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Investigating drivers of Mediterranean coralligenous fish communities using passive acoustic monitoring: the role of thermal environment, day length and moon phases

Gabriella La Manna [a,b,*], Mariangela Moro Merella [a], Riccardo Vargiu [a], Giuseppe Morello [b,c], Gianluca Sarà [b,c], Giulia Ceccherelli [a,b]

[a] *Università di Sassari, Dipartimento di Scienze Chimiche, Fisiche, Matematiche e Naturali, Via Vienna 4, Sassari, Italy*
[b] *National Biodiversity Future Center, Piazza Marina 61, Palermo, Italy*
[c] *Università degli Studi di Palermo, Dipartimento di Scienze della Terra e del Mare, Viale delle Scienze ed. 16, Palermo, Italy*

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ABSTRACT

The Mediterranean coralligenous reef is a vital ecosystem that provides essential habitat for various marine species. However, it faces growing threats due to human activities and climate change, particularly rising sea temperature and marine heat waves. While the impact of thermal anomalies on habitat-forming species is well-documented, their effects on associated fish communities remain understudied. This study investigates the role of the thermal environment, day length, and moon phases in shaping the acoustic community of coralligenous fish using passive acoustic monitoring. Acoustic data collected from two coralligenous reefs in Sardinia, between June and August 2023, revealed seventeen distinct sound types, six of which were attributed to four known species. The Generalized Linear Latent Variable Model highlighted the significant influence of mean daily temperature, temperature variation, and heating events on the abundance of most sound types, with higher temperatures generally correlating with increased sound production. However, some species exhibited reduced vocal activity in response to elevated temperatures, indicating species-specific responses. The study also found that reduced day length and moon phases influenced sound production, even though the thermal descriptors were more important in explaining fish sound abundance. These findings underscore the importance of temperature in shaping the fish acoustic community of coralligenous reefs and provide insights for the potential impacts of climate change on this marine ecosystem. Moreover, the study highlights the need for further research on the effects of sea warming on coralligenous fish assemblages.

1. Introduction

Coralligenous reef is a Mediterranean ecosystem dominated by calcareous organisms, primarily coralline algae and invertebrates such as anthozoans and bryozoans (Ballesteros, 2006). It is typically found between 15 m and 150 m of depth (Martins et al., 2014) in water with dim light condition, low level of nutrients, moderate hydrodynamics and temperature generally below 23 °C (Ballesteros, 2006; Bracchi et al., 2015). It provides ideal habitats for settlement, spawning, recruitment, feeding, and shelter for a wide variety of marine species, and for this reason, it is considered a biodiversity hotspot (Ballesteros, 2006). Furthermore, due to its high species biomass, productivity, and vulnerability, this ecosystem is protected at the European level (92/43/CE Habitat Directive, 2008/56/EC Marine Strategy Framework Directive). However, human-induced stressors such as sediment re-suspension, eutrophication, and mechanical disturbances from fishing and anchoring are threatening this ecosystem. In addition, in recent decades, prolonged periods of unusually warm water, driven by global climatic factors, have become increasingly frequent in the Mediterranean Sea (Ciappa, 2022). Due to the basin small size and the semi-enclosed shape, the Mediterranean Sea is considered a climate hotspot, exposed more rapidly to climate change effects than other oceans (Schroeder et al., 2017; Kubin et al., 2023). In this region, elevated sea temperatures have already led to mass mortality events of key coralligenous species, subsequently reducing biodiversity and threatening the integrity and functioning of the ecosystem (e.g., Ponti

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* Corresponding author. Università di Sassari, Dipartimento di Scienze Chimiche, Fisiche, Matematiche e Naturali, Via Vienna 4, Sassari, Italy.
E-mail address: glamanna@uniss.it (G. La Manna).

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et al., 2014; Rodríguez-Ramilo et al., 2020; Garrabou et al., 2022). Although numerous studies have examined the impact of the thermal environment and its anomalies on habitat-forming species of the coralligenous reefs (Garrabou et al., 2022), to our knowledge no research has yet evaluated their effect on the associated fish assemblages. Temperature deviations from climatology are known to affect fish latitudinal range and vertical distribution (Nagelkerken and Munday, 2016), as well as key behaviors associated with survival and population fitness, such as reproduction and feeding (Brierley and Kingsford, 2009; Ladich, 2018). Thus, the thermal environment can profoundly affect reef complexity and biodiversity, strongly influencing the ecosystem services they provide (including commercial and recreational fishing and SCUBA diving tourism).

