



Environmental alterations and sea warming drive seagrass meadow decline in urbanized coastal areas of the northern Adriatic Sea

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ABSTRACT

Seagrass meadows are important habitat builders, providing food, shelter, and nursery grounds for many species, alongside essential goods and ecosystem services for humanity. However, in the last decades, seagrass meadows have been subjected to numerous pressures, leading to their widespread decline. The northern Adriatic Sea is no exception, with seagrass regression observed notably between 2014 and 2018. This study aims to identify the drivers of the recent seagrass decline in the Gulf of Trieste through a spatial and temporal assessment of seagrass distribution. To assess the relationship between seagrass dynamics and environmental changes, spatiotemporal patterns of environmental variables were analyzed, and generalized additive models were applied for two different time periods: 2009–2013 and 2014–2018. Historical data on seagrass distribution was also collected and compared with the current distribution. Our findings indicate that *Cymodocea nodosa* remains the dominant species on the northern coast of the Gulf, with a decrease of 30 % in Slovenian waters and up to 89 % near Trieste (Italy) during 2014–2018. Analysis of physicochemical variables revealed an increase in seawater temperature across the Gulf and a change in nutrient load, particularly in Slovenia, where it decreased significantly. Models achieved high-performance scores, identifying photosynthetically active radiation, nutrients, temperature, and sediment type as key determinants of seagrass occurrence. Nonetheless, additional local-scale factors likely contributed to lower seagrass' resilience to disturbances. These findings stress the need to develop integrated spatial planning strategies and provide a crucial baseline for future seagrass monitoring and restoration activities.

1. Introduction

Global and local pressures are increasingly altering coastal habitats (Korpinen and Andersen, 2016; Worm and Lotze, 2021), particularly in the Mediterranean Sea, which is experiencing rapid coastal urbanization (Boudouresque et al., 2009; Holon et al., 2015; Lagarias and Stratigea, 2023; Rindi et al., 2020). These impacts are especially critical when keystone species, such as seagrasses, are affected, as their loss triggers

cascading effects on community diversity and composition (Ebenman and Jonsson, 2005; Hughes et al., 2009; Mills et al., 1993). Indeed, seagrass meadows play a key role in shaping coastal ecosystems by providing essential ecological functions, such as food, shelter, nursery grounds for diverse species (Díaz-Gil et al., 2019), and a broad array of ecosystem services (Addamo et al., 2025), including coastal protection (Ondiviola et al., 2014), sediment stabilization (Widdows et al., 2008) and carbon sequestration (Luisetti et al., 2013).

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Seagrass meadows are under pressure worldwide from various anthropogenic impacts leading to considerable decline and local extinction. For instance, *P. oceanica* has declined by up to 34 % over the past 50 years due to multiple stressors (Telesca et al., 2015), such as seabed dredging, coastal development, trawling, anchoring, runoff from urban and agricultural areas, nutrient enrichment and, more recently, rising seawater temperatures (Diaz-Almela et al., 2007; Marba et al., 2014; Orlando-Bonaca et al., 2015, 2019; Repolho et al., 2017; Short et al., 2011; Tuya et al., 2002). The responses of seagrasses to such pressures vary and depend on the adaptation of plants to local conditions, including thermal tolerance (Ferdie and Fourqurean, 2004; Stipich et al., 2022), adaptation to high salinity (Sandoval-Gil et al., 2014) and resistance to nutrient overload (Burkholder et al., 2007). In particular, high nutrient loading can indirectly exacerbate seagrass decline by promoting epiphyte overgrowth, competition with macroalgae, light depletion, and anoxia (Burkholder et al., 2007). However, understanding the causes of decline and quantifying their effects is often challenging due to the interplay of multiple factors and the lack of pre- and post-impact data. In addition, large-scale studies may overlook local impacts or underestimate key drivers of change (Chen, 2021; Edgar et al., 2005; Tamburello et al., 2022).

All four Mediterranean seagrass species occur in the Adriatic Sea, with *Cymodocea nodosa* being the most abundant (Lipej et al., 2004). This species exhibits remarkable phenotypic plasticity, adapting to various natural and anthropogenic stressors through physiological and morphological changes (e.g., Sandoval-Gil et al., 2014). Nevertheless, extensive declines of this species have been recorded in several coastal areas, including the Adriatic Sea (Fabbri et al., 2015; Orth et al., 2006; Short et al., 2011; Tuya et al., 2013, 2014). In the Gulf of Trieste (GoT), the northernmost part of the Adriatic Sea, a sharp regression of *C. nodosa* meadows has also been observed in recent years during our monitoring activities, especially from 2014 to 2018. However, the causes of such

regression remain unclear, and no previous study has systematically assessed the environmental variables that most influence the meadows across the GoT or produced a comprehensive map of their past and current distribution along the entire coastline.

This study aims to fill these gaps by analyzing seagrass monitoring data collected in Slovenian waters in 2009, 2014, and 2018 and in Italian waters in 2014 and 2018. We first compared this data with historical reports to reconstruct seagrass distribution and change in the GoT over the years. Additionally, we analyzed spatiotemporal patterns of water quality variables and applied generalized additive models (GAM) to identify key predictors of *C. nodosa* regression in the GoT between 2014 and 2018. Our findings provide critical insights into the sources of impact on seagrass meadows in the Gulf and highlight the need for integrated spatial planning strategies. Furthermore, this study provides a baseline for future monitoring and restoration efforts aimed at mitigating seagrass loss.

2. Methods

2.1. Study area

The GoT is a relatively shallow sub-basin of the northern Adriatic Sea (NAS), reaching a maximum depth of ~25 m. It includes the entire coastline of Slovenia and the Friuli Venezia Giulia Region (FVG) in Italy, extending between Cape Savudrija and the Tagliamento River mouth (Fig. 1). The general circulation in the NAS is cyclonic, with a northward flow along the eastern side and a southward return flow along the Italian coast on the western side (Artegiani et al., 1997; Ursella et al., 2018). However, the GoT is characterized by different circulation patterns, induced by strong hydrological and meteorological variability. In particular, the basin-scale recirculation during prevailing ENE wind (locally known as Bora or Burja) can flush the entire Gulf in a few days

