

Effect of trampling and digging from shellfishing on *Zostera noltei* (Zosteraceae) intertidal seagrass beds

Joxe Mikel Garmendia¹, Mireia Valle^{2,3}, Ángel Borja¹, Guillem Chust², Dae-Jin Lee⁴, J. Germán Rodríguez¹, Javier Franco¹

¹AZTI, Marine Research Division, Herrera kaia, Portualdea z/g, 20110 Pasaia, Spain.

(JMG) (Corresponding autor) E-mail: jgarmendia@azti.es. ORCID iD: <http://orcid.org/0000-0002-9403-1777>

(AB) E-mail: aborja@azti.es. ORCID iD: <http://orcid.org/0000-0003-1601-2025>

(JGR) E-mail: grodriguez@azti.es. ORCID iD: <http://orcid.org/0000-0003-1565-4851>

(JF) E-mail: jafranco@azti.es. ORCID iD: <http://orcid.org/0000-0002-8629-3558>

²AZTI, Marine Research Division, Txatxarramendi uhartea z/g, 48395 Sukarrieta, Spain.

(MV) E-mail: mvalle@post.com. ORCID iD: <http://orcid.org/0000-0001-8517-8518>

(GC) E-mail: gchust@azti.es. ORCID iD: <http://orcid.org/0000-0003-3471-9729>

³Universidad Laica Eloy Alfaro de Manabí, Facultad de Ciencias del Mar, Ciudadela Universitaria, vía San Mateo s/n, 13052732 Manta, Ecuador.

⁴BCAM - Basque Centre for Applied Mathematics, Alameda Mazarredo 14, 48009 Bilbao, Spain.

(D-JL) E-mail: dlee@bcamath.org. ORCID iD: <http://orcid.org/0000-0002-8995-8535>

Summary: Seagrass beds are among the most valuable ecosystems in the world but they are also among the ones most affected by human activities, and they have decreased significantly in recent decades. In many areas, such as in the Basque Country (northern Spain), seagrass beds occupy areas that are also of interest for human activities such as recreation and shellfishing. They may therefore face a number of pressures that cause damage or irreversible states. Taking into account the limited distribution of seagrass beds in the Basque Country and the interest in their conservation, an eight-month field experiment focusing on the *Zostera noltei* growing season was carried out to evaluate the effect of shellfish gathering. We used generalized linear models to assess different intensities of trampling and digging, as the most important pressures of shellfishing applied to *Zostera noltei* beds. The results indicated that shoot density of *Z. noltei* was negatively altered by trampling treatments and positively affected (as a recovery) by digging treatments. This finding suggests that shellfishing adversely affects seagrass abundance and is potentially responsible for its low density in the Oka estuary. Our findings are important for management and should be taken into account in seagrass conservation and restoration programmes.

Keywords: *Zostera noltei*; seagrass; tidal flats; invertebrate harvesting; impact; field experiment.

Efecto del pisoteo y excavación del marisqueo sobre las praderas intermareales de *Zostera noltei* (Zosteraceae)

Resumen: Las praderas marinas se encuentran entre los ecosistemas más valiosos del mundo; sin embargo, también se encuentran, al mismo tiempo, entre los más afectados por las actividades humanas, por lo que han sufrido un importante declive en las recientes décadas. En algunas zonas, como por ejemplo en el País Vasco (Norte de España), las praderas marinas ocupan superficies que también son de interés para varias actividades humanas (p.ej. paseo, marisqueo); por ello, se enfrentan a diversas presiones que provocan daños o situaciones irreversibles. Teniendo en cuenta la reducida distribución de las praderas marinas en el País Vasco y el interés por su conservación se realizó un experimento de campo de 8 meses de duración, centrado en el periodo de crecimiento de *Zostera noltei*, para evaluar el efecto del marisqueo. Se aplicaron distintas intensidades de pisoteo y excavación (consideradas como presiones más importantes ejercidas por el marisqueo) sobre una superficie de pradera marina. Los resultados obtenidos mediante modelos mixtos lineales generalizados indican que la densidad de hojas de *Z. noltei* respondió negativamente en los tratamientos de pisoteo y positivamente (reflejando una recuperación) en el experimento de excavación. Esto sugiere que el marisqueo afecta negativamente a la abundancia de la pradera marina, y que es potencialmente responsable de su baja densidad en el estuario del Oka. Estas aportaciones resultan relevantes para la gestión de estas zonas y deberían tenerse en cuenta en los planes de conservación y restauración de las praderas marinas.

Palabras clave: *Zostera noltei*; pradera marina; intermareal; extracción de invertebrados; impacto; experimento de campo.

Citation/Como citar este artículo: Garmendia J.M., Valle M., Borja A., Chust G., Lee D.-J., Rodríguez J.G., Franco J. 2017. Effect of trampling and digging from shellfishing on *Zostera noltei* (Zosteraceae) intertidal seagrass beds. Sci. Mar. 81(1): 121-128. doi: <http://dx.doi.org/10.3989/scimar.04482.17A>

Editor: J.S. Troncoso.

Received: May 25, 2016. **Accepted:** November 29, 2016. **Published:** January 26, 2017.

Copyright: © 2017 CSIC. This is an open-access article distributed under the terms of the Creative Commons Attribution (CC-by) Spain 3.0 License.

