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

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Summary

1. 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 ecosystem functions. However, seagrass restoration is often challenging, given the dynamic and stressful environment that seagrasses often grow in.

2. From our world-wide meta-analysis of seagrass restoration trials (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 corre-

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lated with trial performance. Planting techniques can influence restoration success.

3. The meta-analysis shows that both trial survival and seagrass population growth rate in trials that survived 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 have been very small, which may explain the low overall trial survival rate (i.e. estimated 37%).

4. 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.

5. *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 probably 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. Secondly, 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, spreading of risks and enhancing self-sustaining feedback in concert increase success of seagrass restoration.

Key-words: allee effect, coastal ecosystems, ecosystem recovery, global restoration trajectories, positive feedback, seagrass mitigation, seagrass rehabilitation

Introduction

Coastal and estuarine habitats are dynamic environments. Many coastal ecosystems are dominated by one or few 'foundation' species (*cf*. Bruno & 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, for example, by creating shelter and sediment stabilization, resulting in lower water turbidity and amelioration of wave action. This ecosystem engineering by seagrass beds (*cf*. Jones, Lawton & Shachak 1994) forms the basis of key ecosystem services, including erosion control (Hansen & Reidenbach 2012; Christianen *et al*. 2013), carbon sequestration for climate change mitigation (Thorhaug, Raven & Franklin 2009; McLeod *et al*. 2011; Duarte, Sintes & Marbà 2013b; Duarte *et al*. 2013a), fish stock (Watson, Coles & Long 1993; McArthur & Boland 2006; Unsworth *et al*. 2010), and high biodiversity, including iconic and highly endangered species (Hemminga & 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% year^{-1} before 1940 to 7% year $^{-1}$ since 1990 (Waycott *et al*. 2009). Legislation for protection and restoration of seagrass habitat as well as for improving coastal environmental 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 & Janicki 2006; Cardoso *et al*. 2010; Vaudrey *et al*. 2010; but see Valdemarsen *et al*. 2011), but have 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 ecosystem biodiversity and ecosystem services. Restoration efforts have been performed world-wide 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, Kenworthy & Thayer 1998), although a comparative quantitative global overview on the performance of seagrass restoration is lacking and the processes influencing success or failure of restoration programmes 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. Secondly, we study the effect of restoration scale (i.e. initial number of reintroduced plants) on trial survival and population growth rate in trials that survived. A larger restoration scale is hypothesized 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 trials that survived 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 trials that survived positively affected by the numbers of plants or seeds initially planted. This relationship 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 have been very small (55% had fewer than 1000 specimens initially planted), this may explain 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

We compiled data from restoration trials conducted world-wide 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 data set represents a trial, the oldest one from a planting 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); first, we aimed not to 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 trials that survived was calculated as the intrinsic rate of increase of an exponential growth function, log (nsht/nsh0)/t, where nsh0 is the number of shoots (also refers to seeds or seedlings that were used in a few trials) 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 trials that survived.

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 per month) 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. As 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: (i) first 9 months; (ii) between 10 and 22 months (thus including minimally one adverse season); and (iii) 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). Secondly, trial survival (1 or 0) was averaged for each of the three phases and the three averages were multiplied to obtain a conservative estimate of overall trial survival in the long term (i.e. representing a median monitoring duration of 36 months, see Table 1). A total of 1656 out of 1786 trials had one or more data inputs 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 analysed 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: (i) 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 ($\leq$ 9 months); and (ii) long-term planting performance during phase three, which was quantified by assigning scores to the trials that had data monitored in phase three (>22 months, 414 trials), with scores: 0 = lost during phase three, 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 (10–22 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

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
Standardized area at $t = 0$ (m^2)[*]	1108	0·93	0·001	5730
Number of shoots of surviving trials at $t = \text{t}$	487	720	0·43	3.E + 09
Standardized area of surviving trials at $t = \text{t}$ (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	

[*] Areal extent (m^2) was estimated from the standardized area per species (saps), which was calculated from the average diameter of the area that a shoot occupies (spacer length: sl) per species (Marbà & Duarte 1998) and multiplied by the number of shoots (nsh): saps = nsh × π × $(\frac{1}{2}\text{sl})^2$.

