when the state of an estuary mouth (open vs. closed) is considered. In addition, and considering that *Z. capensis* contains two contrasting ecotypes, subtidal (permanently submerged) and intertidal (submerged and exposed with the tidal cycle), the efficacy of both ecotypes in restoration of this species was also investigated. Following a study by van Keulen et al. (2003) and Temmink et al. (2020), it was hypothesized that large-sized cores and compact planting patterns would exhibit significantly increased persistence and spread of the transplants, as both offer increased self-facilitation and sharing of nutrients among cores (Bos & van Katwijk 2007).

Methods

Study Sites

This study was conducted in estuaries in the warm temperate region of South Africa: a temporarily closed estuary (TCE), namely Klein Brak Estuary and Knysna Estuary, which is classified as an estuarine bay (Fig. 1; Van Niekerk et al. 2020). During low freshwater inflow, the mouth of the Klein Brak closes to the sea and water levels fluctuate in response to freshwater input. The estuary is estimated to be in a moderately to heavily modified state (Van Niekerk et al. 2022). Severe reduction in river inflow has resulted in hypersaline conditions and an increase in the frequency and duration of closed mouth conditions.

The Knysna Estuary is the largest tidal estuary in the region and the most important in terms of biodiversity conservation priority; it is both an ecological and an economic asset to South Africa (Claassens et al. 2020). The estuary receives strong tidal flow through its headlands, rendering its mouth perennially open to the sea, with inflow from Knysna River and smaller streams. Knysna is estimated to be in a near natural to moderately modified state (Van Niekerk et al. 2022). For this estuary, water level data were downloaded from www.dws.gov.za (station: K5H003).

Selection of Recipient and Donor Sites, Core Collection, Storage, and Transportation

We followed considerations and criteria from Fonseca (1998) and Tan et al. (2020) during core collection to reduce impacts on donor sites. For intertidal and subtidal ecotypes, cores of 11, 18 and 25 cm Ø (Fig. S1) were collected from two different areas in each estuary. Core collection and transplanting in Knysna Estuary (8–10 February 2021) was conducted during spring low tide. The Klein Brak Estuary mouth was closed at the time of sampling (11–12 February 2021), the estuary was nontidal and thus core collection was not influenced by tides. Collected cores were separated into intertidal and subtidal ecotypes and placed in large plastic trays and buckets covered with cloths soaked in seawater, transferred to transplant sites and planted within 2 hours. In both estuaries, work was carried out under permits from South African National Parks (SANParks; VONH-S/2020-028) and the Department of Forestry, Fisheries and the Environment (DFFE: RES 2021/68).

Planting of Cores

In each estuary, cores ($n = 324$) were transplanted in two sites ~5 m apart, one with subtidal and the other with intertidal plants, each containing two experimental plots (i.e. repeats) ~2 m apart (Fig. 2); four experimental plots were established per estuary. All plots were established perpendicular to the shore in line transects and on the same water level during spring low tide in Knysna Estuary. The same experimental design was used in Klein Brak Estuary with transplants on the same water level; however, cores were transplanted about 3 m shoreward from the water level at the time of this experiment to prevent desiccation stress. Because both study sites did not have wider undisturbed areas for restoration trials, the planting patterns could not be planted parallel to the shore and perpendicular planting seemed more appropriate. Each experimental plot consisted of 11 cm Ø on a transect (with three planting patterns, starting with straight line, followed by compact then star), followed by 18 and 25 cm Ø cores (Fig. 2). Considering the hypothesis that larger cores would exhibit increased survival, it was ideal to include all core sizes in one experimental plot. GPS coordinates were recorded for each experimental plot.

Monitoring Survival Post-Transplant

Monitoring was restricted to counting the number of surviving/visible cores per planting pattern and size in order to minimize disturbances on the transplants. Experimental plots were monitored every week for the first month, every 2 weeks for the second month and once in the following months for three consecutive months. As cores were beginning to die back, monitoring was reduced to once in 2 months for the remainder of the year for a total monitoring period of 12 months. Monitoring was discontinued for 2 months because of flooding following heavy rains in the winter period that left transplants inaccessible (Fig. S2).

