Global analysis of seagrass restoration: the importance of large-scale planting

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Global analysis of seagrass restoration: the importance of large-scale planting.

Subtitle: Large-scale required for seagrass restoration

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Summary

- In coastal and estuarine systems, foundation species like seagrasses, mangroves, saltmarshes, or corals provide important ecosystem services. Seagrasses are globally declining and their reintroduction has been shown to restore seagrass functions. However, seagrass restoration is often challenging, given the dynamic and stressful environment that seagrasses often grow in.
- From our worldwide meta-analysis of seagrass restoration successes (1786 trials), we describe general features and best practice for seagrass restoration. We confirm that removal of threats is important prior to replanting. Reduced water quality (mainly eutrophication), and construction activities led to poorer restoration success than for instance dredging, local direct impact and natural causes. Proximity to and recovery of donor beds were positively correlated to trial performance. Planting techniques can influence restoration success.
- The meta-analysis shows that both trial survival and seagrass population growth rate in survived trials are positively affected by the number of plants or seeds initially transplanted. This relationship between restoration scale and restoration success was not related to trial characteristics of the initial restoration. The majority of the seagrass restoration trials has been very small, which may explain the low overall trial survival rate (i.e., estimated 37%).
- Successful regrowth of the foundation seagrass species appears to require crossing a minimum threshold of reintroduced individuals. Our study provides the first global field evidence for the requirement of a critical mass for recovery, which may also hold for other foundation species showing strong positive feedback to a dynamic environment.

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- ***Synthesis and Applications***: For effective restoration of seagrass foundation species in its typically dynamic, stressful environment, introduction of large numbers is seen to be beneficial and likely serves two purposes. First, a large-scale planting increases trial survival - large numbers ensure the spread of risks which is needed to overcome high natural variability. Second, a large-scale trial increases population growth rate - by enhancing self-sustaining feedback which is generally found in foundation species in stressful environments such as seagrass beds. Thus, by careful site selection and applying appropriate techniques, the spreading of risks and enhancing self-sustaining feedback in concert increase success of seagrass restoration.

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Introduction

Coastal and estuarine habitats are characterised by dynamic and stressful environments. Many coastal ecosystems are dominated by one or few ‘foundation’ species (*cf.* Bruno and Bertness, 2001, species that positively affect the fitness of other species through their modification of the environment). Seagrass beds are a clear example of ecosystems dominated by foundation species. They typically ameliorate stress, usually passively by the mere presence of their structure creating shelter and sediment stabilisation, resulting in lower water turbidity and amelioration of wave action, but also by processes influencing water quality like nutrient uptake. This ecosystem engineering by seagrass beds (cf Jones et al. 1994) forms the basis of key ecosystem services, including erosion control (Hansen and Reidenbach 2012, Christianen et al. 2013), carbon sequestration for climate change mitigation (Thorhaug et al. 2009, McLeod et al. 2011, Duarte et al. 2013a, Duarte et al.

2013b), fisheries habitat support (Watson et al. 1993, McArthur and Boland 2006, Unsworth et al. 2010), and high biodiversity, including iconic and highly endangered species (Hemminga and Duarte 2000).

Seagrasses rank among the most productive yet highly threatened ecosystems on earth with rates of decline accelerating globally from a median of 0.9 % yr^{-1} before 1940 to 7 % yr^{-1} since 1990 (Waycott et al. 2009). Legislation for protection and restoration of seagrass habitat as well as for improving coastal quality has been established in many nations to prevent further losses and facilitate recovery (Duarte 2002, Orth et al. 2006). Water quality improvements have led to seagrass recovery in a limited number of studies (Greening and Janicki et al. 2006, Cardoso et al. 2010, Vaudrey et al. 2010, but see Valdemarsen et al. 2011), but has apparently not slowed the global rate of loss of seagrass substantially. Seagrass restoration is thus a necessary additional instrument to offset the loss of seagrass habitat's ecosystems biodiversity and their services. Restoration efforts have been performed worldwide to compensate or mitigate seagrass losses and have been shown to enhance the associated ecosystem services (Paling et al. 2009). However, seagrass restoration seems to have low performance rates (Fonseca et al. 1998), though a comparative quantitative global overview on the performance of seagrass restoration is lacking and the processes influencing success or failure of restoration programs have not been systematically assessed.

In this paper we use a global, systematic analysis of seagrass restoration to identify characteristics that promote seagrass restoration success and present best practices to support and develop existing restoration guidelines. Second, we study the effect of

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restoration scale (i.e., initial number of reintroduced plants) on the trial survival and population growth rate in survived trials. A larger restoration scale is hypothesised to be beneficial for two reasons: to overcome the stochasticity related to the dynamic environment (e.g., Morris & Doak 2002), and to provide a critical mass for stress amelioration by the starting founders (i.e., the initial planting unit) themselves (cf, Bos & van Katwijk, 2007, van der Heide et al. 2007, 2011, Carr et al. 2010, 2012, Orth et al. 2012). We recorded trial survival and population growth of survived trials in 1786 seagrass restoration trials described in 215 studies. To analyse best practice and to test for confounding effects with restoration scale, we analysed the trial characteristics regarding environmental variables, techniques and species used.

We find both trial survival and population growth rate in survived trials positively affected by the numbers of plants or seeds initially planted. This relation was not confounded by other trial characteristics such as species, method of planting, or environmental characteristics at the recipient sites. As the majority of the seagrass restoration trials has been very small (55% had fewer than 1000 specimens initially planted), this likely explains the low trial survival rates recorded. From this we have derived a conceptual framework to demonstrate how spreading of risks and enhancing self-sustaining feedback in concert increases restoration success.

Materials and methods

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We compiled data from restoration trials conducted worldwide from published articles listed in Web of Science (92 papers), grey literature (120 reports) and own unpublished data (187 trials), from 17 countries, resulting in 1786 trials. Each of the 1786 rows in the dataset represents a trial, the oldest one planted in 1935. A trial consists of one or more shoots or seeds that have the same ‘treatment’, i.e., they are planted at the same location, with similar techniques and treatments in the same year and season, using the same species and plant material. Occasionally, trials from multiple years could not be separated and we recorded the first year or the year of largest effort as the planting year. (Sources used: see Appendix S1 in Supporting Information). The study is not a traditional meta-analysis (e.g. Harrison 2011); firstly, we aimed to not exclude any reported trial (resulting in many missing values); secondly, the recorded characteristics usually have no controls, so effect sizes can only be estimated relatively between categories (e.g. plant material has the categories: seeds, sods, rhizome fragments or seedlings); thirdly, the data did not allow for assignment of a nesting factor like sources or planting teams. This is because very similar trials regarding site and techniques are sometimes based on multiple sources and planting teams, and vice versa, very diverse trials are sometimes listed by single sources or planting teams..

Effect of restoration scale on trial survival and population growth rate

To test for restoration scale effect (i.e., initial number of reintroduced plants) on trial survival we recorded trial survival (1=one or more shoots survived or 0=none of the shoots survived) at the end of the monitoring period and performed survival analyses (see below). The seagrass population growth rate in survived trials was calculated as the intrinsic rate of increase of an exponential growth function, log (nsht/nsh0) / t, where nsh0 is the number of

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shoots[1] at t=zero and nsht is the number of shoots at the end of monitoring after t months. In total, 1060 trials contained data to perform the survival analysis and 486 trials contained data to calculate seagrass population growth rate in survived trials.

