

Soundscape as a proxy for seagrass meadow condition and anthropogenic activity

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ABSTRACT

Soundscape analysis has emerged as a relevant tool in functional marine ecology. However, how habitat-specific variables, environmental and biological components, and external pressures influence acoustic metrics requires further validation. This study investigates how soundscape structure and dynamics are influenced by seagrass meadow conditions, seasonal patterns, and anthropogenic disturbance. To this aim, the soundscape of *P. oceanica* meadows in 16 sites across two Mediterranean Marine Protected Areas was analysed (over 6,600 5-min recordings).

The results revealed a multifaceted and highly site-specific soundscape. Diel cycles were the primary driver of the soundscape, with a significant nocturnal increase associated with fish sounds and the snapping rates of invertebrates. Meadow density and intermediate coverage positively influenced many acoustic metrics, suggesting that more structured meadows supported a more heterogeneous acoustic environment. However, denser meadows exhibited a reduction in low-frequency Sound Pressure Levels, indicating that the canopy acted as an acoustic attenuator. Furthermore, meadows on sandy substrates negatively influenced almost all acoustic metrics compared to those on rocky substrates, which provided more niches for soniferous species and acted as a reflective surface. Boat noise was pervasive and acted as the primary driver of low-frequency Sound Pressure Levels while significantly reducing acoustic complexity and diversity metrics.

In conclusion, acoustic metrics reflected the dynamic interactions between habitat structure, biological processes, and human activity. These findings confirmed that soundscape analysis is a powerful complementary tool for assessing the functional state of *P. oceanica* meadows and that soundscape should be integrated into conservation strategies as a key functional attribute.

1. Introduction

Monitoring marine ecosystems is essential as their stability and survival are increasingly threatened by ongoing local and global stressors (Smit et al., 2021). Identifying these impacts is crucial for enabling timely protection and restoration. Therefore, developing methods that can quantify ecosystem functions beyond structural

metrics - such as their support for biodiversity - and identify human-induced threats is of pivotal importance to gain a more comprehensive understanding of the environment capacity to sustain marine life.

In the pursuit of a deeper understanding, management and protection of marine environments, Passive Acoustic Monitoring (PAM) - the act of listening to and recording sound without adding it to the environment - and soundscape analysis have emerged as increasingly

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relevant tools in marine ecology and conservation (Sueur et al., 2014; Gibb et al., 2019; Mooney et al., 2020; Kemp et al., 2025). Soundscapes are characterized by the ambient sound in terms of its spatial, temporal, and frequency attributes and the types of sources contributing to the sound field (ISO, 2017), including biological sounds (biophony), environmental sounds (geophony), and human-made noise (anthrophony) (Pijanowski et al., 2011). As a non-destructive, autonomous, remote, and cost-efficient approach, PAM enables researchers to capture the continuous acoustic activity of soniferous organisms, many of which are elusive, cryptic or active only at night (Wingfield et al., 2017; Bolgan et al., 2019; Desiderà et al., 2019; Roca and Van Opzeeland, 2020; La Manna et al., 2021), as well as human activities (both legal and illegal), from the noise they produce (La Manna et al., 2014; Carroll et al., 2017; Duarte et al., 2021). Further, sound intensity, complexity, and other acoustic metrics can help in the evaluations of ocean dynamics (Radford et al., 2010; Miksis-Olds et al., 2013; Staaterman et al., 2014) or can serve as proxies for habitat quality and ecosystem restoration success (Bertucci et al., 2016; Ceraulo et al., 2018; Lamont et al., 2022; La Manna et al., 2024; Watson et al., 2025). In fact, acoustic data are increasingly utilized to identify large-scale variations across different habitats or to compare the healthy and degraded states of a single habitat type (Kaplan et al., 2015; Radford et al., 2014; Lamont et al., 2022; Williams et al., 2022; La Manna et al., 2024).

However, evidence on within-habitat soundscape variability remains limited (Azofeifa-Solano et al., 2025), particularly in the temperate context (Havlik et al., 2022). A few exceptions exist concerning biophonic components, which have shown regional variations in seagrass meadows, infralittoral rocky areas, and coralligenous reefs (Bolgan et al., 2019; La Manna et al., 2021; Di Iorio et al., 2018; La Manna et al., 2024). Interpreting complex acoustic signals requires a nuanced understanding of how habitat-specific variables, environmental and biological components, and external pressures influence acoustic metrics and descriptors (Pijanowski et al., 2011; Farina et al., 2014; Dimoff et al., 2021).

This acoustic approach could offer a new perspective for monitoring protected habitats, such as *Posidonia oceanica* meadows, the most iconic and ecologically significant seagrass ecosystem endemic to the Mediterranean Sea (Telesca et al., 2015). As habitat-forming species, *P. oceanica* creates expansive underwater meadows that provide key ecosystem services, including carbon sequestration, coastal protection through wave attenuation, and oxygen production (Costanza et al., 1997; Heck et al., 2003; McLeod et al., 2011; Macreadie et al., 2014; Lamb et al., 2017; Scanu et al., 2022). These meadows serve as essential nurseries, feeding grounds, and refuges for a vast array of marine species, supporting complex food webs vital for the Mediterranean basin (Heck et al., 2003; Telesca et al., 2015). In these habitats, the soundscape reflects the interaction between the physical structure of the plant canopy and the diverse community it hosts (Ceraulo et al., 2018; La Manna et al., 2024). Thus, factors such as meadow density, leaf surface area, and the underlying geomorphology of the sea bottom can significantly affect sound propagation and the composition of the resident acoustic community (Wilson et al., 2013). However, monitoring the functional state of these meadows remains a significant challenge. Traditional monitoring primarily relies on diver-based surveys to assess metrics like coverage, shoot density, and leaf phenology (Buia et al., 2004). While these methods provide essential high-quality data, they are inherently limited by reduced spatial and temporal coverage, high logistical effort, and dependence on favourable environmental conditions. Furthermore, assessing the presence of nocturnal species or the true extent of anthropogenic pressures - such as boat traffic or fishing - is difficult with traditional census techniques (Tyack et al., 2023). Despite its protected status under various international frameworks (e.g., EU Habitats Directive 92/43/EEC and the Barcelona Convention), *P. oceanica* faces significant threats from climate change, coastal development, and direct mechanical damage (Dunic et al., 2021; Ietto et al., 2023). Protecting this habitat is not merely a matter of

conserving a single species, but of maintaining the structural integrity and functional resilience of the entire coastal ecosystem (Scanu et al., 2022). Therefore, there is an urgent need for non-invasive monitoring tools that can provide high-resolution temporal data and a more holistic view of the ecosystem functioning.