Evaluating fish biodiversity in coralligenous reefs is particularly challenging due to their depth and limited accessibility. Furthermore, underwater visual censuses performed by scuba divers cannot be conducted during nocturnal hours when several reef species are instead most active (Duane et al., 2024; La Manna et al., 2024). As a result, coralligenous fish communities remain poorly described, as the most common survey methods are sporadic, exclusively diurnal, and constrained by diving logistics (Di Iorio et al., 2021). However, sporadic research suggests that rocky coralligenous reefs have the highest fish species richness of any other rocky habitat in the Mediterranean Sea (Soldo and Glavičić, 2020; 2021), a finding consistent with the work of Di Iorio et al. (2021), which reported the highest fish sound richness of the Mediterranean Sea in the coralligenous reefs of France and Corsica. Due to the high vulnerability of this ecosystem, efficient and cost-effective monitoring techniques to evaluate the status of animal communities and identify the drivers of their richness and abundance are of pivotal importance (La Manna et al., 2024). The recent use of passive acoustic devices, gaining considerable attention in ecology due to advancements in technology and analysis methods, has proven to be an efficient tool for monitoring and conserving coral reefs, including those in the Mediterranean Sea (Di Iorio et al., 2021; La Manna et al., 2024). In fact, many fish species produce a variety of sounds used for agonistic behavior, territory and nest defense, mate selection, and predator and prey detection (Amorim, 2006). These acoustic signals can be used to detect fish occurrence and behavior in their natural habitats (La Manna et al., 2021; Ferguson et al., 2022).

In this study, we aimed to investigate the drivers influencing the coralligenous fish community, with a focus on the thermal environment, using passive acoustic monitoring. Temperature is considered one of the main drivers influencing fish presence/abundance, vocal activity (number of sounds produced) and temporal patterns of sound production (Amorim, 2006; Papes and Ladich, 2011). However, since many biological sounds may be related to seasonal changes in light conditions (Vieira et al., 2019, 2022) and moon phases (Radford et al., 2008; Staaterman et al., 2014; Monczak et al., 2017; Duane et al., 2024), these factors were also included in our correlative modeling approach to identify which drivers are most associated with coralligenous fish acoustic richness and abundance. The results provide insight for understanding how the thermal environment may influence coralligenous soundscape.

2. Methods

2.1. Acoustic data collection and analysis

Acoustic devices (RASP-URec384k), each featured with a Sensor Technology SQ26 pre-amplified hydrophone (sensitivity −164 dB re: V/m Pa, flat frequency response), a DODOTRONIC programmable recorder (gain 0 dB), battery set, and 400 Gb-SD memory card, were set to record for 15 min every hour (obtaining 6 h of recordings per day at a sampling rate of 192 kHz and 16-bit resolution). This duty cycle was determined by the goal of optimizing recording duration while staying within the battery consumption limits of the recording systems (La Manna et al., 2024). The devices were deployed by scuba divers at a depth of 35–38 m (connecting the device to a 8 kg ballast weights and a buoy) on two coralligenous reefs of the Western Mediterranean Sea in Sardinia (Tavolara Island 40°54′27″N - 9°45′38″E and Santa Teresa Gallura 41°15′25″N - 9°12′12″E, Fig. 1) to collect data on the fish acoustic community (defined as the aggregation of species that produces sounds; Farina and James, 2016) between 16th June and 16th August 2023.

Tavolara Island (TA) is situated within the Tavolara Punta Coda Cavallo Marine Protected Area (MPA), which was established in 1997 and covers an area of 15,280 ha. Santa Teresa Gallura (ST) is located within the Capo Testa Punta Falcone MPA, established in 2018, covering 5,000 ha. At both locations, coralligenous covers hundreds of squared meters and is primarily composed of coralline algae, with lesser amounts of green (e.g., *Halimeda tuna* and *Flabellia petiolata*) and brown algae (e.g., *Dictyotales* spp.). The habitat also supports encrusting and prostrate sponges, as well as Alcyonacea, including the red gorgonian *Paramuricea clavata* (Pinna et al., 2021).

Concurrently to the acoustic data collection, HOBO MX2202 loggers, which recorded local temperature once every hour, were deployed on the same reefs, a few meters apart from the acoustic devices. To characterize the thermal environment four descriptors were calculated: (i) mean daily temperature (the average temperature calculated from hourly temperature recordings taken throughout the day, in °C), (ii) temperature variation (the difference in °C between the mean daily temperature and the mean temperature calculated over the entire study period in each location), (iii) daily temperature shift (the difference in °C between the mean daily temperatures of two consecutive days), and (iv) heating event (a day when the mean daily temperature exceeds the 90th percentile observed throughout the entire period (June–August; Ceccherelli et al., 2020).