The relationship between trial survival and initial number of shoots/seeds (restoration scale) was tested in five categories, 1: <100 shoots/seeds, 2: 100-1000 shoots/seeds, 3: 1000-10,000 shoots/seeds, 4: 10,000-100,000 shoots/seeds, 5: > 100,000 shoots/seeds, using survival analysis (SAS PROC LIFETEST testing whether the scale categories have identical survivor functions using a proportional hazard model). Trial survival after 2 years was estimated using Kaplan-Meier estimation of the survival function using the same SAS procedure. The relationship between population growth rate (increase in number of shoots or seeds month^{-1}) and the five categories of initial number of shoots/seeds scale was analysed and tested using ANOVA.

Estimation of long term trial survival

To estimate long term trial survival, we went through the following steps. Because monitoring periods and frequency differed between trials, and many trials were monitored only once, we first analysed trial survival (1=one or more shoots survived or 0=none of the shoots survived at the moment of monitoring) *per phase*. We distinguished three phases: (1) first 9 months; (2) between 10 and 22 months (thus including minimally one adverse season; and (3) more than 22 months (thus including 2 adverse seasons). In general, adverse seasons can either be autumn/winter (e.g., storms, colds) or summer (e.g., high temperature, high salinity, desiccation). Second, trial survival (1 or 0) was averaged for each of the 3 phases and

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[1] Shoots refer also to seeds or seedlings that were used in few trials

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the three averages were multiplied to obtain a conservative estimate of overall trial survival at the long term (i.e., representing a median monitoring duration of 36 months, see Table 1). 1656 out of 1786 trials had one or more data on trial survival (one or more monitoring events).

Factors affecting restoration performance

To evaluate best practice and to test for confounding effects, 15 trial characteristics were analyzed simultaneously with restoration performance. Restoration performance was expressed by a semi-quantitative measure "integrated success score" which allowed us to evaluate 1289 trials rather than the 478 trials that had quantitative data (which was not sufficient for the evaluation of trial characteristics having many missing values). Integrated success score (ISS) was composed of two metrics: (1) initial trial survival being 1 (or 0) when plants were still present (or had disappeared) in the trial at a monitoring event in phase 1 (≤ 9 months); and (2) long-term planting performance during phase 3 which was quantified by assigning scores to the trials that had data monitored in phase 3 (> 22 months, 414 trials), with scores: 0=lost during phase 3, 1=declined, 2=equal presence and 3=increased since planting. These scores were based upon very diverse monitoring and evaluation methods (i.e., number of shoots, areal development, percentage survival, or textual evaluation, or a combination of those). During the intermediate phase (9-22 months) trials were rarely monitored, therefore these data were only used for the estimation of overall survival of all trials, see above, but not for the evaluation of trial performance. ISS was calculated by multiplying the *mean* initial trial survival by the *mean* long-term trial performance. Both means were calculated per category of the trial characteristics (calculation per trial was not possible because only few trials had data for both metrics). The standard deviation of the

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mean of the integrated success score was computed from the standard deviations of the initial trial survival and the long-term trial performance after initial survival.

Trial characteristics tested were: seagrass species, reason for planting (categories: restore natural values, mitigation for damage, research and test plots), cause of decline (no decline, substrate-related, construction, local direct impact, natural causes and water quality, see Table 2), removal of threats (no threats, complete removal, partial removal), distance from donor site (<1 km, 1-10 km, 10-50 km, >50 km), donor site recovered (yes/no), bioturbation (yes/no), depth (0 – 0.5 m, 0.5-1 m, 1-2m, 2-4 m, >4 m), emergence (subtidal/intertidal), anchoring technique (weights, staples, none and non-weighted frames, see table 3), type of plant material (sods, rhizome fragments, seeds, seedlings, see table 3), fertilisation (yes/no), planting methods (manual/mechanical), habitat manipulation (none, anti-bioturbation measures, sediment stabilisation), protection measures (none, against hydrodynamics, against grazing). The magnitude of response (effect size) describes the difference between integrated success scores (ISS, calculation see above) of the categories with the highest and the lowest value for ISS (i.e., $ISS_{highest} / ISS_{lowest}$); most characteristics do not have a control category, so these differences are relative to each other.

A logistic regression and one-way ANOVA were used to test the effect of 15 trial characteristics on two measures for trial performance, namely initial trial survival (≤ 9 months) and long-term trial success (> 22 months), respectively. All analyses were univariate because the 15 trial characteristics had many missing values (e.g. no studies had information on all 15 characteristics). To identify characteristics that had significantly different performance metrics between their categories, we performed contrast tests (with statistics

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based on the asymptotic chi-square distribution of the Wald statistic) and Tukey's post-hoc tests, respectively. Similarly, to test for possible confounding effects between the initial number of shoots/seeds (=restoration scale) and other trial characteristics, we first used ANOVA to identify characteristics that were significantly affected by the number of shoots/seeds initially planted. To identify whether these characteristics could have confounded effects, we estimated whether the initial number of shoots/seeds correlated positively with total trial performance. A positive correlation between the initial numbers of shoots/seeds and restoration performance indicates the existence of confounding effects.

All statistical analyses were performed in SAS 9.2 (http://support.sas.com, consulted on 25 June 2014 and 15 June 2015).

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Results

Analysis of seagrass restoration trials

Seagrass restoration trials started during the first half of the twentieth century, but efforts remained low until the 1970's, with 20-60 trials initiated per decade. In the 1970's, when seagrass loss started to accelerate (Waycott et al. 2009), the interest in restoring seagrass meadows rapidly increased. Since then, about 450 new trials were initiated globally per decade (Figure S1a). Most (68 %) documented trials were conducted along the temperate and subtropical coastlines of the northern hemisphere (Figure 1). Most restoration areas were previously colonised by seagrass meadows lost due to water quality deterioration (54 %, chiefly eutrophication), coastal construction (15 %) and mechanical destruction of the habitat (8 %), as was reported in the documented trials. The objectives of seagrass restoration were to restore natural values (31 %), mitigate damage and loss (15 %) and gain knowledge (54 %).

One third of the seagrass flora, 26 species, spanning the entire range of size and growth rates among the seagrass flora, was utilised in restoration programs. However, a single species, the temperate *Zostera marina* with the broadest geographical distribution, was utilized in 50% of the reviewed trials. For all seagrass species, rhizome fragments with shoots (55 %) and sods and plugs (24 %) were the most common material planted, whereas seedlings, seeds and seed-bearing shoots have been used in but a few seagrass – most frequently *Z. marina* - restoration programs (12 %, 8 % and 1 %, respectively).

