Recovery of fishery-stressed seagrass meadows is driven by improvements in wastewater management

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A B S T R A C T

As ecosystem engineers, seagrasses provide major benefits to coastal habitats worldwide. Nonetheless, their dynamics remain poorly understood in local areas. Three seagrass (*Zostera noltei*) meadows located within shellfish beds in Galicia (NW Spain) were selected to assess the intra and inter-annual changes in the habitats by considering the effects of harvesting, temperature and sewage pollution. Seagrass cover increased between April and October, when the sediment temperature ranged from 15 to 20 °C, while in terms of long-term dynamics there was a mean gain of 3 % year^{-1} between 2004 and 2023. Shellfishing caused mechanical disturbance within the meadows, but the seasonal changes in cover depended on temperature. However, we pointed out the built of new wastewater treatment plants since 1990 that improved water quality as the main driver of the long-term increase in seagrass cover. Environmental policies that enhance seawater quality and limit harvesting pressure are essential to maintain this positive trend.

1. Introduction

Seagrasses are marine angiosperms that act as key habitat-forming species in shallow estuarine and coastal areas worldwide. In addition to having an important environmental role in providing ecosystem services (carbon sequestration, biodiversity conservation), seagrasses also benefit socio-economic activities, such as commercial fisheries (providing sites for egg laying, nursery habitats, refuge from predation) and cultural projects (snorkeling, informative walks) (Bas Ventín et al., 2015; Montero-Hidalgo et al., 2023). Despite the multiple beneficial services they provide, seagrasses have historically been overlooked in comparison with other ecosystem engineers such as corals and mangroves (Orth et al., 2006; De la Torre-Castro et al., 2014). However, research on seagrasses has become more popular in recent years, as indicated by the increase in the number of related papers published per year, from 200 in 2000 to 1000 in 2020 (see Orth and Heck, 2023). Nonetheless, there remain some research gaps. For example, the temporal change in seagrass cover is a new research hotspot that may shed light on how the effects of diverse anthropogenic and environmental stressors have modified these habitats.

A general decline in seagrass meadows has been reported in the past two or three decades in studies involving various seagrass species in different areas of the US (Corbett, 2006; Lefcheck et al., 2017; Capistrant-Fossa and Dunton, 2024), Europe (Cochón and Sánchez, 2005; Martin et al., 2010) and Oceania (Seddon et al., 2000; Kendrick et al., 2002). The potentially most damaging impacts were found to be related to water quality degradation. Waycott et al. (2009) reported that an alarming global decline in seagrass meadows (110 km^2 year^{-1}) has occurred since 1980. This decline may have caused enormous loss of ecosystem services and goods in coastal-dependent societies, mainly those sustained by small scale fisheries (SSF) in developing countries (De la Torre-Castro et al., 2014). Nonetheless, despite an estimated global net loss of 5602 km^2 since 1880 (Dunic et al., 2021), the decline has recently stabilised and has even been reversed in some regions (e.g. de los Santos et al., 2019). However, the extent of reversal differs widely. Thus, e.g. a multispecific seagrass bed regained 17,000 ha in 50 years (1984–2015) within the Chesapeake Bay (Atlantic coast of the US, Lefcheck et al., 2018). In a local bed of *Zostera noltei* Hornemann, cover increased by 212 ha from 2010 to 2018 in the Merja Zerga lagoon (Atlantic coast of Morocco, Benmokhtar et al., 2023) and a fragmented *Z. noltei* bed gained 370 ha from 1985 to 2012 after alternating periods of losses and recovery in the Loire Estuary (Atlantic coast of France, Zoffoli et al., 2021).

Estuarine habitats are dynamic and their suitability for hosting seagrass meadows depends on several biotic and abiotic factors. Biological processes (e.g. bioturbation, herbivory, detritivory, diseases) can modify

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the establishment and fragmentation of meadows. However, anthropogenic pressure (including pollution, dredging and filling, fishing and shellfishing, and wastewater discharge) is the major driver of the long-term dynamics of seagrass cover (Cochón and Sánchez, 2005; Waycott et al., 2009; Dunic et al., 2021). The stressors involved have negative consequences on environmental indicators such as light attenuation, water salinity and temperature, benthic substrate, wave exposure, flow velocity and tidal exposure (Erftemeijer et al., 2023). The negative effects of these anthropogenic activities have long been known and 20.25 % of the marine seagrass species are classified as threatened or near threatened on the IUCN's Red List (https://www.iucnredlist.org/). However, specific conservation measures only started to be implemented in the second half of the last decade, as seagrass meadows have generally been overlooked (Orth et al., 2006; Norlund et al., 2016). Nonetheless, local management actions, including the restoration and regulation of wastewater discharges, have since been successfully carried out (de los Santos et al., 2019). For instance, a significant reduction in nutrient inputs to fjords in Denmark resulted in an increase in the depth reached by the seagrass *Zostera marina* Linnaeus (Riemann et al., 2016).

In Galicia (NW Iberian Peninsula), one of the most fishing-dependent regions in the European Union (Villasante et al., 2016), small scale fisheries (SSFs) are economically crucial to coastal communities (Pita et al., 2019). These soft-bottom beds are exploited both on foot in intertidal areas and afloat in subtidal by local harvesters who collect up to 21 bivalve species (including cockles, clams, razor clams and scallops) by sediment raking and digging (Fig. S1A). As part of estuarine ecosystems, the shellfish beds are inhabited by a number of non-commercial species where highlight the presence of the ecosystem engineers *Z. noltei* and *Z. marina* that form dense patches in some areas (Román et al., 2020; Román et al., 2023).

Until the 2000s, the social perception of seagrasses among Galician shellfishers was predominantly negative, and conflicts between shellfish harvesters and conservationists have been reported since 1900 (Bas Ventín et al., 2015; Fernández et al., 2022). Because of the socioeconomic importance of shellfishing activities, authorized removal of extensive seagrass meadows is regularly carried out with tractors and ploughs (see Fig. S1B and C; Fernández et al., 2022) that together with coastal dredging and filling may lead negative consequences on the seagrass population dynamics (Cochón and Sánchez, 2005; Sanmartí et al., 2021). Notwithstanding, seagrass meadows provide services to other species, acting as refuges from predation, nursery areas and thermal and saline buffers (Wong, 2013; Román et al., 2022; Román et al., 2024) which could improve commercial stocks and thus increase the shellfishery economic benefits. To improve the management of seagrass meadows that inhabit productive beds, the first step is to know the distribution and abundance of seagrass meadows at different spatial and temporal scales.