Each acoustic recording was visually and aurally inspected using Raven Pro 1.6 (Cornell University) displaying the spectrogram 180 s at a time with frequencies between 0 and 8.5 kHz (FFT length = 8,192, Hamming window, 50 % overlap). Fish sounds that were clearly distinguishable and identifiable in both the oscillogram and spectrogram, with an amplitude at least twice that of the background noise (suggesting the emitter's proximity to the device), were classified and counted using known fish sounds from the Mediterranean Sea (Bonacito et al., 2001, 2002; Codarin et al., 2012; Parmentier et al., 2010, 2018; Picciulin et al., 2012, 2013, 2018, 2020; Kéver et al., 2012, 2015, 2016; Bertucci et al., 2015; Di Iorio et al., 2018; Bolgan et al., 2019), following the methodological framework initially outlined by Desiderà et al. (2019), which was based on the acoustic features of the sound types, and adapted for this study (Table 1; see La Manna et al., 2024).

2.2. Statistical analysis

Generalized linear latent variable models (GLLVM; Niku et al., 2019) were applied to relate the abundance of each fish sound (expressed as the number of each sound type per day) to four descriptors of the thermal environment: three continuous variables (mean daily temperature, temperature variation, and daily temperature shift) and one categorical variable [heating event, with two levels (0 = no heating event; 1 = heating event)]. Further, day length (continuous variable) and moon phase [categorical variable with four levels: first quarter (lunar days 5–11), full moon (lunar days 12–19), third quarter (lunar days 20–26) and new moon (lunar days 27-4) have also been included as explanatory variables since they can both influence fish abundance and behavior. Day length and moon phase were obtained using the R-packages suncalc (Thieurmel and Elmarhraoui, 2025) and lunar (Lazaridis, 2022), respectively. Before the analysis, continuous variables, were checked for collinearity (Pearson's correlations): none of them were collinear thus they were all included in the models.

GLLVM are designed to manage multivariate abundance data, by expanding the standard generalized linear modeling framework to incorporate latent variables, which can address the covariation between