Seagrass restoration trials were on the average small scale with fewer than 409 shoots/seeds and a 0.93 m^2 standardised plant area (i.e., the area that these shoots/seeds would occupy in a full cover or coalesced situation, calculated per species), although occupied areas extended to 3 to 4 orders of magnitude larger with far greater number of shoots/seeds for the larger trials (figure 1, table 1). Monitoring was on the average 12 months or less (50 %). However, monitoring duration extended beyond 2 years for 27.5 % of the restoration trials and the longest monitoring period was 38 years (*Thalassia testudinum* in Florida, planted in 1973 (Thorhaug 1974 and unpublished data) (table 1)).

Analysis of best practice of seagrass restoration

Traditional seagrass restoration guidelines recommend careful site selection, i.e. a sheltered location with an adequate light environment, and recommend reversal of habitat

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degradation prior to restoration. Data on shelter and light availability were very scarce and were not included in the analysis. Analysis of the planting depth range showed a weak optimum of intermediate depths. Shallow depth (< 0.50 m) had poorest restoration success, with intertidal sites performing worst (magnitude of response 2.5, Table S1).

The review shows the importance of removal of threats (Table S1). Worldwide, causes of decline are generally known in restoration trials (78% of the cases). However subsequent restoration success varies with different causes: particularly restoration following losses derived from reduced water quality (usually eutrophication) are less successful than, for example, those derived from construction activities (68%), substrate manipulations like dredging and filling (43%), or in areas where there has been no seagrass decline (36%). Recovery and proximity of donor beds were positively correlated to trial performance, with magnitudes of response of 6.4 and 3.9 respectively (Figure 2). Bioturbation can lead to severely reduced initial trial survival and long-term population expansion of survived trials (Table S1). The review shows no consistent correlation between restoration performance and planting season (results not shown).

Seedlings consistently perform worse than any other plant material used, whereas seeds have intermediate scores; anchoring of rhizome fragments using weights gives better success scores than any other combination of plant material and anchoring technique (Figure 2). The magnitude of response to anchoring technique and plant material was 7.1. Any anchoring (weights, staples, frames or using sods) improved the *initial* survival of plants by 84 % on average ($p < 0.0001$, Table S2). The application of weights (sand bags, stones, shells) improved later success scores by 45 % whereas other anchoring methods do not

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contribute to the later success scores (Table S2). Mechanical planting methods improved initial survival, but somewhat reduced later success scores as compared to manual planting methods (Table S2). Habitat manipulations and protection measures had no positive effect on success (Table S2). Fertilization, if applied (only in 9 cases with long-term data) improved success scores with a magnitude of response of 2.4. Note that for some species fertilization has been demonstrated to inhibit survival and growth (e.g., *Posidonia australis*, Cambridge & Kendrick 2009), illustrating that our meta-analysis provides general trends and averages regarding planting procedures which may not hold for all species or sites.

The effect of trial scale on restoration success

Trial survival (proportional hazard model $P < 0.01$) and seagrass population growth rate in survived trials (in number of shoots or standardised area, month^{-1}) were directly related to the initial number of shoots or seeds planted. After 23 months, estimated survival of small trials was 22 % (<100 shoots/seeds planted), but trial survival increased to 42 % for the largest scale trials (>100,000 shoots/seeds planted, figure 3a). Likewise, the population growth rate (as increase in number of shoots) in seagrass restoration trials initiated at less than 1000 shoots/seeds was negative, whereas population growth rates for trials with more than 10,000 planted shoots/seeds were positive (figure 3b). The positive effect of restoration scale on both trial survival and population growth rate in survived trials suggests the existence of a threshold of scale of the trial required for restoration progress between 1000 - 10,000 shoots/seeds.

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The ‘better performing’ sites, species and techniques were generally near zero or (weakly) negatively correlated to initial planting scale (Table S3). This robustly shows the absence of confounding effects in the relationship between restoration scale and restoration success.

Discussion

Best practice of seagrass restoration

Experiences of seagrass restoration efforts worldwide have been collated in the form of transplantation guidelines (e.g., Addy 1947; Phillips 1980; Thorhaug 1981; Fonseca et al. 1998; Campbell 2002; Short et al. 2002; van Katwijk et al. 2009; Cunha et al 2012), largely based on regional studies and a few species. They recommend careful site and species selection, i.e. a sheltered location with an adequate light environment, and recommend reversal of habitat degradation prior to restoration. They provide best practices addressing anchoring techniques, habitat manipulations, type of plant material used, planting mechanisms, and strategies to cope with the large stochasticity related to the dynamic seagrass environment. However, the drivers of success in seagrass restoration programs have not been objectively and systematically assessed globally, which has been a key factor in preventing improvements based on past experiences (e.g., our analysis shows the absence of a learning curve, Figure S1b). Still, it should be reminded that a global analysis like ours can only provide generalities, and local and regional expertise remains vital for seagrass restoration success.

The importance of shelter and sufficient light is tentatively confirmed in our semi-quantitative worldwide analysis by the slightly better performance of plantings at intermediate planting depths (i.e., very shallow sites probably suffer from wave dynamics,

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whereas very deep sites are light-limited). Direct evidence cannot be obtained as information on local energy regimes and light availability is largely lacking in literature. Our review confirms the importance of removal of threats. Restoration following losses derived from reduced water quality (usually eutrophication) are less successful than, for example those derived from construction activities, substrate manipulations like dredging and filling, or in areas where there has been no seagrass decline.

Recovery and proximity of donor beds were positively correlated to trial performance. Donor bed proximity indicates nearby seagrass presence, which, together with its recovery potential demonstrates that the environment is suitable for seagrass growth (e.g. Orth et al. 2006). The positive role of donor proximity may additionally be due to 'type-matching' or genetic provenance; the use of local plants could be beneficial due to the presence of locally adapted gene complexes in adjacent meadows (Hämmerli and Reusch 2002; Fonseca 2011; Sinclair et al. 2013). Third, it may also be correlated with the donor material being in better physiological condition when planted given the minimum time between collection and planting.

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Regarding planting procedures, the most important factors affecting the success of revegetation trials were anchoring technique and plant material (combined magnitude of response 7.1). During the first months after planting, any anchoring of rhizome fragments or seedlings enhanced survival in comparison to no anchoring. Subsequently, the application of weights (sand bags, stones, shells) significantly improved later success scores in comparison to frames, staples or sods. Weights may mitigate significant water dynamics whereas light frames or staples may become set into motion by water dynamics and thus destabilise the rooting process of the plantings in the long-term. Seedlings consistently perform worse than rhizome fragments, sods or seeds. Mechanical planting methods achieved a somewhat lower success than manual planting methods though initial survival is higher; potentially this reflects the exploratory nature of many of these mechanical planting methods (e.g. Paling et al., 2001).

Large restoration trials have generally performed better

The performance of seagrass restoration was largely dependent on the trial scale, since trial survival and population growth rate in restoration trials were directly related to the initial number of shoots or seeds planted. For example, after 23 months, estimated survival of small trials was 22 % (<100 shoots/seeds planted), but trial survival increased to 42 % for the largest scale trials (>100,000 shoots/seeds planted). Likewise, the population growth rate (as increase in number of shoots) in the seagrass restoration trials initiated at less than 1000 shoots/seeds was negative, whereas population growth rates for trials with more than 10,000 planted shoots/seeds were positive, and thus appear to effectively restore the seagrass meadow. The positive effect of restoration scale on both trial survival and population growth rate of survived trials suggests the existence of a threshold of scale of the trial required for restoration progress between 1000 - 10,000 shoots/seeds. Note that the threshold for success will vary over time and in space, depending on factors such as stress levels and natural variability. 55% of the seagrass restoration trials worldwide had less than 1000 shoots or seeds initially planted, which may have contributed to the low overall trial survival from 1786 trials (conservatively estimated to be 37% after median 36 months).