Holes as a result of core collection in donor sites were monitored over the same time frame as transplants followed by an

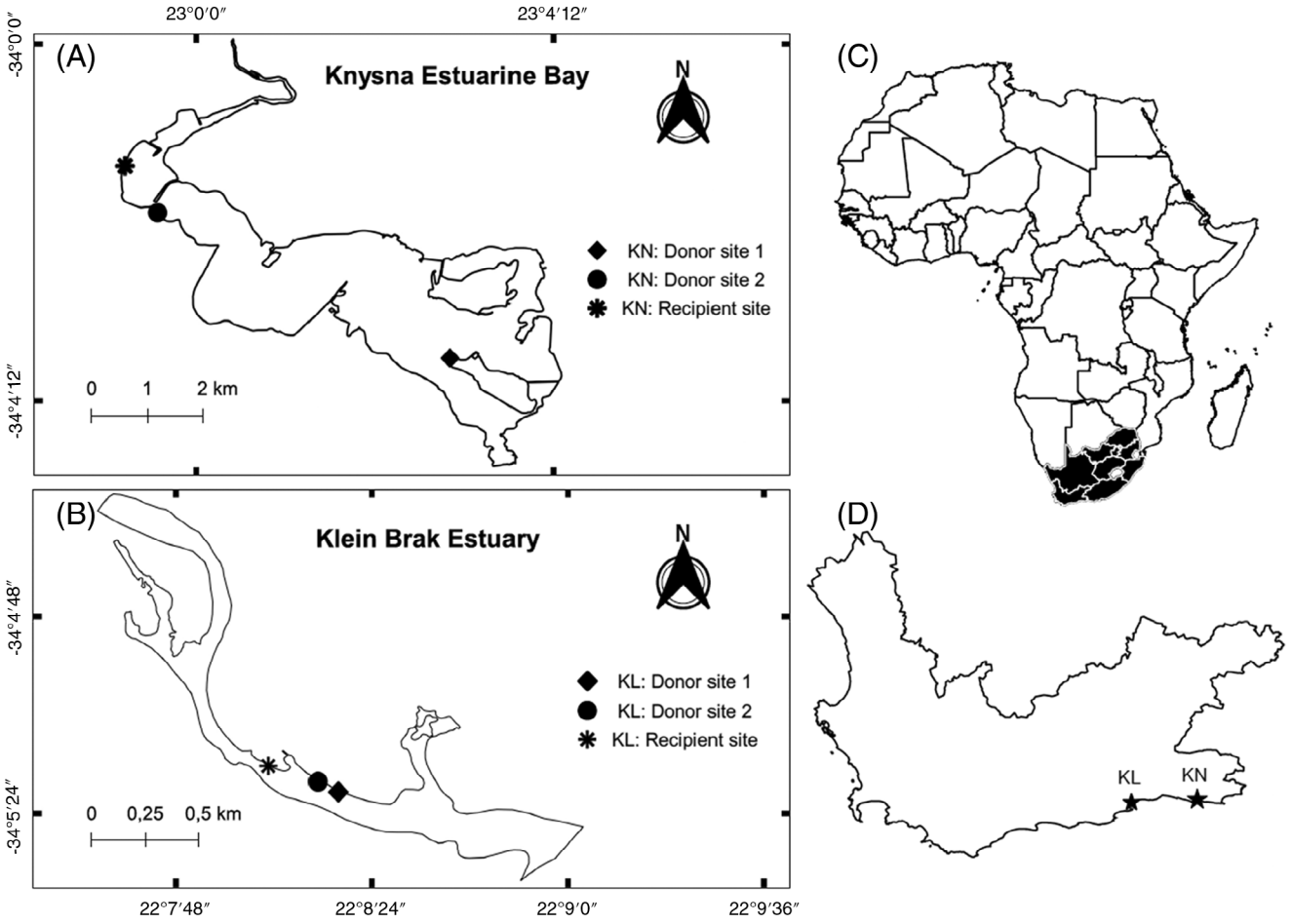


Figure 1. Location of sampling sites in Knysna (A) and Klein Brak (B) systems, position of South Africa within Africa (C) and study sites within the Western cape of South Africa (D). KL = Klein Brak Estuary, KN = Knysna Estuary.