To date, several acoustic metrics have been developed to summarize amplitude, temporal and frequency-related acoustic features into single values representing soundscape variability and complexity (e.g., Buxton et al., 2018; Wilford et al., 2021; Minello et al., 2021; Pieretti et al., 2017, 2020; Alcocer et al., 2022). Although their reliability for assessing species richness and abundance is still debated - largely due to sensitivity to signal-to-noise ratios and parametrization (e.g., Bolgan et al., 2018; Chen et al., 2023; Kemp et al., 2025; Sugai and Costa-Pereira, 2025) - researchers increasingly use combinations of these metrics to characterize soundscapes and distinguish among varying habitat conditions (e.g., Bertucci et al., 2020; Roca and Van Opzeeland, 2020; Sánchez-Giraldo et al., 2021; Williams et al., 2022; Mattmüller et al., 2024; Minello et al., 2021; Buscaino et al., 2025; Valenzisi et al., 2025; Poveda-Martínez et al., 2026). Indeed, acoustic patterns within an environment can serve as an effective proxy for its overall ecological integrity (Sánchez-Giraldo et al., 2021).

The objective of this study was to investigate how the soundscape structure, complexity, and dynamics in *P. oceanica* meadows, are influenced by habitat structural conditions in terms of shoot density, leaf surface area, coverage and bottom type, as well as by temporal patterns and anthropogenic disturbance. By analysing over 6,600 5-min recordings taken in 16 sites across two Mediterranean Marine Protected Areas (MPAs), we evaluated the suitability of PAM and an ensemble of manual and automatically processed acoustic metrics as a non-invasive complementary tool for assessing the seagrass ecological conditions. The prediction is that the soundscape depends on meadow canopy conditions, associated biodiversity, and anthropogenic activities affecting seagrass ecosystem functioning. These results will contribute to validating soundscape approaches for tracking shifts in ecological conditions (Wilford et al., 2021; Tyack et al., 2023).

2. Methods

2.1. Study area and data collection

Data collection was performed within *P. oceanica* meadows of two Mediterranean MPAs: Capo Caccia-Isola Piana in Sardinia (hereafter Capo Caccia) and Capo Gallo-Isola delle Femmine in Sicily (hereafter Capo Gallo). Specifically, 10 sites were selected in Capo Caccia and 6 in Capo Gallo among a range of protection restrictions, all within a depth range of 15 - 20 m (Fig. 1).

Within each site, three areas spaced approximately 20 m apart were selected. In each area, bottom type, meadow continuity, percentage coverage (visually estimated over a 5 m radius around a fixed point) and meadow density (using 40 × 40 cm quadrats, n=3) were recorded. Furthermore, to characterize the seagrass canopy, six *P. oceanica* shoots were collected from each area (N=18 per site) and subsequently transported to the laboratory for phenological analysis. For each shoot, the number of leaves, leaf width and length were measured to calculate the total leaf surface area. The sites across the two MPAs encompass a wide range of fine-scale structural conditions. This gradient includes highly variable shoot densities (ranging from 250 to >550 shoots/m²), meadow coverage (ranging from heavily fragmented patches with <50% coverage to continuous meadows with 90–100% coverage), number of leaves per shoot (from 3 to 7), and leaf surface area (from 183 to 291 cm²). The combination of these variables provides a robust proxy for above-ground biomass and canopy volume, which may directly shape the local soundscape by influencing acoustic propagation and hosting soniferous species. Furthermore, these parameters are widely recognized as reliable and standard descriptors of *Posidonia oceanica* meadow status under European environmental legislation (e.g., the EU Water