It is critical to point out that seagrass restoration performance is not only related to the trial scale, but also to site characteristics and planting procedures, and may differ between

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species (as shown in our meta-analysis). This could potentially lead to confounding effects; the larger scale trials may target more suitable sites and techniques than smaller scale trials. However, the 'better performing' sites, species and techniques were generally (weakly) *negatively* correlated to initial planting scale. This robustly indicates the absence of such confounding effects in the positive relationship between restoration scale and restoration success.

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Large restoration scales may generally benefit restoration successes

Plantings (or new colonisations) are vulnerable to extinction by a multitude of factors, including (i) the variability in external factors of influence (environmental variability), and (ii) positive density dependence or positive feedback (e.g., Morris & Doak 2002). A large-scale planting (particularly when covering a large areal extent) increases the range of environmental conditions experienced by the plants, and hence the likelihood of encountering suitable conditions for positive growth. The local environment is likely heterogeneous due to for example local accumulation of organic matter or macroalgae, bioturbation or mere stochastic variation in water dynamics rising from the hydrodynamic regime. When strong positive feedback occurs, a critical threshold population density is needed to initiate self-facilitating processes (e.g., Morris & Doak 2002, van der Heide et al. 2007, Nystrom et al. 2012). Our meta-analysis of global seagrass restoration supports that both processes occur in seagrass beds. With increasing numbers of initially planted individuals (i) the survival percentage increased, which relates to spreading of risks to overcome environmental variability, and (ii) the population growth rate increased, which relates to positive feedback. Given the typically dynamic and stressful coastal environment of seagrass habitats, and the large number of already identified positive feedbacks in seagrass beds (e.g. Bos and van Katwijk 2007, van der Heide et al. 2007, 2011, Carr et al. 2010, 2012, Orth et al. 2012), this finding may not be surprising. However, our study is the first to show this occurs in seagrass restoration trials at a global scale. To our knowledge, this is the first time this principal has been globally demonstrated as an example of foundation species restoration trends in coastal environments.

Our finding implies that – after careful site and species selection - large-scale plantings are highly preferable in the typically dynamic and/or stressful environments of (former) seagrass beds. To not risk planting under the suggested threshold, it is even advisable to use a larger planting scale than estimated by the planters. However, we recognize this is costly both with respect to extracting donor material as well as operational costs (though regained ecosystem services may compensate and eventually surpass these investment costs, e.g. Duarte et al. 2013b).

If managers decide on a larger number of individuals in a restoration project, these large numbers can be used to increase the density (to reach the threshold for density-dependent feedback, i.e., planting density > density required to restore self-sustaining feedback), but also to increase the spatial extent (in order to spread risks, i.e., the spatial extent of the planting > extent of environmental variability – note that environmental variability relates to spatial heterogeneity resulting from both natural variability and stochasticity). We have depicted the synergy to employ both, in a conceptual framework (figure 4). For a given number of plants available for restoration, focus could be more on either increasing spatial extent or increasing planting density. Clearly, in highly dynamic systems with large unpredictable disturbances, environmental forcing will overrule benefits from restoring feedback, and spreading of risks is of paramount importance (for seagrass beds indicated by

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e.g., Suykerbuyk et al. submitted this journal). In those cases a focus on large spatial extent is preferable. Reversely, in less dynamic environments, positive feedback may accelerate restoration processes (for seagrass beds indicated by e.g., McGlathery et al. 2012, for shellfish beds e.g. indicated by Schulte et al. 2009), and local high planting densities could be aimed at. This choice should depend upon the wisdom of the local seagrass experts. Our framework implies an 'irony of the test plot': the test plot has the lowest chances for trial survival and subsequent population expansion of all. A surviving and expanding test plot could indicate a bonanza or an exceptionally benign environment, but it can also indicate mere luck. (Note that seagrass restoration practitioners use relatively large numbers of shoots in what are still called 'test plots', so we did not show this effect for 'test plots' in our meta-analysis). Our results indicate that also a slowly recovering, sparse seagrass bed may benefit from additional planting.

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A large restoration scale is even more beneficial in situations with potential bistability: a conceptual framework

Our study shows strong positive feedback, i.e., at low initial numbers of shoots/seeds (fewer than 1000), the population growth becomes negative. This means that the initial stages of a restoration trial of foundation species may generate bistability, where two alternative and potentially persistent ecosystem regimes are possible (Nystrom et al. 2012).

Bistability has been proposed in seagrass systems (e.g., van der Heide et al. 2007, 2008, Carr et al. 2010, 2012). In a framework with alternative stable states, thresholds (tipping points) exist above which self-sustaining feedback promotes recovery (figure 5a). Below the threshold, the planting extirpates, in line with our findings. Note that our findings represent an average situation – individual systems may not show threshold behaviour. From this framework we have demonstrated that, in order to reach a tipping point for recovery it helps to combine (i) increasing the presence of self-facilitating seagrass as a foundation species (vertical wide arrow in Figure 5b and referring to positive density dependence or allee effects, i.e., via reduction of environmental stress by the species engineering activity, Morris & Doak 2002) and (ii) externally reducing the environmental stress (horizontal wide arrow in Figure 5b). Environmental stress has a mean component, and a variance component due to natural variability. The mean component can obviously be reduced by for example habitat rehabilitation and is not related to transplantation scale. The variance component can be tackled by spreading of risks. Spreading of risks is accomplished using large numbers of individuals and hence the spatial extent of the plot, which increases the variability of environmental conditions within the plot and hence the likelihood that favourable conditions are encountered by at least some of the planting (cf. Morris & Doak 2002; our study). Thus, increasing the initial number of shoots/seeds may increase restoration performance via the two pathways that concertedly help to reach the tipping point for recovery in a situation with alternative stable states (figure 5b).

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Figure legends

Figure 1. Map of 1786 trials analysed (green dots represent trials). Frequency diagrams of the initial scale of the restoration trials per bioregion show that most trials start with less than 1000 shoots. Blue lines separate the bioregions.

Figure 2. Performance of seagrass restoration trials in relation to cause of decline prior to planting, distance from and recovery of the donor site and plant material and anchoring techniques. The semi-quantitative integrated succes score and its standard error of the mean were calculated from initial survival and long-term performance after initial survival, see materials and methods. The categories for causes of decline and anchoring techniques are elaborated in table 2 and 3 respectively. Rhiz.fr. = rhizome fragments

Figure 3. Positive effects of restoration scale (number of initially planted shoots) on the trial survival and population growth rate of seagrass in survived trials. (a) Kaplan-Meier-estimated trial survival after ≥ 23 months, ± confidence interval (proportional hazard model over entire period: $p=0.0070$); (b) Log mean population growth rate (log of increase in number of shoots mo^{-1}) ± standard error of the mean, ANOVA $p<0.0001$, $df=4$.