Figure 2. Experimental design showing core sizes, planting patterns of both intertidal and subtidal ecotypes for each study site.

additional 6 months for a total of 18 months. Resulting holes were considered recovered once the entire hole was filled with adjacent sediment. Thereafter, the expansion of seagrass into these areas was noted.

Data and Statistical Analyses

Transplant survival (as number of cores remaining per transplanting pattern) and recovery of resulting holes in donor sites were recorded in number of weeks (i.e. count data). The dataset did not meet assumptions of normality. As such, generalized linear models (GLMs) were used for all analyses. To choose an appropriate model based on a link function, a model with the lowest Akaike information criterion (AIC) was used for further interpretations. Before interpretations of a model, a dredge function (MuMIn package) was used to remove variables that were not significant.

For all fitted models, half-normal plots (with simulated envelopes) were used to assess the goodness of fit using the *hnp* package. If, having fitted a Poisson model, the variance was greater than the average (i.e. overdispersion, Durmuş & Güneri 2020), then assumptions of the Poisson model were deemed violated and negative binomial (NB; glm.nb function in *MASS* package) regression models were used. Predictor variables were core size, planting pattern, and ecotype. All GLMs were carried out in R (version 4.1.1). *ggplot2* and *gridExtra* were used for graphical presentations.

Results

Survival of Transplanted Cores

All data can be accessed at www.github.com/vonderheydenlab/Mokumo_SeagrassRestoration. At both study sites, cores survived for 12 weeks, although the loss of cores differed between core size and planting pattern. In the Knysna Estuary, no significant differences were observed in terms of planting patterns ($p = 0.364$), core sizes ($p = 0.332$), or ecotypes (i.e. intertidal vs. subtidal: $p = 0.418$; Fig. 3). In the Klein Brak Estuary, no significant differences were observed in terms of core sizes ($p = 0.539$) and ecotypes ($p = 0.506$); however, there was a significant difference for transplant pattern ($p < 0.05$) in which transplants from the compact pattern exhibited ~25% increased survival as compared to star-like pattern and straight-line pattern. There was no significant difference ($p = 0.995$) between straight line and star-like patterns (Fig. 3).

When transplant survival was compared between study sites, significant differences were observed in terms of core sizes, where all core sizes and ecotypes of Knysna transplants indicated increased survival (Fig. 4). Water levels from the Klein Brak varied considerably throughout the duration of the study (Fig. S2), through both dry periods and flood events, including "blackwater events" (Fig. S3).

Donor Site Monitoring and Recovery

In terms of recovery of resulting holes in donor sites (number of weeks each hole was visible) in Knysna, there was no significant difference ($p = 0.25$) between ecotypes (Fig. 5). There was, however, a significant difference ($p < 0.05$) in terms of recovery by core size hole, where smaller holes exhibited fastest recovery. There was no significant difference between medium-sized and large-sized resulting holes ($p < 0.05$). The same trend was observed in Klein Brak Estuary for both ecotypes (intertidal and subtidal; Fig. 5; $p > 0.05$), with holes resulting from the smallest core size recovering faster. There was a significant difference in recovery rate by study site ($p = 0.049$) with Knysna indicating faster recovery due (Fig. 5). A once-off monitoring event in February 2023 in Knysna additionally showed seagrass had re-established itself over all donor holes (Fig. S4).

Discussion

This study presents the first attempt, in South Africa, to transplant cores of *Z. capensis* in different sizes and planting patterns within the context of restoring functional seagrass meadows. Specifically, the focus was to determine whether core size and planting pattern impacts transplant survival. Our work included two estuarine system types, each with unique environmental and physical characteristics, providing novel insights into restoration attempts across dynamic ecosystems. Using the Knysna and Klein Brak as examples, transplanting did not lead to established seagrass patches, as all cores, regardless of core size or transplant pattern, died within 12 weeks of planting. Given decades of pioneering and foundational seagrass restorations with reviewed transplanting techniques and methods, and the growing large-scale restoration practices globally (Sinclair et al. 2020; Tan et al. 2020), the current study provides valuable insights into the potential for transplants as a method for seagrass restoration, by identifying opportunities and challenges for future seagrass restoration work. Understanding local restoration successes in South African estuarine systems will lay the foundation and improve conservation of endangered seagrass species and expand ecological restoration trials to recover damaged meadows in other estuaries.