Seagrass habitat mapping is a growing field of interest (Orth and Heck, 2023) where various techniques can be used based on available funds and research goals (Kovacs et al., 2018). In the last two decades, multispectral images from Landsat 8 (30 m/pixel) and Sentinel-2 (10 m/pixel) satellites have become freely accessible worldwide. However, historical mapping using these images is hampered due to their low-resolution and the absence of images for early 2000s (Benmokhtar et al., 2023). High-resolution orthoimagery (<0.5 m/pixel) can overcome these issues, although its suitability for semi-automated object-based analysis remains uncertain due to the absence of multispectral bands. Nonetheless, the value of these orthoimages for visual photointerpretation of seagrass meadows has been widely demonstrated (e.g. Martin et al., 2010; Román et al., 2020).

Seagrasses inhabiting productive shellfish beds are subjected to prevailing environmental challenges (e.g. global warming, pollution) and are also affected by several shellfishing-related activities (sediment raking, digging, trampling and ploughing), which make these meadows even more dynamics. The main aim of this study was to understand the

spatiotemporal changes of three fishery-stressed *Z. noltei* meadows. With that purpose, three specific objectives were assessed in three Galician shellfish beds where *Z. noltei* inhabits: (1) to register the seasonal meadow shifts, (2) to determine the long-term dynamic of these meadows, and (3) to investigate the role of harvesting effort, temperature and wastewater treatment as drivers of variability.

## 2. Material and methods

2.1. Study area

The Rías Baixas (Galicia, NW Iberian Peninsula, Fig. 1A) are flooded tectonic valleys oriented in a northeast-southwest direction. They are strongly influenced by the NW Iberian Upwelling System, which causes important upwelling events in spring and summer during northerly winds (Alvarez et al., 2005, 2008) and makes the Galician coast one of the most productive marine areas in Europe. The dynamics of three *Z. noltei* meadows located in the most productive shellfish beds in three different rías were investigated, and the size of each meadow was determined. The sites were chosen because of the presence of the seagrass *Z. noltei*, which forms patches of different density (Román et al., 2023), and also because the meadows have been physically disturbed by bivalve shellfisheries over a period of decades. From north to south, the Testal site is situated within the northernmost and shortest Ría de Noia, where the River Tambre discharges $1.7 \cdot 10^9$ m^3 year^{-1}; the O Sarrido site is located in the south coast of the widest Ría de Arousa mainly influenced by the rivers Ulla ($2.5 \cdot 10^9$ m^3 year^{-1}) and Umia ($5.2 \cdot 10^8$ m^3 year^{-1}); and the A Seca site is situated in the inner part of the Ría de Pontevedra, mostly affected by the river Lérez ($6.7 \cdot 10^8$ m^3 year^{-1}). All of the sites are mesotidal estuarine areas with long emersion periods (up to 3.5–4 h).

2.2. Mapping methods

To estimate the short-term changes in the seagrass meadows under study, eight field surveys were conducted in situ in 2020 (January, April, May and October), 2021 (January, March and September) and 2023 (September) during spring low tides. The perimeter of the area covered by *Z. noltei* was geo-referenced by a researcher walking along the edges of the meadows with a portable GPS of sub-metric precision (Mobile Mapper 50, Spectra Geospatial). Sampling was carried out in the three intertidal shellfish beds on three consecutive days to prevent date-dependent differences. The same zones within each bed were always checked: the entire bed in Testal and the most important areas in O Sarrido and A Seca because of tidal time constraints in these (larger) beds (see Fig. 1A). Once recorded, the polygons were exported as shape files compatible with the open-source software QGIS v. 3.12.

In order to assess the state of the seagrass within each meadow, three 100 m-long transects were delimited, parallel to the coastline and 50 m apart, with the aid of a tape measure. The transects were established before and at the end of the plant growing season, namely in spring and autumn of 2020 (March and October) and 2021 (April and September) and autumn 2023 (September). The transects were tracked with a portable GPS, and the same positions were inspected each time. The site condition was visually determined at one metre intervals along the transect and categorized as recently harvested, *Z. noltei* or bare sediment (Fig. 1B).

The long-term dynamics of these seagrass meadows were analysed by using a series of aerial orthoimages derived from the Aerial Orthophotography National Plan (PNOA) that are freely available at the Spanish Centre of Geographic Information (CNIG, https://centrodedescargas.cnig.es/CentroDescargas/index.jsp). Four sets of high-resolution aerial photographs taken in the middle and the end of the annual growth season were selected for use: from September 2004 (0.45 m/pixel), July 2010 (0.22 m/pixel), July 2017 (0.22 m/pixel) and June 2020 (0.18 m/pixel). As the 2023 orthoimage was still not available from PNOA, the
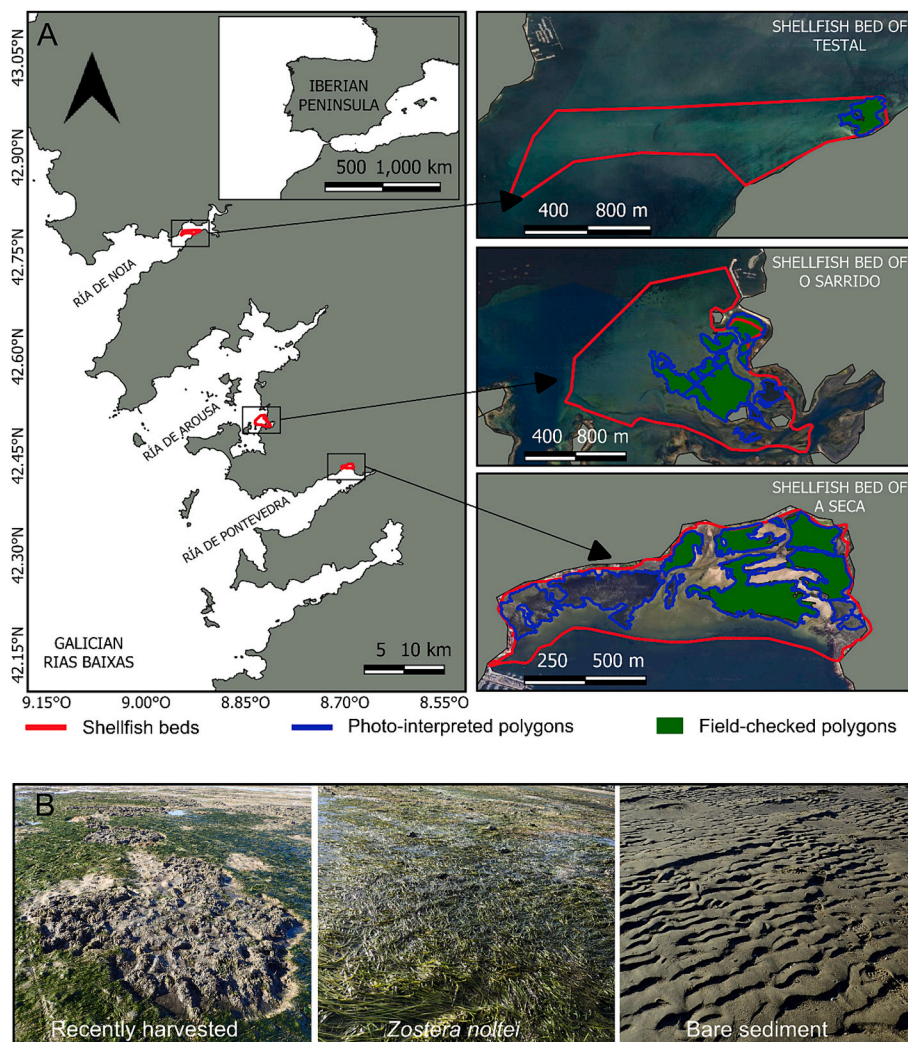
Fig. 1. A) Maps showing the study area and the shellfish beds under study. B) Photographs of the habitats along the transects, showing gaps of bare sediment due to recent harvesting, patches of *Z. noltei* and large areas of bare sediment.