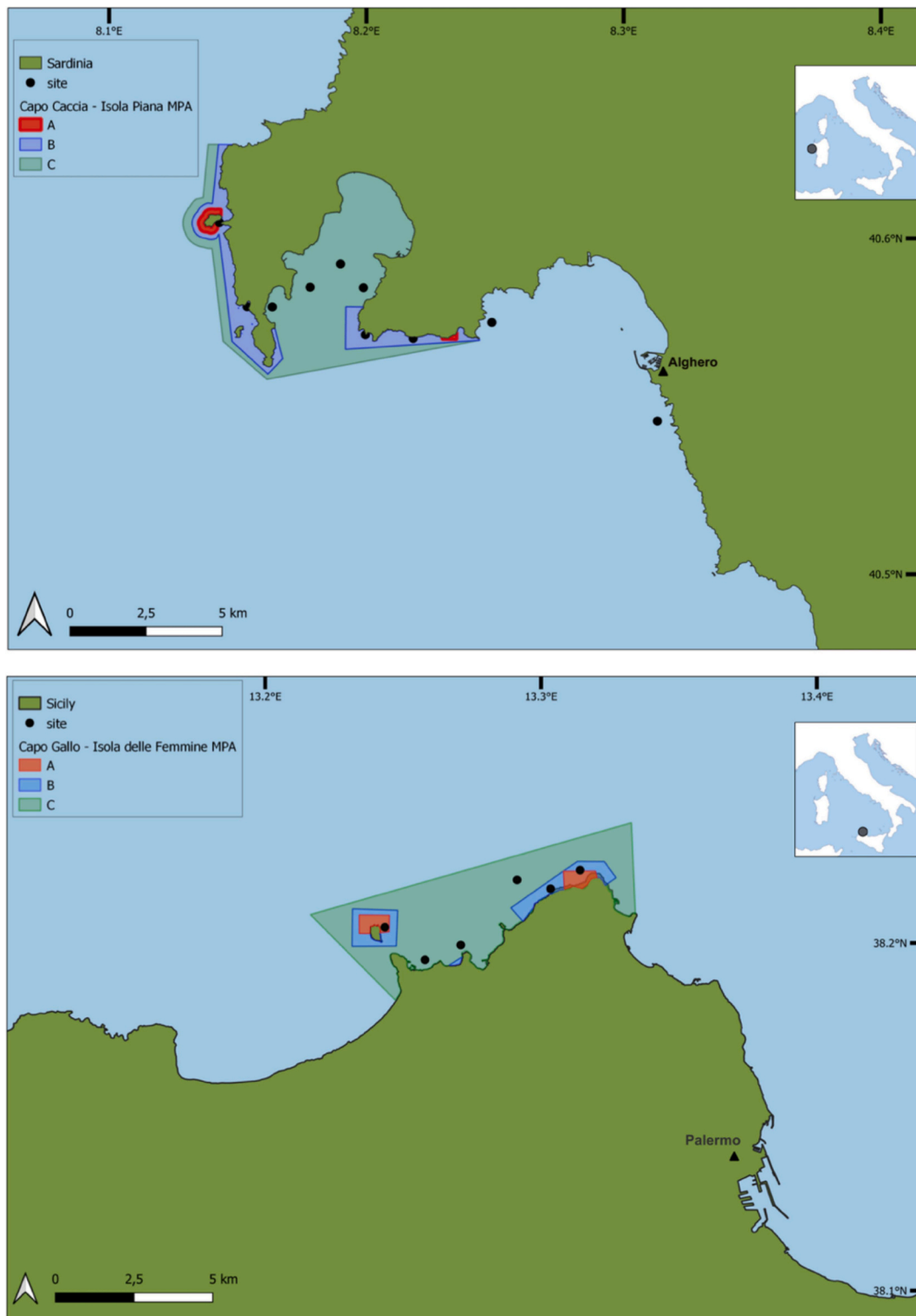


Fig. 1. Study areas and sampling sites (black dots) in the two MPAs of Sardinia and Sicily. A = full protection zone; B = general protection zone; C = partial protection zone.

Framework Directive 2000/60/EC and the Marine Strategy Framework Directive 2008/56/EC).

In each site, an autonomous underwater acoustic recorder (URec384k-Nauta RCS; hereafter URec) was deployed by scuba divers and secured using a mooring system consisting of 5 kg ballast weights and a subsurface buoy. The URec units were equipped with Sensor Technology SQ26 pre-amplified hydrophones, featuring a sensitivity

range between -166 and -175 dB re: $V/\mu Pa$ and a flat frequency response up to 30 kHz. Hardware specifications included a DODO-TRONIC programmable recording interface (0 dB gain), a dedicated battery pack, and SD memory cards with capacities ranging from 256 to 512 GB. Recording was conducted for three consecutive days per deployment, spanning 24 hours daily. The devices operated on a duty cycle of 15-minute recording intervals (followed by 45-minute pauses

each hour) and each session was saved as three 5-minute .wav files.

To account for varying levels of recreational boat traffic, data collection was conducted during low tourist season (June 2025) and high tourist season (August 2025). This sampling period also represents the annual peak of fish acoustic activity, as it corresponds to the spawning season and maximum territorial behavior for most Mediterranean coastal soniferous species (Buscaino et al., 2016). To minimize the contribution of transient abiotic noise from wind and waves, all recordings were performed under calm meteorological conditions, specifically characterized by a sea state and wind force below 2 on the Douglas and Beaufort scales, respectively.

2.2. Acoustic analysis

The acoustic data were processed through a combination of manual inspection and automated signal processing. Each recording was analysed both aurally and visually using Raven Pro 1.6 (Cornell University), with spectrograms viewed in 300-s windows across a frequency bandwidth of 0–8.5 kHz, using a Fast Fourier Transform (FFT) of 8,192 points, a Hamming window, and a 50% overlap. Fish acoustic signals clearly identifiable in both waveform and spectrogram were manually selected and categorized by comparing them with known sounds from the Mediterranean Sea. Following the classification framework described by Desiderà et al. (2019) and subsequent applications (La Manna et al., 2021, 2024a, 2024b, 2025), seven distinct sound types were identified (Table 1a). For each 5-minute recording, total fish acoustic abundance (FAAb), impulsive sounds from invertebrates (e.g., snapping shrimps), and boat noise were identified and annotated. To measure the persistence of both biological and anthropogenic soundscape components, three indices were used - namely Invertebrate Sound Proportion (ISP), Fish Sound Proportion (FSP), and Boat Sound Proportion (BSP) - calculated as the percentage of time, over the 5-minute interval, each sound type (impulsive invertebrate sounds, fish sounds, and boat noise, respectively) was detectable. To further characterize the soundscape complexity and diversity, a suite of widely used acoustic metrics (e.g., Pieretti and Danovaro, 2020; Minello et al., 2021; Mattmüller et al., 2024) was calculated using PAMGuide (Merchant et al., 2015), Soundecology (Villanueva-Rivera and Pijanowski, 2019) and Seewaves packages in R (Sueur et al., 2008) (Table 1b). Absolute sea ambient noise levels were estimated as Sound Pressure Levels (SPL, dB re 1 μ Pa rms) calculated specifically within the 0.1–2 kHz frequency range (SPL2), to isolate fish sound (Picciulin et al., 2012, 2013; Di Iorio et al., 2018; Bolgan et al., 2019) and anthropogenic components (boat noise; Erbe et al., 2016a, 2016b; La Manna et al., 2021), and in the 2–32 kHz range (SPL32) to capture high-frequency biological activity, such as snapping shrimp snaps and other invertebrate sounds (Buscaino et al., 2016). The Acoustic Complexity Index (ACI) was computed to track the intensity variations between successive time bins. High ACI values correspond to high intensity variability, typically associated with healthy or restored habitats (Roca and Van Opzeeland, 2020; Williams et al., 2022; La Manna et al., 2024) or biological activity (McWilliam and Hawkins, 2013; Staaterman et al., 2014; Bertucci et al., 2016; Buscaino et al., 2016; Pieretti et al., 2017; Bolgan et al., 2018; La Manna et al., 2024). Bioacoustic Index (BI) reflects the accumulated acoustic energy in the frequency bands where biological signals are most prominent (Boelman et al., 2007) and, in the marine context, has been shown to be effective in detecting some impulsive sounds, such as sperm whale clicks (Fergusson et al., 2023) or fish chorus in some contexts (Siddagangaiah et al., 2019) and it can reflect higher spectral heterogeneity of the soundscape (Mattmüller et al., 2024). In this study, both ACI and BI were calculated in the frequency bands 0.1–2 kHz (ACI2, BI2) and 2–32 kHz (ACI32, BI32). The Acoustic Diversity Index (ADI) and the Acoustic Evenness Index (AEI) were calculated to measure the variety and richness of an acoustic environment by analysing the distribution of sound across the frequency spectrum, based on the Shannon and the Gini indexes, respectively. High ADI and low AEI values indicate a diverse