INTRODUCTION

Seagrass beds are among the most valuable ecosystems in the world (Costanza et al. 2014), but they are also among those most affected by human activities (Pitanga et al. 2012) and have decreased significantly in recent decades (Short and Wyllie-Echeverria 2000), now occupying a much lower area than in the past (Short et al. 2011). This reduction in coverage has been related to direct and indirect human activities (Hastings et al. 1995, Baden et al. 2003), along with global climate change (Short et al. 2006). Seagrasses provide valuable goods and services (Cullen-Unsworth and Unsworth 2013), and their habitat is specifically targeted for conservation and restoration (Green and Short 2003, Cunha et al. 2012).

Seagrass meadows can be found in the intertidal and subtidal zones along temperate and tropical coastal areas and require specific conditions to grow and develop (Green and Short 2003). *Zostera* is the most widespread seagrass genus throughout the world, with 14 species currently recognized (Short et al. 2011). The species *Zostera noltei* is the dominant intertidal seagrass along the Atlantic coast of Europe and northern Africa (Moore and Short 2006), and its meadows are associated with flat areas within soft bottoms (sand mud mixtures) sheltered from high water current (Valle et al. 2015).

Among the several pressures and impacts affecting seagrasses, those occurring in the intertidal zone are mainly caused by human presence in general (Eckrich and Holmquist 2000, Pitanga et al. 2012), and by shellfish activity for human consumption and for live

bait in particular (Boese 2002, Dolch and Reise 2010, Nordlund and Gullström 2013).

Although it is evident that shellfish harvesting exerts a high pressure on seagrass meadows (Pitanga et al. 2012), there is only limited research that demonstrates the magnitude of the impact: e.g. Alexandre et al. (2005) and Cabaço et al. (2005) in Portugal; Feigné et al. (2007, in Auby et al. 2011) in France; and Park et al. (2011) in Korea. We therefore aimed to assess the effect of shellfishing activity on *Z. noltei* beds in an estuary with extensive intertidal flats, where we hypothesized that recreational and shellfishing activities (in terms of digging and trampling) are negatively affecting the development (i.e. shoot density) of the seagrass. This objective was addressed by undertaking a field-based experiment in which we tested the effect of trampling and digging on *Z. noltei* seagrass beds within sandy environments.

MATERIALS AND METHODS

Study area

We selected the Oka estuary located in the southeastern Bay of Biscay (Fig. 1) to perform the field experiment. This estuary has the largest *Z. noltei* meadows within the Basque coast (87% of the total seagrass bed area in the region, Garmendia et al. 2013), but a decline from 18.82 ha in 2008 to 16.65 ha in 2012 within the middle section of the estuary was recently detected (Garmendia et al. 2013). This area of the estuary supports potentially negative uses for seagrass development, such as recreational and shellfishing activities. Although, according to the Fishing Directorate of the

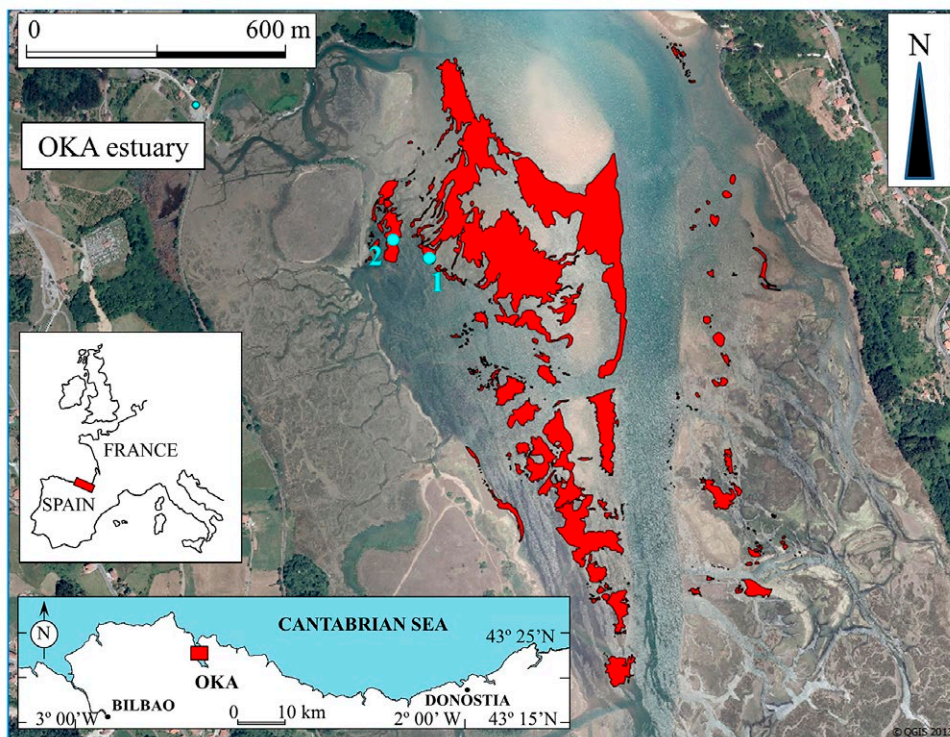


Fig. 1. – Study area. Middle section of the Oka estuary. In red, area occupied by seagrasses in 2012. Location of experiment areas: plot 1; plot 2.