Google Earth image corresponding to September 2023 was used instead. The selected orthoimages of the intertidal fishing beds are cloudless and shadowless, but they were not all taken at the same tidal height. However, as the seagrass meadows are shallow, of depth approximately 2 m even during high tide, the orthoimages were used in the survey except those for Testal in July 2010 and O Sarrido in July 2017. Polygons showing the distribution of the *Z. noltei* meadows within the shellfish beds were delimited by photointerpretation in QGIS by using the Spanish national coordinate system (ETRS89/UTM zone 29 N).

2.3. Validation of the orthoimage measurements

The photo-interpreted polygons from July 2020 and September 2023 were compared with the actual limits of the meadows geo-referenced in situ in October 2020 and September 2023, respectively, by superimposing them in QGIS and calculating the coinciding/non coinciding areas. As the O Sarrido and A Seca beds were not fully inspected during field sampling, validation was carried out considering only the field-checked polygons (i.e. important zones that constitute >50 % of the total area covered by the meadows, see limits in Fig. 1A).

2.4. Drivers of seagrass variation

The sediment temperature (accuracy ±0.1 °C) was recorded in situ every 30 min, at depths of 2 and 7 cm (meadow rhizosphere), with two temperature loggers (EnvLogger version 2.4, https://electricblue.eu/) attached to PVC sticks buried vertically in three intertidal zones (low, mid and high) in the three beds, between January 2020 and September 2023.

Shellfishing effort, which directly affects the seagrass meadows (Garmendia et al., 2021), was inferred by the number of licences issued for each shellfish bed yearly between 2004 and 2020 (obtained from the management plans (https://www.pescadegalicia.gal/). Different harvesting intensities within the shellfish beds were also considered, by creating a grid of points separated by 100 m on each shellfish bed. A technical assistant from the fisher's guilds managing the shellfish bed then assigned each point to one of the following harvest intensity categories: (0) not harvested in the last two years, (1) harvested twice a year, (2) harvested seasonally, (3) harvested bimonthly, (4) harvested monthly or (5) harvested weekly.

The potential effects of untreated wastewater discharges on the long-term dynamics of *Z. noltei* meadows were assessed by tracing the installation of wastewater treatment plants (WWTPs) in the three rías (Ría de Noia, Ría de Arousa and Ría de Pontevedra) from data provided by the Autonomous Government of Galicia (information restricted to WWPTs with a capacity higher than 2000 equivalent inhabitants, https://augasdegalicia.xunta.gal/).

2.5. Data analysis

The short-term spatial variability in the *Z. noltei* meadows (tracked in situ with a portable GPS) was analysed by overlapping in QGIS the layers registered in each field sampling in order to detect any differences in the size of meadows within the beds. In addition, the areas of the field georeferenced polygons were calculated using the QGIS default tool *calculator* and graphically represented as a time series (January 2020–September 2023) to study seasonal and annual shifts.

Transects used to assess the state of the seagrass within the meadows were modelled by running a multinomial logistic regression with the type of habitat as a response variable (3 levels: recently harvested, *Z. noltei* and bare sediment) and the fixed factor Sampling date (5 levels: March 2020, October 2020, April 2021, September 2021 and September 2023). In addition, the monthly sediment temperature data for the different depths of sensor and intertidal heights were averaged to yield the monthly mean temperature at the rhizosphere level. The differences in sediment temperatures across years were then compared by one-way ANOVA with the fixed factor Year (3 levels: 2020, 2021 and 2022).

The long-term changes in the meadows were determined by comparing the photo-interpreted maps of 2004 and 2023 with the default tools *union* and *difference* from QGIS to estimate the meadow loss and gain in this century. Nonetheless, changes within the period were also tracked by calculating the areas occupied by *Z. noltei* in the intermediate orthoimages (2010, 2017 and 2020).

Differences in number of harvesters throughout the years were checked by one-way ANOVA with the fixed factor Year (20 levels: from 2004 to 2023). Generalized linear models (GLMs) with a binomial distribution of errors (logit link function) were used to compare the binary response variable Habitat (2 levels: vegetated vs unvegetated) and the fixed factor Harvesting intensity (6 levels: not harvested in the last two years, harvested twice a year, seasonally, bimonthly, monthly and weekly). Finally, the WWTPs installed in the Ría de Noia, Ría de Arousa and Ría de Pontevedra were categorized according to the year of construction: before the 2000s, from 2000 to 2009 and from 2010 to the present. The categories were displayed on a spatial map to facilitate interpretation.

All statistical analyses were performed using R Statistical Software (R Core Team, 2021). The average values were reported as means ± standard deviation (sd), and statistical significance was established at $p = 0.05$. Any significant effects detected were further explored with a post hoc Tukey's multiple comparisons test. The normality of the residuals and the homogeneity of variances were checked with Shapiro-Wilk tests and residuals plots, respectively. The binomial models were checked for overdispersion and corrected with a quasi-binomial structure when required (Zuur et al., 2009). All data were processed and graphically represented using the *tidyverse* R package (Wickham et al., 2019), and Habitat probability was plotted by applying the family binomial to the smoothing function *geom_smooth*. The one-way ANOVA, multinomial and binomial models were conducted using *car* (*aov* function, Fox and Weisberg, 2019), *nnet* (*multinom* function, Venables and Ripley, 2002) and the default *stats* (*glm* function) R packages, respectively.