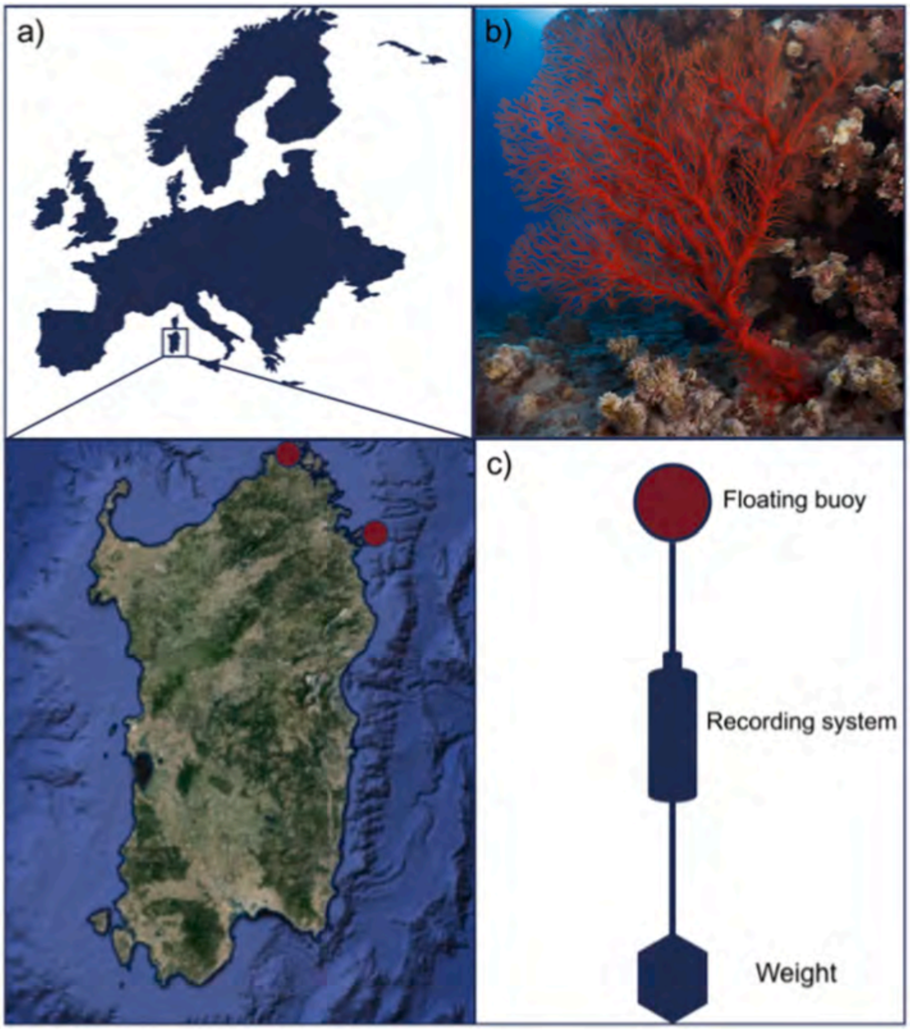

Fig. 1. Panel a): study sites and sampling locations; panel b): coralligenous reef; panel c): mooring scheme of the passive acoustic monitoring device.

species that is not explained by the explanatory variables (including species interactions and correlations caused by missing covariates). A forward selection model approach based on the Akaike information criterion (AIC) was used to first select the optimal number of latent variables and then the best combination of explanatory variables (Zuur et al., 2009). The R-package gllvm (version 1.3.1; Niku et al., 2019) was used to run the model. Model residuals were checked using the plot. gllvm-function of the gllvm package.

The associations between acoustic richness (calculated as the number of different sound type per day of recording) and acoustic abundance (calculated as the total number of fish sounds per day of recording) and the explanatory variables previously described were tested using two separate generalized linear mixed models (GLMMs) with a Poisson and Negative binomial distribution, respectively. GLMMs are an extension of generalized linear models that allow for the inclusion of random effects, by modeling the covariance structure generated by the grouping of data (Zuur et al., 2009). A forward selection procedure was applied to select the best models based on Akaike's information criterion (AIC) (Zuur et al., 2009). The best model was validated through graphical inspection of residuals (i.e., residuals vs. fitted values to assess homogeneity and residuals vs. each explanatory variable to check for independence). The GLMMs were performed using the package glmmTMB. In both GLLVMs and GLMMs, sampling day was included as a random effect to account for the likely correlation in fish sound abundance and richness within the same day, due to similar environmental conditions. Statistical significance was set at $p < 0.05$.

3. Results

Overall, in the two coralligenous reefs 22,665 sounds (12,840 at TA and 9,825 at ST) were extracted and analyzed. Seventeen different sound types were identified, six associated with four known species/taxa (*Sciaena umbra*, *Ophidion rochei*, *Scorpaena* spp., and *Epinephelus marginatus*) and eleven related to species which have not been identified, yet (Table 1).

The GLLVM (applied to all sound types except PS1, due to its scarce occurrence) revealed a significant association between the explanatory variables and the abundance of most sound types. Higher mean daily temperatures were associated with higher abundances of almost all sound types, except for those emitted by *Scorpaena* spp. (UFPS), which showed a reduced abundance, and slightly with the abundance of sounds emitted by *Sciaena umbra* (RPS) (Fig. 2a). Greater temperature variation was linked to lower abundance of three frequency-modulated sound types (LDS, DS, and DSS), one pulsed sound (PS4), and one sound produced by *Epinephelus marginatus* (SB) (Fig. 2b). The presence of heating events was associated with lower abundance of almost all sound types (Fig. 2c), except for the sound emitted by *Scorpaena* spp. (UFPS), which was more abundant. Additionally, reduced day length was linked to lower abundances of SFM, UFPS, RPS, and PS4 (Fig. 2d). Moon phases were associated with the abundance of many sound types, both positively and negatively (Fig. 3). To assess the factors most influencing fish sound abundance, candidate models were compared using the Akaike Information Criterion (AIC). The model that included thermal

Table 1
Acoustic properties (mean ± se) for each sound type at TA (Tavolara) and ST (Santa Teresa) sites during the study period: peak frequency (the frequency in Hz with the highest power), duration (total duration of the sound in sec), number of pulses and pulse rate (ratio between the duration and the number of pulses).