Fig. 2. – Shellfish gathering in the Oka estuary. A, bivalve harvesting; B, live bait harvesting with vacuum sucker; C and D, sediment alteration as a result of both methods of shellfish harvesting.

Basque Government, the number of professional shellfish collectors has decreased in recent years, the number of illegal gatherers seems to be increasing (personal communication from shellfish collectors). According to the last update from the local fisher association in 2013, in the Oka estuary there are four professional shellfish collectors targeting bivalve molluscs (clams) and three professional collectors targeting live bait (worms, crustaceans and razor clam). Recreational collectors are also allowed in this estuary, and are mainly present during summer period. Although the number of recreational activities cannot be estimated a priori, the high number of tourists visiting the towns close to the estuary suggests that recreational shellfish collectors clearly exceed professional collectors by at least a factor of 5 (observed in our samplings). The open season for professional clam shellfishing, based on management measures established in order to protect clam populations, is from October to February (sometimes extended to March). However, live bait collection is allowed throughout the year. Extraction effort is limited by the low tides. Regarding awareness of the users to *Z. noltei* meadows, although they have heard something about seagrass importance, they are not concerned about its conservation and they do not avoid trampling on seagrass meadows during their activity.

Experimental set up: pressure effect of trampling and digging

The field experiment assessed the effect of two pressures observed on *Z. noltei* beds in the estuary (Fig. 2): (1) trampling (carried out by both collectors and walkers) and (2) hoe digging (carried out by shellfishers). The experiment started in May 2013 and ended in December 2013. Experiments to assess the effect of trampling and hoe digging were performed at two muddy sand sites (or plots) with similar sand and mud contents (plot 1, 80% sand and 20% mud; plot 2, 70% sand and 30% mud) (Fig. 1). The effect of trampling was assessed through a field experiment whose aim was to reflect different pressure levels (Fig. 3). Three lanes (A, B and C) were defined inside two plots of 5×4 m each with homogenous cover of *Z. noltei* (average density: plot 1, 1790±391 shoots m⁻²; plot 2, 1341±341 shoots m⁻²). The first lane (A) was the control lane with no intervention; the second lane (B) was a low-pressure lane with 20 laps per month; and the third lane (C) was a high pressure lane with 50 laps per month. The pressure was exerted once a month for 4 months (Table 1). The effect of digging was assessed through a field experiment consisting of four lanes (A, B, C and D) (Fig. 4). This experimental setup was based on

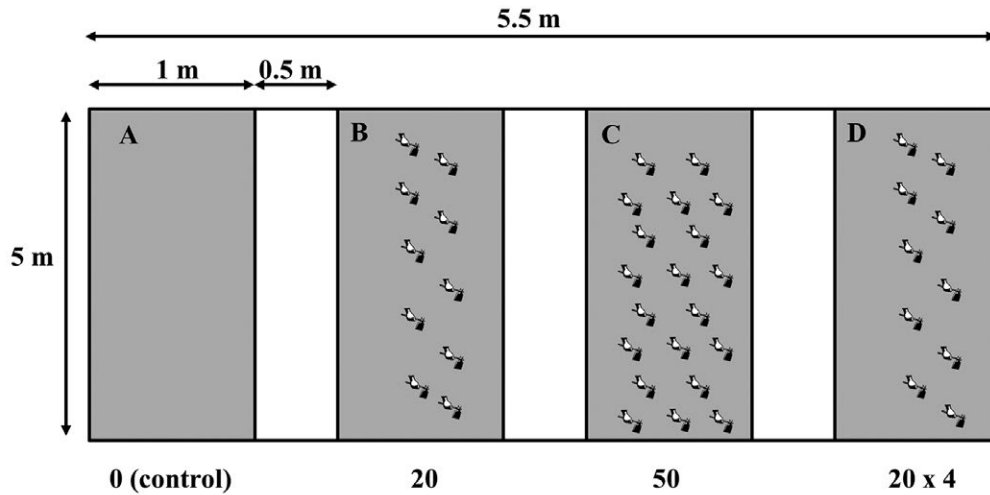


Fig. 3. – Trampling experiment: lane A, control, 0 footsteps; lane B, light pressure, 20 laps per month; and lane C, heavy pressure, 50 laps per month. In grey, experimental lanes.

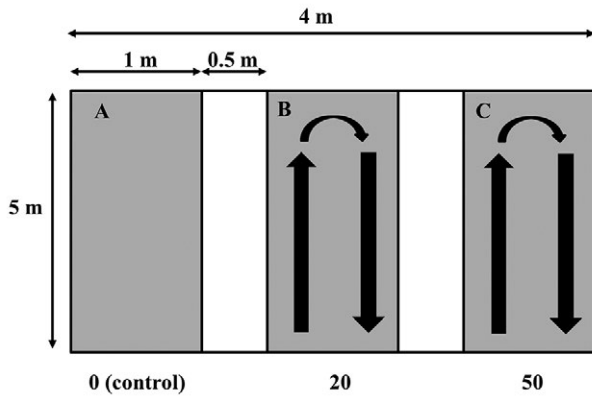


Fig. 4. – Digging experiment: lane A, control, 0 hoes; lane B, light pressure, intermittent, 20 hoes; lane C, heavy pressure, intermittent, 50 hoes; and lane D, continuous pressure, weekly, 20 hoes (4 times). In grey, experimental lanes.