3. Results

3.1. Short-term evolution and potential causes

The short-term dynamics of *Z. noltei* meadows were similar in the three shellfish beds and were characterized by the presence of remnant patches in the high and mid intertidal zones, and by more variable patches in the low intertidal zone (Fig. 2A, B and C). Seagrass cover was greater in the O Sarrido site throughout the study period, followed in
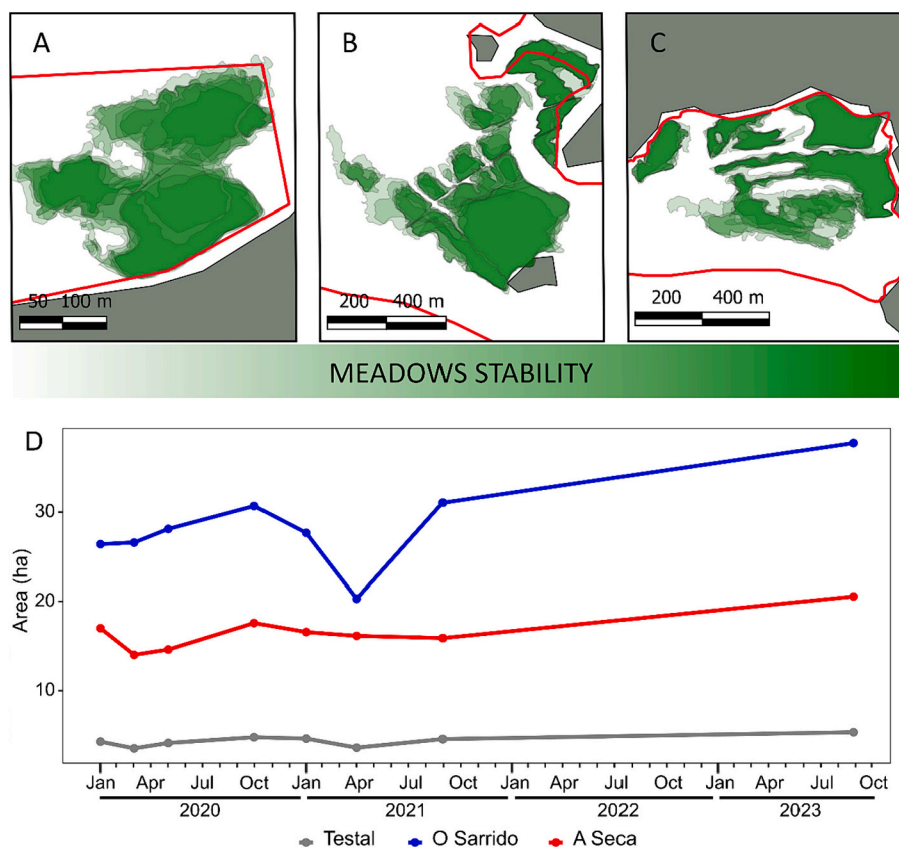

Fig. 2. Superimposed layers of *Z. noltei* polygons from each field sampling in A) Testal, B) O Sarrido and C) A Seca. Areas where *Z. noltei* is not usually present are shown in light green and areas that are frequently covered are shown in dark green. D) Short-term changes in the area covered by seagrass in each shellfish bed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

order by A Seca and Testal (Fig. 2D). Seasonal changes were observed in the three meadows between 2020 and 2023, i.e. an increase in area from spring to the early autumn with minimal cover in March (3.52, 26.59 and 14.03 ha at Testal, O Sarrido and A Seca, respectively) and maximal cover in October (4.76, 30.68, 17.59 ha at Testal, O Sarrido and A Seca, respectively) in 2020 and 2021. Notably, between January and April 2021, there was a significant decrease in the *Z. noltei* cover at O Sarrido from 27.67 ha in January to 20.29 ha in April (Fig. 2D). The area occupied by all three meadows was greater in 2023 than in the previous years (5.33, 37.75 and 20.56 ha at Testal, O Sarrido and A Seca, respectively).

Harvesting activities within the meadows are not very common, as the presence of these characteristics "gaps" (see Fig. 1B and Fig. S1A) did not cover 25 % of surveyed points along the transects in any case (Fig. 3A); however, a notable impact on the state of these well-established meadows was observed, particularly in March 2020 in the O Sarrido and A Seca sites and in April 2021 in the Testal site. The spatial distribution of the different habitat conditions along the transects differed significantly on each sampling date in the Testal site, with a wide variability in *Z. noltei* patches, bare sediment and harvested areas. The analyses also revealed significant differences in habitat condition

Table 1

Summarised results of the one-way ANOVAs used to test for differences across years in both sediment temperature (2020, 2021 and 2022) and number of harvesting licences issued (2004–2023). Significant effects are indicated in bold.

Shellfish bed	Source of variation	Sediment temperature			No. of licences issued		
		df	F	p	df	F	p
Testal	Year	2	0.02	0.97	9	0.62	0.45
O Sarrido	Year	2	0.63	0.59	19	0.93	0.35
A Seca	Year	2	0.14	0.82	19	9.68	**0.01**

