Increasing the chance of a successful restoration of *Zostera noltii* meadows

Mireia Valle [a,b,*], Joxe M. Garmendia [c], Guillem Chust [a], Javier Franco [c], Ángel Borja [c]

[a] AZTI-Tecnalia, Marine Research Division, Txatxarramendi ugartea z/g, 48395 Sukarrieta, Spain
[b] Universidad Laica Eloy Alfaro de Manabí, Central Research Department, Ciudadela Universitaria, Vía San Mateo s/n, 13-05-2732 Manta, Manabí, Ecuador
[c] AZTI-Tecnalia, Marine Research Division, Herrera Kaia, Portualdea z/g, 20110 Pasaia, Spain

ABSTRACT

Seagrass meadows are essential and ecologically important habitats in marine ecosystems providing physical, biological, economic and social benefits. Concern over their decreasing trends has triggered the development of many restoration programs worldwide. This research aims to define adequate strategies to restore *Zostera noltii* meadows through the application of field based experiments. To this end, we undertook transplant experiments to test: (i) the influence of the sediment type on the survival and growth of the transplants; (ii) the utility of habitat modelling in the selection of appropriate recipient locations for seagrass transplantation; and (iii) the time required for the natural recovery of the donor beds. Results showed a greater growth of *Z. noltii* within sandy sediments in comparison to muddy sediments. Nevertheless, long-term survival of transplants was observed for muddy environments sheltered from high water current. Applied habitat suitability model rightfully predicted the success of the transplant, suggesting such models as appropriate management-decision tools for selecting transplant sites. Although donor bed recovery was assessed using different strategies (a hole in mud and a filled hole in sand), from a similar state as starting point (i.e., hole filled), seagrass recovered quicker in sandy sediment. In the light of our results several considerations in order to increase the chance of a successful restoration are stated to provide a sound basis to plan and implement further restoration projects of *Z. noltii.*

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Although seagrass meadows are considered ecologically important habitats in coastal marine ecosystems (Orth et al., 2006), providing several physical, biological, economic and social benefits (Cullen-Unsworth and Unsworth, 2013), their habitat is being lost and fragmented overall (Waycott et al., 2009; Short et al., 2011). Consequently, efforts to restore seagrass meadows are increasing widely (Paling et al., 2009; Cunha et al., 2012). Particularly in Europe, restoration efforts have focused on the transplantation of *Zostera marina* (e.g. van Katwijk et al., 1998; Bos and van Katwijk, 2007) and *Posidonia oceanica* (e.g.

Molenaar and Meinesz, 1995; Piazzi et al., 1998; Sánchez-Lizaso et al., 2009), whilst the restoration of *Zostera noltii* (e.g. Martins et al., 2005; van Katwijk et al., 2009; Suykerbuyk et al., 2012) and *Cymodocea nodosa* (e.g. Cunha et al., 2009) is less common.

According to literature, optimal survival of transplants mainly depends on sediment type and the transplant site selection (e.g. Seddon, 2004; Bos and van Katwijk, 2007; Busch et al., 2010; Fonseca, 2011; Renton et al., 2011). Thus, we aimed to evaluate those factors in the restoration of the intertidal seagrass *Z. noltii*. To this end, our objectives were to test: (i) the influence of the sediment type on the survival and growth of the transplants; (ii) the utility of habitat modelling in the selection of appropriate recipient locations for seagrass transplantation; and (iii) the time required for the natural recovery of the donor beds. These studies were designed to determine the most effective methods to maximize the success of a future large-scale restoration, with minimum impact on the donor beds.

* Corresponding author at: Universidad Laica Eloy Alfaro de Manabí, Central Research Department, Ciudadela Universitaria, Vía San Mateo s/n, 13-05-2732 Manta, Manabí, Ecuador.
E-mail address: mireia.valle@uleam.edu.ec (M. Valle).

2. Materials and methods

2.1. Study area, donor and recipient sites

This research has been developed in a temperate coastal area, in two estuaries within the Basque coast (SE Bay of Biscay, north of Spain; Fig. 1). In this coastal area, 7 out of the 12 estuaries are classified under the type 'estuaries with extensive intertidal flats' according to the European Water Framework Directive (2000/60/EC; Borja et al., 2004) and, therefore, appropriate for hosting *Z. notlii* meadows. However, the presence of this seagrass is restricted to 3 estuaries (Fig. 1) and has been recently listed as an endangered species within the Catalogue of Threatened Species in the Basque Country (BOPV, 2011). The decline of *Z. noltii* in this region might be partially explained by the general degradation of the estuaries over the last two centuries due to human pressures (Borja et al., 2006). Although water quality has considerably improved as a result of effective water treatment (Tueros et al., 2009), the natural recolonization of locally extinct seagrass populations in this coastal area would need long recovery time as suggested by the few and small extant populations, as sources of seeds and fragments, and by low dispersal rates of *Z. noltii* populations (Coyer et al., 2004; Diekmann et al., 2005; Chust et al., 2013). Thus, in order to assist the species to recolonize these estuaries, the local government has supported this research program to evaluate factors influencing the restoration of *Z. noltii* and to prevent further loss of this seagrass.

Donor sites where selected within the Oka estuary (Fig. 1), which has the best preserved and largest *Z. noltii* meadows within this region, hosting up to 87% of the seagrass beds surface (Garmendia et al., 2013) and where the genotypic diversity (i.e., number of unique individuals within populations) of *Z. noltii* meadows is the highest (0.74) in comparison to the other estuaries where *Z. noltii* occurs (Bidasoa 0.51 and Lea 0.20; Chust et al., 2013).

The recipient site (Butroe estuary, Fig. 1) was chosen on the basis of water quality, physical environment and similarity to the estuaries where the species is currently present (i.e., Oka, Lea and Bidasoa; Garmendia et al., 2010).