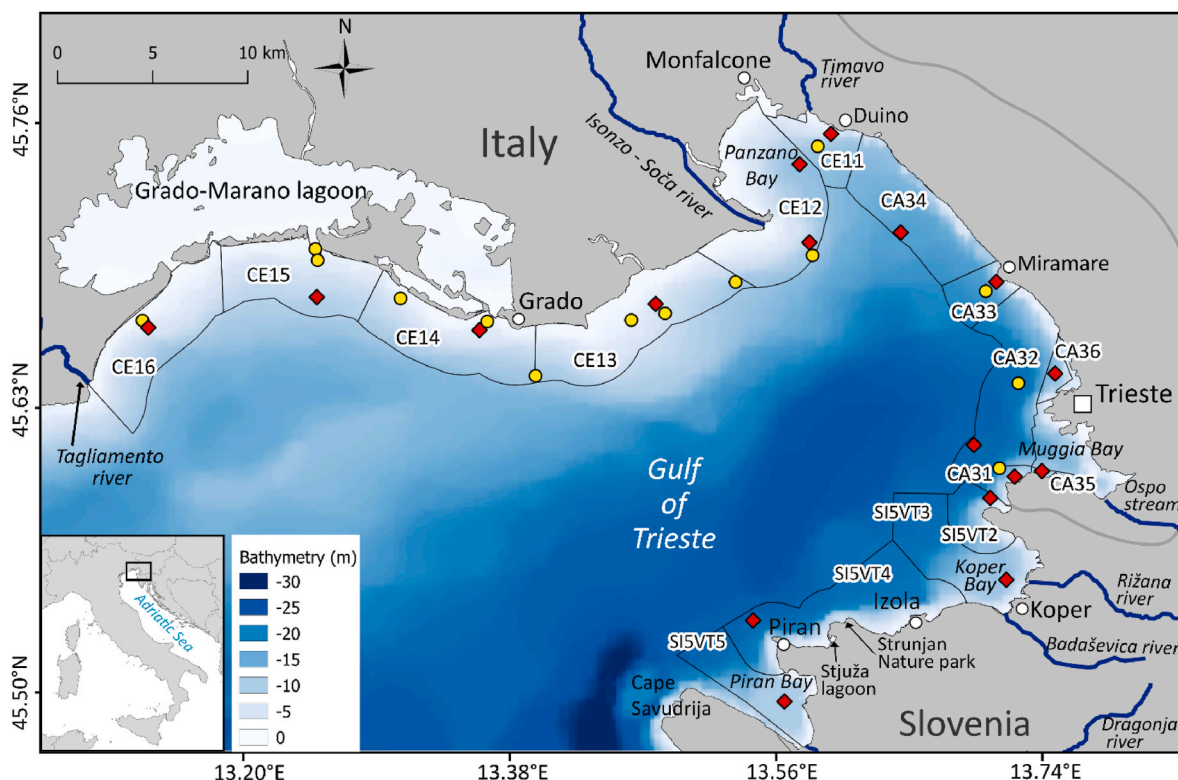


Fig. 1. The Gulf of Trieste with the sampling stations (yellow dots and red diamonds) and the coastal water bodies (designed with a code) of the water quality monitoring programs considered for this study. Red diamonds indicate stations where nutrients, along with other variables, are also collected. Areas of the Gulf considered in this study: Slovenia (SLO) (water bodies SI5VT2, SI5VT3, SI5VT4, SI5VT5), northern coast (NC) (water bodies CE11-16) and eastern coast (EC) (water bodies CA31-36).

(Kuzmić et al., 2006). The average salinity is about 37 psu, mainly influenced by the freshwater inflow from the Isonzo-Soča River and maximum summer seawater temperatures reach 28 °C (data from VIDA oceanographic buoy, <https://www.nib.si/mbp/en/>).

The northern coast of the GoT, from the Tagliamento River to the Panzano Bay, is predominantly low and sedimentary and it is strongly influenced by freshwater inputs from two major estuaries: the Isonzo-Soča and the Tagliamento rivers. These rivers represent the largest freshwater input and the primary source of land-based nutrients (Fig. 1). Additionally, a substantial exchange of water masses occurs also between the Grado-Marano lagoon and the sea, facilitated by six channels. Conversely, river inputs in the other areas of the Gulf are low and contribute less than 10 % to the freshwater balance (Cozzi et al., 2012). The eastern coast of the Gulf, stretching from Panzano Bay to Muggia Bay in Italy, is high and rocky, with several submarine springs. The Slovenian coastline in the southeastern part of the Gulf features steep flysch cliffs and alluvial deposits at the river mouths (Fig. 1). Both the Slovenian and eastern Italian coasts of the Gulf are highly urbanized and have undergone major changes in recent decades, following intensive economic and tourist development, especially near the ports of Trieste and Koper (Kolega, 2015; Orlando-Bonaca et al., 2012, 2019). Currently, less than 18 % of the Slovenian coastline (Turk, 1999; Turk et al., 2007) and 45 % of the FVG coastline (Zanchini and Manigrasso, 2017) remains in a near-natural state.

2.2. Seagrass distribution

Following the EU Water Framework Directive (WFD, European Commission, 2000) and the Marine Strategy Framework Directive (MSFD, European Commission, 2008), which mandate the assessment of seagrass extent and status, the Marine Biology Station Piran (NIB), in cooperation with the University of Maribor monitored seagrass distribution along the entire Slovenian coastline (46.7 km) in 2009, 2014 and 2018. Monitoring activities in FVG (93 km) were carried out in 2014 and 2018 by the University of Trieste, with the support of the staff of the Miramare Marine Protected Area and the National Institute of Oceanography and Applied Geophysics - OGS.

In Slovenia, seagrass maps were developed by combining field-based methods and remote sensing technology (Ivajnsiĉ et al., 2022). Supervised image classification (Maximum Likelihood Classifier) was applied to Google Earth satellite imagery (2018) and to high-resolution near-infrared ortho-photo (pixel size 0.25 m) by using ground control polygons derived from seagrass field mapping conducted in 2014 (Ivajnsiĉ et al., 2022). In Italy, the seagrass meadow was mapped by underwater surveys, with georeferenced markers recorded at the meadow edges. Each marker included species-specific information. For the area between Punta Tagliamento and the Isonzo-Soča River mouth, 30 parallel and perpendicular transects to the coastline were recorded using Side-Scan Sonar. Data was simultaneously collected by divers to check seagrass presence/absence. Data was analyzed using ESRI ArcGIS 9.x software and SONAR DeepView software. The data and the corresponding maps were processed using QGIS 2.6 (QGIS.org, 2014. QGIS Geographic Information System. QGIS Association. www.qgis.org).

Historical data on seagrass distribution in the GoT was gathered through a literature review, encompassing peer-reviewed journals, online databases, and local grey literature. All studies containing qualitative or quantitative information on seagrass occurrence were considered (Table S1). Occurrence data was georeferenced using the free and open-source Geographic Information System QGIS 3.22 (QGIS.org, 2022. QGIS Geographic Information System. QGIS Association. www.qgis.org).

2.3. Spatiotemporal pattern analysis of water quality variables

Monthly data on physicochemical variables (temperature (TEMP), salinity (SAL), pH (PH), dissolved oxygen (DOX), chlorophyll-a (CPHL),

nitrate (NTRA), nitrite (NTRI), ammonium (AMON) and phosphate (PHOS)) at the seawater surface from 2009 to 2018 was obtained from 31 sampling stations, involved in the water quality monitoring programs of the Regional Environmental Protection Agency of FVG (ARPA-FVG) in Italy and by the NIB and the Agency of the Republic of Slovenia for the Environment (ARSO) in Slovenia (Fig. 1). Nutrient sampling was limited to selected stations (red diamonds in Fig. 1). The N:P ratio (N:P) was calculated at each station based on the concentrations of inorganic nitrogen (DIN) and phosphorus (DIP), excluding values below the detection limit. The sampling stations were distributed over 12 coastal water bodies (WBs) in Italy and four WBs in Slovenia, defined by ARPA-FVG and by the Slovenian Ministry of Environment and Spatial Planning, respectively, according to the environmental characteristics of each area (Fig. 1). In this study, we considered only the data at the sea surface, as nutrients are not measured at the sea bottom in Italy.

To assess the environmental conditions before and after 2014, when a notable regression of *Cymodocea nodosa* meadows was observed (see '1. Introduction' and '3. Results' sections), the monthly mean values of the variables were calculated for two five-year periods (2009–2013 and 2014–2018). Percent variation between the periods was calculated for each area of the Gulf with similar geomorphological and environmental features: Slovenian coast (SLO) (WBs: SI5VT2, SI5VT3, SI5VT4, SI5VT5, Fig. 1), northern Italian coast (NC) (WBs: CE11-16, Fig. 1) and eastern Italian coast (EC) (WBs: CA31-36, Fig. 1). Spatiotemporal differences between areas and years (fixed factors) were tested by two-way permutation-based analysis of variance, followed by pairwise comparisons with 9999 permutations to resolve differences between levels of factors in pairs, using the 'lmPerm' package (Wheeler et al., 2016) in R software version 4.03 (R Core Team, 2021; www.r-project.org).

2.4. Relationship between seagrass change and environmental factors

2.4.1. Data processing for modeling

C. nodosa presence/absence in 2014 and 2018 was used as a response variable in the species distribution models. We did not use the seagrass data collected in 2009 in Slovenia to build the models, as the species showed only minor changes during that year (see Section 3, 'Results'), and no data were available for FVG for the same period to make results comparable. Vector layers of seagrasses for both years were rasterized in GIS, assigning values '1' or '0' to each pixel to indicate presence or absence, respectively.

Relevant predictor variables were selected based on expert opinion and prior studies (Baldan et al., 2024; Boscutti et al., 2015; Chefaoui et al., 2018, 2016; De la Hoz et al., 2018; Duarte, 1995; Fernández-Torquemada and Sánchez-Lizaso, 2006; Marba et al., 1996). These variables were chosen considering their potential relationship with seagrasses and their availability across the study area (Table S2).