Eckrich and Holmquist (2000) and aimed to be a proxy of single one-off pressure (with two different levels of pressure) and a constant pressure; to this end four lanes were defined inside two plots of 5×5.5 m each with homogenous cover of *Z. noltei* (average density: plot 1, 1632±337 shoots m⁻²; plot 2, 848±299 shoots m⁻²). The first lane (A) was the control lane with no intervention; the second lane (B) was the low intermittent pressure lane with 20 hoe digs per month; the third lane (C) was the high intermittent pressure lane with 50 hoe digs per month; and the fourth lane (D) was a constant pressure lane with 20 hoe digs per week. The pressures were exerted during the first month (Table 1).

In both field experiments, changes in *Z. noltei* shoot densities were monitored (Table 1). Samples were taken at time 0 (before pressure), month 2, month 4, and month 7 (Table 1). The samples consisted of (1) photographs and (2) measurements of shoot density (25×25 cm quadrats, 3 replicates in plot 1 and 2 in plot 2; first sampling randomly and resampling the same squares, non-destructive sampling).

Statistical analysis

Seagrass data were analysed using a generalized linear mixed model (GLMM; Breslow and Clayton 1993, Jiang 2007) in order to determine whether the shoot density, i.e. shoots m² (with Poisson errors), differed according to treatments and across time (for trampling and digging). GLMMs are an extension of generalized linear models (McCullagh and Nelder 1989) to include both fixed and random effects. The control lane was considered to reflect the natural development of the seagrass. The aim was to test the effect of treatment (i.e. trampling and digging) over time (where time 0 is the time before pressure) and with a control treatment. Hence, the interaction between treatment and time was included and the variability within each plot across time was accounted for with a random effect.

As imposed by the nested experimental design in two replicates (plots), the model considered the repeated measurements of two plots. The statistical analysis was done using the statistical software R using the glmer function of the library lme4 (Zuur et al. 2009, Bates et al. 2015).

Table 1. – Chronogram of the experiments. Measurements (Me), pressure (P) and both (Me/P). W, week; M, month. The same experimental design was replicated in plot 1 and in plot 2.

Experiment		M 0								
		W 0	W 1	W 2	W 3	M 1	M 2	M 3	M 4	M 7
Trampling	Lane A	Me					Me		Me	Me
	Lane B	Me/P				P	Me/P	P	Me/P	Me
	Lane C	Me/P				P	Me/P	P	Me/P	Me
	Lane D	Me					Me		Me	Me
Digging	Lane B	Me/P					Me		Me	Me
	Lane C	Me/P					Me		Me	Me
	Lane D	Me/P	P	P	P		Me		Me	Me
	Lane A	Me								

Table 2. – Means (and standard deviation) for plant shoot density (shoots m⁻²) in both pressure experiments (trampling and digging). Treatments: A, no pressure; B, light pressure; C, heavy pressure; D, continuous pressure.

Experiment	Time	Treatment			
		A	B	C	D
Trampling	0	1785.6 (451.0)	1520.0 (190.7)	1526.4 (578.9)	
	2	2284.8 (304.3)	1654.4 (679.6)	646.4 (533.7)	
	4	2195.2 (932.0)	1452.8 (1103.2)	355.2 (387.1)	
	7	2268.8 (326.8)	1548.8 (896.8)	828.8 (655.4)	
Digging	0	1254.4 (468.3)	1145.6 (495.2)	1497.6 (555.5)	1376 (588.4)
	2	1689.6 (833.2)	1033.6 (908.2)	1104 (722.2)	1267.2 (591.4)
	4	1568.0 (1191.4)	1203.2 (729.9)	1369.6 (434.4)	1731.2 (803.9)
	7	1692.8 (800.5)	1542.4 (968.7)	1945.6 (399.1)	2083.2 (235.5)

Table 3. – Generalized linear mixed model (GLMM) results indicating probability values for plant shoot density in both pressure experiments (trampling and digging). GLMM includes fixed effects (treatment and time), interaction between treatment and time, and random effects for plot replicates. In bold, significant p-values (<0.05) for fixed effects. Treatments: B, light pressure; C, heavy pressure; D, continuous pressure.

Experiment	Fixed effects	Estimate	p-value
Trampling	Treatment B	-0.231	<0.001
	Treatment C	-0.537	<0.001
	Time	0.026	0.145
	Treatment B : Time	-0.027	<0.001
	Treatment C : Time	-0.133	<0.001
Digging	Treatment B	-0.293	<0.001
	Treatment C	-0.115	<0.001
	Treatment D	-0.091	<0.001
	Time	0.043	0.075
	Treatment B : Time	0.018	<0.001
	Treatment C : Time	0.019	<0.001
	Treatment D : Time	0.036	<0.001

RESULTS

Mean values (and standard deviation) for plant shoot density in both pressure experiments (trampling and digging) are shown in Table 2. In the trampling experiment, while at site A densities increased by 27% from time 0 to time 7 months, at site B no clear differences were found during the experiment, and at site C the densities had decreased by 23% at time 4 months. On the other hand, in the digging experiment, after 7 months the densities had increased in all the treatments. No clear differences were found between treatments, except for time 2 months, when a slight decrease in densities was found in treatments B, C and D (10%, 26% and 8%, respectively), whereas an increase of 35% was observed in treatment A.