2.2. Transplanting procedure

Extraction and planting of seagrass sods (i.e., planting units, PUs, hereafter) was selected as the technique to be applied in all the transplants (Appendix A, Fig. 1). PUs consisted of seagrass sods of 38 cm long and 27 cm width (aerial surface of 1026 cm^2) including shoots, roots, and rhizomes with associated sediment (10–15 cm depth; Appendix A, Fig. 1). Extraction and plantation tasks were undertaken during low tide and lasted approximately three hours each working day. PUs were extracted from the donor bed and placed in wooden boxes (Appendix A, Fig. 1), which were covered with wet sheets to avoid desiccation during the field work. The PUs were transported by road to the recipient sites (one hour approx.). The wooden boxes were then placed in the intertidal flat of the recipient estuary, in a sheltered and not easily-visible location. Next day at the lowest tide, sods were planted in previously excavated holes of 10–15 cm depth.

In order to ensure that possible transplant failure was not related to the transplanting procedure and the associated stress, control transplants were carried out. Six control PUs were harvested following the same methodology during the field works in years 2011 and 2012. Control PUs were first extracted and introduced in wooden boxes and then covered with wet sheets during the time elapsed in the donor bed (approx. 2 h). Once the extraction work was finished, the harvested control PUs were returned to their original site following the same transplanting methodology used in the recipient site. Shoot density in the control PUs was sampled during one year and was compared to the shoot density in the natural undisturbed bed.

Table 1
Grain size classification for sandy and muddy sites (Wentworth, 1922).

Grain size (μm)	Wentworth class	Sandy site (%)	Muddy site (%)
<63	Silt	48.6	70.5
62.5–125	Very fine sand	7.7	7.4
125–250	Fine Sand	21.0	12.4
250–500	Medium sand	21.7	8.7
500–1000	Coarse sand	1.0	1.0

2.3. Influence of sediment type

To assess the influence of the sediment type on survival and growth of the transplants, 8 PUs were planted in the Butroe estuary in early spring 2009. Four PUs were transplanted in sandy sediment and four PUs in muddy sediment (Table 1). Transplants were planted 125 m apart. The sandy site was very close to the river channel at 0.2 m height above mean sea level, while the muddy site was close to the river edge at 0.5 m. Shoot density and horizontal growth (occupied aerial surface) were sampled monthly during 15 months. Differences between paired means of the measured variables (shoot density and horizontal growth) for sandy and muddy sediments were analyzed using a paired t-test (McDonald, 2009). Here, paired t-test is used since the variables (shoot density and growth) for each PU treatment (sandy and muddy sediment) are measured at the same date conditions and repeated for different dates.

2.4. Habitat suitability model

Restoration of seagrass beds should be preceded by careful site selection (e.g. van Katwijk et al., 2009; Fonseca, 2011). To this end habitat suitability modelling represents a promising approach to determine suitable locations for transplantation (Guisan and Zimmermann, 2000; Franklin, 2009; Valle et al., 2011).

In order to assess the usefulness of habitat suitability modelling in the restoration process, 9 PUs were planted in the Oka estuary in different locations where the species was not occurring and the habitat presented different probability of suitability according to a habitat suitability model developed for this estuary (Valle et al., 2014). The model was generated applying a Generalized Additive Model (GAM; Hastie and Tibshirani, 1996) and included topographical, sedimentological and hydrographical variables which are thought to influence the distribution of *Z. noltii*. We selected this model owing its high accuracy explaining the distribution of the *Z. noltii* in the Oka estuary (97% of deviance explained).