Mean, minimum, and maximum water quality variables at the sea surface (PH, SAL, DOX, TEMP, summer temperature (TSUM), CPHL, NTRA, NTRI, AMON, PHOS, N:P) were calculated for each sampling station in two five-year periods (2009–2013, 2014–2018). Data was interpolated over the entire study area using a multilevel b-spline algorithm in GIS (Lee et al., 1997). Monthly mean and maximum seawater velocity (Vmean, Vmax), and mean kinetic energy of ocean currents (KEmean) at surface, from 2009 to 2018, were extracted from a high-resolution numerical simulation of the NAS. The simulation is based on the Massachusetts Institute of Technology general circulation model (MITgcm), a three-dimensional finite volume model for geophysical fluid dynamics (Marshall et al., 1997). The computational domain extends north of 43.5°N with a horizontal resolution of 1/128° (about 600 and 850 m in the zonal and meridional direction, respectively) and 27 unevenly spaced levels in the vertical direction. The NAS model is a downsampling of the Copernicus Marine Environment Monitoring Service (CMEMS; <https://marine.copernicus.eu/>) implemented as part of the CADEAU project (Silvestri et al., 2020). It explicitly considers the main rivers flowing into the basin and it is forced by a

high-resolution limited-area atmospheric model. Further details on the simulation features and setup are provided in [Silvestri et al. \(2020\)](#) and [Bandelj et al. \(2020\)](#). Hydrodynamic data was then averaged over the two five-year periods and rasterized in GIS. Bathymetry (DEPTH) was derived from the General Bathymetric Chart of the Oceans with a resolution of 15 arc-seconds (GEBCO Compilation Group, 2019; www.gebco.net). Sediment grain size (SED) given as phi-scale (ϕ), was obtained from a detailed sedimentological map produced by interpolating the raw data (3-metric IDW) with a grid resolution of 1 km ([Bostock et al., 2018](#)). The interpolation distance metrics used were the geographic distances and the water depth difference ([Bostock et al., 2018](#)). The phi diameter, introduced by Krumbein (1938, 1934) as a practical means of visualizing and analyzing sediment grain size, is calculated as the negative logarithm to the base 2 of the particle diameter (in millimeters), thus higher values indicate finer sediments (i.e., silt and clay). Since PAR and diffuse attenuation coefficient (Kd) are not available from the monitoring programs carried out in the GoT before 2014, monthly data at the sea surface from 2009 to 2018 was provided by Level-3 standard mapped image derived from the Aqua MODIS sensor, with a 4 km grid cell size, available on NASA Ocean Color Web (oceancolor.gsfc.nasa.gov; Ocean Biology Processing Group, NASA Goddard Space Flight Center, Ocean Ecology Laboratory, 2018). PAR on the seafloor (PARz) was computed using the Lambert-Beer formula (Eq. 1) as previously done in other studies on seagrasses (e.g., [Duarte, 1991](#); [Obrador and Pretus, 2008](#)):

$$I_z = I_0 e^{-kz} \quad \text{Eq. 1}$$

where z is the depth derived from GEBCO, I_0 is the surface PAR derived from the satellite imagery, and k is the diffuse attenuation coefficient. The mean values of PAR on the seafloor were then calculated for the two five-year periods. The distance of seagrasses from estuaries and lagoon channels (DIST) was calculated in GIS as the Euclidean distance from the first edge of the freshwater inputs to the center of each pixel of the seagrass raster layers. The effects of ports/marinas (PORTS) and mariculture (MAR) on the seagrasses was considered by drawing a 500 m radius around them. The resulting vector layers were rasterized in GIS, and we assigned '1' to all pixels within the radius and '0' to the pixels outside of it to indicate the presence or absence of the impact. The choice of 500 m from the impact source is arbitrary, but can be considered as a buffer area where seagrasses may be affected (see for instance, [Cabaço et al., 2008](#); [Pergent-Martini et al., 2006](#); [Tuya et al., 2014](#)).

All layers were standardized to a raster format with a 100 m cell size to match the spatial scale of the sampling area and species. Computation of the models was limited to the 10 m isobath, representing the maximum seagrass depth in the GoT. All GIS file manipulations and computations were performed in QGIS 3.22 (QGIS.org, 2022). QGIS Geographic Information System. QGIS Association. www.qgis.org.

2.4.2. Model development

GAMs were implemented to explain spatiotemporal changes in *C. nodosa* occurrence between 2014 and 2018 as a function of environmental factors in the two five-periods (2009–2013 and 2014–2018). Due to the different pressures, geomorphology, environmental conditions and seagrass occurrence, separate models were run for the three areas (SLO, EC and NC). For NC, where no seagrass changes were observed in 2018 compared to 2014 (see the '3. Results' section), data was averaged over the entire period and models did not include time intervals.

Data exploration followed the protocol by [Zuur et al. \(2010\)](#). The presence of possible outliers in the predictor variables was determined by using boxplots and Cleveland dotplots ([Cleveland, 1993](#)). Multicollinearity among predictors was assessed by Pearson's correlation ($r < 0.7$) using the 'Hmisc' package ([Harrell Jr, 2022](#)) and the Variance Inflation Factor ($VIF < 5$) using the 'car' package in R ([Fox and Weisberg,](#)

2018). This process resulted in a subset of 12 largely uncorrelated variables for the SLO model, 15 for the NC model and 13 for the EC model, which were used as initial inputs to the models (Table S3, Fig. S1).

Interactions between the selected predictors and time ('years') were also included in the models using a smoothing function. If they were not significant or did not improve the models, they were removed, and the explanatory power of each predictor was tested with or without smooth term. A backward selection procedure was used to find the best models based on the Akaike Information Criterion (AIC), with the lowest AIC value indicating the best fit ([Burnham and Anderson, 2003](#)), the highest explained deviance and by retaining only statistically significant variables ($p < 0.05$). The dataset was split into a training dataset (70 %) for calibration and in a testing dataset (30 %) for validation, repeating the process ten times.

Model performance was evaluated by the area under the receiver operating characteristic (ROC) curve (AUC) using the 'ROCR' package in R ([Sing et al., 2005](#)), the True skill statistic (TSS) (i.e., sensitivity + specificity – 1 ([Allouche et al., 2006](#))) and the Root Mean Squared Error (RMSE) using the 'Metrics' package in R ([Hamner et al., 2018](#)). To determine the optimal threshold for optimizing the confusion matrix scores (i.e. trade-off between specificity and sensitivity) and to transform predicted probability into binary values (presence-absence), we tested a range of thresholds based on the ROC curve and compared them with the result obtained using the 'optimalCutoff' function from the 'InformationValue' package in R ([Prabhakaran, 2016](#)). Model goodness-of-fit was also assessed by checking potential patterns in the residuals of the models against each covariate ([Zuur and Ieno, 2016](#)). All GAMs were fitted through a binomial distribution with a logistic link function, using the 'mgcv' package in R ([Wood and Wood, 2015](#)). Effect plots of the best GAMs were generated using the 'mgcViz' package in R ([Fasiolo et al., 2020](#)). Relative importance of the variables was assessed by using the 'gam.hp' package in R ([Lai et al., 2024](#)). The model outputs were rasterized using the 'ggplot2' package in R ([Wickham, 2016](#)) showing the logistic probability of occurrence (from 0 to 1) in the study area. All analyses were carried out with R software version 4.03 (R Core Team, 2021; www.r-project.org).

3. Results

3.1. Seagrass distribution

3.1.1. Historical distribution

Most studies reporting on the historical distribution of seagrasses in the GoT were qualitative (Table S1). These studies typically listed the observed species, their locations and, in some cases, provided details of depth ranges and sediment type.