between sampling dates in O Sarrido and A Seca, although the differences were mainly caused by the high probability of finding recently harvested areas in March 2020 (~20 %). Thus, the distribution was similar in the O Sarrido site between September 2021 and 2023 (post hoc group d) as well as in the A Seca site between October 2020 and September 2023 (post hoc group b) (Fig. 3A). In addition, the probability of occurrence of bare sediment areas along the transects was higher in March 2020 and April 2021 than after the seagrass growing season (September–October), when the probability of *Z. noltei* occurrence was higher in all three sites.
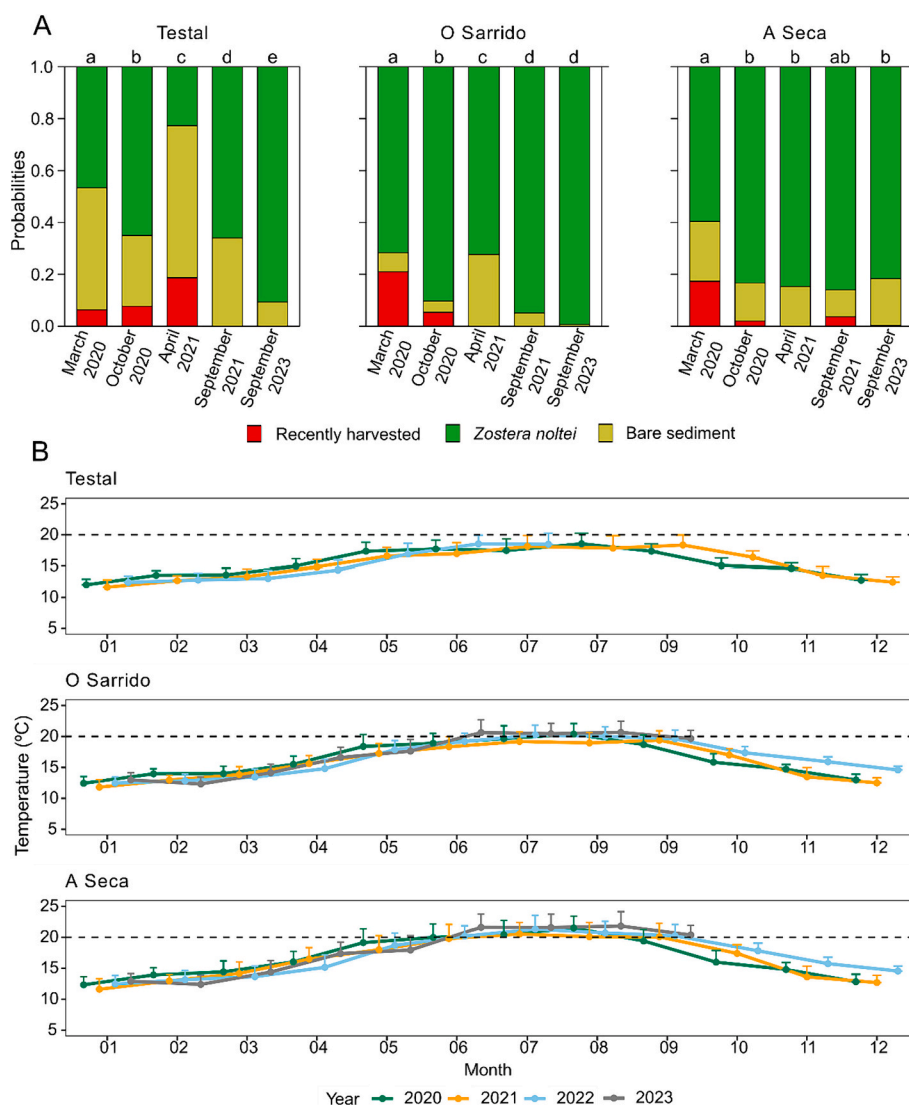
Fig. 3. A) Results of multinomial logistic regression of temporal analysis of the habitat conditions recorded along the transects in each shellfish bed. Groupings of letters above the bars denote the results of post hoc Tukey's test for the overall dynamics (including the three categories of habitat condition). B) Monthly mean sediment temperatures recorded at the rhizosphere level in each shellfish bed. Dashed horizontal lines represent the reference temperature of 20 °C.
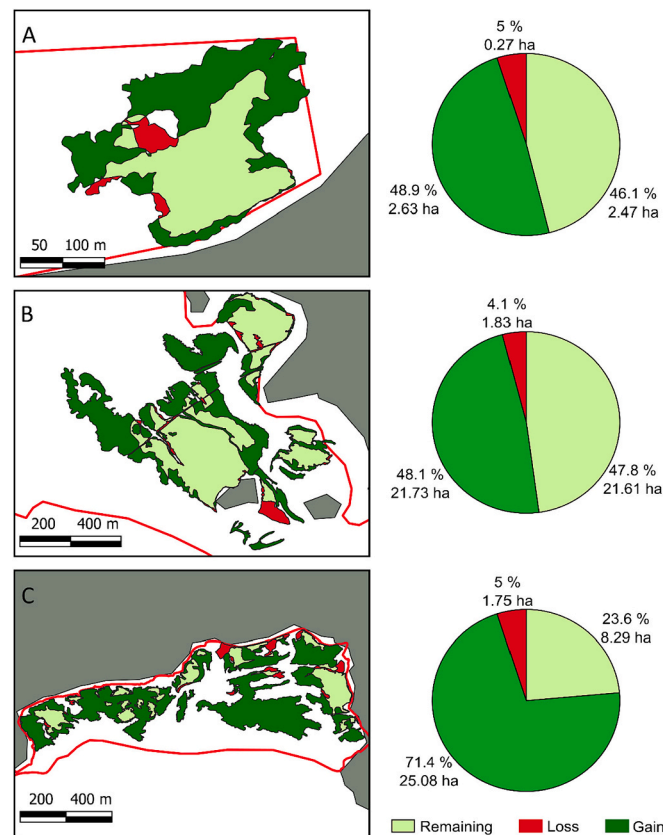
Fig. 4. Long-term changes (2004–2023) in the area occupied by *Z. noltei* meadows in the shellfish beds: A) Testal, B) O Sarrido and C) A Seca.

Temperatures at the rhizosphere level followed the expected seasonal pattern in all three beds; monthly mean values ranged from 15 to 20 °C between April and October, and lower temperatures were recorded in autumn and winter (Fig. 3B). Although higher temperatures were sometimes recorded in the summer of 2023, the monthly mean temperatures did not differ significantly across the study period in any of the shellfish beds (Table 1). Nonetheless, the monthly sediment temperatures were higher in the fishing beds located in the southern rías since Testal did not reach 20 °C, while that temperature was usually exceeded from June to September in O Sarrido (up to 20.64 ± 2.08 in August 2023) and, particularly, in A Seca (up to 21.81 ± 2.33 in August 2023). In that sense, the mean sediment temperatures throughout the study period were 15.3 ± 2.42, 16.23 ± 2.84 and 16.70 ± 3.31 °C in Testal, O Sarrido and A Seca, respectively (Fig. 3B). Within the shellfish beds, the sediment temperatures were more constant in the low intertidal zone because the immersion periods were longer than in the mid and high intertidal zone, where exposure to aerial temperatures led to greater thermal oscillations (Fig. S2).

3.2. Long-term changes and potential causes

Validation of the photo-interpreted maps of *Z. noltei* cover derived from PNOA and Google Earth orthoimages demonstrated the high accuracy and applicability of this mapping method relative to the georeferenced field maps (Fig. S3). In 2020 (PNOA), the percentage of coincident areas exceeded 85 % for both methods (Fig. S3A, B and C), while in 2023 (Google earth) the value ranged from 83.7 in the Testal site to 90.8 in the O Sarrido site (Fig. S3D, E and F). The accuracy of the photointerpretation method was therefore adequate with both types of orthophotos, although minor errors were detected in some cases as in the O Sarrido site in 2020 and the Testal site in 2023, when ~10 % of the total area included in the field sampling was not captured in the orthoimages (Fig. S3B and D).

The *Z. noltei* cover within the shellfish beds increased greatly between 2004 and 2023, although the gain was not homogeneous along the shellfish beds (Fig. 4). The trends were similar in the Testal and O Sarrido sites, where the *Z. noltei* cover increased 2.63 and 21.73 ha, respectively, representing an almost twofold increased in the area occupied in 2004 (Fig. 4A and B). However, seagrass cover in the A Seca site underwent an extraordinary increase, of 25.08 ha, which was three times higher than the area previously covered by remnant patches (Fig. 4C). Loss of *Z. noltei* was scarcely observed throughout the study period, representing only ~5 % of the current seagrass cover in the three beds. While *Z. noltei* was mainly situated in the high intertidal zone in 2004, a large increase towards the mid and low intertidal zones was observed in 2023 (Fig. 4). In particular, the greatest increases in seagrass cover were observed in the periods 2010–2020 in the Testal site (from 1.81 to 4.79 ha), 2004–2017 in the O Sarrido site (from 23.45 to 34.76 ha) and 2020–2023 in the A Seca site (from 9.49 to 17.08 ha) (Fig. 5). By contrast, slight decreases were observed in the Testal and O Sarrido sites during the periods 2004–2010 and 2017–2020, respectively (Fig. 5).