PUs were planted in March 2010 along a gradient of suitability (from low to high suitability; Fig. 2). Three PUs were placed in the southernmost location of the intertidal flat (OK1; low suitability, 28 ± 10%), three PUs in the middle part (OK2; high suitability, 98 ± 2%), and the last three PUs were located in the northernmost location (OK3; high suitability, 96 ± 1%). This gradient of suitability was primarily dependent on depth. To determine whether the model was useful for selecting the recipient site, the agreement between the transplants' success (i.e., survival and high shoot density) and the habitat suitability value (i.e., probability of occurrence) were compared. To assess this agreement, survival and shoot density in each PU were monthly sampled and compared to the observed density in natural undisturbed beds close to the donor site during one year. Considering the observed densities in the last sampling, a linear regression model was fitted between the mean shoot density, as the dependent variable, and the habitat suitability value, as the independent variable.
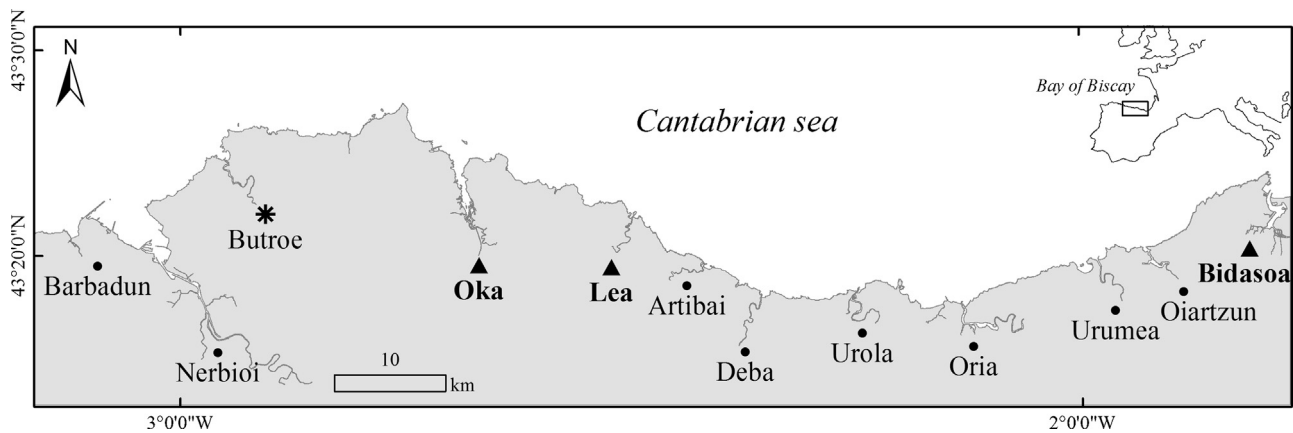
Fig. 1. Estuaries within the Basque coast (SE Bay of Biscay, north of Spain). Estuaries where *Zostera noltii* naturally occurs (in bold, black triangles). Butroe estuary, recipient of transplant material (highlighted by an asterisk).
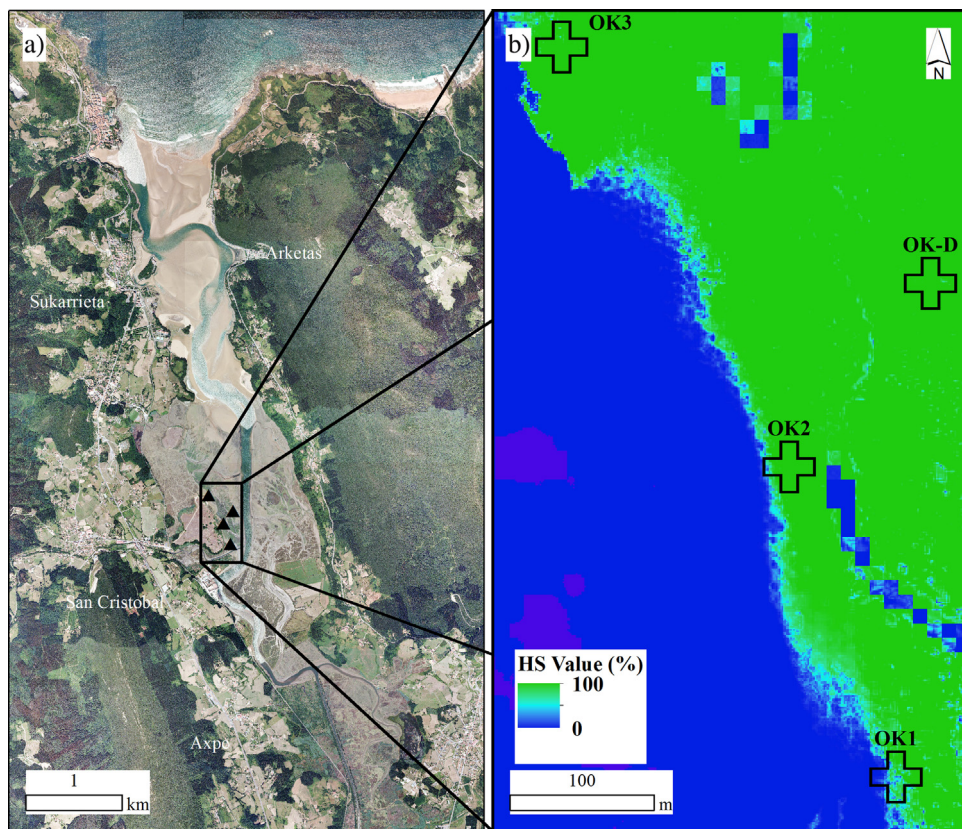

Fig. 2. a) Oka estuary where transplant and donor sites are located (black triangles). b) Habitat suitability map zoom to the transplants sites (OK1, OK2 and OK3) and donor site (OK-D).

2.5. Donor bed recovery

The time required for a natural recovery of the donor bed was assessed in 2010, 2011 and 2012. The donor site selected in 2010 was established in muddy sediment, whereas the donor sites from 2011 and 2012 were established in sandy sediment. In addition to sedimentological differences, two strategies were implemented after the extraction of the transplanting stock. In 2011 and 2012 the dug holes were replenished (i.e. covered) with surrounding sandy sediment (Appendix A, Fig. 2). In 2010 no action was undertaken after the extraction of PUs (Appendix A, Fig. 3).

In 2010 donor bed monitoring consisted of bimonthly measurement of depth in the dug hole and field photographs during the first year; thereafter a sparser sampling rate was followed (4 months between samplings). In 2011 and 2012 donor beds were monitored by monthly field photographs until total recovery was observed. Once regrowth was observed, shoot density was sampled in the donor beds and compared to surrounding natural undisturbed *Z. noltii* meadows.