Transplant Pattern May Influence Core Survival

Previous studies indicated that transplanting using the clumping/compact patterns increases restoration success, especially in isolated transplants (Temmink et al. 2020). We observed no significant differences in Knysna, but compact patterns in Klein Brak indicated better survival rates in the short-term. The naturally occurring seagrass in this system only grows on a narrow horizontal strip within the lower intertidal zone, where the compact cores were transplanted. With the mouth closed, Klein Brak experienced no tidal flows and some cores dried due to desiccation stress as water levels receded. As monitoring continued, the Klein Brak Estuary experienced a strong flooding event 3 months post-transplant, restricting access to field sites. When access became possible as water levels decreased, none of the transplanted cores could be located, indicating that local flow regimes are crucial determinants of seagrass restoration success.

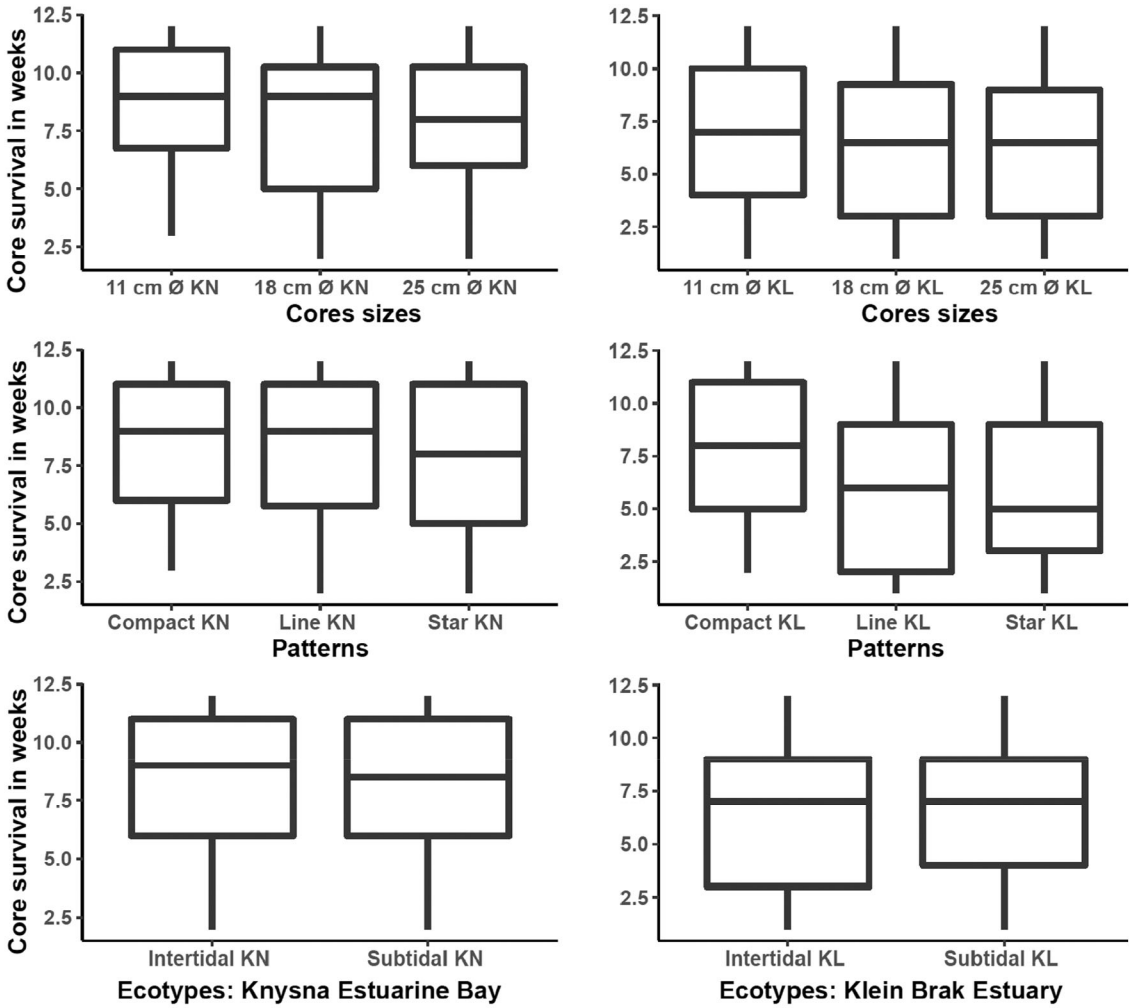


Figure 3. Differences in the survival of core sizes, planting patterns and ecotypes of transplants in Knysna Estuarine Bay and Klein Brak Estuary after 3 months. Central bar: median values; box: interquartile range; whiskers: full range of the data, excluding outliers.

Transplanting Intertidal and Subtidal Ecotypes

Studies have indicated that phenotypic differences in ecotypes can reflect selective responses to contrasting microenvironments (Kim et al. 2020). In this study, there was no significant differences in terms of transplanting by ecotypes, which suggests that either sub-or-intertidal plants are suitable donor material for restoration purposes. In terms of choosing a tidal