Sound name	Sound description	Site	Peak frequency (Hz)		Duration (s)		Number of pulses		Pulse rate		Species Taxa	Reference
			Mean	± se	Mean	± se	Mean	± se	Mean	± se		
APPPS	Accelerating pulse series with alternating pulse period.	TA	235	15.4	7.1	0.52	54.6	3.3	0.1	0.003	*Ophidion rochey*	Picciulin et al., 2018; present study
RPS	Stereotyped pulse series which may be repeated irregularly (I-call), regularly (R-call) or in chorus	ST	287	0.79	0.51	0.001	5.75	0.02	0.09	0.0002	*Sciaena umbra*	Picciulin et al., 2012, 2013; present study
		TA	305	1.20	0.45	0.002	4.21	0.02	0.11	0.0002		
UFPS	Ultra-fast amplitude modulated pulse series with a pseudo-harmonics appearance	ST	872	2.44	0.22	0.01	15.65	0.18	0.01	0.0001	*Scorpaena* spp.	Di Iorio et al., 2018; Bolgan et al., 2019; present study
SB	A single boom	TA	121	3.78	0.06	0.001	–	–	–	–	*Epinephelus marginatus*	Bertucci et al., 2015; present study
HSB	A single boom with higher peak frequency	ST	253	8.55	0.03	0.001	–	–	–	–	Unknown	Present study
		TA	196	1.59	0.03	0.001	–	–	–	–		
LPS	Low frequency pulse series	ST	188	0.001	0.5243	0.28	3.00	0.58	0.17	0.09	*Epinephelus marginatus*	Bertucci et al., 2015; present study
PS1	Series of pulses	TA	599	12	22.04	1.59	24.13	1.98	0.98	0.05	Unknown	Present study
PS2	Series of pulses	ST	298	6.22	0.81	0.02	6.17	0.12	0.13	0.003	Unknown	Present study
		TA	260	2.50	0.79	0.009	5.84	0.04	0.13	0.001		
PS3	Series of pulses	ST	736	38.15	0.30	0.04	3.41	0.44	0.10	0.011	Unknown	Present study
		TA	631	5.61	0.30	0.008	2.90	0.04	0.095	0.002		
PS4	Series of pulses	TA	597	4.94	7.15	0.15	6.55	0.14	1.124	0.02	Unknown	Present study
PS5	Series of pulses	ST	316	6.75	0.41	0.01	3.26	0.07	0.12	0.004	Unknown	Present study
		TA	250	2.00	0.42	0.001	3.12	0.02	0.13	0.001		
PS6	Series of pulses	TA	598	2.16	2.05	0.027	2.62	0.02	0.75	0.01	Unknown	Present study
LDS	Down sweep frequency modulated sound, with multi-harmonic appearance	ST	142	7.85	0.22	0.03	–	–	–	–	*Epinephelus marginatus*	Bertucci et al., 2015; present study
		TA	125	1.61	0.38	0.02	–	–	–	–		
DS	Down sweep frequency modulated sound	ST	319	13.85	0.15	0.02	–	–	–	–	Unknown	Desiderà et al., 2019; present study
		TA	377	3.62	0.14	0.001	–	–	–	–		
DSS	Consecutive series of down sweep frequency modulated	ST	304	10.66	1.12	0.11	–	–	–	–	Unknown	Desiderà et al., 2019; present study
		TA	356	4.76	0.91	0.03	–	–	–	–		
FM	Frequency modulated sound	ST	348	146.98	0.14	0.02	–	–	–	–	Unknown	Present study
		TA	449	9.15	0.11	0.01	–	–	–	–		
SFM	Series of frequency modulated sound	TA	578	1.86	2.44	0.06	–	–	–	–	Unknown	Present study

descriptors (mean daily temperature, temperature variation, and heating events) had a lower AIC value (Table 2) compared to those that included day length and moon phase, indicating that the thermal descriptors were more important in explaining the abundance of coralligenous fish sounds. However, the final best models also included day length and moon phase (Table 2), suggesting that both should also be considered when interpreting the patterns of coralligenous fish acoustic community. The explanatory variables accounted for 96 % of the covariation in sound abundance, suggesting that they are key factors influencing the covariance of coralligenous fish sounds. The correlation plot derived from the GLLVM analysis revealed patterns of residual association among the 16 fish sound types. After accounting for the variation explained by environmental covariates, most sound types appeared uncorrelated or showed slight positive correlations (dark blue clusters in Fig. 4). In contrast, only UFPS—the sound attributed to *Scorpaena* spp.—exhibited negative correlations (dark red squares in Fig. 4) with some sound types (e.g., PS5, DSS, DS, LDS).

Acoustic richness (per day) ranged from 8 to 14 sound types at TA and from 2 to 9 at ST, while acoustic abundance ranged from 45 to 672 at TA and from 3 to 585 at ST. Acoustic richness and abundance were positively linked with higher mean temperatures. Acoustic richness was also lower in the presence of heating events, while acoustic abundance was higher at full moon compared to the other lunar phases (Table 3, Fig. 5).