Historical records indicate that *Zostera marina* and *Zostera noltei* were once dominant in the GoT, particularly in the early 20th century. [Teghet \(1906\)](#) described the Gulf as being predominantly colonized by meadows of these two species, especially in inlets such as Panzano Bay and Muggia Bay, and along the eastern coast (Figs. S2, S3, S6), even if the exact location of *Z. noltei* was not reported by the author. These meadows extended to depths of –18 m on sandy substrates and –14 m on mud. *Z. marina* remained abundant along both the Italian and Slovenian coasts after thirty years, while *Z. noltei* was reported only in some inlets ([Benacchio, 1938](#)) (Figs. S2, S3, S6). However, by the 1960s and 1970s, *Z. noltei* was still present, while *Z. marina* distribution had significantly declined. The species became restricted to shallow areas, down to 2 m depth, and regions with lower salinity, such as the Timavo River mouth ([Simonetti, 1966, 1973](#)) (Figs. S2, S3, S6). This contraction in distribution is thought to be due, in part, to infections by *Labyrinthula macrocystis*, a myxomycete pathogen known to affect *Z. marina* globally. The pathogen confined the species to locations near freshwater inflows, where cooler temperatures and reduced salinity mitigated the effects of the infection ([Simonetti, 1973](#)). [Zavodnik and Jaklin \(1990\)](#) also reported a sharp decline in *Z. marina* populations along the Istrian

Peninsula coasts by 1988. Meanwhile, *Z. noltei* persisted in shallow areas with lower salinity. Since the 1990s, a few studies have addressed the occurrence of Zosteraceae in recent decades. *Z. marina* and *Z. noltei* were recorded near Miramare between 1988 and 1990, although most of the meadows had disappeared after a flood event (Bressan and Odorico, 1996) (Figs. S2, S3, S6). Mazzella et al. (1998) collected samples of *Z. marina* off Grado at 1 m depth to conduct a comparative study of seagrass phenology (Figs. S2 and S6). In Slovenia, small populations of *Z. noltei* mixed with *Cymodocea nodosa* were reported in the Strunjan Nature Park (Lipej et al., 2003, 2004; Turk and Lipej, 2006), and in the Koper Bay (Turk et al., 2002) (Figs. S3 and S6). *Z. marina* was occasionally found as small patches in the mouths of rivers, streams, and lagoons, with the only substantial meadow observed in Koper Bay (Faganeli et al., 1997; Lipej et al., 2004; Turk et al., 2002; Turk and Lipej, 2006) (Figs. S2 and S6). Within the Stjuža lagoon (part of the Strunjan Landscape Park) *Zostera* spp. co-occurred with *C. nodosa* (Šajna and Kaligarič, 2005).

C. nodosa was not mentioned in the earliest records (Techet, 1906) and was only sparsely reported by 1938, being limited to areas near Trieste and Koper Bay (Benacchio, 1938) (Figs. S4 and S6). However, its presence increased over the following decades. By the 1960s and 1970s, it had become the dominant species in sedimentary infralittoral zones, accounting for more than 80 % of seagrass coverage (Simonetti, 1966, 1973) (Figs. S4 and S6). It occupied depths up to 7 m on sand and 5 m on mud. Its expansion likely came at the expense of other seagrass species, such as *Posidonia oceanica* and *Zostera* spp., filling areas left by their decline. This shift may have been influenced by environmental changes, including reduced water quality and the presence of pathogens affecting other species (Simonetti, 1966, 1973). Similarly, Zavodnik & Jaklin (1990), in the late 1980s, observed a considerable expansion of the *C. nodosa* range, colonizing sites that were previously dominated by *P. oceanica* or *Zostera* species along the Istrian Peninsula. Since the 1990s, *C. nodosa* was found to be widespread from 2 to 10 m deep, along the whole coastline, with the exception of the highly urbanized areas near the ports of Koper and Trieste (Bressan and Odorico, 1996; Faganeli et al., 1997; Falace et al., 2009; Lipej et al., 2003, 2004; Makovec and Turk, 2006; Mazzella et al., 1998; Orlando-Bonaca and Lipej, 2005; Peduzzi and Vuković, 1990; Šajna and Kaligarič, 2005; Turk, 2006; Turk et al., 2002; Turk and Lipej, 2006; Vuković and Turk, 1995) (Figs. S4 and S6).

Regarding *P. oceanica*, it was historically rare, west of the Isonzo-Soča River, even if the exact location was not reported on map by the author (Techet, 1906). However, by 1938 it had been observed in several areas, including Muggia Bay, off the town of Grado, and between Koper Bay and Piran Bay (Benacchio, 1938) (Figs. S5 and S6). Despite these occurrences, by the 1960s and 1970s, *P. oceanica* was only confirmed off the Grado-Marano lagoon and was missing elsewhere (Simonetti, 1966, 1973) (Figs. S5 and S6). Its decline continued, with Zavodnik and Jaklin (1990) reporting a sharp decrease in populations along the Istrian Peninsula by 1988. Afterwards, the extent and status of *P. oceanica* have been assessed in various studies that highlighted a spotty distribution. Numerous small patches, occasionally interspersed with *C. nodosa* and *Z. noltei*, were recorded along the coastline between Izola and Koper spanning approximately 1 km long and 50 m wide (0.63 ha), at depths of 0.5–4 m (Faganeli et al., 1997; Makovec and Turk, 2006; Orlando-Bonaca and Bressan, 1998; Orlando-Bonaca and Lipej, 2005; Turk, 2006; Turk et al., 2002; Turk and Lipej, 2006; Turk and Vuković, 1998; Vuković and Turk, 1995). The most detailed maps were provided by Vuković and Turk (1995) and Turk et al. (2002) (Fig. S5). Other small patches were reported off Grado (Falace et al., 2009; Ruggiero et al., 2002). These meadows represent the northernmost occurrence of *P. oceanica* in the Mediterranean and form a monoclonal population (Ruggiero et al., 2002) (Fig. S5).

3.1.2. Recent distribution

Seagrass monitoring in Slovenia (since 2009) and Italy (since 2014)

showed that *C. nodosa* remains the most abundant seagrass species in the GoT. In Italy, contiguous *C. nodosa* meadows were recorded in 2014 along the NC, from the Tagliamento River mouth to Panzano Bay (Fig. 2). Further stands were also spotted close to Miramare and at Lazzaretto, on the Italy-Slovenia border. However, most of the *C. nodosa* beds reported in the literature before 2009 on the coast between Duino and Miramare were no longer present by 2014 (Fig. 2, S4, S6). In 2018, there were no detectable changes on the NC, whereas on the EC, from Miramare to Lazzaretto, over 89 % of the meadows had disappeared (Fig. 2). Close to Duino (i.e., Villaggio del Pescatore), *Z. noltei* replaced *C. nodosa*. In SLO, *C. nodosa* is widespread along most of the coastline. Between 2009 and 2014, the extent of these meadows decreased by only 1.2 %, mostly off the port of Koper (Fig. S7). However, from 2014 to 2018, *C. nodosa* meadows decreased by up to 30 %, primarily in the Koper Bay, the Piran Bay and off the Stjuža lagoon (Fig. 3).

Z. noltei was observed in 2014 only near Duino and in small patches at Lazzaretto, but in 2018 it was no longer found at Lazzaretto (Fig. 2). Due to depth restrictions, the shallowest (<1 m depth) northern coast, which is periodically exposed to the tides, was not surveyed, so additional *Zostera* spp. meadows may have gone undetected. In SLO, a monospecific meadow of *Z. noltei* has been recorded north of the port of Koper (Ivajnsič et al., 2022). In contrast, *Z. marina* was not detected in any of the surveys (Fig. 3).

The distribution of *P. oceanica* has remained unchanged, with the species persisting in small patches (665 m²) off Grado on rocky substrate, and along a 1 km stretch between Izola and Koper in SLO (6750 m² (Lipej et al., 2018)) (Figs. 2–3, S5, S7, S8, S9). Although exposed to notable anthropogenic disturbance, these patches currently appear to be stable.

3.2. Spatiotemporal pattern analysis of water quality variables

Nutrients, especially NTRA, PHOS, and N:P, showed marked variations across different areas and time periods. The NC consistently had the highest mean concentrations of NTRA, AMON, NTRI and N:P in both time periods, whereas the mean PHOS in SLO was almost twofold higher than in Italy during 2009–2013 (Fig. 4). Between 2014 and 2018, nutrient trends differed both by nutrient type and area (Fig. 4). In SLO, the mean PHOS, NTRA, and AMON consistently decreased by 67 %, 44 %, and 42 %, respectively, while the mean NTRI increased by 17 %. In contrast, the EC recorded increases in the mean PHOS (14 %), NTRA (105 %) and NTRI (58 %), while in the NC, the mean PHOS nearly doubled (98 %), and the mean NTRA and NTRI increased by 24 % and 50 %, respectively. Both the NC and EC experienced a slight decrease in mean AMON (12 %) with respect to the larger decrease observed in SLO (Fig. 4). As for the mean N:P, a consistent increase (124 %) was measured in SLO during the second period, ascribable to the marked decrease in mean PHOS. A slight increase (10 %) was also recorded in the EC, whereas the NC experienced a 26 % decrease (Fig. 4). These spatial and temporal variations were further supported by a statistically significant interaction term for the mean NTRA ($p = 0.01$), PHOS ($p < 0.001$) and N:P ($p = 0.03$) (Table S4). Pairwise comparisons revealed significant differences in the two time periods in all areas, except for the mean PHOS and N:P in the EC and the mean NTRA and N:P in the NC (Table S5). Pairwise comparisons also confirmed differences between areas across both time periods for all nutrients, except for the mean PHOS between the NC and EC in both time periods and for the mean NTRA and N:P between SLO and EC during 2009–2013. Notably, the mean PHOS in SLO during 2014–2018 did not differ significantly from the mean PHOS in the NC or EC in the earlier period. In addition, significant temporal differences were observed for the mean AMON and NTRI, and significant differences between the three areas for the mean AMON (Tables S4 and S5).