Figure 4. Framework depicting the synergy to investing in spatial extent and planting density, and the trade-off, given a high but limited number of plants, to invest relatively more in either spatial extent or in planting density. A large investment in high numbers may be needed for best restoration practice in dynamic systems to capture windows of opportunity generated by spatial heterogeneity (horizontal axis: spreading of risks, or spatial extent of planting, m^2) and to reach threshold required to initiate self-sustaining feedback (vertical

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axis: recovery of feedback, or planting density, m^{-2}). Knowledge of the local environment is essential to choose the best planting strategy.

Figure 5. How large initial numbers of foundation individuals (i.e., a large-scale restoration) are particularly needed when alternative stable states are likely and a critical threshold needs to be crossed, as in our study object. (a) Situation with alternative stable states. The dotted line indicates tipping points for recovery and collapse: above this line self-sustaining feedback propellers the system to high presence of the foundation species through natural recovery. Below this line the system will collapse towards a state without the foundation species. (b) How reintroduction (vertical arrow) and stress reduction (horizontal arrow) concertedly help to reach a tipping point for recovery. Large numbers of initial numbers of foundation individuals considerably increase the chance to reach a tipping point for recovery, via dual action: (i) obviously the reintroduction itself is scale dependent due to positive feedback, but also (ii) large numbers are needed to overcome the variable and stochastic part of environmental stress (left part of horizontal arrow, indicated by 'var'), by spreading of risks in time and space.

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Supporting Information.

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Sources for the dataset

Table S1: Effect of species and environmental characteristics on restoration performance.

Table S2: Effect of planting techniques on restoration performance

Table S3: Tests for confounding effects

Figure S1: Numbers per decade and learning curve of seagrass restoration trials

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Table 1. Overview of results and characteristics of the trials. Phase 1 ≤ 9 months, phase 2: 10-22 months and phase 3 ≥ 23 months. The number of samples (N) depended on the availability of the data.

	N	median	min	max
number of shoots at t=0	1109	409	2	3E+06
standardised area at t=0 (m^2)[a]	1108	0.93	0.001	5730
number of shoots of surviving trials at t=t	487	720	0.43	3.E+09
standardised area of surviving trials at t=t (m^2)	487	1.26	0.0001	9.E+06
monitoring time t (months)	1715	12	0.70	456
growth rate* of surviving trials (months^{-1})	486	-0.005	-2.996	1.251
population growth rate phase 1	189	-0.082	-2.996	1.251
population growth rate phase 2	173	0.025	-0.453	0.406
population growth rate phase 3	124	0.029	-0.354	0.245

	N	%	Median monitoring time (months)
overall trial survival**		37 %	
trial survival phase 1	1034	70 %	5.7
trial survival phase 2	677	67 %	12
trial survival phase 3	412	79 %	36

[a] Areal extent (m^2) was estimated from the standardised area per species (saps), which was calculated from the average diameter of the area that a shoot occupies (spacer length, sl)

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per species (Marbà and Duarte 1998) and multiplied by the number of shoots (nsh): saps = nsh x π x (½sl)^2.

*Growth rate refers to increase in number of shoots .

**The overall trial survival refers to the survival of trials, not shoots, and has been estimated by multiplying the actual trial survival rates within each of the three phases, i.e. 70% x 67% x 79% (note that most trials have only one or two monitoring dates).

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Table 2. Classification of causes of decline of the meadows in the area of the restoration trial

Main target of disturbance	Types of disturbance	Impact
Local direct impact	Trawl fishing Boat/vessel damage Dumping Mining in meadow	Mechanical damage & removal
Water quality	Thermal pollution	Heat stress
	Eutrophication	Nutrient stress / algal overgrowth / sulfide toxicity
	Oil or chemical pollution	Chemical impact
	Turbidity increase	Lack of light
Substrate	Dredging	Temporary increased turbidity
	Filling	Smothering (by sediment)
	Erosion (of seagrass bed sediment)	Temporary increased sediment dynamics Changes in sediment type (e.g. replacement by less favourable sediment)
Natural cause	Wasting disease	Infection, thinning, mortality
	Storms Beach erosion Overwash	Unstable sediment, loss of anchoring
Construction	Large scale construction (e.g. sea walls, ports, bridges); reclamation	Removal of part or entire seagrass meadow

Table 3. Categories of anchoring techniques and plant material as distinguished in this study

Anchoring technique categories: **weights** are provided by rocks, shells, bricks or sandbags and include the TERFS method: Transplanting Eelgrass Remotely with Frame System (Short et al. 2002); **staples** include rods, bamboo’s, pegs, sprigs and washers; **frames** include anchoring techniques that attach the planting material to frames, grids, quadrates, nets, mats or meshes that are not weighted and do not include TERFS.

Plant material comprise the categories **sods:** intact units of native sediment with roots, rhizomes and leaves, sometimes also referred to as plugs and peat pots (the latter are only included here if the sediment is included in the transplantation), **rhizome fragments** with shoots, also sometimes referred to as turions or sprigs; **seeds** and **seedlings.**