[†] 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% × 67% × 79% (note that most trials have only one or two monitoring dates).

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/sulphide 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

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 a few trials had data for both metrics). The standard deviation of the 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, 1–2 m, 2–4 m, >4 m), emergence (subtidal/intertidal), anchoring technique (weights, staples, none and non-weighted frames; explanation: 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, bamboos, pegs, sprigs and washers; frames include anchoring techniques that attach the planting material to frames, grids, quadrats, nets, mats or meshes that are not weighted and do not include TERFS), type of plant material (sods, rhizome fragments, seeds, seedlings; explanation: sods are intact units of native sediment with roots, rhizomes and leaves, sometimes also referred to as plugs and peat pots – peat pots 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), fertilization (yes/no), planting methods (manual/mechanical), habitat manipulation (none, anti-bioturbation measures, sediment stabilization), 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. $\mathrm{ISS_{highest}}/\mathrm{ISS_{lowest}}$); 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 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).

Results

ANALYSIS OF SEAGRASS RESTORATION TRIALS

Seagrass restoration trials started during the first half of the twentieth century, but efforts remained low until the 1970s, with 20–60 trials initiated per decade. In the 1970s, 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 (Fig. S1a). Most (68%) documented trials were conducted along the temperate and subtropical coastlines of the northern hemisphere (Fig. 1). Most restoration areas were previously colonized 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 utilized in restoration programmes. 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 programmes (12%, 8% and 1% respectively).

Seagrass restoration trials were on average small scale, with fewer than 409 shoots/seeds and a 0·93 m^2 standardized plant area (i.e. the area that these shoots/seeds