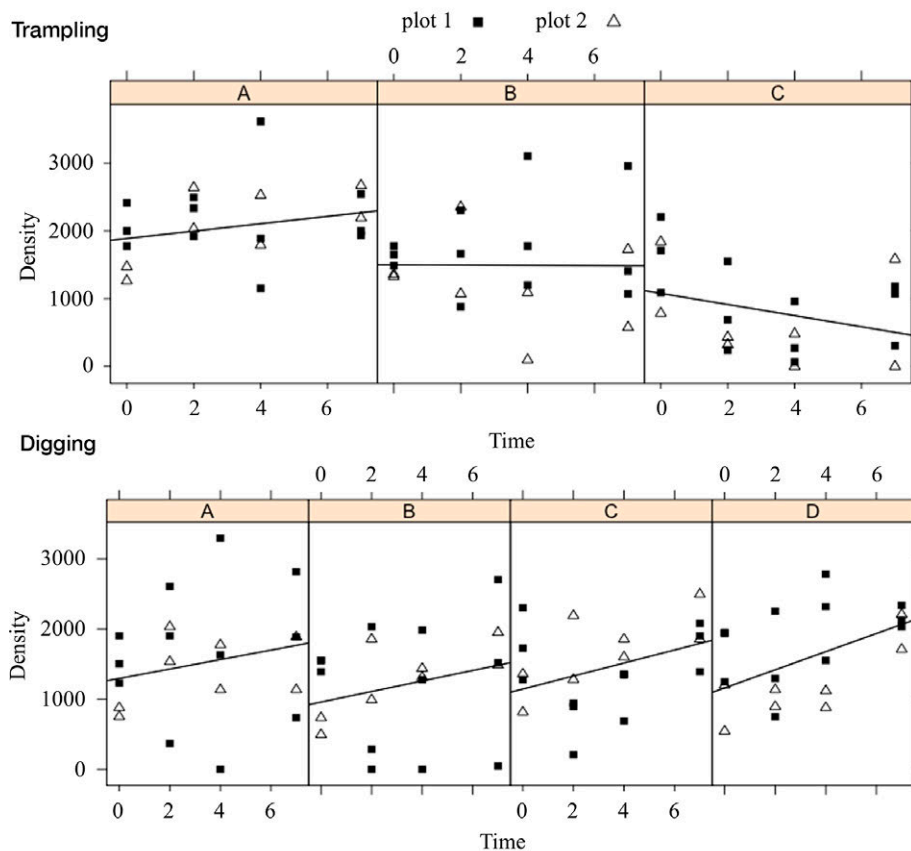


Fig. 5. – Generalized linear mixed model (GLMM) results showing shoot density (shoots m⁻²) of *Z. noltei* during both field experiments: Trampling (above) and Digging (bottom). Degrees of pressure in the trampling experiment: A, control, no pressure; B, low pressure; C, high pressure. Degrees of pressure in digging experiment: A, control, no pressure; B, low intermittent pressure; C, high intermittent pressure; and D, constant pressure. The lines represent the GLMM fitted to data.

Results from the GLMM applied to the trampling experiment (Table 3) showed significant negative differences in *Z. noltei* shoot density in the interactions between lanes B and C and time ($p < 0.0001$, Fig. 5A) in comparison with the control (lane A). This can be observed in changes in slopes over time on both plots between trampling treatments in Figure 5A: *Zostera* shoot densities increased throughout the growing season in the control lane (treatment A), appeared to be stable following moderate trampling (treatment B), and clearly declined under the impact of intense trampling (treatment C). This result indicates that applied pressure in both lanes (B, low trampling pressure; and specially C, high trampling pressure) affected negatively the shoot density in comparison with the control lane (A).

Results from the GLMM applied to the digging experiment (Table 3) showed significant positive differences in *Z. noltei* shoot density in the interactions between lanes B, C and D and time ($p < 0.0001$, Fig. 5B). As in the case of trampling, *Zostera* shoot densities also increased throughout the growing season in the control lane (treatment A). However, the slopes in the B, C and D lanes were slightly higher than in the control (Fig. 5B). This result indicates that applied pressures (B, low intermittent pressure, C, high intermittent pressure, and D, constant pressure) positively affected the shoot density in comparison with the control (A). Given that in the digging experiment pressure was only applied between time 0 and time 2, we interpreted this result as recovery of shoot density in times 4 and 7 (Table 3).

DISCUSSION

Most human activities in estuaries, such as pressure from trampling exerted by simply walking on seagrass, can cause direct physical damage to estuarine plants. At first, this impact might not seem very high because walkers move continuously (without stops) and do not usually produce major footprints and sediment movements except in very fine and soft sediment. Furthermore, the walk normally occurs in areas with relatively compact sediment. Similar to the findings of Eckrich and Holmquist (2000) and Travaille et al. (2015), our trampling experiment reduced the shoot density in seagrass beds in the Oka estuary. Trampling impact was in the Oka estuary negatively was shown to affect the survival and growth rate of *Z. noltei* planting units in a restoration project carried out by Valle et al. (2015). The impact of trampling increases with standing (which facilitates the sinking of the walker and the physical alteration of the substratum), slower movement and intensified trampling on a small area, which usually occurs when somebody is looking for something in the sediment, as in the case of shellfishing.