Table 1

Summary of the fish sounds and acoustic metrics used in the study. (a) Classification of detected fish sounds, including descriptions of their acoustic structure and taxonomic attribution when possible. (b) Overview of the acoustic metrics used to characterize the soundscape, including the measured acoustic component, the specific settings, the corresponding reference and R packages used for calculation.

a) Fish sound	Description	Reference
DS	Down sweep frequency modulated sound with decreasing frequency and peak frequency ≥ 200 Hz (emitted by unknown species)	Desiderà et al., 2019
SB	Low-frequency single booms attributed to <i>Epinephelus marginatus</i>	Bertucci et al., 2016
PS	Irregular pulse series with peak frequency ≥ 200 Hz	Desiderà et al., 2019
FPT	Fast pulse trains	Desiderà et al., 2019
RPS	Stereotyped pulse series which may be repeated irregularly (I- call), regularly (R- call) or in chorus emitted by <i>Sciaena umbra</i>	Picciulin et al., 2012, 2013
APPPS	Accelerating pulse series with alternating pulse period emitted by <i>Ophidion rochei</i>	Picciulin et al., 2018
UFPS/kwa/	Ultra-fast amplitude modulated pulse series with a pseudo-harmonic appearance emitted by <i>Scorpaena</i> spp.	Di Iorio et al., 2018; Bolgan et al., 2019
b) Acoustic metrics	Measured component	Setting
Fish acoustic abundance	Total number of fish sounds per 5-minute recording.	–
Acoustic Complexity Index (ACI)	Intensity variation over time. Two frequency limits have been defined: ACI2 (0.1–2 kHz) to account for fish acoustic signals; ACI32 (2–32 kHz) to account for invertebrate acoustic signals. Accumulated energy in biological frequency bands. Two frequency limits have been defined: BI2 (0.1–2 kHz) to account for fish acoustic signals; BI32 (2–32 kHz) to account for acoustic signals from invertebrates.	Hamming-window; window lengths = 8192 points; overlap = 50%. Frequency resolution = 11.72 Hz; temporal resolution of 0.085 s
Bioacoustic Index (BI)	–	Boelman et al., 2007 Soundecology
Acoustic Evenness Index (AEI)	Distribution (evenness) of sound across bands.	Size of frequency bands = 50 Hz; dB threshold = -40 dB
Acoustic Diversity Index (ADI)	Variety and richness of spectral distribution.	Size of frequency bands = 100 Hz; dB threshold = -40 dB
Acoustic Entropy (H)	Degree of complexity and disorder (Spectral $\times$ Temporal). Total acoustic energy levels (in decibels) calculated in two frequency bands: SPL2 (0.1–2 kHz) to account for fish acoustic signals and boat noise; SPL32 (2–32 kHz) to account for acoustic signals from invertebrates.	–
Sound Pressure Level (SPL)	–	Hamming-window; window lengths = 2048 points; overlap = 50%

soundscape where acoustic energy is spread across multiple frequency bands (such as different species of fish and invertebrates, occupying various acoustic niches), while low ADI and high AEI values indicate a less diverse or "poorer" soundscape, where sound is concentrated in only a few frequency bands or the environment is relatively silent. Acoustic Entropy (H) is a metric used to quantify the degree of complexity and disorder within an acoustic signal. It is calculated as the product of two components: spectral entropy (H_f), which measures the distribution of energy across the frequency spectrum, and temporal entropy (H_t), which measures the distribution of energy over time. The index ranges from 0 to 1, where values near 0 represent a soundscape dominated by a single frequency or a very regular, repetitive pulse, while values near 1 represent a high degree of disorder, typical of a soundscape containing a wide variety of overlapping signals or random noise (Parks et al., 2014; Kaplan et al., 2015; Rice et al., 2017; Staatterman et al., 2017) (Table 1b).

2.3. Statistical analysis

The acoustic metrics were calculated for each 5-minute recording and then averaged across the three recordings per hour (N=2,215) to obtain a single hourly mean value. Initial soundscape characterization was performed by calculating hourly means and standard errors (SE) of each acoustic metric across spatial and temporal scales (Suppl. Mat. Fig. S1 – S4). Additionally, the mean values of all metrics were plotted by sampling site to facilitate the visualization of their spatial patterns (Suppl. Mat. S5 – S7).

A Spearman rank correlation analysis was performed between acoustic metrics and the biological (ISP and FSP) and anthropogenic (BSP) components of the soundscape to provide a basis for interpreting the complexity of the acoustic environment.

In order to identify the specific drivers of each acoustic metric, ten Generalized Linear Mixed Models (GLMMs) were developed. Based on the distribution of the response variables, appropriate link functions were selected (Gaussian or Gamma for continuous acoustic metrics and Negative binomial for count data, FAAb). The following spatial, temporal and ecological predictors were included in the models as fixed effects: i) MPA (categorical variable with two levels: Capo Caccia and Capo Gallo); ii) SEASON (categorical variable with two levels: low tourist season and high tourist season); iii) TIME (categorical variable with two levels: day and night); iv) meadow density, number of leaves per shoot and leaf surface (continuous covariates); v) COVERAGE (categorical variable with three levels: <50%, 60-80% and 90-100%); vi) BOTTOM TYPE (categorical variable with two levels: rocky and sandy); vii) BOAT (categorical variable with two levels: yes and no). Site and Date were included as random effects to account for the nested structure of the sampling design and temporal autocorrelation. Prior to model fitting, multicollinearity among predictors was assessed using the Generalized Variance Inflation Factor (GVIF). Only predictors with a $GVIF^{1/(2 \cdot df)} < 2$ were retained in the final models. Specifically, the number of leaves per shoot was found to be highly collinear with meadow density; therefore, only density was included in the subsequent analyses. Model selection was performed through a backward stepwise procedure based on the Akaike Information Criterion (AIC). Model validation was performed using the DHARMA package (Hartig, 2016). Specifically, we inspected scaled quantile residuals through Q-Q plots to assess the distributional assumptions and used residual-versus-predicted plots to check for homoscedasticity. Additionally, residuals were plotted against each predictor to ensure that no non-linear patterns or systematic biases remained unaccounted for in the fixed effects. No significant deviations or patterns were detected, confirming the suitability of the selected model structures and link functions. Standardized effect sizes and 95% confidence intervals were calculated and visualized to compare the relative influence of each predictor across all models.