2.6. Field measurements and data processing

All transplants were visited monthly during the first year for in situ measurements. Shoot density was sampled deploying a 10×10 cm quadrat inside the PUs and counting the number of surviving shoots. Sampled density was expressed in shoot m^{-2}.
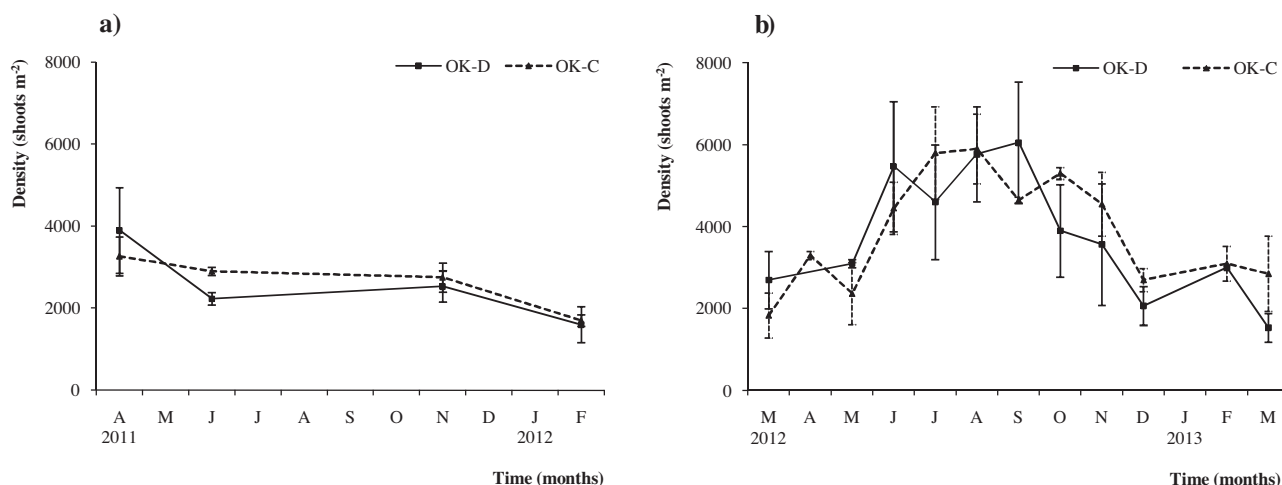
Fig. 3. Mean (±Standard Deviation) shoot density of *Zostera noltii* in control planting units (OK-C) and natural undisturbed bed close to donor sites (OK-D), a) data from 2011 transplants; (b) data from 2012 transplants.

Density was sampled in the densest area of the PU; this criteria was selected to avoid possible bias due to shoot burial (due to sediment deposition and algae) in areas of the quadrats. Horizontal growth was calculated using field photographs of the PUs. Photographs were processed using an image processing and analysis software (ImageJ) to estimate the aerial surface of one PU based on the presence of shoots (or leaves). Subsequently, an areal extent ratio index was calculated as the ratio between the areal extent in the time t and the initial areal extent of the PU (i.e., an areal extent ratio index of 2 means that a PU has doubled its initial aerial surface).

3. Results

3.1. Transplanting procedure

In both control trials, PUs showed a very similar seasonal dynamics to the natural bed (Fig. 3), indicating that the used transplanting procedure, using sods and spring timing, was not affecting the success rate of the PUs.

3.2. Influence of sediment type

Z. noltii shoot density was observed to be significantly higher from the 2nd to the 9th month (paired *t*-test, $p = 0.003$) in the PUs established in sandy sediment (average value 3143 ± 768 shoots m^{-2}) than in those in muddy sediment (average value 2360 ± 550 shoots m^{-2}; Fig. 4). Measured areal extent ratio index was also found to be significantly different between both treatments (paired *t*-test, $p = 0.005$), observed average values were 3.26 ± 2.24 in sandy sediments and 1.27 ± 0.57 in muddy sediments. However, after the tenth month the development in the PUs within sandy sediment appeared to be negatively influenced by burial due to the displacement of sand occurring close to the main channel (Fig. 4). In June 2010 (15 months after the planting), a river flood event, which eroded a large amount of sediment in this zone, caused the loss of all PUs in the sandy site (Fig. 4).

The sandy sediment appeared to be more suitable for root growth and establishment than muddy sediment during the first months (sandy PUs showed an areal extent ratio index greater than 5, while in muddy PUs it was lower than 2; Fig. 5). Nevertheless, long-term survival of transplanted PUs was better in muddy environments. After 5.5 years a PU in the muddy site still survives (25% in terms of number of transplanted PUs), it has increased 8 times

its aerial surface (200% in terms of transplanted area) and shows a positive growing trend.

3.3. Habitat suitability model accuracy

An initial average density value of 5000 shoots m^{-2} was observed in all PUs transplanted. Whilst shoot density in PUs from OK1 site (low suitability value) showed a decreasing trend after the second month and a maximum areal extent ratio index of 0.77, PUs in OK2 and OK3 sites (high suitability value) showed a good general condition after transplantation (i.e., similar density trends to the natural population; Fig. 6). Areal extent ratio index in OK2 increased steady from 0.89 to 3.6. OK3 suffered an external impact in winter which suddenly interrupted its development (its areal extent ratio index decreased from 1.2. in November to 0.41 in December) and led to an important decrease in shoot density (Fig. 6). The external impact might be related to trampling by shellfish-gatherers which were observed several times within the PUs of this site during the monitored year, negatively affecting the transplants. Observed mean shoot density during the last sampling month (June 2011) in each site was: 300 ± 173 shoots m^{-2} within OK1; 3800 ± 872 shoots m^{-2} within OK2; and 1967 ± 651 shoots m^{-2} within OK3. In turn, the density in the natural donor population (OK-D) was 4500 shoots m^{-2}. The linear regression model fitted between the shoot density of the PUs and the habitat suitability value, showed a significant relation ($p = 0.007$) and presented an adjusted R^2 of 0.63 (Fig. 7), indicating a positive relation between habitat suitability and the success of transplants.