Shellfishing combines both trampling and digging (Cochón and Sánchez 2005). Feigné et al. (2007, in Auby et al. 2011) concluded that collection of clams carried out on foot and by hand in Arcachon (France) has a strong impact on *Z. noltei* seagrass. Similarly, Cabaço et al. (2005) concluded that shellfishing nega-

tively affects *Z. noltei* populations, despite the high recovery capacity of this species. In the Formosa estuary, Portugal, Cabaço et al. (2005) found that the high frequency and intensity of disturbance caused by shellfishing (especially in summer) prevents the total recovery of the seagrass meadow. These authors pointed out that seagrass can withstand the disturbance of shellfishing provided that, after an isolated disturbance, it is left to recover for one month. However, survival and recovery of the plant will depend on the type of physical damage (cutting or breakage), its magnitude and, if it is only a burial disturbance, on the burying magnitude (deep level and dwell time), as *Z. noltei* can only tolerate some degree of burial due to its high sensitivity to this disturbance (Cabaço et al. 2008). Furthermore, several authors have found a direct effect of shellfishing on seagrass density (Short and Wyllie-Echeverria 1996, Cabaço et al. 2005, Park et al. 2011), even with low-intensity pressure (Alexandre et al. 2005), but they refer to the activity of harvesting in general and do not specify the shellfishing method as we do here. In contrast, our digging experiment, where pressure was applied between time 0 and time 2, did increase the shoot density, which we associated with the recovery of seagrass in times 4 and 7.

In addition to the direct impact of shellfishing in seagrass abundances, the disturbances produced by gatherers can also affect benthic communities in different ways (García-García et al. 2015): by altering nutrient availability, by altering abundance and diversity of infaunal and epifaunal invertebrates, and by fostering a higher growth of green algae such as *Ulva* sp. It seems that *Ulva* sp. grows faster in the holes or puddles caused by shellfishing than on muddy platforms and in tidal ponds (van Alstyne et al. 2011), becoming an extra pressure for seagrass (Brun et al. 2003).

However, Boese (2002) does not consider recreational shellfishing as an important threat for intertidal seagrass, at least in the case of *Z. marina*. This author points out that seagrass remains in areas that have been heavily disturbed for decades by recreational gatherers, suggesting that long-term effects are minor. Nevertheless, the fact that seagrass does not disappear should not be considered as a minor alteration, since this seagrass would probably have reached larger surface areas if there had been no such shellfishing or if it were of a lower intensity. This might be happening in the Oka estuary, where the number of professional gatherers has decreased in the past decade, but the pressure on seagrass beds is not decreasing, probably due to an increase in the number of non-professional gatherers (especially illegal gatherers). According to Cabaço et al. (2008), the impact of an alteration will depend on the magnitude and frequency of disturbance, so recovery will also vary depending on the damage caused (Short and Wyllie-Echeverria 1996).

As the number of professional clam gatherers has decreased in the last decade, new licences, which are compulsory for shellfishing in the Oka estuary, have not been issued in recent years. This is supposed to be positive for seagrass conservation since the shellfishing pressure is apparently decreasing. However, the

increase in recreational and, especially, illegal gatherers is alarming, mainly due to their lack of awareness of the magnitude of the impact they cause and because they are an unidentified (and therefore inaccessible) audience for addressing environmental awareness campaigns.

In these areas, in which different human interests coexist, it is crucial to develop management and conservation plans according to the natural habitats and the activities carried out, especially when the survival of a species or habitat of great interest is at risk. *Z. noltei* is the only seagrass occurring in the Basque coastal estuaries, and is presently restricted to 3 (Oka, Lea and Bidasoa) out of the 12 estuarine ecosystems of the coast (Valle et al. 2015). It has therefore been listed as an endangered species within the Basque Catalogue of Threatened Species of Wild and Marine Fauna and Flora (23 February 2011). In addition, the Oka estuary includes a wide variety of ecosystems of international importance and is the best preserved estuary in the region. It is the main part of Urdaibai designated as a Biosphere Reserve by UNESCO in 1984. It was also included as a Ramsar site under the Ramsar List of Wetlands of International Importance (year 1992), and in the Natura 2000 Network (Specially Protected Bird Area, SPBA ES0000144, Birds Directive 79/409/EEC) (1994). The Urdaibai shoreline and marshes have recently been chosen among the Atlantic biogeographic region Sites of Community Importance to be designated a Special Area of Conservation (SAC) (ES2130007, Habitats Directive 92/43/EEC) (2013). In such an important natural area, the management strategy must be (re)defined, recognizing the importance of communication, exchanging information, sharing responsibilities and managing the participation of all users (Guimarães et al. 2012).

The high frequency and intensity of current shellfishing disturbance in the Oka estuary will negatively affect the natural development of *Z. noltei*. To stop this trend of seagrass regression, shellfishing impact must be monitored and managed. The goods and services provided by seagrasses must be highlighted in order to promote less aggressive shellfishing techniques (Cochón and Sánchez 2005). Knowledge of the importance of a resource is the first step towards its management, protection and sustainable use (de la Torre and Rönnbäck 2004, Guimarães et al. 2012).