zone for transplantation, Wegoro et al. (2022) noted a strong effect of depth in the restoration of *Syringodium isoetifolium*, where survival decreased with increasing depth. In shallower depths, restoration may be more successful due to light availability, making transplants grow faster and establish more quickly (Ferretto et al. 2021).

The Effect of Cores Size on Transplant Success

van Keulen et al. (2003) indicated that 15 cm Ø cores for *Posidonia sinuosa* and *Amphibolis griffithii* had better persistence and survival rates, especially under high-energy conditions, due to improved sediment stability as well as less disturbance to the rhizosphere. Matheson et al. (2022) indicated that 5 cm Ø cores for *Z. muelleri* were also effective, suggesting that optimal core size is likely to be species-specific. For example, for *Z. capensis* in Mozambique, Amone-Mabuto et al. (2023) noted that 7.5 cm Ø cores had higher survival rate compared to 4.5 cm Ø. *Syringodium isoetifolium* also indicated better survival of 10 cm Ø compared to 7 cm Ø cores (Wegoro et al. 2022). For this study, no significant differences were observed in transplanting for the different core sizes in either study site. However, using small cores will at least decrease population impacts on donor meadows and make handling easier (Matheson et al. 2022; this study). It is important to note that although additional methods such as the use of plugs (plant and associated sediment) or sprigs (plant without sediment) have been utilized in restoration (Hou et al. 2021), success rates have differed across countries and study sites, suggesting that best practices for planting techniques are often estuary or site-specific (Wegoro et al. 2022).