3.4. Donor bed recovery

In 2011 and 2012, the donor sites were completely recovered after one year (i.e., no apparent external impact remained and replacement of donor material with regrowth of rhizomes and shoots occurred, being shoot density into the hole similar to natural, non-disturbed meadows in the area; Appendix A, Figs. 4 and 5). In 2010, sediment in the donor site was muddy and the dug hole was not replenished. In this case, more than 24 months were needed to naturally cover the hole and to start the recovery of the vegetative material (Appendix A, Fig. 6). However, after 43 months a nearly complete recovery was also observed in this donor site (2.5 years more than in 2011 and 2012 trials; Appendix A, Fig. 6).
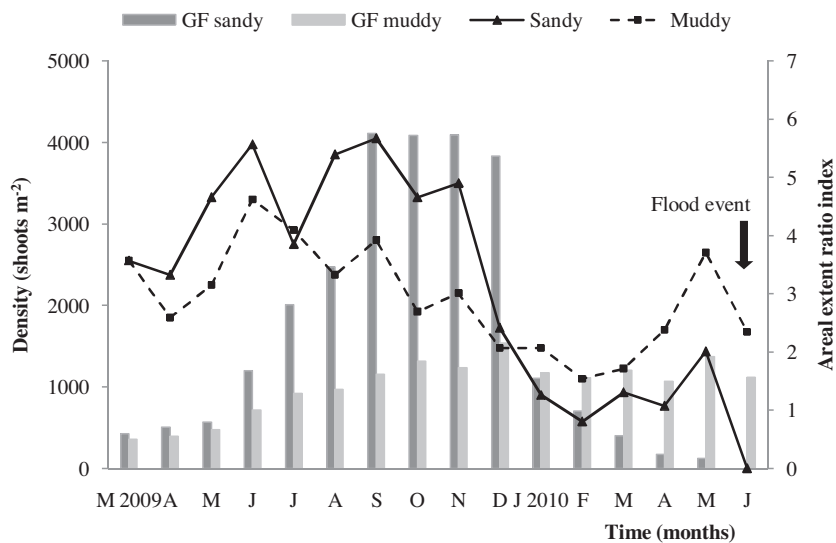
Fig. 4. Mean shoot density (shoots m⁻²) of *Zostera noltii* in PUs planted in sandy sediment and in muddy sediment (lines). Columns indicate the areal extent ratio index of sandy PUs (dark grey) and muddy PUs (light grey).
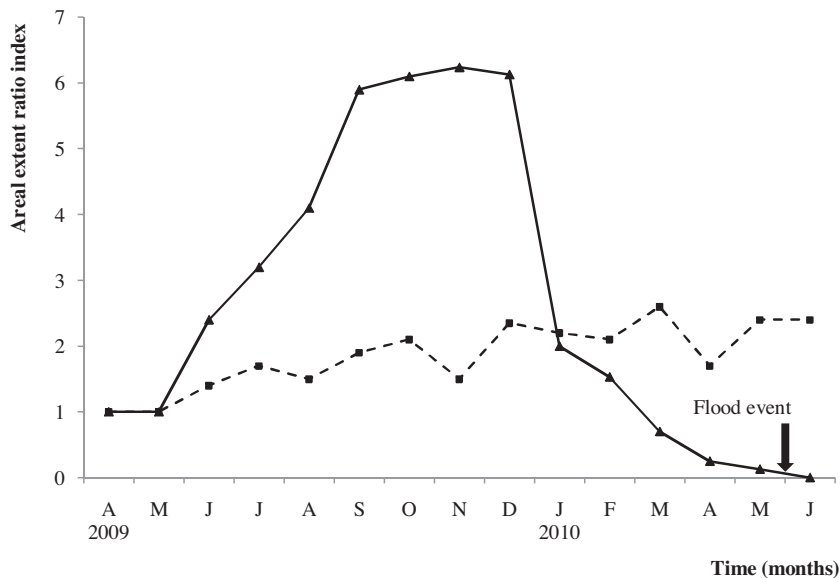

Fig. 5. Areal extent ratio index evolution for a PU within sandy sediment (solid line and triangles) and a PU within muddy sediment (dashed line and rectangles).

4. Discussion

4.1. Transplanting procedure

Control PUs showed similar dynamics in shoot density to natural populations, thus extraction and planting of sods of ca. 1000 cm² and 10 cm depth was found to be an adequate transplanting procedure for *Z. noltii*. This procedure remains a mainstay of vegetative transplantations (Fonseca, 2011) as it has been found to yield the highest chances of success (Fonseca et al., 1998). As explained by Fonseca (1994) and Paling et al. (2001), this method minimizes disruption to root and rhizome tissues allowing the development of the transplanted shoots and a successful transplant establishment.

Transplanting period was also found to be adequate. We transplanted in early spring, when belowground biomass is well developed, but the growing season has not fully started yet (i.e., higher percentage than aboveground biomass; Vermaat and Verhagen, 1996). This period also coincides with the season where temperature and light conditions start increasing (Martins et al., 2005).