Changes in the other physicochemical variables between 2009–2013 and 2014–2018 were less pronounced. The NC consistently had the lowest mean values for TEMP, SAL, and PH, and the highest for DOX in

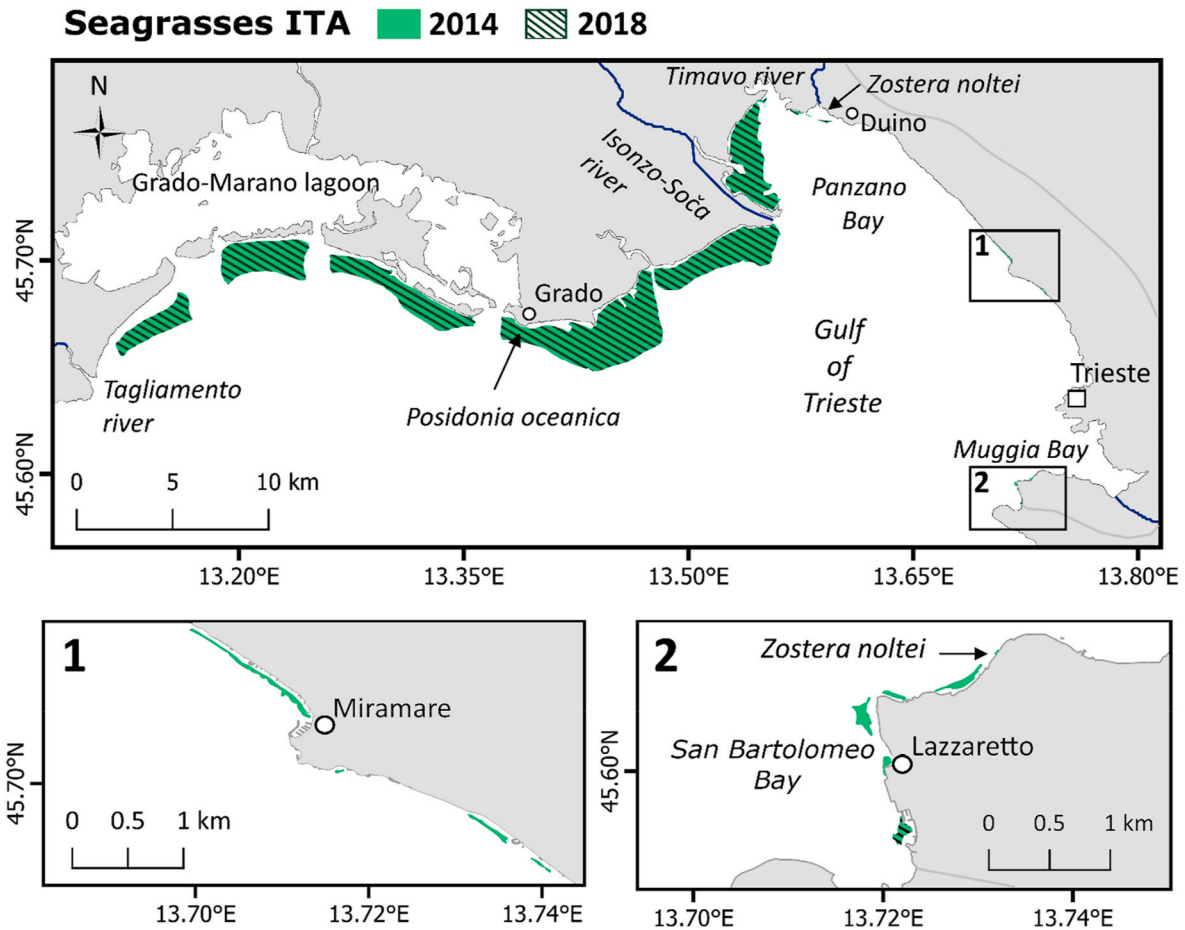


Fig. 2. Comparison of seagrass distribution between 2014 and 2018 in FVG Region (Italy) with an enlargement for the area of Miramare and San Bartolomeo Bay. Most of the seagrass meadows shown in the figure consist of *Cymodocea nodosa*. Any occurrences of other species are also indicated in the figure.

both periods (Fig. 4). Specifically, the mean TEMP was nearly 1 °C lower than in the other areas. By contrast, the mean CPHL in SLO was slightly higher than in Italy during the first period (Fig. 4). In the second period, most variables increased throughout the entire GoT, except for the mean SAL in the NC, which decreased by 5 %, and the mean DOX in SLO (−1 %). The interaction term for the mean SAL was statistically significant ($p = 0.01$) (Table S4) and pairwise comparisons confirmed that the NC consistently differed from the other two areas in both periods, but no statistically significant year-to-year differences were detected within each area (Table S5). Analysis of variance also revealed significant differences among areas and years for the mean PH ($p < 0.001$) and TEMP ($p < 0.05$) (Table S4), and among areas for the mean DOX ($p < 0.001$), although SLO and the EC did not differ in any comparison (Table S5). The mean CPHL did not vary significantly between areas but was significantly different between the two time periods ($p = 0.005$) (Table S4).

3.3. Relationship between seagrass change and environmental factors

The final model for SLO retained four variables, all statistically significant ($p < 0.05$): mean PARz, the interactions of the factor 'years' with maximum PHOS, maximum AMON and mean TSUM (Table S6). The interaction between 'years' and mean PARz was not statistically significant, and applying a smooth term to the variable did not improve its contribution to the explained deviance of the model (Fig. 5). Effect plots showed that the probability of seagrass occurrence increases gradually with nutrients (maximum PHOS and maximum AMON), while the increase in mean TSUM leads to a sharp decrease in the probability of seagrass presence, with the effect being more pronounced in the period

2014–2018 (Fig. 5). The model explained nearly 50 % of the deviance ($R^2 = 0.486$, $R^2_{adj.} = 0.497$). Individual contribution of mean PARz and mean TSUM to the explained deviance of the model was 0.17 and 0.12, while the individual contribution of maximum AMON, maximum PHOS and years was 0.10, 0.04 and 0.06, respectively.

Changes in seagrass presence between 2014 and 2018 in the EC were primarily predicted by mean PARz, mean TSUM, SED, and mean N:P, all of which had smooth terms, and were all statistically significant ($p < 0.05$) (Table S6). The time factor 'years' also resulted statistically significant ($p < 0.001$), but not in interaction with the other terms. The model indicated that seagrass occurrence is positively influenced by an increase in mean PARz, up to 20 E/m²/day, and by the increase in SED, suggesting a higher likelihood of seagrass occurrence on fine sediments (Fig. 5). Conversely, increases in mean N:P and mean TSUM, as observed in SLO, lead to a gradual decline in seagrass presence. The 'years' factor revealed a clear decline in seagrasses from 2014 to 2018 (Fig. 5). The model explained 77.5 % of the deviance ($R^2 = 0.775$, $R^2_{adj.} = 0.56$), individual contribution of mean TSUM was 0.23, while for mean PARz was 0.21 and for mean N:P was 0.18. Individual contribution of the 'years' factor and SED was about 0.09 and 0.07, respectively.