The changes in the number of harvesting licences issued between 2004 and 2023 was site-dependent. The number of licences issued for Testal has remained rather constant since 2012 (first year with available data). However, the number varied more widely in O Sarrido, decreasing from 249 in 2004 to 220 in 2023, and in A Seca, increasing significantly from 166 to 267 in the same period (Fig. S4, Table 1). Thus, the harvesting pressure was similar throughout the study period in terms of number of harvesters per bed, except in the A Seca site. However, harvesting was spatially heterogeneous within the beds and the effects on the presence of *Z. noltei* differed among shellfish beds (Fig. 6). In the Testal site, the presence of *Z. noltei* was significantly lower in frequently harvested areas than in the other zones; however, as the meadow was restricted to a small area in the upper intertidal zone, this finding should be considered with caution. Likewise, in both the O Sarrido and A Seca shellfish beds, a significant negative trend in the presence of *Z. noltei* was
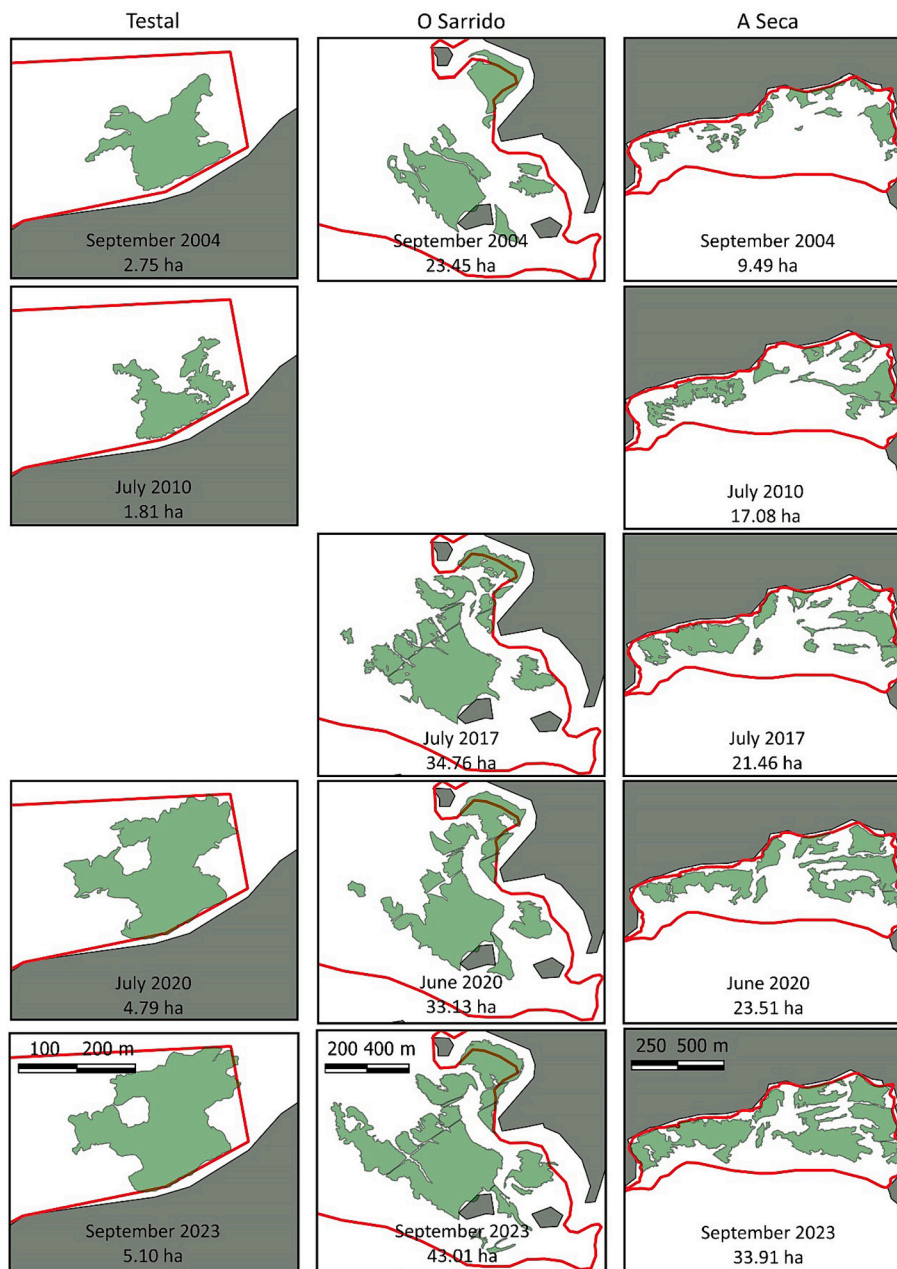
Fig. 5. Details of the changes in the *Z. noltei* cover in each shellfish bed. Orthoimages were not available for O Sarrido in 2010 or Testal in 2017.

associated with higher harvesting intensity, with seagrass cover being lower in intensively harvested areas. Nonetheless, shellfish harvesting and seagrass meadows coexist in some areas (Fig. 6), demonstrating the high degree of resilience of the seagrass to intense harvesting (seasonal or bimonthly work), as the probability of *Z. noltei* occurrence remained ~50 % in these cases.

The installation of new WWTPs was continuous, but asynchronous in the Rías Baixas in the period considered (Fig. 7). The Ría de Noia did not have any WWTPs until 2008, when the first was built. Another three WWTPs were then constructed in the area in the following six years. The first WWTP discharging in the Ría de Arousa was constructed in 1994, where there are now a total of 12 WWTPs, most of which were built between 2000 and 2010. The Ría de Pontevedra has three WWTPs, the most recent constructed in 2000. Nonetheless, the oldest WWTP (Placeres, built in 1993) has been modified several times since its construction because the treatment did not meet the standards established in the environmental directives.