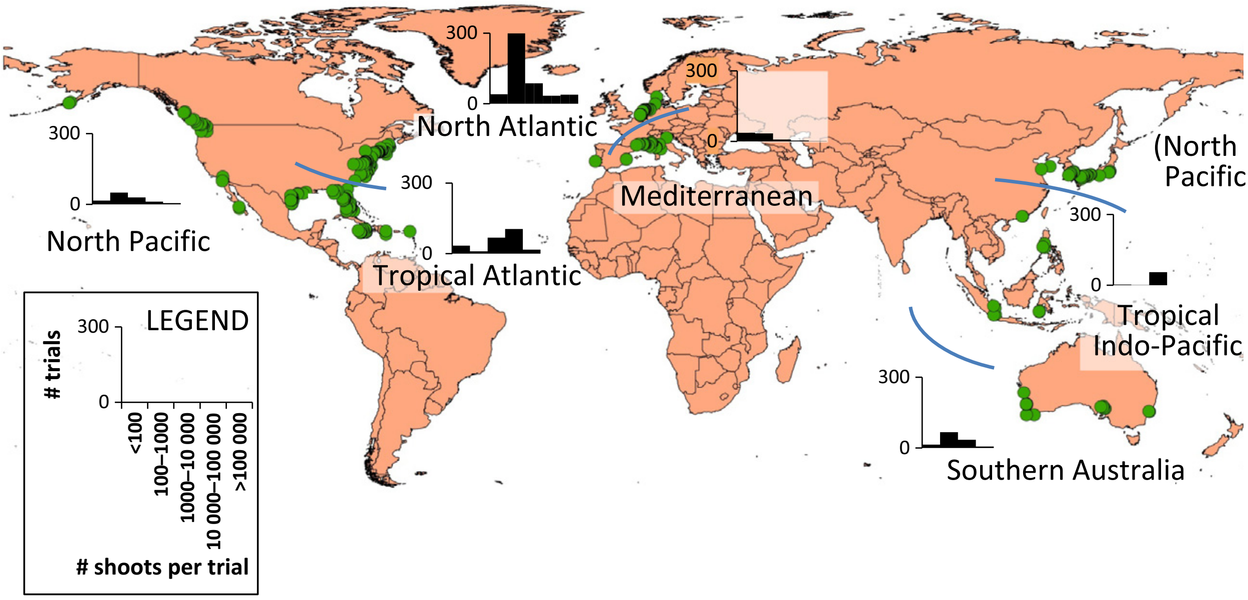

Fig. 1. Map of 1786 trials analysed (green dots represent trials). Frequency diagrams of the initial scale of the restoration trials per bioregion show that most trials start with <1000 shoots. Blue lines separate the bioregions.

would occupy in a full cover or coalesced situation, calculated per species), although occupied areas extended to three to four orders of magnitude larger with far greater numbers of shoots/seeds for the larger trials (Fig. 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 A. Thorhaug, unpublished data) (Table 1)).

ANALYSIS OF SEAGRASS RESTORATION BEST PRACTICE

Traditional seagrass restoration guidelines recommend careful site selection, i.e. a sheltered location with an adequate light environment, and recommend reversal of habitat 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 analysis shows the importance of removal of threats (Table S1) and world-wide, 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 with trial performance, with magnitudes of response of 6·4 and 3·9 respectively (Fig. 2). Bioturbation can lead to severely reduced initial trial survival and long-term population expansion of trials that survived (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 (Fig. 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 ($P < 0{\cdot}0001$, Table S2). The application of weights (sand bags, stones, shells) improved later success scores by 45%, whereas other anchoring methods did not contribute to the later success scores (Table S2). Mechanical planting methods improved initial survival, but somewhat reduced later success scores as compared with manual planting methods (Table S2). Habitat manipulations and protection measures had no positive effect on success (Table S2). Fertilization, if applied (only in