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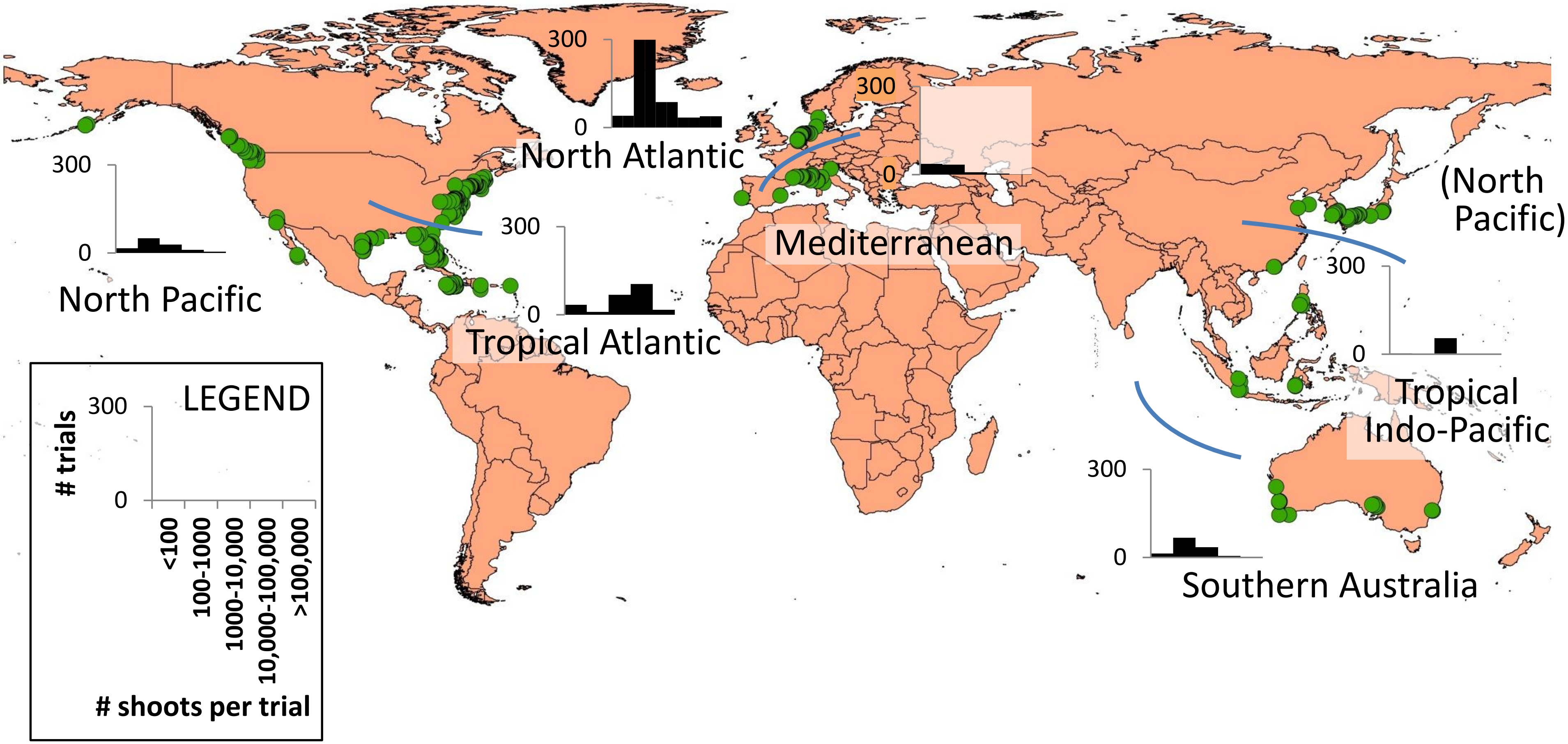
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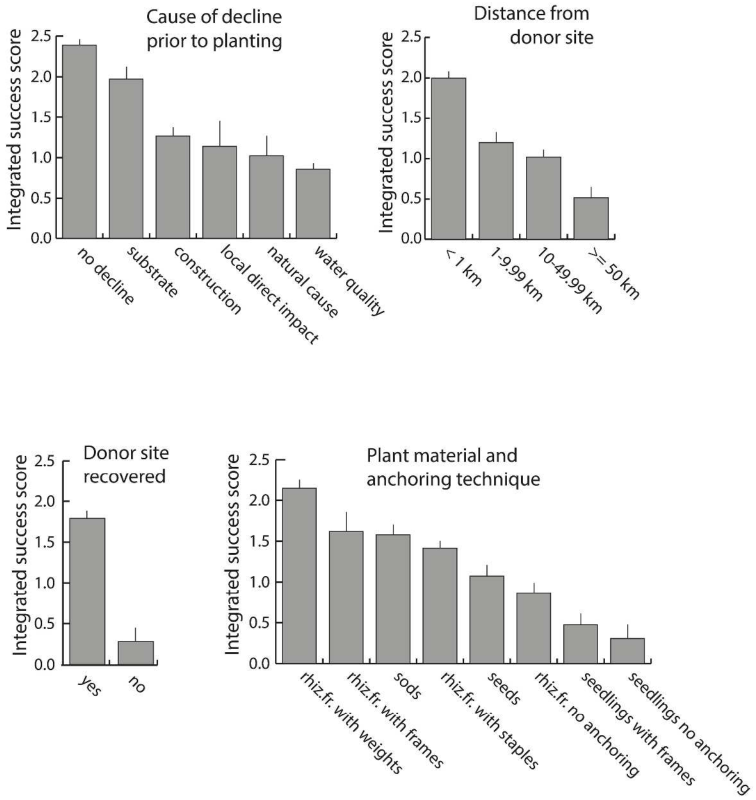

Figure 2. Performance of seagrass restoration trials in relation to cause of decline prior to planting, distance from and recovery of the donor site and plant material and anchoring techniques. The semi-quantitative integrated succes score and its standard error of the mean were calculated from initial survival and long-term performance after initial survival, see materials and methods. The categories for causes of decline and anchoring techniques are elaborated in table 2 and 3 respectively. Rhiz.fr. = rhizome fragments
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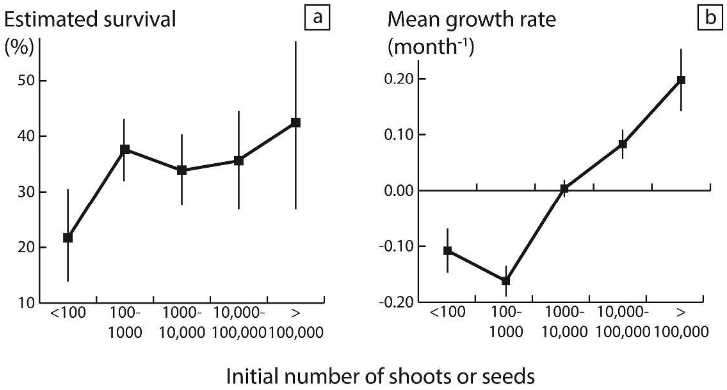

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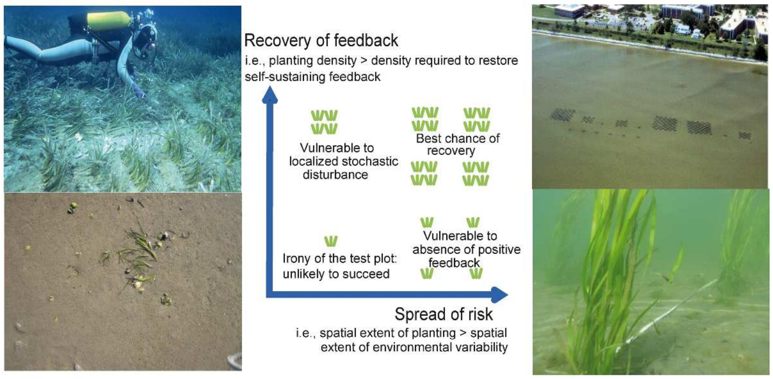

Figure 4. Framework depicting the trade-off to investing in either planting density or spatial extent, and the synergy to invest in both. A large investment in high numbers may be needed for best restoration practice in dynamic systems to capture windows of opportunity generated by spatial heterogeneity (horizontal axis: spreading of risks, or spatial extent of planting, m2) and to reach threshold required to initiate self-sustaining feedback (vertical axis: recovery of feedback, or planting density, m-2). Knowledge of the local environment is essential to choose the best planting strategy.
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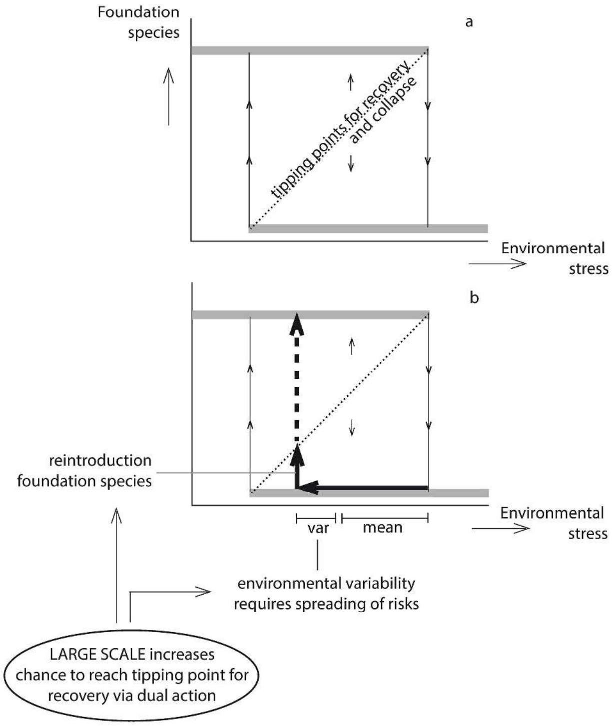