4.2. Influence of sediment type

We found a greater areal extent ratio index in the PUs established in sandy sediment in comparison to those transplanted in muddy sediment during the first growing season (Figs. 4 and 5). Nevertheless, the long-term survival of transplanted PUs was observed within muddy environments sheltered from high currents. These findings suggest that sediment type affects the growth, whereas location contributes to survival, and confirm that sheltered locations are essential for longer-term survival of transplanted seagrass plots (van Katwijk et al., 2009). Marbà and Duarte (1995) also confirmed that high sediment mobility maintains seagrass beds in a continuous state of colonization involving spatially asynchronous patch growth and subsequent mortality.
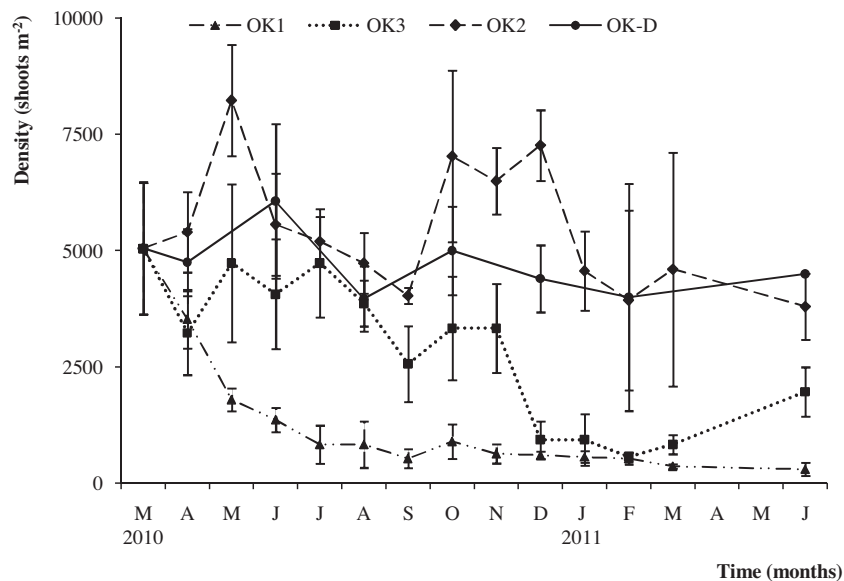
Fig. 6. Mean (±SD) shoot density (shoots m^{-2}) of *Zostera noltii* in PUs from OK1, OK2 and OK3 sites; and of the natural population at the donor site (OK-D).
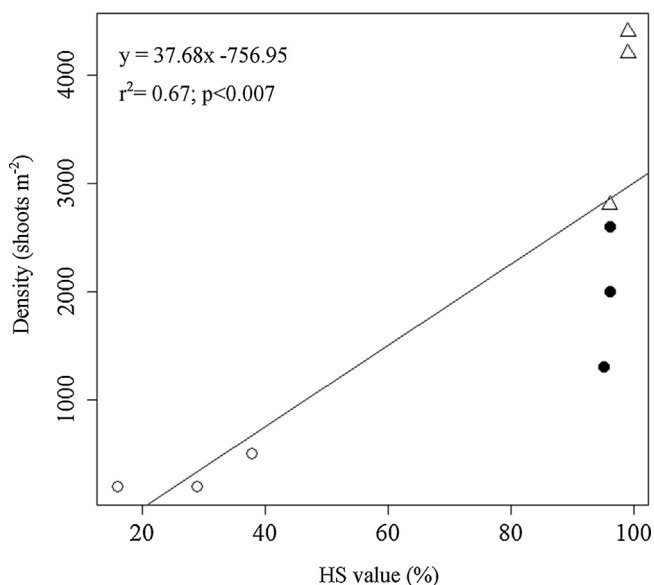

Fig. 7. Linear regression plot between the mean shoot density (shoots m^{-2}) as the dependent variable and the habitat suitability (HS) value (%) as the independent variable. Open circles (PUs from OK1), open triangles (PUs from OK2) and black dots (PUs from OK3).

to a more sheltered zone. When a bigger restoration project is planned, transplanted seagrass beds could be left in place because they will create their own mutual sheltering effect since they can act as ecosystem engineers and modify their abiotic environment (Jones et al., 1997). Vermaat et al. (1987) demonstrated along a transect gradient how mutual sheltering provides defense against adverse conditions such as current velocities with concomitant high chances of uprooting.

4.3. Habitat suitability model

Mapping suitable sites for restoration practices has been recommended by several authors (e.g. Kelly et al., 2001; Bekkby et al., 2008; van Katwijk et al., 2009). Here the usefulness of a habitat suitability model (Valle et al., 2014) for the selection of an appropriate recipient site has been tested; the model rightfully predicted the success of the transplant. We have shown that planting within predicted suitable sites increased the chance of a successful restoration. Thus, the observed positive relation between success of PUs (i.e., shoot density) and habitat suitability values indicates that the habitat suitability model predicts adequate locations for transplants. Therefore, building a habitat suitability model to support the selection of the most suitable recipient sites is highly recommended in order to improve the essential guideline on seagrass transplantation: careful site selection (e.g. van Katwijk et al., 2009; Marion and Orth, 2010). The habitat suitability model should be built within the first stage of the restoration programme and should be subjected to experts' opinion (Kelly et al., 2001). Before deciding the location of the transplants, the potential uses (e.g., recreational, boating, shellfish collectors) of the suitable sites must also be considered. In this sense, the trampling disturbance we found in the PUs from OK3 (highly suitable site) probably negatively affected the transplants (marked decrease in shoot density and in areal extent ratio index) and consequently, a highly suitable site, was close to become not suitable due to human pressure (i.e., transit zone).

4.4. Donor bed recovery

Z. noltii seagrass combines a very high branching rate (Vermaat and Verhagen, 1996) with a moderately fast rhizome elongation rate suggesting that it is likely capable of fast patch growth (Cunha et al., 2004). These growth rates were observed in the sandy donor

After 5.5 years we reported a survival rate of 25% for the transplants located in muddy sediment. Besides this observed survival rate, which is close to the survival rate documented by Fonseca et al. (1998), the PU from the muddy site showed a very successful spatial expansion: it increased eight times in extent and 200% of the initially transplanted overall area is maintained.

Although long-term survival was only documented for the muddy site, considering the exponential areal expansion rates of the PUs transplanted in the sandy site, spring culture of transplants can be recommended for small scale restoration projects. This might be done selecting sandy environments as initial location to acclimate and enhance the growth of the PUs before definitive transplantation. However, this strategy should consider possible occurrence of punctual and unpredictable events (such as floods or storms) and therefore, once the PUs have grown, transplants should be moved from sandy locations (i.e. exposed environment)

site where the hole created after the extraction of PUs was replenished (i.e., filled) with surrounding sediments, confirming that this species can rapidly recover by clonal growth after modest sediment disturbance as documented by Han et al. (2012). In muddy donor population where no replenish was undertaken, the recovery lasted much longer, suggesting that both, the sediment type and the presence of the hole, probably contributed to the delayed recovery. Thus, to minimize the impact produced in the donor beds, selection of sandy environment and filling excavations are found to be adequate strategies. Bourque and Fourqurean (2014) also suggested filling excavations as an important step on seagrass restoration.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.aquabot.2015.07.002

References

BOPV, 2011. Orden de modificación del catálogo vasco de especies amenazadas de la fauna y flora silvestre y marina. BOPV-Basque Country Oficial Bull. 37, 12 pp.