4. Discussion

Seagrasses play an important role in coastal ecosystems worldwide. Understanding the spatiotemporal changes in seagrass cover is therefore essential to enable development of appropriate conservation policies in the current context of climate change. General patterns of changes in seagrass cover have been described at both global (e.g. Waycott et al., 2009; Dunic et al., 2021) and continental scale (e.g. de los Santos et al., 2019). However, seagrass meadows are very dynamic systems that are exposed to a great variety of local anthropogenic and environmental factors, provoking different dynamics across nearby beds (Román et al., 2020; Barañano et al., 2022). The present study investigated intra-annual trends in seagrass cover in three shellfish beds in the Galician Rías Baixas. Seagrass cover was maximum in early autumn, and *Z. noltei* was scarce in continuously harvested beds. In addition, the long-term changes (2004–2023) clearly demonstrated an increase in the total area occupied by seagrass meadows within the three shellfish beds, with
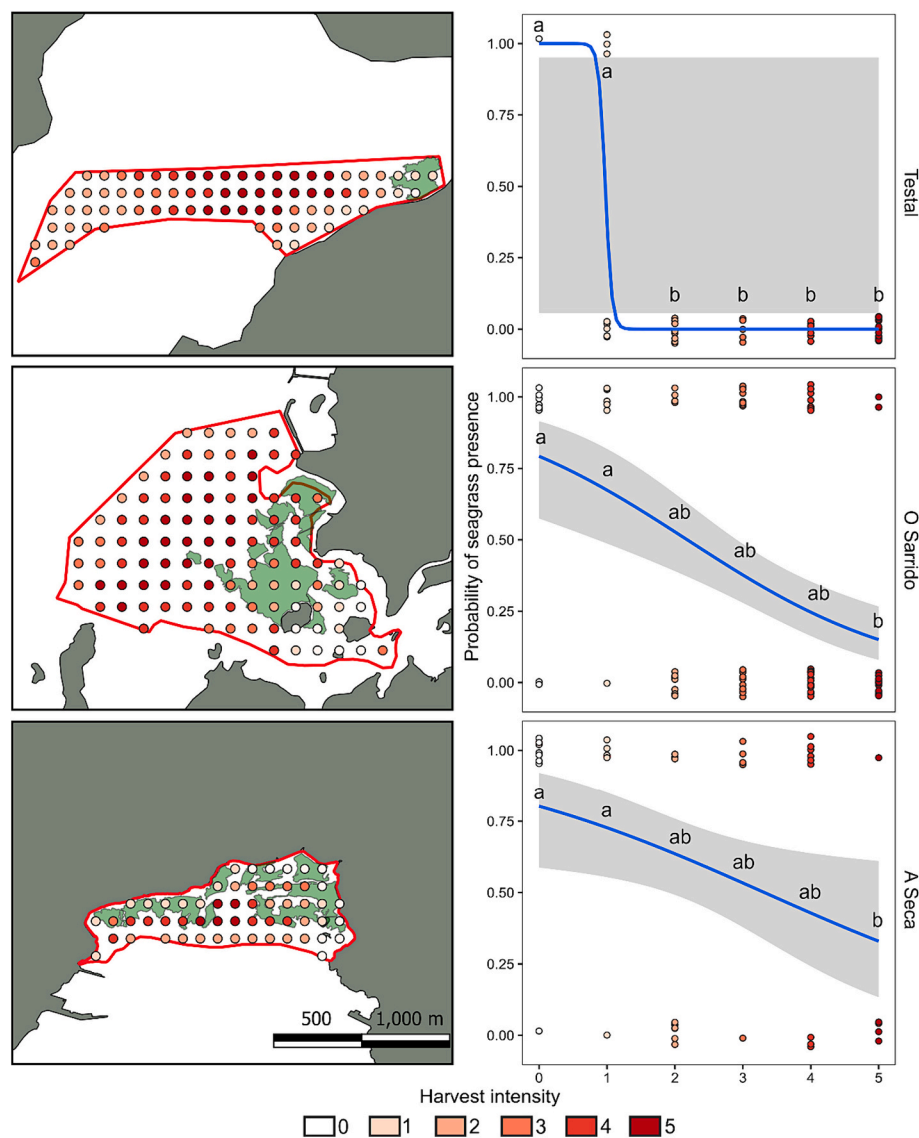
Fig. 6. Maps of each shellfish bed with a grid of points separated by 100 m on the left. Harvesting intensity was determined at each point and is denoted in different colours. Probability of seagrass presence in relation to each level of harvesting intensity for each shellfish bed on the right. Blue lines are the predictions of LOESS models with shaded 95 % confidence interval, and dots indicate the observations made at in each level. Groupings of letters above the line indicate the results of the post hoc Tukey's test. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

a mean increase of ~3 % year^{-1}, probably as a result in the reduction of untreated sewage loads discharged in the area.

The seasonal dynamics of *Z. noltei* followed a typical unimodal pattern, with a marked growing season between spring and early autumn, as expected for this species along western European coasts (Peralta et al., 2005). For instance, in 2020, the seagrass cover increased by 11.62, 16.19 and 3.4 % in the Testal, O Sarrido and A Seca sites respectively. The study findings showed that harvesting activities can modify the intra-annual changes in seagrass cover because it causes gaps of bare sediment, even within well-established patches. These changes could lead to a long-term lack of resilience derived from chronic effects on meadow resistance and recovery (Unsworth et al., 2015). A similar effect has been described in a nearby subtidal *Z. marina* meadow, where the periodical disturbances associated with harvesting have caused a highly fragmented and discontinuous seagrass matrix (Barañano et al., 2022). Nonetheless, we suggest temperature and light availability as the main environmental drivers of the intra-annual variability detected in the studied meadows as had previously been evidenced in a field study of seasonal seagrass fluctuations (Soissons et al., 2018). During the

growing season, the sediment temperature in the three beds ranged from 15 to 20 °C, which appears to be an optimum range for temperate seagrass species (Nejrup and Pedersen, 2008). However, the highest temperatures (close to 20 °C) were recorded in the O Sarrido and A Seca shellfish beds, which could explain the larger area covered by *Z. noltei* in these beds than in the Testal (coldest) bed. Indeed, temperatures above 16 °C, closer to ~20 °C, are associated with formation of larger numbers of longer leaves in *Z. marina* plants (Beca-Carretero et al., 2021).

Although most global trends described so far have revealed a historical decline in seagrass cover (Orth et al., 2006; Waycott et al., 2009; Dunic et al., 2021), some recent studies have detected an increase in the size of local meadows in the past two decades (e.g. Calleja et al., 2017; de los Santos et al., 2019; Zoffoli et al., 2021; Benmokhtar et al., 2023). In line with these recent findings, our results highlighted a robust positive trend for the size of seagrass meadows in the three shellfish beds to increase between 2004 and 2023. The increase in size ranged from 2.4 % year^{-1} (Testal and O Sarrido) to 3.6 % year^{-1} (A Seca), values which are within the range reported in previous studies, such as 4 % year^{-1} in the Merja Zerga lagoon, Morocco (Benmokhtar et al., 2023) and 2.2 %
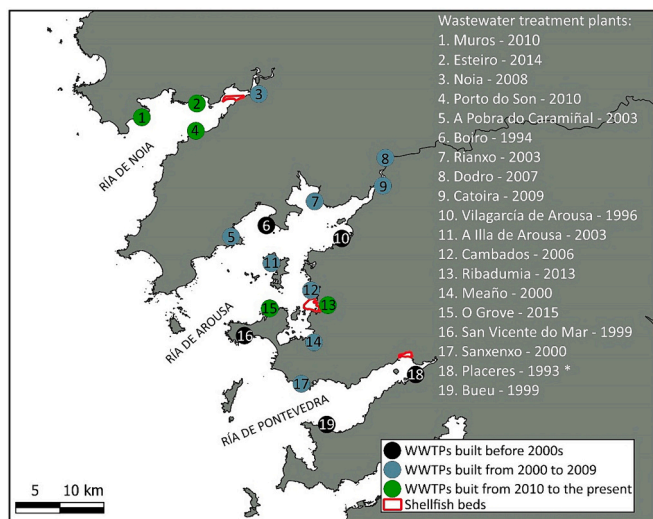
Fig. 7. Study area including wastewater treatment plants (WWTPs), ordered from north to south and categorized in relation to the year of construction. The information is restricted to WWTPs with a capacity higher than 2000 equivalent inhabitants. *The Placeres WWTP has been renovated several times since construction.