Figure 5. How large initial numbers of foundation individuals (i.e., a large-scale restoration) are particularly needed when alternative stable states are likely and a critical threshold needs to be crossed, as in our study object. (a) Situation with alternative stable states. The dotted line indicates tipping points for recovery and collapse: above this line self-sustaining feedback propellers the system to high presence of the foundation species through natural recovery. Below this line the system will collapse towards a state without the foundation species. (b) How reintroduction (vertical arrow) and stress reduction (horizontal arrow) concertedly help to reach a tipping point for recovery. Large numbers of initial numbers of foundation individuals considerably increase the chance to reach a tipping point for recovery, via dual action: (i) obviously the reintroduction itself is scale dependent due to positive feedback, but also (ii) large numbers are needed to overcome the variable and stochastic part of environmental stress (left part of horizontal arrow, indicated by ‘var’), by spreading of risks in time and space.
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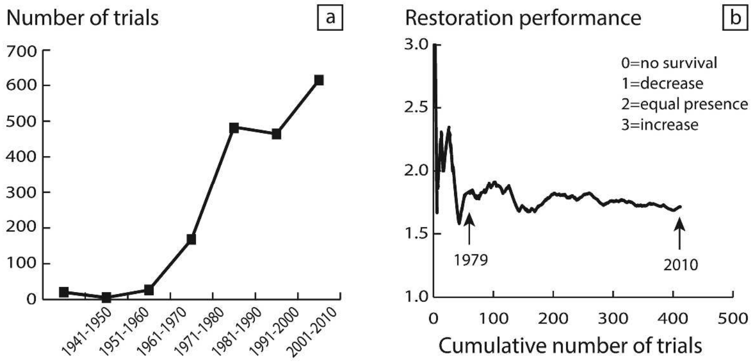

Figure S1. Despite increasing numbers of seagrass restoration trials initiated per decade, accumulated experience has not yet improved the performance of subsequent trials. (a) Increase of numbers of reviewed trials during the last 8 decades (2 trials initiated in 2011 are not depicted); (b) Learning curve: the average restoration performance score (representing the 415 trials monitored >22 months, scores 0=no trial survival, 1=decrease, 2=equal presence and 3=increase) as function of the cumulative number of trials since 1972 remains low after some initial fluctuations.

Learning curve
297x420mm (300 x 300 DPI)

Supplementary Information Table S1. Restoration success in relation to general and environmental characteristics. Initial trial survival (< 10 months, scores 0=no survival and 1=survival) and long term trial success (>22 months, scores 0=no survival, 1=decrease, 2=equal presence and 3=increase) in relation to general characteristics, plant and environmental characteristics and planting techniques. Integrated success score is the multiplication of initial trial survival and long term trial success. Logistic regression of initial trial survival and anova p-values of long term trial success are presented per variable. Number of plantings (N) and estimated mean scores are presented per category with differing letters in superscript denoting logistic regression contrasts in initial trial survival and Tukey posthoc significant differences in long term trial success at an alpha level of 0.05.

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	Initial trial survival (< 10 months)		Long term trial success (> 22 months)		integrated success score
Variable	N	p-value and estimated mean	N	p-value and estimated mean	
Reason for planting		<0.0001		0.0185	
restore natural values	318	0.53^{B}	119	1.49^{B}	0.79
mitigation	90	0.86^{A}	138	1. 80^{AB}	1.55
research	275	0.91^{A}	123	1.65^{B}	1.50
test plots	218	0.58^{B}	24	2.25^{A}	1.31
Source		0.0055		0.0004	
grey literature	395	0.73^{A}	213	1.92^{A}	1.40

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web of science	632	0.65^{B}	201	1.50^{B}	0.98
Cause of decline[1]		<0.0001		<0.0001	
no decline	103	0.92^{A}	22	2.59^{A}	2.38
substrate	60	0.85^{AB}	31	2.32^{AB}	1.97
construction	132	0.81^{B}	110	1.56^{B}	1.26
local direct impact	36	0.69^{BC}	14	1.64^{B}	1.13
natural cause	68	0.56^{C}	12	1.83^{AB}	1.02
water quality	475	0.56^{C}	144	1.53^{B}	0.86
Removal of threats		0.0043		<0.0001	
no threats	93	0.92^{A}	22	2.59^{A}	2.41
complete removal	30	0.70^{B}	26	2.39^{A}	1.67
partial removal	344	0.78^{B}	157	1.62^{B}	1.26
Distance from donor site		<0.0001		<0.0001	
< 1 km	151	0.74^{B}	46	2.70^{A}	2.00
1-9.99 km	103	0.88^{A}	70	1.36^{B}	1.20
10-49.99 km	324	0.66^{B}	92	1.54^{B}	1.02
>= 50 km	155	0.32^{C}	44	1.64^{B}	0.52
Donor site recovered		<0.0001		<0.0001	
yes	217	0.88^{A}	111	2.05^{A}	1.80
no	68	0.31^{B}	22	0.91^{B}	0.28
Bioturbation was a factor		0.0005		<0.0001	

no	258	0.78^{A}	116	2.05^{A}	1.60
yes	28	0.46^{B}	42	1.71^{B}	0.79
Depth		<0.0001		0.0014	
0-0.49 m	169	0.55^{C}	51	1.29^{B}	0.71
0.5-0.99 m	175	0.45^{C}	20	2.20^{A}	0.99
1-1.99 m	195	0.69^{B}	71	1.48^{AB}	1.02
2-3.99 m	112	0.86^{B}	37	2.05^{A}	1.76
>4 m	97	0.93^{A}	80	1.30^{B}	1.21
Emergence		<0.0001		<0.0001	
subtidal	702	0.72^{A}	318	1.88^{A}	1.35
intertidal	238	0.50^{B}	84	1.05^{B}	0.53

[1] Explanation see Table 2.

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Supplementary Information Table S2. Restoration success in relation to planting procedures.

Explanation see table S1.