Mean PARz, SED, minimum NTRA, and minimum TEMP were the four main contributors to the model for the NC, all of which were statistically significant ($p < 0.001$) (Table S6). The relationship between seagrasses and mean PARz was positive, and occurrence gradually increases as the minimum NTRA increases. The relationships of seagrasses with SED and minimum TEMP were both negative and linear, as the smooth term applied to these factors did not improve the explained deviance of the model. Specifically, seagrasses decreased with increasing SED, suggesting a lower probability of finding the species on

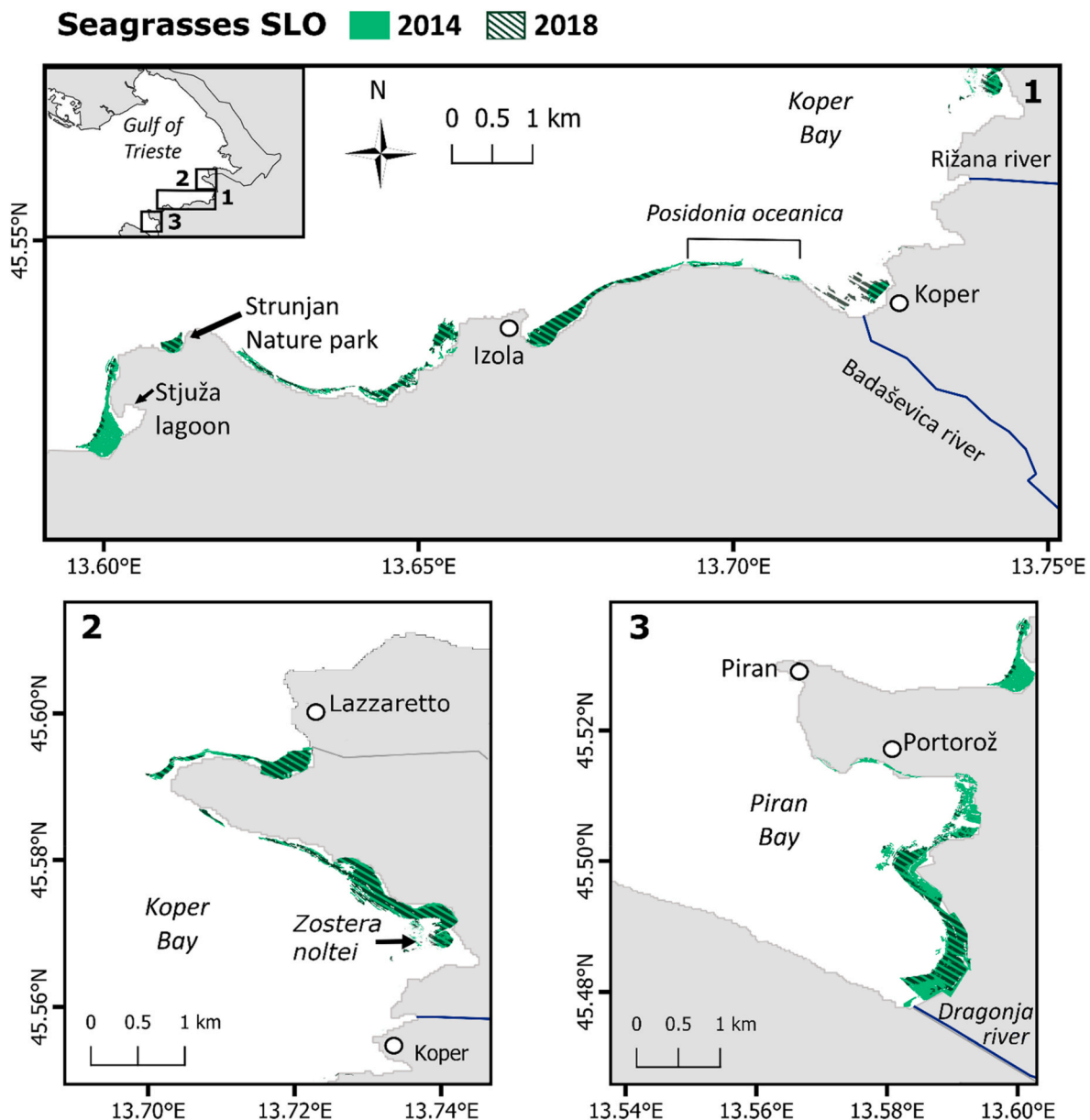


Fig. 3. Comparison of seagrass distribution between 2014 and 2018 in Slovenia. Most of the seagrass meadows shown in the figure consist of *Cymodocea nodosa*. Any occurrences of other species are also indicated in the figure.

finer sediments. In addition, the model showed that seagrass presence decreases linearly with increase in minimum TEMP, although to a lesser extent (Fig. 5). The cumulative contribution of these factors to the explained deviance of the model was 38.4 % ($R^2 = 0.384$, $R^2_{adj.} = 0.40$). The most influential factor was mean PAR_z, with an individual contribution of nearly 0.18, followed by SED (0.10), minimum NTRA (0.06), and minimum TEMP (0.05).

All models exhibited high performance scores. The AUCs values were greater than 80 %: 0.86 for the SLO model, 0.83 for the NC, and 0.88 for the EC. The TSS for the SLO model was 0.72, (specificity = 0.91 and sensitivity = 0.81), and similarly for EC (TSS = 0.76, specificity = 0.99; sensitivity = 0.77). In contrast, the TSS for the NC model was lower (0.66), with specificity of 0.77 and sensitivity of 0.89 (Table 1).

The areas predicted to have suitable conditions for seagrass occurrence matched up with the seagrass distribution recorded during monitoring activities, demonstrating that the models accurately predicted the presence or absence of seagrasses in the study area (Fig. S10). The highest suitability areas (>0.6) were found as expected on the NC,

given the widespread presence of seagrasses, especially west of the Isonzo-Soča River. In SLO, the model accurately predicted the presence of seagrasses with high probability (>0.75) in San Bartolomeo Bay, Piran Bay and close to the Rižana and Badaševica rivers. In the EC, seagrasses were predicted only in San Bartolomeo Bay (0.3), near Miramare (0.6) and in a single spot between Miramare and Duino (<0.2) where seagrasses were only recorded in the past and not in 2014 and 2018 (Fig. S10).

4. Discussion and conclusions

In this study, we provided the first detailed mapping of seagrasses in the GoT, establishing a baseline for future monitoring. The most abundant species is *Cymodocea nodosa*, while *Zostera* spp. and *Posidonia oceanica* exhibit a patchy distribution, confined to certain areas. In particular, *P. oceanica* has been reduced to small patches off the coast of Grado (Italy), protected within a Natura 2000 site (ZPS/ZSC IT3330008), and between Izola and Koper (SLO). Although *C. nodosa*, as