4. Discussions

This study aimed to investigate the factors influencing the coralligenous fish acoustic community in the Mediterranean Sea, focusing on the thermal environment, day length, and moon phases. Using passive acoustic monitoring, we identified seventeen distinct sound types within two coralligenous reefs, six of which were associated with four known species (*Sciaena umbra, Ophidion rochei, Scorpaena* spp., and *Epinephelus marginatus*). The results of the Generalized Linear Latent Variable Model (GLLVM) indicated that the explanatory variables—thermal environment, day length, and moon phases—were significantly associated with the abundance of most sound types, with temperature playing a particularly prominent role in shaping the observed acoustic patterns.

The strong association between higher mean daily temperature and increased sound abundance for nearly all sound types emphasizes the importance of the thermal environment in coralligenous fish acoustic activity. This finding aligns with previous studies documenting the effects of temperature on fish behavior, including vocalizations

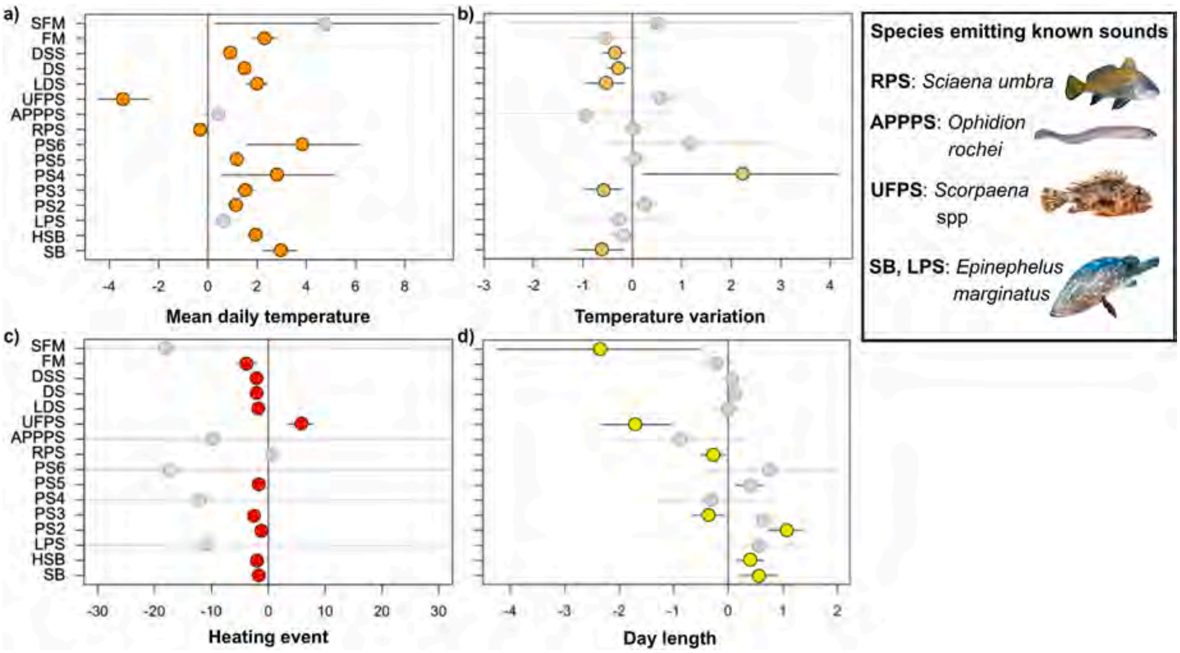

Fig. 2. Output of the negative binomial GLLVM. Coefficient plots containing the point estimates and 95 % confidence intervals for the effect of a) mean daily temperature, b) temperature variation, c) heating event and d) day length for the 16 fish sound type abundance. Colored circles located to the right of the zero-crossing show positive coefficients (thus association), while those positioned to the left show negative coefficients. Gray circle and lines denote intervals containing zero and thus not significant for the model.