Bekkby, T., Rinde, E., Erikstad, L., Bakkestuen, V., Longva, O., Christensen, O., Isachsen, E., Isæus, M., 2008. Spatial probability modelling of eelgrass (Zostera marina) distribution on the west coast of Norway. ICES J. Mar. Sci. 65, 1093–1101.

Borja, Á., Franco, J., Valencia, V., Bald, J., Muxika, I., Belzunce, M.J., Solaun, O., 2004. Implementation of the European water framework directive from the Basque country (northern Spain): a methodological approach. Mar. Pollut. Bull. 48, 209–218.

Borja, Á., Galparsoro, I., Solaun, O., Muxika, I., Tello, E.M., Uriarte, Á., Valencia, V., 2006. The European water framework directive and the DPSIR, a methodological approach to assess the risk of failing to achieve good ecological status. Estuar. Coast. Shelf Sci. 66, 84–96.

Bos, A.R., van Katwijk, M.M., 2007. Planting density, hydrodynamic exposure and mussel beds affect survival of transplanted intertidal eelgrass. Mar. Ecol. Prog. Ser. 336, 121–129.

Bourque, A.S., Fourqurean, J.W., 2014. Effects of common seagrass restoration methods on ecosystem structure in subtropical seagrass meadows. Mar. Environ. Res. 97, 67–78.

Busch, K.E., Golden, R.R., Parham, T., Karrh, L.P., Lewandowski, M.J., Naylor, M.D., 2010. Large-scale Zostera marina (eelgrass) restoration in Chesapeake Bay, Maryland, USA. Part I: a comparison of restoration methods in the patuxent and potomac rivers. Restor. Ecol. 18, 490–500.

Chust, G., Albaina, Á., Aranburu, Á., Borja, Á., Diekmann, O.E., Estonba, Á., Franco, J., Garmendia, J.M., Iriondo, M., Muxika, I., Rendo, F., Rodríguez, J.G., Ruiz-Larrañaga, O., Serrão, E.Á., Valle, M., 2013. Connectivity, neutral theories and the assessment of species vulnerability to global change in temperate estuaries. Estuar. Coast. Shelf Sci. 131, 52–63.

Coyer, J.A., Diekmann, O.E., Serrao, E.A., Procaccini, G., Milchakova, N., Pearson, G.A., Stam, W.T., Olsen, J.L., 2004. Population genetics of dwarf eelgrass Zostera noltii throughout its biogeographic range. Mar. Ecol. Prog. Ser. 281, 51–62.

Cullen-Unsworth, L.C., Unsworth, R., 2013. Seagrass meadows, ecosystem services, and sustainability. Environ.: Sci. Policy Sustain. Dev. 55, 14–28.

Cunha, A.H., Duarte, C.M., Krause-Jensen, D., 2004. How long time does it take to recolonize seagrass beds? In: Borum, J., Duarte, C.M., Krause-Jensen, D., Greve, T.M. (Eds.), European Seagrasses: An Introduction to Monitoring and Management. EU project Monitoring and Managing of European Seagrasses, Conpenhagen, Denmark, pp. 72–76.

Cunha, A.H., Assis, J.F., Serrão, E.A., 2009. Estimation of available seagrass meadow area in Portugal for transplanting purposes. J. Coast. Res. 56, 1100–1104.

Cunha, A.H., Marbá, N.N., van Katwijk, M.M., Pickerell, C.H., Henriques, M., Bernard, G., Ferreira, A., Garcia, S., Garmendia, J.M., Manent, P., 2012. Changing paradigms in seagrass restoration. Restor. Ecol. 20, 427–430.

Diekmann, O.E., Coyer, J.A., Ferreira, J., Olsen, J.L., Stam, W.T., Pearson, G.A., Serrao, E.A., 2005. Population genetics of Zostera noltii along the west Iberian coast: consequences of small population size, habitat discontinuity and near-shore currents. Mar. Ecol. Prog. Ser. 290, 89–96.

European Water Framework Directive, 2000. Directive 2000/60/EC of the European parliament and of the council establishing a framework for the community action in the field of water policy. http://ec.europa.eu/environment/water/water-framework/index_en.html

Fonseca, M.S., Kenworthy, W.J., Thayer, G.W., 1998. Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters. In: NOAA Coastal Ocean Program Decision Analyses Series No. 12. NOAA. Coastal Ocean Office, Silver Spring, MD, Washington, DC, 222 pp.

Fonseca, M.S., 1994. A guide to transplanting seagrasses in the Gulf of Mexico. Texas A&M University Sea Grant College Program, TAMU-SG-94-601, College Station, 26 pp.

Fonseca, M.S., 2011. Addy revisited: what has changed with seagrass restoration in 64 years? Ecological Restoration 29, 73–81.

Franklin, J., 2009. Mapping Species Distribution Spatial Inference and Prediction. Cambridge University Press, New York, 320 pp.

Garmendia, J.M., Rodríguez, J.G., Borja Á, Franco, J., 2010. Clasificación de los estuarios del PaÍs Vasco como zonas potenciales para la restauración de praderas intermareales de Zostera noltii. Rev. Investig. Mar. 17, 40–61.

Garmendia, J.M., Valle, M., Borja Á, Chust, G., Franco, J., 2013. Cartografía de Zostera noltii en la costa vasca: cambios recientes en su distribución (2008–2012). Rev. Investig. Mar. 20, 1–22.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.