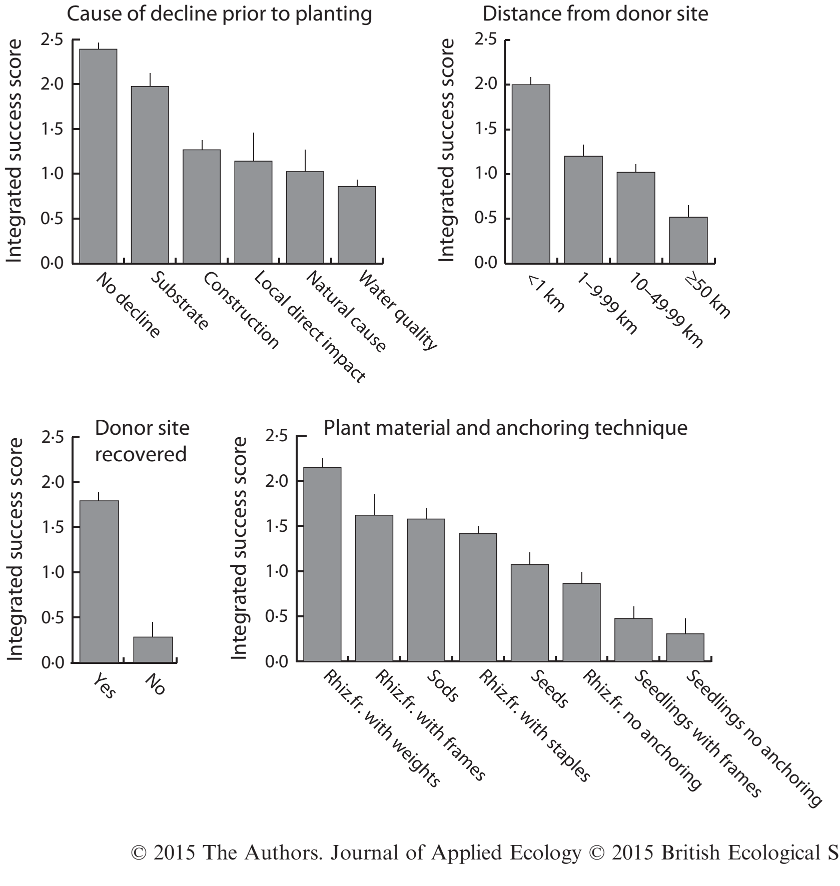

Fig. 2. Performance of seagrass restoration trials in relation to cause of decline prior to planting, distance from and recovery of the donor site and plant material and anchoring techniques. The semi-quantitative integrated success score and its standard error of the mean were calculated from initial 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 in Materials and methods respectively. Rhiz.fr. = rhizome fragments.

nine 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 $P < 0{\cdot}01$) and seagrass population growth rate in trials that survived (in number of shoots or standardized area per month) 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, Fig. 3a). Likewise, the population growth rate (as increase in number of shoots) in seagrass restoration trials initiated at <1000 shoots/seeds was negative, whereas population growth rates for trials with more than 10 000 planted shoots/seeds were positive (Fig. 3b). The positive effect of restoration scale on both trial survival and population growth rate in trials that survived suggests the existence of a threshold of scale of the trial required for restoration progress between 1000 and 10 000 shoots/seeds.

The 'better performing' sites, species and techniques were generally near zero or (weakly) negatively correlated with initial planting scales (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 world-wide have been collated in the form of transplantation guidelines (e.g. Addy 1947; Phillips 1980; Thorhaug 1981; Fonseca, Kenworthy & Thayer 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 programmes 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, Fig. S1b). Still, it should be stated 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 world-wide analysis by the slightly better performance of plantings at intermediate planting depths (i.e. very shallow sites probably suffer from wave dynamics, 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 the literature. Our analysis confirms the importance of removal of threats. Restorations 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 with 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

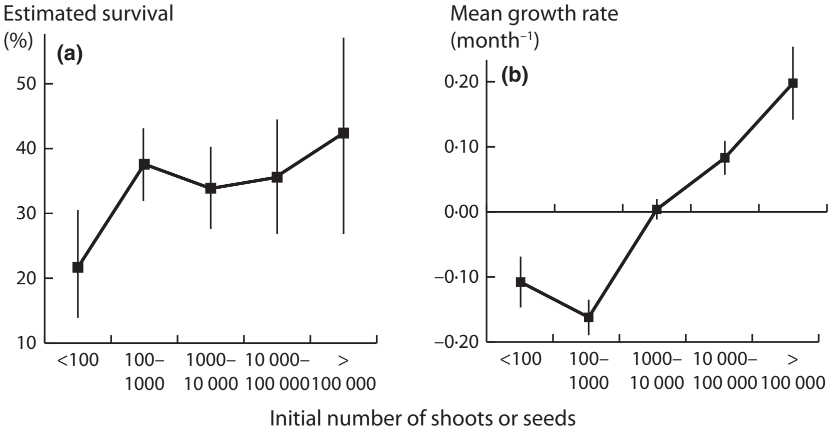

Fig. 3. Positive effects of restoration scale (number of initially planted shoots) on trial survival and population growth rate of seagrass in trials that survived. (a) Kaplan–Meier-estimated trial survival after ≥ 23 months, ±confidence interval (proportional hazard model over entire period: $P = 0{\cdot}0070$); (b) Log mean population growth rate (log of increase in number of shoots mo^{-1}) ±standard error of the mean, ANOVA $P < 0{\cdot}0001$, d.f. = 4.

adapted gene complexes in adjacent meadows (Hammerli & Reusch 2002; Fonseca 2011; Sinclair *et al.* 2013). Thirdly, it may also be correlated with the donor material being in better physiological condition when planted, given the minimum time between collection and planting.