	Initial trial survival (< 10 months)		Long term trial success (> 22 months)		integrated success score
Variable	N	p-value and estimated mean	N	p-value and estimated mean	
Anchoring technique[1]		<0.0001		<0.0001	
weight (including TERFS)	106	0.76^{A}	35	2.69^{A}	2.07
staple	301	0.79^{A}	129	1.78^{B}	1.41
none	417	0.52^{B}	142	1.73^{B}	0.95
frame	93	0.82^{A}	54	0.93^{c}	0.76
Type of plant material[1]		<0.0001		<0.0001	
sods	149	0.79^{A}	116	1.79^{A}	1.41
rhizome fragments	570	0.71^{A}	210	1.90^{A}	1.35
seeds	88	0.58^{B}	22	1.77^{A}	1.03
seedlings	179	0.55^{B}	49	0.67^{B}	0.37
Anchoring technique combined with plant material[1]		<0.0001		<0.0001	

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rhizome fragments + weights	85	0.78^{A}	34	2.77^{A}	2.16
rhizome fragments + frames	39	0.87^{A}	14	1.86^{B}	1.62
sods (no anchoring)	103	0.85^{A}	71	1.85^{B}	1.57
rhizome fragments + staples	283	0.81^{A}	115	1.76^{B}	1.43
seeds (no anchoring)	80	0.55^{B}	20	1.95^{AB}	1.07
rhizome fragments (no anchoring)	148	0.45^{B}	32	1.91^{AB}	0.86
seedlings + frames	35	0.8^{A}	32	0.59^{C}	0.47
seedlings (no anchoring)	112	0.43^{B}	14	0.71^{C}	0.31
Fertilization		<0.0001		0.0021	
fertilized	83	0.92^{A}	9	2.89^{A}	2.66
not fertilized	931	0.66^{B}	391	1.66^{B}	1.10
Planting method		0.0325		0.008	
manual	601	0.69^{B}	290	1.88^{A}	1.30
mechanical	41	1.00^{A}	34	1.35^{B}	1.35
Habitat manipulation		0.0004		<0.0001	
none	428	0.71^{B}	215	2.03^{A}	1.44
anti-bioturbation measures	21	1.00^{A}	15	1.33^{B}	1.33
sediment stabilisation	59	0.80^{AB}	28	0.50^{C}	0.40
Protection measures		<0.0001		0.2433	
none	419	0.72^{A}	240	1.87	1.35
against hydrodynamics	34	0.35^{B}	7	1.57	0.55

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against grazing	18	0.33^B	12	1.33	0.44

[1] Explanation of categories, see Table 3

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Supplementary Information Table S3. Tests for confounding effects. Relationship between initial number of shoots (log-transformed) and 15 trial characteristics (listed in column 1) is depicted in column 4 by the average number of shoots after log-transformation; the p-value and Tukey posthoc tests (alpha level of 0.05) show significant number of shoots between categories. Differing letters in superscript denote Tukey posthoc significant differences at an alpha level of 0.05. The number of trial (N) are presented in column 3. The correlation between integrated success score (column 2, see Table S1 and S2) and estimated mean number of shoots per category (column 4) is presented in column 5. Only trials were included that also evaluated the number of shoots at the end of monitoring) are presented per category. There are no confounding effects as the correlation coefficients are all negative or near zero.

	Integrated success score		Initial planting scale log (number of shoots)	potential confounding effects
Characteristics		N	p-value and estimated mean	Correlation coefficient
Seagrass species			>0.0001	-0.55
Posidonia australis	2.71	19	6.34^{AB}	
Posidonia oceanica	1.68	51	4.77^{B}	
Halodule wrightii	1.36	58	8.74^{AB}	
Zostera marina	1.18	202	6.44^{AB}	
Posidonia sinuosa	1.01	5	8.52^{AB}	
Syringodium filiforme	0.98	17	9.78^{A}	
Zostera noltii	0.92	27	7.67^{AB}	

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Thalassia testudinum	0.83	51	8.12^{AB}	
Amphibolis antarctica	0.63	1	6.22^{AB}	
Reason for planting			<0.0001	-0.25
restore natural values	0.79	41	8.31^{A}	
mitigation	1.55	105	8.82^{A}	
research	1.50	152	4.83^{C}	
test plots	1.31	96	7.06^{B}	
Cause of decline[1]			<0.0001	-0.46
no decline	2.38	57	4.77^{C}	
substrate	1.97	95	9.05^{A}	
construction	1.26	102	6.14^{BC}	
local direct impact	1.13	22	9.58^{A}	
natural cause	1.02	16	9.41^{A}	
water quality	0.86	147	7.1^{B}	
Removal of threats			<0.0001	-0.79
no threats	2.41	54	4.73^{C}	
complete removal	1.67	35	8.94^{A}	
partial removal	1.26	213	7.66^{B}	
Distance from donor site			0.0004	0.15
< 1 km	2.00	118	8.01^{A}	
1-9.99 km	1.20	69	7.26^{AB}	
10-49.99 km	1.02	114	6.66^{B}	
>= 50 km	0.52	43	8.05^{A}	
Donor site recovered			n.s.	
yes	1.80	260	7.96	
no	0.28	14	8.49	

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Bioturbation was a factor			0.0002	-1.0
no	1.60	284	7.61^{B}	
yes	0.79	10	10.63^{A}	
Depth			<0.0001	-0.18
0-0.49 m	0.71	29	6.6^{B}	
0.5-0.99 m	0.99	34	9.61^{A}	
1-1.99 m	1.02	105	8.41^{A}	
2-3.99 m	1.76	93	7.07^{B}	
>4 m	1.21	79	5.16^{C}	
Emergence			N.S.	
subtidal	1.35	377	7.59	
intertidal	0.53	42	7.02	
Anchoring technique^{2}			<0.0001	-0.13
weight (including TERFS)	2.07	84	6.52^{B}	
staple	1.41	133	5.25^{C}	
none	0.90	202	8.96^{A}	
frame	0.76	32	5.2^{C}	
Type of plant material^{2}			<0.0001	0.023
sods	1.41	79	9.04^{B}	
rhizome fragments	1.35	329	6.59^{C}	
seeds	1.03	16	11.97^{A}	
seedlings	0.92	37	6.62^{C}	
Anchoring technique combined with plant material^{2}			<0.0001	0.01
rhizome fragments + weights	2.16	73	6.70^{ED}	
rhizome fragments + frames	1.62	24	4.81^{F}	

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sods (no anchoring)	1.57	67	9.29^{B}	
rhizome fragments + staples	1.43	131	5.24^{EF}	
seeds (no anchoring)	1.07	16	11.97^{A}	
rhizome fragments (no anchoring)	0.86	93	8.65^{CB}	
seedlings + frames	0.47	5	3.99^{F}	
seedlings (no anchoring)	0.31	25	7.24^{CD}	
Fertilization			<0.0001	-1.00
fertilized	2.66	54	5.73^{B}	
not fertilized	1.10	429	7.36^{A}	
Planting method			n.s.	-
manual	1.30	324	7.89	
mechanical	1.35	20	9.05	
Habitat manipulation			n.s.	
none	1.44	332	7.52	
anti-bioturbation measures	1.33	11	9.45	
sediment stabilisation	0.40	6	8.03	
Protection measures			n.s.	
none	1.35	319	7.54	
against hydrodynamics	0.55	8	6.69	
against grazing	0.44	5	7.03	

[1] Categories are explained in Table 2

[2] Categories are explained in Table 3

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Supplementary material s1

Supporting Information Appendix S1. Sources for the dataset. Data accessibility: data are intended to be stored at Radboud University Repository

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