Finally, the overall influence of spatial, temporal, ecological and anthropogenic predictors on the general soundscape structure was investigated using a Redundancy Analysis (RDA). The RDA was

performed on the matrix of acoustic metrics (response variables), which were transformed to account for different scales and units. Explanatory variables included MPA, TIME, BOTTOM TYPE, Density, Leaf surface, and BOAT, while SEASON was excluded due to its low influence detected by the GLMMs. The significance of the full model and of each individual predictor was assessed using ANOVA-like permutation tests (999 permutations). The adjusted coefficient of determination (R_{adj}^2) was used to estimate the proportion of variance explained by the canonical axes.

All statistical analyses were conducted in R (R Core Team, 2023) using the vegan package (Oksanen et al., 2022) for RDA and glmmTMB (Brooks et al., 2017) for GLMMs. Model outputs, including standardized effect sizes and 95% confidence intervals, were extracted and tidied using the broom.mixed (Bolker and Robinson, 2022) and dplyr (Wickham et al., 2023) packages to facilitate comparison across different acoustic metrics. Data visualizations were generated using the ggplot2 package (Wickham, 2016).

3. Results

3.1. General results

Boat noise was detected in 60% of recordings, while biological sounds from invertebrates (e.g., snapping shrimp and other pulsed sounds) and fish were present in 99% and 70% of samples, respectively. The analysis of acoustic metrics revealed distinct spatial and temporal variations across the study areas (Suppl. Mat. S1 – S7).

The correlation matrix revealed several links between acoustic metrics and soundscape components. Specifically: i) high-frequency acoustic metrics (ACI32, BI32, SPL32), H, and AEI were strongly correlated with ISP; ii) low-frequency metrics (ACI2, BI2) showed weak correlations with BSP; and iii) BI2 was the only metric moderately correlated with FSP. Thus, several of the selected acoustic metrics serve as proxies for the biological activity of invertebrates within the meadow soundscape, though no such relationship was found for fish (Fig. 2).

3.2. Predictors of acoustic metrics

The GLMMs identified distinct sets of drivers for each acoustic metric (Fig. 3; full statistical summaries in Tables S8–S16). TIME emerged as a dominant factor: the nocturnal hours exerted a strong, significant positive influence on all acoustic metrics, except for ACI32, AEI and SPL2, while SEASON was not retained in most of the model selections, except for AEI, ADI and ACI32. MPA and habitat-specific factors further influenced the acoustic metric responses: Capo Gallo was characterized by significantly higher SPL and BI values, across both frequency bands, FAAb and H, while Capo Caccia exhibited higher AEI value. Regarding habitat structure: i) meadow density positively influenced ACI32 and ADI and negatively influenced SPL, in both frequency bands, and BI2; ii) leaf surface positively influenced SPL, in both frequency bands, and H, and negatively influenced AEI; iii) higher meadow coverage positively influenced FAAb, H and SPL, in both frequency bands. Meadows on sandy bottom negatively influenced all acoustic metrics, except for AEI and FAAb. Finally, anthropogenic disturbance represented by the presence of boats positively influenced SPL2 while showing a significant negative influence on ACI2, ACI32, BI2 and FAAb (Fig. 3).

3.3. Multivariate drivers of *P. oceanica* meadow soundscape

The Redundancy Analysis (RDA) demonstrated that the ecological and anthropogenic variables considered significantly explained the variance in the soundscape structure ($R_{adj}^2 = 43\%$). The first two canonical axes accounted for a cumulative proportion of 81.37% of the explained variance (RDA1: 62.75%; RDA2: 18.62%). The remaining unconstrained variance (57%) suggests that while the current model captures the primary drivers, additional unmeasured factors also

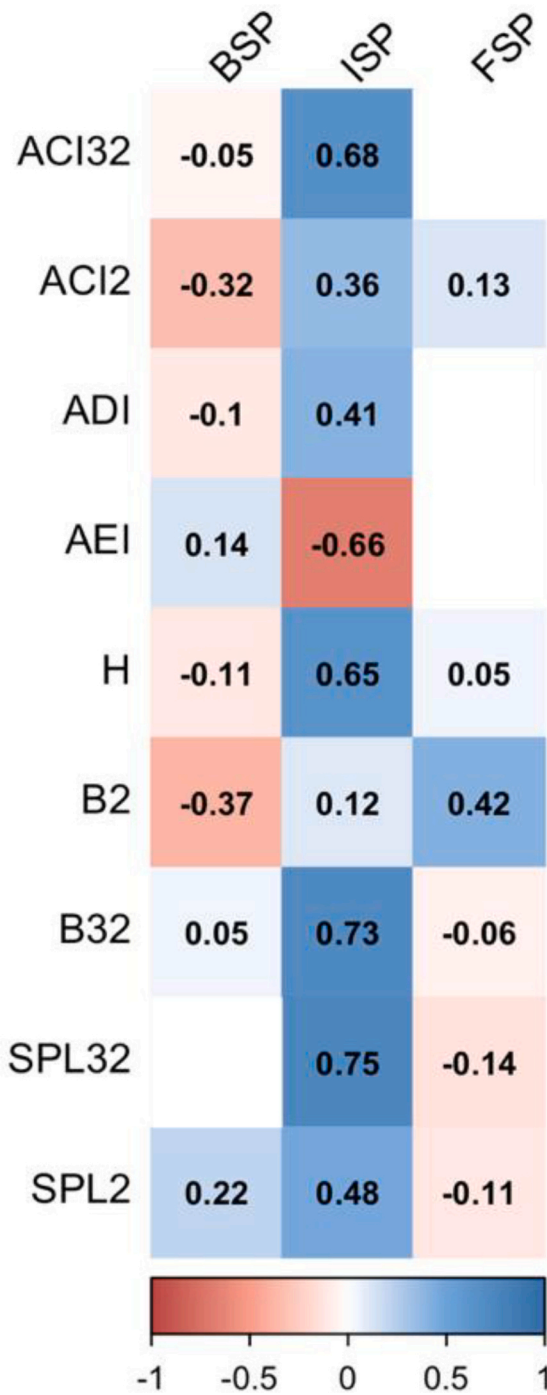


Fig. 2. Spearman's rank correlation matrix between acoustic metrics (rows) and soundscape components (columns). The colour scale represents the Spearman's rho coefficient, ranging from -1 (dark red, strong negative correlation) to +1 (dark blue, strong positive correlation). Numerical values indicate the correlation coefficients; empty cells represent non-significant correlations. BSP = Boat Sound Proportion, ISP = Invertebrate Sound Proportion, FSP = Fish Sound Proportion.