CONCLUSIONS

From our experiments we can conclude that *Zostera noltei* was affected by the alteration produced by trampling. Further experimentation and monitoring is needed for final confirmation of the potential impacts, especially in the case of digging. It should also assess, for example, the interaction between digging and trampling and enlarge the experimental sample size. All this will help to provide a more robust assessment of direct impacts on seagrasses in this area.

Solving the lack of knowledge of shellfish gatherers about seagrass meadows and their importance could be a key element for estuarine habitat conservation.

Lack of information is a threat when activities are carried out in vulnerable natural environments: users are unaware of the severity of the impact that their activity produces. It is therefore necessary to increase understanding (especially among shellfish gatherers) of the importance of seagrass in marine ecosystems and how it can be conserved.

ACKNOWLEDGEMENTS

The authors would like to thank the Urdaibai Biosphere Reserve Board for giving permission to carry out field experiments and Itziar Canive for her help in the experiment. This work was funded by the Basque Water Agency (URA) through a cooperation agreement signed with AZTI for research on the application of Directive 2000/60/EC in the coastal area of the Basque Country. The research of Dae-Jin Lee was also supported by the Basque Government through the BERC 2014-2017 programme and by the Spanish Ministry of Economy and Competitiveness (MINECO) through the BCAM Severo Ochoa excellence accreditation SEV-2013-0323. This paper is contribution number 800 of the Marine Research Division (AZTI).

REFERENCES

- Alexandre A., Santos R., Serrão E. 2005. Effects of clam harvesting on sexual reproduction of the seagrass *Zostera noltii*. *Mar. Ecol. Prog. Ser.* 298: 115-122.
<https://doi.org/10.3354/meps298115>
- Auby I., Bost C.-A., Budzinski H., et al. 2011. Régression des herbiers de zostères dans le Bassin d'Arcachon: état des lieux et recherche des causes. Rapport Ifremer RST/LER/AR 11.007 Gironde Conseil Général, Arcachon, 195 pp.
- Baden S., Gullström M., Lundén B., et al. 2003. Vanishing seagrass (*Zostera marina*, L.) in Swedish coastal waters. *Ambio* 32: 374-377.
<https://doi.org/10.1579/0044-7447-32.5.374>
- Bates D., Maechler M., Bolker B., et al. 2015. Fitting Linear Mixed-Effects Models using lme4. *J. Stat. Soft.* 67(1): 1-48.
<https://doi.org/10.18637/jss.v067.i01>
- Boese B.L. 2002. Effects of recreational clam harvesting on eelgrass (*Zostera marina*) and associated infaunal invertebrates: in situ manipulative experiments. *Aquat. Bot.* 73: 63-74.
[https://doi.org/10.1016/S0304-3770\(02\)00004-9](https://doi.org/10.1016/S0304-3770(02)00004-9)
- Breslow N.E., Clayton D.G. 1993. Approximate inference in Generalized Linear Mixed Models. *J. Am. Stat. Assoc.* 88: 9-25.
<https://doi.org/10.2307/2290687>
- Brun F.G., Vergara J.J., Navarro G., et al. 2003. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. *Mar. Ecol. Prog. Ser.* 265: 85-96.
<https://doi.org/10.3354/meps265085>
- Cabaço S., Alexandre A., Santos S. 2005. Population-level effects of clam harvesting on the seagrass *Zostera noltii*. *Mar. Ecol. Prog. Ser.* 298: 123-129.
<https://doi.org/10.3354/meps298123>
- Cabaço S., Santos R., Duarte C.M. 2008. The impact of sediment burial and erosion on seagrasses: A review. *Estuar. Coast. Shelf S.* 79: 354-366.
<https://doi.org/10.1016/j.ecss.2008.04.021>
- Cochón G., Sánchez J.M. 2005. Variations of seagrass beds in Pontevedra (North-Western Spain): 1947-2001. *Thalassas* 21: 9-19.
- Costanza R., de Groot R., Sutton P., et al. 2014. Changes in the global value of ecosystem services. *Global Environ. Chang.* 26: 152-158.
<https://doi.org/10.1016/j.gloenvcha.2014.04.002>
- Cullen-Unsworth L., Unsworth R. 2013. Seagrass meadows, ecosystem services, and sustainability. *Environment* 55: 14-28.
<https://doi.org/10.1080/00139157.2013.785864>
- Cunha A.H., Marbà N., Van Katwijk M., et al. 2012. Changing paradigms in seagrass restoration. *Restor. Ecol.* 20: 427-430.