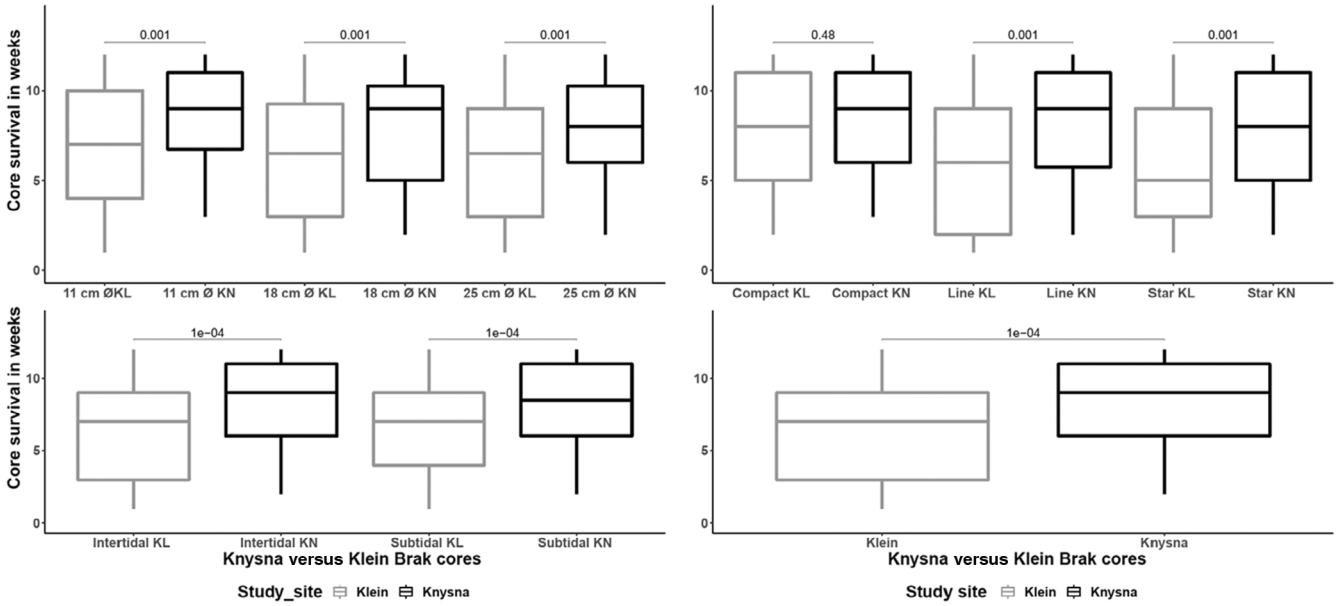


Figure 4. Differences in core sizes, transplant patterns, ecotypes, and the overall transplant survival between study sites after 3 months.

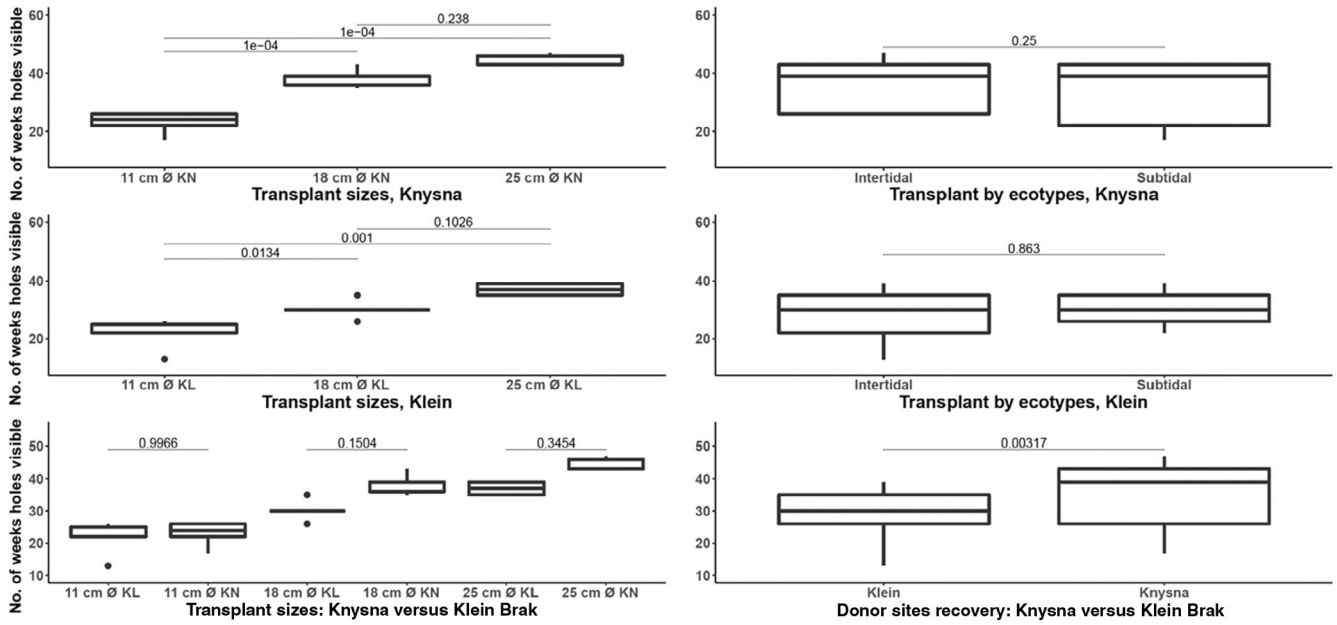


Figure 5. Differences in recovery of donor sites (*y*-axis = number of weeks holes were visible within a calendar year) between Knysna Estuarine Bay and Klein Brak Estuary.