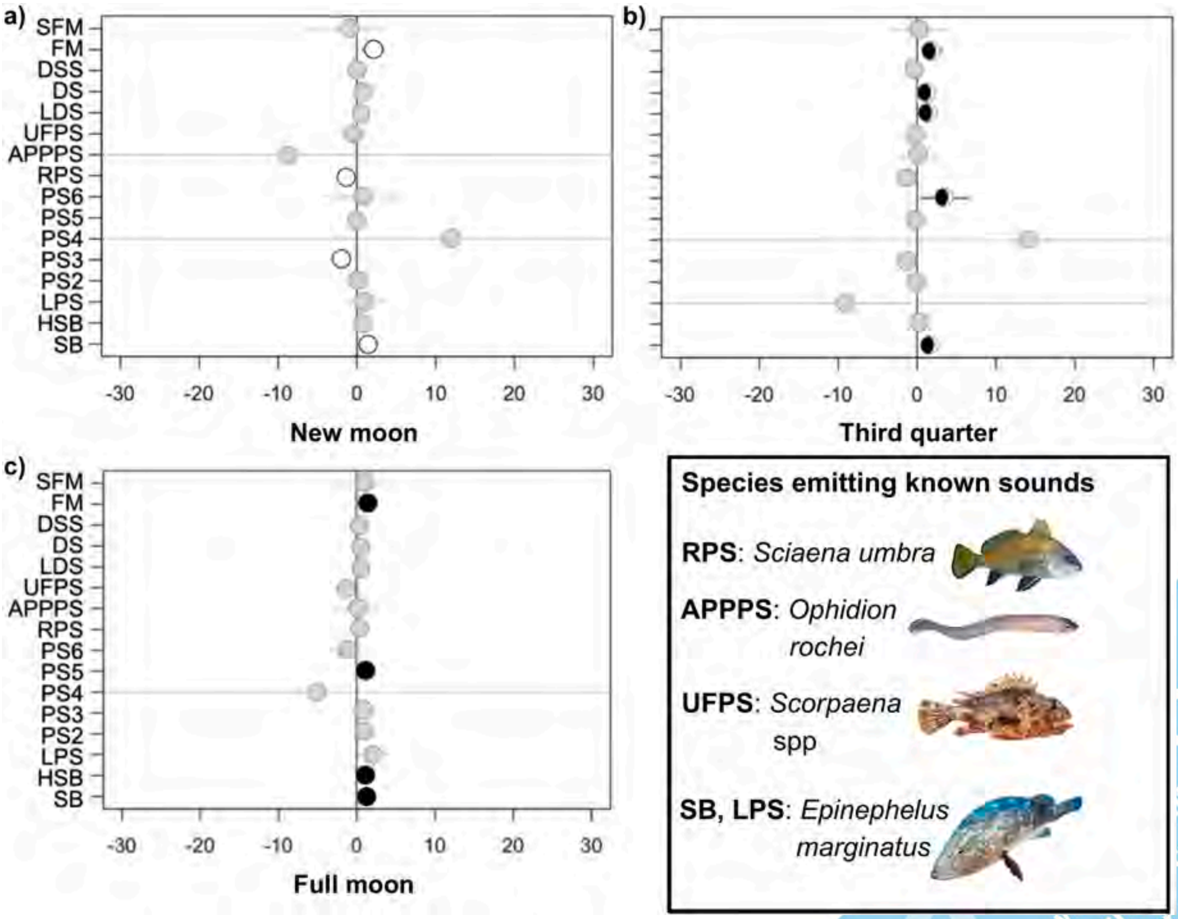

Fig. 3. Output of the negative binomial GLLVM. Coefficient plots containing the point estimates and 95 % confidence intervals for the effect of moon phase for the 16 fish sound type abundance. Colored circles located to the right of the zero-crossing show positive coefficients (thus association), while those positioned to the left show negative coefficients. Gray circle and lines denote intervals containing zero and thus not significant for the model.

Table 2
GLLVMs comparisons. In bold the best model based on the AIC values. All models included sampling day as random terms.

Model formula	df	AIC
Null model (LV = 0)	161	6451
Null model (LV=1)	**177**	**6429**
Null model (LV = 2)	192	6460
Sound abundance ~ Mean daily temperature	65	6654
Sound abundance ~ Temp variation	65	6790
Sound abundance ~ Daily shift	65	6823
Sound abundance ~ Heating event	65	6804
Sound abundance ~ Mean daily temperature + Temp variation	81	6635
Sound abundance ~ Mean daily temperature + Daily shift	81	6657
Sound abundance ~ Mean daily temperature + Heating event	81	6575
Sound abundance ~ Mean daily temperature + Temp variation + Heating event	97	6552
Sound abundance ~ Mean daily temperature + Daily shift + Heating event	97	6582
Sound abundance ~ Mean daily temperature + Daily shift + Heating event + Temp variation	113	6561
Sound abundance ~ Moon phase	97	6752
Sound abundance ~ Day length	65	6713
Sound abundance ~ Mean daily temperature + Temp variation + Heating event + Day length	113	6470
Sound abundance ~ Mean daily temperature + Temp variation + Heating event + Moon phase	145	6506
Sound abundance ~ Mean daily temperature + Temp variation + Heating event + Day length + Moon phase	**161**	**6423**