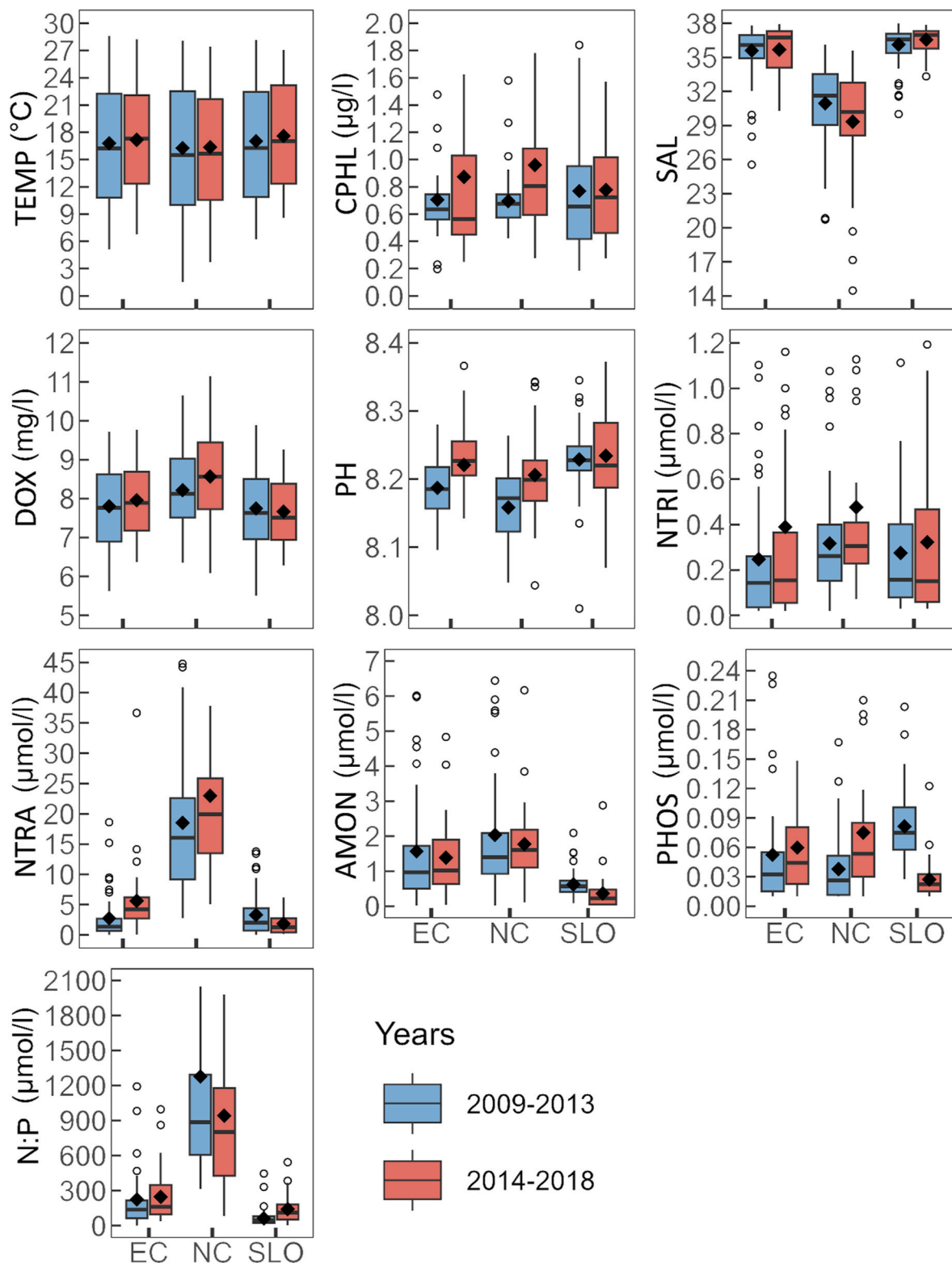


Fig. 4. Boxplots of the physicochemical variables measured by the water quality monitoring programs in the Gulf of Trieste and calculated on the two five-year periods. Black diamonds indicate the mean value. TEMP: temperature; CPHL: chlorophyll-a; SAL: salinity; DOX: dissolved oxygen; PH: pH; NTRI: nitrites; NTRA: nitrates; AMON: ammonium; PHOS: phosphates; N:P: N:P ratio. SLO: Slovenia, EC: eastern coast, NC: northern coast.

a pioneer species, is tolerant to moderate stressful conditions (Terrados and Ros, 1992), field surveys have detected a severe decline since 2014, especially along the EC (Miramare, Grignano, Sistiana) and in SLO. Contrarily, only minor changes were recorded in SLO between 2009 and 2014 (1 %). The most stable seagrass meadows are currently located

along the NC, where the largest and most continuous meadows (ca. 55 km²) are found, under significant freshwater influence.

Our findings indicate that changing environmental conditions have played a primary role in the recent regression.

In particular, nutrients were identified as key predictors of seagrass

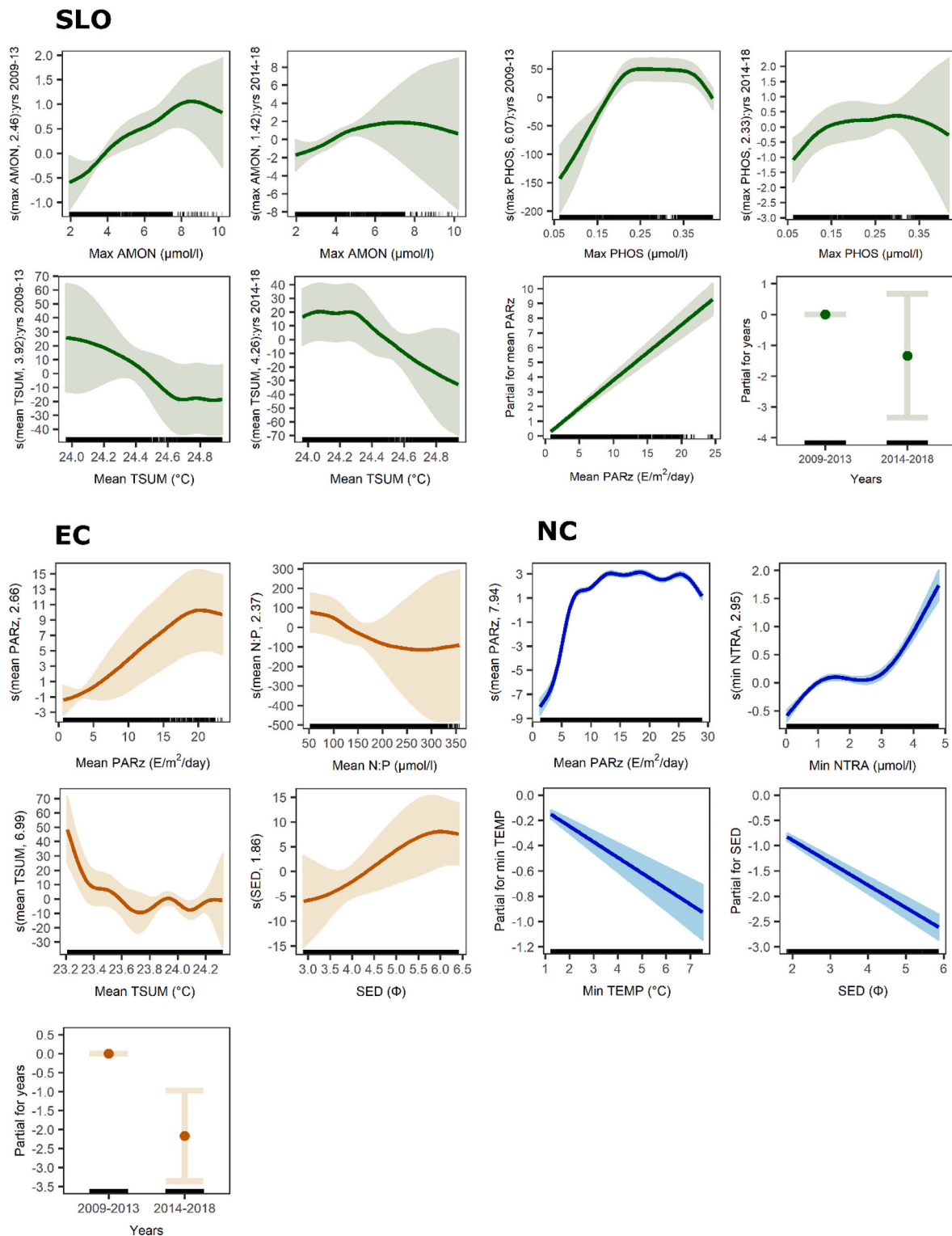


Fig. 5. Effect plots of the best models for the three coastal areas. The y-axis represents the partial effect of the smooth or linear terms of each explanatory variable on the logit of the response variable. Tick marks on the x-axes show the distribution of the observed data. The shaded areas indicate the 95 % confidence intervals. SLO: Slovenia, EC: eastern coast, NC: northern coast.

occurrence in all models of the three areas, and the results showed that an increase in nutrient content correlated with greater seagrass presence. Notably, in SLO, the interaction with the 'years' factor was significant for both maximum AMON and maximum PHOS. Spatiotemporal analysis of water quality variables showed that nutrient levels in SLO dropped significantly after 2014, especially PHOS (-67 %), but also

AMON and NTRA. This decrease in nutrients is probably the result of EU legislation aimed at reducing PHOS in detergents, thereby decreasing nutrient load in wastewater in SLO (Regulation (EU) No 259/2012, 2012). On the contrary, along the Italian coastline of the GoT, an increase in nutrient levels was recorded in the second period analyzed in our study. This result is not surprising, since in recent years there has

Table 1

Performance scores of the best models for each area. SLO: Slovenia, EC: eastern coast, NC: northern coast.