contribute to the overall acoustic variability in the soundscape. The ANOVA permutation test confirmed the robustness of the model. Among the explanatory variables, BOTTOM TYPE emerged as the primary driver of soundscape variation, followed by Density and TIME. COVERAGE and BOAT also exerted significant, although secondary, influence on the marine seagrass soundscape (Table 2).

The ordination revealed a clear separation between the two MPAs

(Fig. 4). Capo Caccia (green ellipse) was characterized by ACI2, ACI32 and BI32. These acoustic metrics, together with FAAb, showed a strong positive relationship with seagrass density and intermediate meadow coverage levels (Cov 60-80%). Furthermore, they were positively associated with the night vector. Capo Gallo (blue ellipse) exhibited a closer association with SPL in both frequency bands (SPL2, SPL32) and BOAT. A marked gradient was observed along RDA1, where the vector for sandy bottom was diametrically opposed to the ACI2, ACI32 and BI32. Sandy bottom, higher *P. oceanica* leaf surface and highest meadow coverage were strongly associated with AEI and negatively associated with BI, ACI and ADI (Fig. 4).

4. Discussion

In this study, the suitability of a set of acoustic metrics to capture the overall patterns of the *P. oceanica* meadow soundscape in the Mediterranean Sea was investigated. The results revealed a multifaceted soundscape driven by a complex interplay of spatial, temporal, ecological, and anthropogenic factors and provided preliminary evidence on how the tested sources translate into soundscape patterns (Bradfer-Lawrence et al., 2022).

4.1. Spatial and temporal factors

Most of the acoustic metrics were influenced by the factor MPA, and the clear separation between Capo Caccia and Capo Gallo in the RDA ordination plot suggests that *P. oceanica* meadow soundscape can be highly spatially structured. Particularly, the Capo Caccia soundscape was characterized by complexity indices (ACI) linked to good meadow conditions (high coverage and density), while Capo Gallo soundscape was more influenced by high Sound Pressure Levels (SPL32), correlated with the invertebrate sound proportion (ISP). Further, the alignment of SPL2 vectors with boat presence confirms that the acoustic footprint in this area is primarily driven by anthropogenic noise, rather than by fish sounds (FAAb). As a result, Capo Gallo has the loudest but least complex soundscape. This phenomenon can occur when one specific source, such as a very high density of a single soniferous species, specific grazing activity, or single source of anthropogenic noise, dominates the frequency band. Conversely, Capo Caccia seems to be characterized by more diverse soundscape components.

Concerning the temporal pattern, the strong nocturnal peak observed across almost all acoustic metrics confirms the dominance of the diel cycle in shaping the soundscape of Mediterranean coastal waters, consistent with other studies (e.g., Buscaino et al., 2016; Ceraulo et al., 2018; La Manna et al., 2021; 2024). This nocturnal increase is likely associated with the acoustic activity of fish species and the intensified activities of snapping shrimps or other invertebrates, due to reproductive or foraging behaviour that intensifies under low-light conditions (Radford et al., 2008; Pieretti et al., 2017; Azofeifa-Solano et al., 2025). Conversely, few seasonal effects were found, except for the high-frequency Acoustic Complexity Index and the Acoustic Diversity index (ACI32 and ADI). This pattern is likely due to the short seasonal range considered in the study, which was primarily designed to capture variations in tourism and related boat traffic.

4.2. Meadow structure- and anthropogenic- related factors

The relationship between meadow structure and acoustic metrics revealed complex interactions. The positive influence of shoot density and intermediate coverage on ACI, BI, FAAb and ADI suggest that dense meadows may support a more heterogeneous acoustic environment even when partially fragmented. However, the observed reduction in SPL in denser meadows indicates that the physical presence of the canopy might act as an acoustic attenuator or "filter", as already postulated for seagrasses and other similar marine habitats (Ceraulo et al., 2018; Cox et al., 2025). In fact, seagrass leaves are characterized by the presence