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 destabilize 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, although 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 <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 trials that survived suggests the existence of a threshold of scale of the trial required for restoration progress between 1000 and 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. Fifty-five per cent of the seagrass restoration trials world-wide have <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 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 with initial planting scale. This robustly indicates the absence of such confounding effects in the positive relationship between restoration scale and restoration success.

LARGE RESTORATION SCALES MAY GENERALLY BENEFIT RESTORATION SUCCESSES

Plantings (or new colonizations) 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 probably 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; Nyström *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 & 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 and operational costs (although regained ecosystem services may compensate and eventually surpass these investment costs, e.g. Duarte, Sintes & Marbà 2013b).

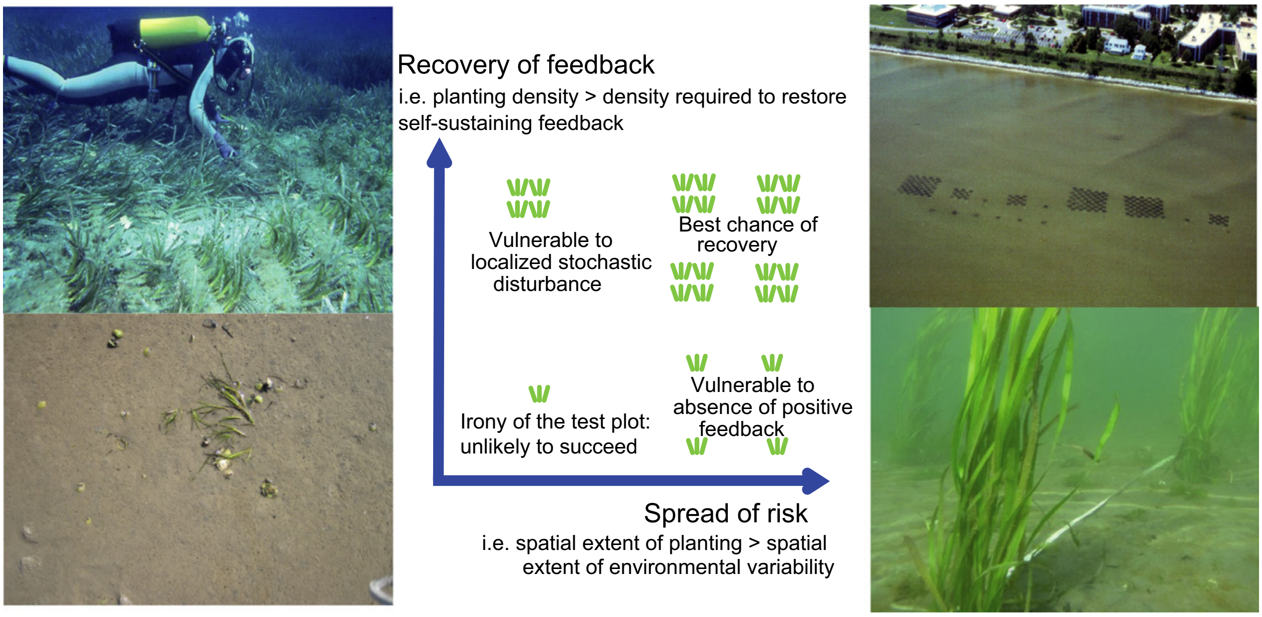

Fig. 4. Framework depicting the synergy to investing in spatial extent and planting density, and the trade-off, given a high but limited number of plants, to invest relatively more in either spatial extent or in planting density. A large investment in high numbers may be needed for best restoration practice 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 axis: recovery of feedback, or planting density, m^{-2}). Knowledge of the local environment is essential to choose the best planting strategy. Photo courtesy, clockwise: A. Meinesz, R.J. Orth, C. Durance, A.R. Bos.