GAM	Explained deviance	AUC	TSS	Specificity	Sensitivity	RMSE
SLO	48.6 %	0.86	0.72	0.91	0.81	0.31
EC	77.5 %	0.88	0.76	0.99	0.77	0.10
NC	38.4 %	0.83	0.66	0.77	0.89	0.36

been an additional supply of nutrients through the Isonzo-Soča River, likely due to the use of fertilizers in agriculture and field runoff (Gianni et al. in prep.). Nevertheless, our data confirm very low concentrations of PHOS and, consequently, a high N:P ratio, indicating phosphorus limitation (Atkinson and Smith, 1983) and oligotrophic conditions, as also reported in other studies (Giani et al., 2012; Grilli et al., 2020; Mentaschi et al., 2024; Mozetič et al., 2010; Solidoro et al., 2009). According to scientific literature, seagrasses can be limited by either nitrogen or phosphorus; however, nitrogen concentrations are typically higher than those required to saturate growth, making phosphorus generally the limiting nutrient (Leoni et al., 2008; Perez et al., 1991, 1994). In our case, the sharp decrease in phosphorus concentrations after 2014 had likely a direct impact on seagrasses in SLO, while in EC, persisting phosphorus limitation may have amplified the effects of other stressors on seagrasses in recent years, rather than directly causing the recent extensive regression observed. Phosphorus limitation has also been suggested as a possible contributing factor in the decline of *Fucales* (e.g., *Cystoseira* s.l., *Fucus viriosides*) in the NAS (Descourvières et al., 2024; Falace et al., 2024; Orlando-Bonaca et al., 2021).

Along with nutrients, TEMP was also identified as a significant factor in all models, specifically minimum TEMP in the NC and the mean summer TEMP in the EC. An increase in temperature was recorded between the two five-year periods, which correlated with a lower likelihood of seagrass occurrence. This effect was less pronounced in the NC than in the EC and SLO, which is likely due to the mitigating influence of the Isonzo-Soča River discharge. This outcome was expected, as sea TEMP has long been recognized as one of the primary limiting factors for seagrasses, affecting their biology at multiple levels (morphological, physiological, and molecular) (Nguyen et al., 2021; Repolho et al., 2017). Rising temperature is particularly detrimental to seagrasses because it increases the plant light requirements and the consumption of stored carbohydrates to fulfil the increased metabolic demands (Collier and Waycott, 2014; Litsi-Mizan et al., 2023; Massa et al., 2009). The depletion of carbon reserves further exacerbates the effects of warming and the ability of plants to cope with additional stressors (Egea et al., 2018; Soissons et al., 2018; Terrados and Ros, 1995). Recent studies have shown that seawater temperatures in the NAS are increasing by 0.36 % per year (Grilli et al., 2020). Consequently, the effects of rising temperatures driven by climate change on seagrasses are expected to intensify in the future, possibly leading to their functional extinction (Duarte et al., 2018).

Several coastal construction activities and sediment resuspension have recently been documented along the EC (e.g., Grignano and Sisti-ana) (authors' pers. obs.) and reported as local factors contributing to seagrass decline in Piran and Strunjan (SLO) (Ivajnsič et al., 2022; Lipej et al., 2018). Coastal interventions are known to cause physical removal of plants, change sediment type, modify hydrodynamic conditions and increase turbidity (Boudouresque et al., 2009; Cabaço et al., 2010; Tuya et al., 2002). Light availability on the sea floor was one of the most significant factors in our models, showing a positive effect in all areas. A reduction in light may have exacerbated the negative effects of temperature and/or nutrient changes and fostered seagrass regression. Unfortunately, the outlook for the future is concerning, as GoT coastline is highly urbanized, especially in the EC and SLO. According to the latest reports on coastal consumption in Italy, 61.5 km of the 120 km coastline in the FVG region has been irrevocably altered by urbanization. Half of this is occupied by ports and industrial facilities, while only 8 % of the

coastline is protected (Nanni et al., 2023; Zanchini and Manigrasso, 2017). It can be assumed that additional coastal works will be required in the future to sustain the extensive infrastructure that is currently in place. Therefore, careful management of construction activities and implementation of mitigation measures are urgently needed.

Our results indicated that the probability of seagrass occurrence in the EC was higher on fine-grained sediments, whereas in NC it increased with grain size. Two key factors may account for this outcome. A first explanation is that seagrass presence is closely related to the prevailing sediment type in each area: sand in the NC and clay/silt in the EC (Ogorelec et al., 1991). Secondly, nutrients, especially PHOS, are more readily available in fine-grained sediments than in sandy and carbonate sediments. Thus, in the EC, where PHOS can be a limiting factor, seagrasses tend to thrive in fine sediments. In contrast, in the NC, the proximity of the Isonzo-Soča River and the lagoon mouths enhances nutrient availability in the water, enabling seagrasses to also colonize coarse sediments. However, the growth of seagrasses may be influenced by the physical and geochemical properties of certain sediment types, rather than the grain size itself (Koch, 2001). Further studies are needed to explore these dynamics more into detail.

All three models successfully predicted the presence of seagrasses in both the NC and SLO and agreed well with the actual distribution. In contrast, the model for the EC exhibited lower precision, which is likely due to the limited number of positive cases (i.e., seagrass presence) in the dataset. Remarkably, the model predicted the presence of seagrasses near Duino, an area where the species was previously found (before 2010) and which is characterized by the presence of underwater springs. As expected, the models identified areas close to rivers and freshwater inputs as most suitable for seagrasses, as these regions typically have higher nutrient levels and lower seawater temperatures.

Although we are confident in our results, the present study has certain limitations. Specifically, our data on dissolved nutrients in the water column may not fully capture the effects of nutrient concentration as they do not account for nutrient sources in the sediment. Indeed, rooted macrophytes also obtain phosphorus and nitrogen from the sediments (Hemminga, 1998). Consequently, seagrasses may not have experienced nutrient limitations or alterations, at least in some areas. Moreover, using physicochemical variables collected at the sea surface to study benthic species could potentially be misleading. However, in the GoT, seagrasses thrive in shallow waters (0–10 m depth) where surface dynamics significantly influence the seabed. Therefore, as previous studies in this area have shown (Falace et al., 2015; Solidoro et al., 2009), surface data can serve as a reasonable proxy for the bottom layer.

Alongside the pressures identified in our study, it is likely that a combination of other factors, many of which may have gone unnoticed or unquantified, has contributed to both the recent and historical regression of seagrass meadows in certain areas of the Gulf. These include occasional and localized pressures, such as flooding, landslides and sewage discharges from land and vessels, as well as a low genetic diversity due to predominant asexual reproduction. Finally, chemical pollutants, grazing and pathogens may also have affected the meadows, but not enough data is available.

Recently, there has been growing interest in large-scale studies that leverage powerful modeling techniques (e.g. Baldan et al., 2024; Chefaoui et al., 2016; Hao et al., 2019; Melo-Merino et al., 2020; Neiva et al., 2016; Rubbens et al., 2023). These approaches are invaluable in overcoming the challenges associated with the difficulty of collecting data at basin-scale due to limited resources, and in predicting the potential range shift of species under climate change scenarios (Guisan and Zimmermann, 2000; Pearson and Dawson, 2003). Nevertheless, large-scale studies often fail to capture local dynamics and may not fully elucidate the specific factors responsible for species regression. Although mitigation of the impacts of human activities, establishment of marine protected areas, and restoration efforts are valuable strategies, their feasibility should be carefully assessed on a case-by-case basis. Therefore, local studies, such as the one presented here, remain crucial

for a better understanding of marine habitat dynamics and the development of conservation measures tailored to local conditions.

In conclusion, this study elucidates a suite of key factors influencing seagrass health in the GoT and identifies critical zones of increased vulnerability exposed to multifactorial pressures. These insights underscore the urgent need for targeted conservation strategies and long-term monitoring, given the intrinsically dynamic nature of seagrass ecosystems. Future research should endeavor to further unravel the complex interplay between natural variability and anthropogenic impacts to refine management practices and ensure the resilience of these vital marine habitats.

CRediT authorship contribution statement

Fabrizio Gianni: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Annalisa Falace:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Martina Orlando-Bonaca:** Writing – review & editing, Investigation, Funding acquisition, Data curation. **Saul Ciriaco:** Writing – review & editing, Software, Investigation, Data curation. **Danijel Ivajnsić:** Writing – review & editing, Visualization, Resources, Data curation. **Sara Kaleb:** Investigation. **Lovrenc Lipej:** Writing – review & editing, Investigation, Funding acquisition, Data curation. **Borut Mavrič:** Investigation, Funding acquisition, Data curation. **Stefano Querin:** Writing – review & editing, Software, Formal analysis, Data curation. **Vinko Bandelj:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2025.109563>.

Data availability

Data will be made available on request.

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