Han, Q., Bouma, T.J., Brun, F.G., Suykerbuyk, W., van Katwijk, M.M., 2012. Resilience of Zostera noltii to burial or erosion disturbances. Mar. Ecol. Prog. Ser. 449, 133–143.

Hastie, T., Tibshirani, R., 1996. Generalized additive models. Stat. Sci. 1, 297–318.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Kelly, N.M., Fonseca, M., Whitfield, P., 2001. Predictive mapping for management and conservation of seagrass beds in North Carolina. Aquat. Conserv.: Mar. Freshwater Ecosyst. 11, 437–451.

Marbà, N., Duarte, C.M., 1995. Coupling of seagrass (Cymodocea nodosa) patch dynamics to subaqueous dune migration. J. Ecol. 83, 381–389.

Marion, S.R., Orth, R.J., 2010. Factors influencing seedling establishment rates in Zostera marina and their implications for seagrass restoration. Restor. Ecol. 18, 549–559.

Martins, I., Neto, J.M., Fontes, M.G., Marques, J.C., Pardal, M.A., 2005. Seasonal variation in short-term survival of Zostera noltii transplants in a declining meadow in Portugal. Aquat. Bot. 82, 132–142.

McDonald, J.H., 2009. Handbook of Biological Statistics, 2nd ed. Sparky House Publishing, Baltimore, Maryland, 287 pp.

Molenaar, H., Meinesz, A., 1995. Vegetative reproduction in Posidonia oceanica: survival and development of transplanted cuttings according to different spacings; arrangements and substrates. Botanica Marina 38, 313–322.

Orth, R.J., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. Bioscience 56, 987–996.

Paling, E.I., van Keulen, M., Wheeler, K.D., Phillips, J., Dyhrberg, R., 2001. Mechanical seagrass transplantation in Western Australia. Ecol. Eng. 16, 331–339.

Paling, E.I., Fonseca, M.S., van Katwijk, M.M., van Keulen, M., 2009. Seagrass restoration. In: Perillo, G., Wolanski, E., Cahoon, D., Brinson, M. (Eds.), Coastal Wetlands: An Ecosystem Integrated Approach. Elsevier, Amsterdam, The Netherlands, pp. 687–713.

Piazzi, L., Balestri, E., Magri, M., Cinelli, F., 1998. Experimental transplanting of Posidonia oceanica (L.) Delile into a disturbed habitat in the Mediterranean Sea. Bot. Mar. 41, 593–602.

Renton, M., Airey, M., Cambridge, M.L., Kendrick, G.A., 2011. Modelling seagrass growth and development to evaluate transplanting strategies for restoration. Ann. Bot. 108, 1213–1223.

Sánchez-Lizaso, J.L., Fernández-Torquemada, Y., González-Correa, J.M., 2009. Evaluation of the viability of Posidonia oceanica transplants associated with a marina expansion. Bot. Mar. 52, 471–476.

Seddon, S., 2004. Going with the flow: facilitating seagrass rehabilitation. Ecol. Manag. Restor. 5, 167–176.

Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Sidik Bujang, J., Calumpong, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freeman, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Kenworthy, W.J., La Nafie, Y.A., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., van Tussenbroek, B., Vergara, S.G., Waycott, M., Zieman, J.C., 2011. Extinction risk assessment of the world's seagrass species. Biol. Conserv. 144, 1961–1971.

Suykerbuyk, W., Bouma, T.J., van der Heide, T., Faust, C., Govers, L.L., Giesen, W.B.J.T., de Jong, D.J., van Katwijk, M.M., 2012. Suppressing antagonistic bioengineering feedbacks doubles restoration success. Ecol. Appl. 22, 1224–1231.

Tueros, I., Borja, Á., Larreta, J., Rodríguez, J.G., Valencia, V., Millán, E., 2009. Integrating long-term water and sediment pollution data, in assessing

chemical status within the European Water Framework Directive. Mar. Pollut. Bull. 58, 1389–1400.

Valle, M., Borja, Á., Chust, G., Galparsoro, I., Garmendia, J.M., 2011. Modelling suitable estuarine habitats for *Zostera noltii*, using ecological niche factor analysis and bathymetric LiDAR. Estuar. Coast. Shelf Sci. 94, 144–154.

Valle, M., Chust, G., del Campo, Á., Wisz, M.S., Olsen, S.M., Garmendia, J.M., Borja, Á., 2014. Projecting future distribution of the seagrass *Zostera noltii* under global warming and sea level rise. Biol. Conserv. 170, 74–85.

Vermaat, J.E., Verhagen, F.C.A., 1996. Seasonal variation in the intertidal seagrass *Zostera noltii* Hornem: coupling demographic and physiological patterns. Aquat. Bot. 52, 259–281.

Vermaat, J.E., Hootsmans, M.J.M., Nienhuis, P.H., 1987. Seasonal dynamics and leaf growth of *Zostera noltii* Hornem., a perennial intertidal seagrass. Aquat. Bot. 28, 287–299.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, K.L., Hughes, R.G., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106, 12377–12381.

Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30, 377–392.

van Katwijk, M.M., Schmitz, G.H.W., Hanssen, L.S.A.M., den Hartog, C., 1998. Suitability of *Zostera marina* populations for transplantation to the Wadden Sea as determined by a mesocosm shading experiment. Aquat. Bot. 60, 283–305.

van Katwijk, M.M., Bos, A.R., de Jonge, V.N., Hanssen, L.S.A.M., Hermus, D.C.R., de Jong, D.J., 2009. Guidelines for seagrass restoration: importance of habitat selection and donor population, spreading of risks, and ecosystem engineering effects. Mar. Pollut. Bull. 58, 179–188.