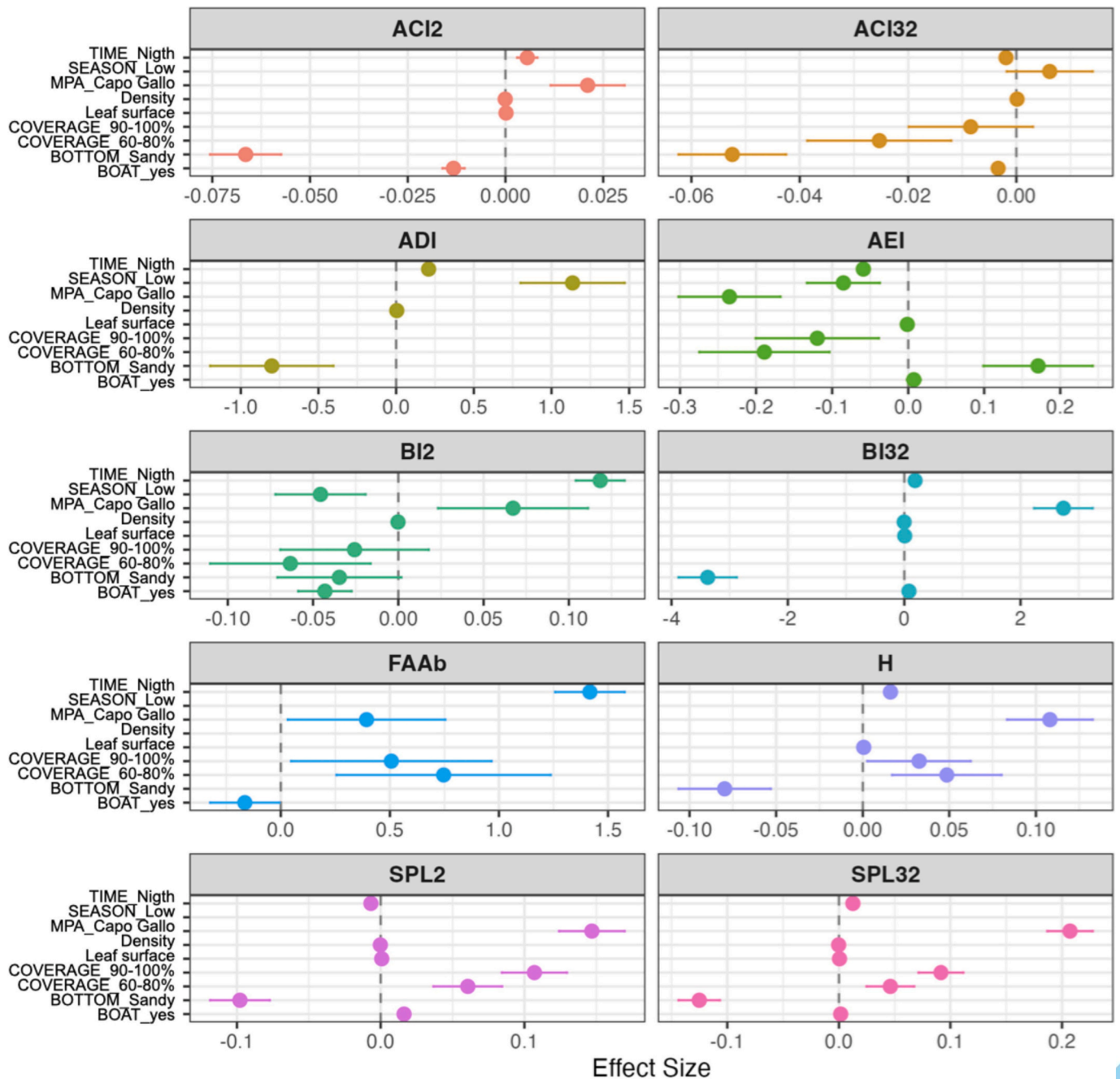


Fig. 3. Standardized effect sizes of environmental and anthropogenic predictors on acoustic metrics derived from Generalized Linear Mixed Models (GLMMs). The plots display the estimated coefficients (points) and their corresponding 95% confidence intervals (horizontal lines) for each acoustic metric. Predictors are considered significant when their confidence intervals do not overlap the zero. Positive values indicate a positive relationship with the metrics, while negative values indicate an inverse relationship. Categorical variables are shown relative to their respective reference levels (i.e. TIME: night vs. day; SEASON: low vs. high; BOTTOM TYPE: sandy vs. rocky; BOAT: yes vs. no). The varying scales of the x-axes reflect the standardized effect sizes for each specific model.

Table 2

Results of the ANOVA-like permutation test (999 permutations) for the Redundancy Analysis (RDA).

Predictor	Df	Variance	F-statistic	p-value
COVERAGE	2	0.4789	81.933	0.001
BOTTOM TYPE	1	1.1544	394.993	0.001
Density	1	0.4811	164.604	0.001
Leaf surface	1	0.0303	10.360	0.001
TIME	1	0.3291	112.599	0.001
BOAT	1	0.0528	18.084	0.001
Residual	2215	6.4734		

of gases (associated with the production of oxygen) inside and around the plants, which can modify the speed of sound through a meadow (Miksis-Olds and Miller, 2006; Wilson and Dunton, 2009; Wilson et al., 2013). Further, *P. oceanica* meadow density, reflecting the number of shoots and leaves, can attenuate sound, a phenomenon already documented in terrestrial forests (e.g., Lu et al., 2024). Thus, the reduction of SPL at low frequency, which is positively correlated to the boat presence and related noise, can be due to the attenuation related to the meadow structure (Ceraulo et al., 2018). Conversely, the increase in SPL at high frequency where leaf surface is higher may be due to the larger number of invertebrate species (e.g., sea urchins, molluscs and crustaceans) that produce indirect sounds during their grazing activities on the leaf

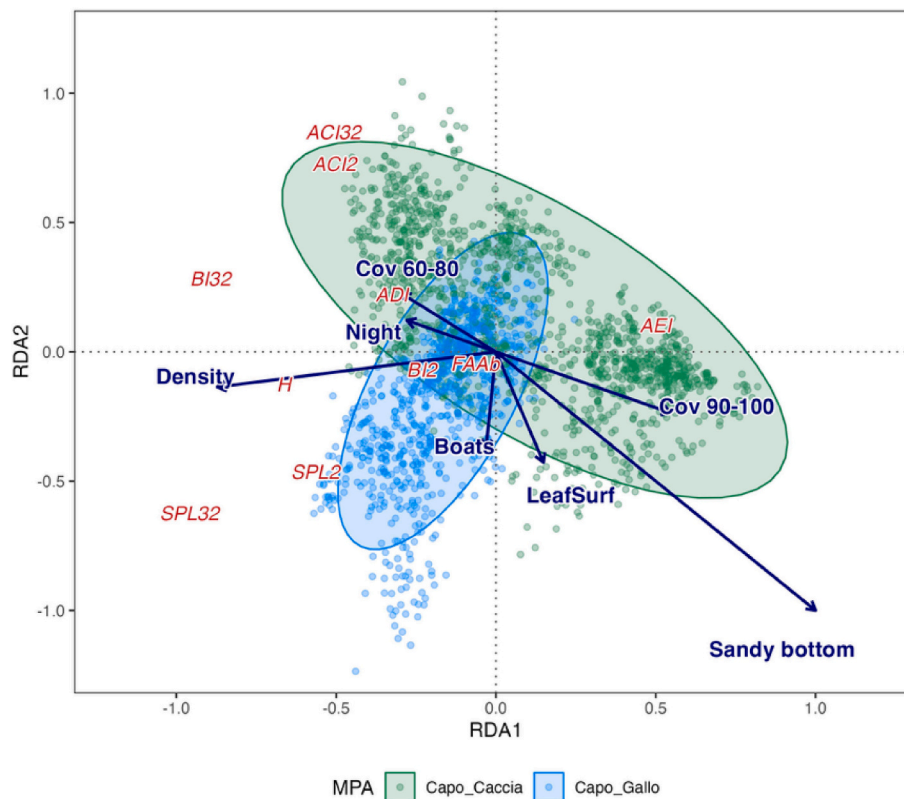


Fig. 4. RDA ordination biplot illustrating the relationship between acoustic metrics (in red) and predictors (dark blue vectors). The length and direction of the vectors represent the strength and correlation of each variable with the canonical axes. Sites are grouped by MPA: Capo Caccia (green points and ellipse) and Capo Gallo (blue points and ellipse).