- <https://doi.org/10.1111/j.1526-100X.2012.00878.x>
de la Torre-Castro M., Rönnbäck O. 2004. Links between humans and seagrasses—an example from tropical East Africa. *Ocean Coast. Manage.* 47: 361-387.
<https://doi.org/10.1016/j.ocecoaman.2004.07.005>
- Dolch T., Reise K. 2010. Long-term displacement of intertidal seagrass and mussel beds by expanding large sandy bedforms in the northern Wadden Sea. *J. Sea Res.* 63: 93-101.
<https://doi.org/10.1016/j.seares.2009.10.004>
- Eckrich C.E., Holmquist J.G. 2000. Trampling in a seagrass assemblage: direct effects, response of associated fauna, and the role of substrate characteristics. *Mar. Ecol. Prog. Ser.* 201: 199-209.
<https://doi.org/10.3354/meps201199>
- García-García F.J., Reyes-Martínez M.J., Ruiz-Delgado M.C., et al. 2015. Does the gathering of shellfish affect the behavior of gastropod scavengers on sandy beaches? A field experiment. *J. Exp. Mar. Biol. Ecol.* 467: 1-6.
<https://doi.org/10.1016/j.jembe.2015.02.016>
- Garmendia J.M., Valle M., Borja Á., et al. 2013. Cartografía de *Zostera noltii* en la costa vasca: cambios recientes en su distribución (2008-2012). *Rev. Invest. Mar.* 20: 1-22.
- Guimarães M.H.M.E., Cunha A.H., Nzinga R.L., et al. 2012. The distribution of seagrass (*Zostera noltii*) in the Ria Formosa lagoon system and the implications of clam farming on its conservation. *J. Nat. Conserv.* 20: 30-40.
<https://doi.org/10.1016/j.jnc.2011.07.005>
- Green E.P., Short F.T. 2003. World atlas of seagrasses. Prepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, USA, 298 pp.
- Hastings K., Hesp P., Kendrick G.A. 1995. Seagrass loss associated with boat moorings at Rottne Island, Western Australia. *Ocean Coast. Manage.* 26: 225-246.
[https://doi.org/10.1016/0964-5691\(95\)00012-Q](https://doi.org/10.1016/0964-5691(95)00012-Q)
- Jiang J. 2007. Linear and Generalized Linear Mixed Models and their applications. Springer-Verlag, New York, 257 pp.
- McCullagh P., Nelder J. 1989. Generalized Linear Models. Monographs on statistics and applied probability, 37. Chapman and Hall, London, 511 pp.
- Moore K.A., Short F.T. 2006. *Zostera*: biology, ecology and management. In: Larkum A.W.D., Orth R.J., Duarte C.M. (eds), *Seagrasses: Biology, Ecology and Conservation*. Springer, Netherlands, pp. 361-386.
https://doi.org/10.1007/978-1-4020-2983-7_16
- Nordlund L.M., Gullström M. 2013. Biodiversity loss in seagrass meadows due to local invertebrate fisheries and harbour activities. *Estuar. Coast. Shelf Sci.* 135: 231-240.
<https://doi.org/10.1016/j.ecss.2013.10.019>
- Park S.R., Kim Y.K., Kim J.H., et al. 2011. Rapid recovery of the intertidal seagrass *Zostera japonica* following intense Manila clam (*Ruditapes philippinarum*) harvesting activity in Korea. *J. Exp. Mar. Biol. Ecol.* 407: 275-283.
<https://doi.org/10.1016/j.jembe.2011.06.023>
- Pitanga M.E., Montes M.J.F., Magalhaes K.M., et al. 2012. Quantification and classification of the main environmental impacts on a *Halodule wrightii* seagrass meadow on a tropical island in northeastern Brazil. *Ann. Brazilian Acad. Sci.* 84: 35-42.
<https://doi.org/10.1590/S0001-37652012005000010>
- Short F.T., Wyllie-Echeverria S. 1996. Natural and human-induced disturbance of seagrasses. *Environ. Conserv.* 23: 17-27.
<https://doi.org/10.1017/S0376892900038212>
- Short F.T., Wyllie-Echeverria S. 2000. Global seagrass declines and effects of climate change. In: Sheppard C. (ed.), *Seas at the millennium: an environmental evaluation*, 10-11. Elsevier Science, Amsterdam.
- Short F.T., Koch E.W., Creed J.C., et al. 2006. SeagrassNet monitoring across the Americas: case studies of seagrass decline. *Mar. Ecol.* 27: 277-289.
<https://doi.org/10.1111/j.1439-0485.2006.00095.x>
- Short F.T., Polidoro B., Livingstone S.R., et al. 2011. Extinction risk assessment of the world's seagrass species. *Biol. Conserv.* 144: 1961-1971.
<https://doi.org/10.1016/j.biocon.2011.04.010>
- Travaille K.L., Salinas-de-León P., Bell J.J. 2015. Indication of visitor trampling impacts on intertidal seagrass beds in a New Zealand marine reserve. *Ocean Coast. Manage.* 114: 145-150.
<https://doi.org/10.1016/j.ocecoaman.2015.06.002>
- Valle M., Garmendia J.M., Chust G., et al. 2015. Increasing the chance of a successful restoration of *Zostera noltii* meadows. *Aquat. Bot.* 127: 12-19.
<https://doi.org/10.1016/j.aquabot.2015.07.002>
- van Alstyne K.L., Flanagan J.C., Gifford S.A. 2011. Recreational clam harvesting affects sediment nutrient remineralization and the growth of the green macroalga *Ulva lactuca*. *J. Exp. Mar. Biol. Ecol.* 401: 57-62.
<https://doi.org/10.1016/j.jembe.2011.03.002>
- Zuur A.F., Ieno E.N., Walker N.J., et al. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science, New York.
<https://doi.org/10.1007/978-0-387-87458-6>