Recovery of Donor Sites

The recovery of donor sites was strongly dependent on the size of core collected, with medium and large cores more negatively impacting donor meadows, although there were no significant differences in recovery rates of holes between intertidal or subtidal areas. As such, the use of small cores for restoration of *Z. capensis* is recommended. In addition, recovery of donor sites may greatly depend on the geology of the estuary site. For example, the second donor site at the upper estuary of Knysna indicated signs of accretion which may have played a significant role in filling up of resulting holes.

Recommendations for Ongoing Restoration Trials in South Africa

It is crucial to understand that *Z. capensis* in South Africa occurs in estuaries with significantly different conditions and

intra-estuarine variation. For example, intertidal zones in Knysna vary widely in form, with extensive tide-washed sands at the lower reaches and steeply sloping banks with soft and mobile sediments elsewhere. Finer particle substrates contribute to light attenuation during high tides and burial of transplants during low tides greatly influencing restoration outcomes (Zabarte-Maeztu et al. 2020). The present trial was conducted at the upper reaches of Knysna in muddy substrates and it may be that transplants were affected by smothering due to mobile sediments.

Climate change and the demand for freshwater have exerted pressures on TCEs in terms of precipitation and alterations in freshwater inflow patterns. As such, TCEs may remain closed for longer periods of time and more frequently than usual, hampering restoration trials due to water level fluctuations, turbidity, and desiccation. As shown by the Klein Brak site, rapidly changing physicochemical conditions in South African estuaries poses serious challenges for seagrass restoration as this affects survival of transplants, with potential donor sites indicating seasonal dynamics, mainly due to dynamic flooding cycles of estuaries. Although it may be important to conduct restoration trials and fine-tuning methods and techniques in predominantly open estuaries, it is important to note that the available intertidal zones are limited in extent, thus restricting opportunities for restoration.

Restoration trials are of high importance to mitigate the loss of seagrasses in the region. As such, it is important to identify permanent, larger meadows as those may provide opportunities for fine-tuning techniques and practices with fewer impacts. Spatiotemporal monitoring of these sites and the need to protect them from anthropogenic factors such as bait-digging, and associated trampling, is essential for a successful restoration in South Africa. Once large and permanent meadows are identified per estuary and tidal zone (i.e. intertidal and subtidal) effective "no-take bait zones" can be declared to protect such meadows. Only Knysna and Langebaan have some formal protection of *Z. capensis* (Adams 2016), but those are reportedly not effective. For example, SANParks implemented the no-take bait rule in some areas of Knysna, yet Barnes and Claassens (2020) note that bait collection and trenching are common at these sites as there is no policing.

As much as it is important to identify large, permanent meadows, it is also important to identify meadows that are dynamic and understand spatiotemporal changes in cover, as well as those requiring rehabilitation. Expanding meadows laterally instead of focusing on transplanting in isolated areas is likely to lead to higher restoration success. Due to the lack of seeds and flowers in *Z. capensis* (Adams 2016), core transplanting has been the only solution for restoration, even though preliminary attempts at moving cores between estuaries were unsuccessful (Adams 2016). Phair et al. (2019) and Jackson (2021) show high genomic differentiation of *Z. capensis* meadows. Given that restoration success is increased when choosing donor materials from genetically and similar sites, this is an important consideration in the South African context. Jackson (2021) reported low intrapopulation clonality, contrary to expectations of isolated *Z. capensis* populations, suggesting sexual reproduction may be more prevalent than assumed. This is supported by field sightings of flowers and seeds in several populations. As such, manipulations of populations under controlled conditions, may provide restoration attempts of *Z. capensis* with seed rearing opportunities, further expanding restoration efforts in the region.

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Supporting Information

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

Figure S1. Core sizes (25, 18, and 11 cm Ø) of transplants in Klein Brak Estuary.
Figure S2. Minimum and maximum water level data for DWS monitoring station.
Figure S3. Stained water ("black water") during flooding of Klein Brak Estuary.
Figure S4. Donor site 7-month post-transplanting and 21 months post-transplanting, and 36 months post-transplanting.

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