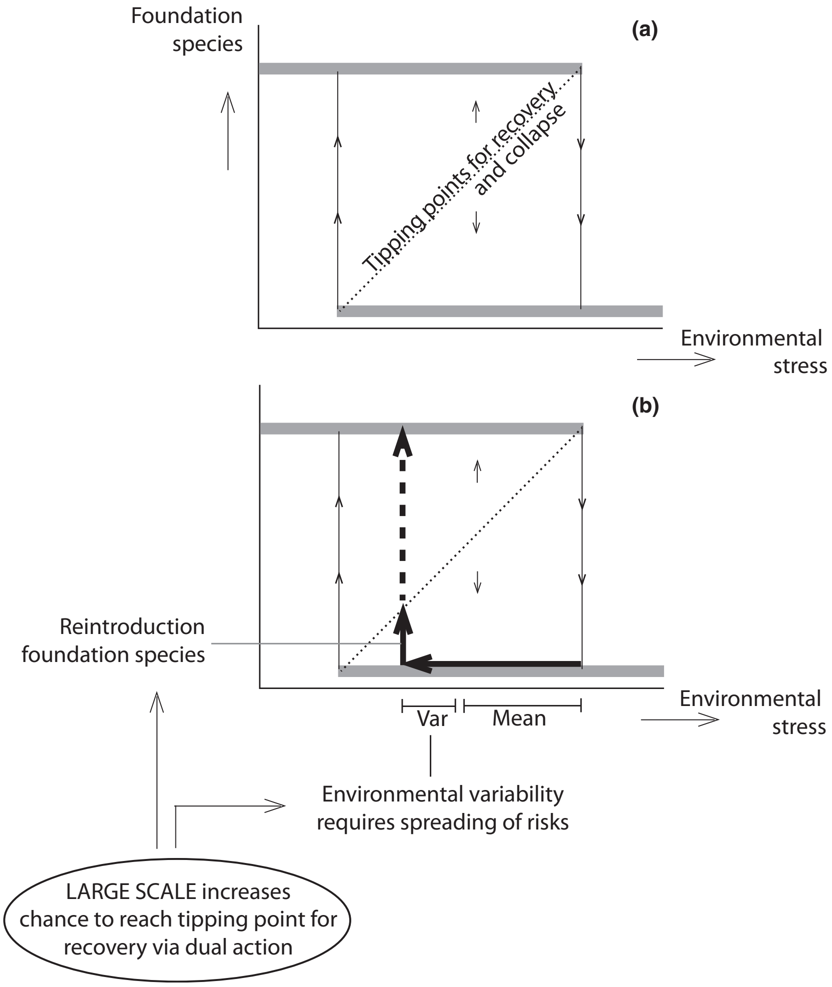

Fig. 5. How large initial numbers of foundation individuals (i.e. a large-scale restoration) are particularly needed when alternative stable states are likely and a critical threshold needs to be crossed, as in our study object. (a) Situation with alternative stable states. The dotted line indicates tipping points for recovery and collapse: above this line, self-sustaining feedback propels the system to a 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 reach a tipping point for recovery. Large initial numbers of foundation individuals considerably increase the chance of reaching 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.

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 (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 (Fig. 4). For a given number of plants available for restoration, the 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, e.g. Suykerbuyk *et al.* 2016). In those cases a focus on large spatial extent is preferable. Conversely, 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, Burke & Lipcius 2009), and local high planting densities could be aimed at. This choice should depend upon the knowledge of the local seagrass experts. Our framework implies an 'irony of the test plot': the test plot has the lowest chance 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 also indicate that a slowly recovering, sparse seagrass bed may benefit from additional planting.

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 (Nyström *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 (Fig. 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, 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 Fig. 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 Fig. 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 reach the tipping point for recovery in a situation with alternative stable states (Fig. 5b).

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Data accessibility

The data base of restoration trials is available from 1 November 2016 onwards at Data Archiving and Networked Services (DANS) doi: 10.17026/dans-x9h-expgl (van Katwijk 2015).

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Supporting Information

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

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

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

Table S2. Effect of planting procedures on restoration performance.

Table S3. Tests for confounding effects.

Appendix S1. Sources for the data set.