epiphytes (Cox et al., 2025). The meadow coverage also showed significant positive relations with FAAb, suggesting that more continuous meadows provide the necessary substrate and shelter for some soniferous species, consistent with the meadow role of fish nursery and refuge (Bell and Harmelin-Vivien, 1982; Vassallo et al., 2013).

The finding that sandy bottom negatively influenced almost all acoustic metrics (except AEI and FAAb) underscores the role of geomorphology in shaping the acoustic 'identity' of the seagrass habitat, consistently with Wilson et al. (2013). The soundscape of meadows established on sandy bottoms was characterized by higher evenness (high AEI) and lower complexity (low ACI and BI) compared to those on rocky substrates. This suggests that the synergy between the seagrass canopy and the specific seabed type likely influences both the associated community composition and the local sound propagation properties. Rocky bottoms inherently provide more niches for cryptic soniferous species, such as gobies and various crustaceans, and act as a reflective surface that may enhance local sound reverberation (Ceraulo et al., 2018; Desiderà et al., 2019; Watson et al., 2025). This acoustic reflection can lead to higher perceived Sound Pressure Levels and a more complex biological soundscape in rocky areas compared to mobile substrates. In contrast, sandy bottoms often act as acoustic absorbers, particularly at higher frequencies, and typically support less acoustically diverse communities due to their lower structural complexity (Piercy et al., 2014; Ceraulo et al., 2018; Biggs and Erisman, 2021).

Boat noise was a pervasive component of the soundscape, detected in 60% of the recordings. The GLMMs and RDA biplots clearly highlight that boat presence is the primary driver of low-frequency Sound Pressure Levels (SPL2). More importantly, the significant negative influence of boat presence on several acoustic complexity and diversity metrics suggests that anthropogenic noise may mask or suppress biological signals, other than influencing acoustic metrics (Parks et al., 2014).

4.3. Monitoring applications and management implications

This study confirms the effectiveness of a suite of acoustic metrics as reliable proxies for monitoring ecological and anthropogenic dynamics of *P. oceanica* meadows, consistent with previous research linking acoustic patterns to ecological integrity (Fuller et al., 2015; Burivalova et al., 2018; Gottesman et al., 2020). By significantly reducing field effort and the logistic constraints of more traditional techniques, PAM offers a cost-effective and complementary tool for seagrass monitoring, enabling the collection of high-resolution temporal data that traditional diver-based surveys cannot capture. Thus, integrating PAM and soundscape analysis into standard seagrass monitoring protocols would allow managers to better assess meadow functional state, including the presence of ecologically or commercially important species and the actual exposure of the community to noise pollution.

However, several limitations must be addressed. Correlation analysis revealed that while high-frequency metrics (e.g., SPL32, ACI32, BI32) effectively track invertebrate activity, low-frequency metrics are frequently confounded by the spectral overlap between fish vocalizations and boat noise. Thus, regardless of the analytical approach—whether based on manual or automatically processed acoustic metrics or emerging machine learning methods (Williams et al., 2022)—soundscape data alone cannot currently be used to predict species richness or assess absolute biodiversity status (Alcoer et al., 2022; Sethi et al., 2023; Sugai and Costa-Pereira, 2025). Instead, a suite of manual and automatically processed metrics (with proper and clearly defined parametrization) can be used to reflect the dynamic interactions between habitat structure, biological processes, and human activity. Thus, a more realistic application is to use soundscapes to guide targeted ecological studies (Sethi et al., 2023). By establishing site-specific acoustic baselines, monitoring can detect shifts in habitat condition or evaluate the effectiveness of boating regulations within

valuable coastal habitats. Moreover, as climate change continues to shift species ranges, the long-term monitoring of biophony may enable early detection of ecological transitions, providing a warning system of restructuring biological communities. Such information could prioritize field surveys in locations exhibiting sustained, anomalous changes in the acoustic community.

In conclusion, soundscape analysis should not be viewed as a stand-alone tool for determining the ecological status of *P. oceanica* meadows, but as a fundamental component of an integrated monitoring framework. This holistic approach would be essential for safeguarding both the structure and functioning of the seagrass ecosystem, using the soundscape as a crucial attribute which, beyond serving as a proxy for associated biodiversity, provides critical sensory cues for larval orientation and settlement (Simpson et al., 2005), thereby maintaining the ecological integrity of the system. Consequently, the soundscape should be recognized as a core element of marine environments and integrated into conservation strategies as a key functional attribute (Sánchez-Giraldo et al., 2021).

CRediT authorship contribution statement

Gabriella La Manna: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Giuseppe Morello:** Writing – original draft, Investigation, Formal analysis. **Mariangela Moro Merella:** Writing – original draft, Investigation, Formal analysis. **Alessia Crobu:** Writing – original draft, Investigation, Formal analysis. **Arianna Pansini:** Writing – original draft, Investigation, Formal analysis. **Ivan Guala:** Writing – original draft, Investigation, Formal analysis. **Franco Paolo Mancuso:** Writing – original draft, Investigation, Formal analysis. **Maria del Mar Bosch-Belmar:** Writing – original draft, Investigation, Formal analysis. **Maria Cristina Mangano:** Writing – original draft, Investigation, Formal analysis. **Gianluca Sarà:** Writing – original draft, Supervision, Funding acquisition, Conceptualization. **Giulia Ceccherelli:** Writing – original draft, Supervision, 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.ecolind.2026.115290>.

Data availability

Data will be made available on request.

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