year^{-1} in Chesapeake Bay, USA (Lefcheck et al., 2018). However, the changes were not linear, and alternating periods of loss and gain were observed, as typically occurs in seagrass ecosystems (Calleja et al., 2017; Zoffoli et al., 2021). For instance, in the Indian River lagoon, Florida, the area occupied by seagrass meadow increased by 7000 ha between 1994 and 2009 and then decreased by 19,000 ha in the following 8 years (Morris et al., 2022). Colonization of unvegetated areas mainly depends on clonal growth from well-established meadows, although the recruitment of new seedlings can also play a key role in stabilizing new patches and, even more important, in colonizing isolated areas with optimum habitat conditions (Borum et al., 2004). Given that seagrasses often disappear from and then recolonize the same areas, conservation policies should aim to protect not only the meadows, but also nearby areas, as recolonization could occur within a few years (Munsch et al., 2023).

One potential explanation for the increase in *Z. noltei* cover within shellfish beds is a reduction in the historical harvesting effort, as occurred in the nearby intertidal of A Ramallosa (Román et al., 2020); however, this effect was probably not significant in the sites under study, because the number of licences issued did not decrease throughout the study period. Nonetheless, negative effects of harvesting and associated impacts (e.g. trampling and sediment moving) on seagrass patches have often been demonstrated (Guimarães et al., 2012; Garmendia et al., 2021). The Galician shellfishers who work both on foot in the intertidal zone and from aboard vessels in the subtidal zone have a particularly negative perception of dense seagrasses meadows, which make shellfish harvesting more difficult (Bas Ventín et al., 2015). The shellfishers' actions often cause fragmentation of the meadows and loss of biodiversity (Barañano et al., 2022; Román et al., 2023). In this study, we observed that seagrass did not generally recolonize areas that are harvested monthly or weekly but that a period of inactivity could enable recolonization, as suggested in some studies conducted after the Covid-19 lockdown (Zoffoli et al., 2021; Benmokhtar et al., 2023). Thus, although harvesting activities allowed the long-term seagrass progression and recovery, these impacts generally restricted the colonization to areas with a lower harvesting pressure.

The study findings also showed that the construction of new WWTPs and the renovation of older ones in the past two decades may have enhanced seagrass cover by reducing nutrient discharges into the estuaries. In this context, Erftemeijer et al. (2020) reported an improvement

of water quality derived from a reduction in the discharge of untreated water as the main driver of recovery of 9 seagrass species in South Australia. In the Galician Rías Baixas, the nitrite and phosphate concentrations decreased in the period 2002–2011 (Doval et al., 2016), and this trend is expected to continue in line with the implementation of environmental politics against eutrophication (e.g. Marine Strategy Framework Directive; European Commission, 2008) and improved wastewater treatment. Reductions in nutrient loads over the last 20 years have promoted expansion of seagrass cover in different parts of the US (Lefcheck et al., 2018), Europe (de los Santos et al., 2019) and Oceania (Fernandes et al., 2022; Erftemeijer et al., 2023), with the consequent improvement of ecosystem functioning. Roca et al. (2015) demonstrated the efficacy of the wastewater load reductions, derived from the construction of new WWTPs, to enhance several biochemical seagrass indicators such as nitrogen, $\delta^{15}N$, phosphorus and total non-structural carbohydrates content in rhizomes. In addition, the reduction in habitat degradation may have enhanced the resilience of the studied meadows (Unsworth et al., 2015), as the small patches observed in 2004 were found to be less fragmented in 2023. Thus, although the changes in seagrass cover are not instantaneous and were only detected approximately 6 years after improvement in water quality (Fernandes et al., 2022), the management actions implemented to reduce nutrient loads have proved cost-effective.

The present study focused on analysing the intra and inter-annual changes in *Z. noltei* cover in three different shellfish beds, where the effects of some environmental and anthropogenic pressures were analysed. The observed short-term dynamics confirmed the typical unimodal pattern in temperate species, with an association between spring and summer temperatures (15–20 °C) and growth. The retrospective analysis (2004–2023) revealed a long-term trend for seagrass cover to increase greatly in the three beds covering the high intertidal zone and also several parts of the mid and low intertidal zones. Given that a reduction in the historical fishing pressure was ruled out, we suggest that the recovery was mainly a consequence of improved quality of the seawater owing to the installation of new WWTPs along the Galician Rías Baixas. The increase in seagrass cover is consistent with the findings of recent studies worldwide (Lefcheck et al., 2018; de los Santos et al., 2019, Erftemeijer et al. 2020) and thus, the global trend of seagrass decline, reported in the early 2000s (Orth et al., 2006; Waycott et al., 2009), seems to have stabilised or even been reversed in some areas. This positive pattern could be included into the global campaign of ocean optimism, which tries to recognise successful environmental actions to promote the social hope and collaboration in ocean conservation (see Balmford and Knowlton, 2017). Nevertheless, the findings should be considered with caution as the dynamics of seagrass meadows are very variable (Calleja et al., 2017, Morris et al. 2022). In addition, there is a high degree of variability at small spatial scales which is even higher within productive shellfish beds (Cochón and Sánchez, 2005; Román et al., 2020; Barañano et al., 2022). Therefore, environmental policies aimed at improving water quality must include the establishment of areas with restricted harvesting pressure, because seagrass colonization has been demonstrated to be limited in areas that are continuously exposed to bivalve fishery activities. Furthermore, improved harvesting practices could favour recovery of seagrasses. For example, removal of shoots instead of the entire plants and harvesting smaller areas have been demonstrated to improve the resilience of seagrasses, especially that of fast-growing species (e.g. Sanmartí et al., 2021).

CRediT authorship contribution statement

Salvador Román: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Celia Olabarria:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Marta Román:** Writing – review & editing, Methodology, Conceptualization. **Elsa Vázquez:**

Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2024.116282.

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