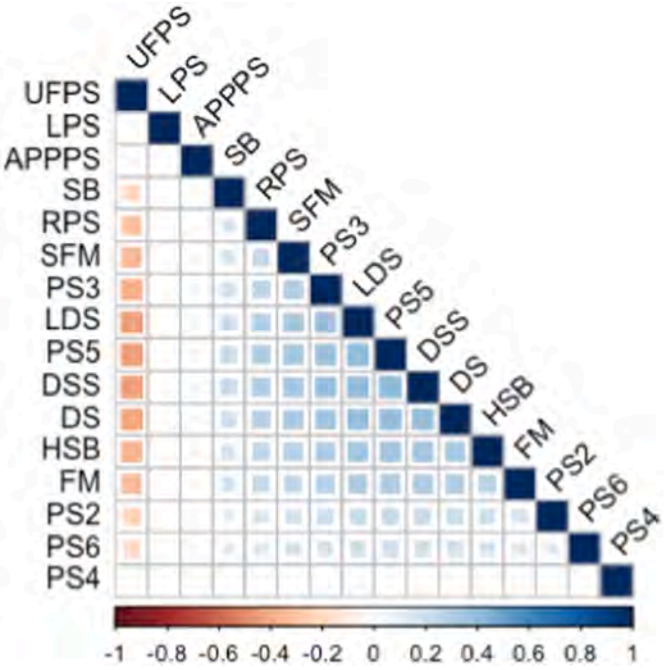

Fig. 4. Correlation across response variables (induced by the latent variable of the GLLVM), estimating the correlation patterns across fish sound types explained by the environmental predictors.

(Connaughton et al., 2000; Amorim, 2006; Papes and Ladich, 2011; Ladich and Schleinzer, 2015; Rice et al., 2016; Montie et al., 2015, 2016, 2017; Monczak et al., 2017; Ladich and Maiditsch, 2020; Vieira et al., 2022). Fish in many ecosystems rely on temperature cues to regulate important biological functions such as reproduction, feeding, agonistic interactions, and territory defense, which can influence their acoustic behavior (Montie et al., 2015; Ladich, 2018; Vieira et al., 2022). The positive correlation between temperature and sound abundance suggests that warmer conditions may stimulate fish activity or promote sound-producing behaviors. However, the correlation was not uniform across all species or sound types. For example, *Scorpaena* spp. (UFPS) exhibited reduced vocal activity in response to higher temperatures, indicating that some species may be more sensitive to temperature changes than others, possibly due to ecological adaptations (Ladich, 2018).

Table 3
GLMMs outputs on A) acoustic richness and B) acoustic abundance. Significant p-values are in bold. All models included sampling day as random terms. R^2 marginal considers only the explained variance of the fixed terms, while R^2 conditional accounts for both the fixed and random terms.

A) Acoustic richness	Estimated	Std. Error	Z value	P-value
(Intercept)	−0.159	0.224	−0.709	0.478
Mean daily temperature	0.101	0.010	9.971	**<2e-16**
Heating event	−0.505	0.129	−3.896	**9.8e-05**
Daily shift	−0.048	0.032	−1.479	0.139
R2 marg 51 %; R2 cond 52 %				

B) Acoustic abundance	Estimated	Std. Error	Z value	P-value
(Intercept)	9.505	2.795	3.401	0.001
Mean daily temperature	0.044	0.018	2.483	**0.013**
Daily shift	−0.068	0.046	−1.488	0.137
Day length	−0.351	0.180	−1.947	0.051
Moon phase:full moon	0.398	0.187	2.124	**0.034**
Moon phase:new moon	−0.578	0.280	−2.064	**0.039**
Moon phase:third quarter	−0.109	0.212	−512	0.608
R2 marg 77 %; R2 cond 100 %				

Greater temperature variation was associated with lower abundance of several sound types, particularly frequency-modulated sounds (LDS, DS, DSS), pulsed sounds (PS4), and one of the sounds produced by *Epinephelus marginatus* (SB). This observation is consistent with the idea that sudden or fluctuating temperature changes may disrupt the environmental stability required for optimal biological function in marine organisms (Munday et al., 2008). Heating events were also found to be associated with lower abundances of most sound types and acoustic richness, suggesting that prolonged periods of unusually warm water may lower acoustic abundance and richness, likely due to stress, changes in metabolic rates, or shifts in behavior (Monczak et al., 2017; Ladich et al., 2018). However, the increased vocal activity of *Scorpaena* spp. during heating events could reflect a species-specific adaptation to extremely warming conditions, possibly linked to territorial behaviors or species-specific interactions stimulated by higher temperature events.

Reduced day length was associated with lower abundances of sounds emitted by several species, including SFM, UFPS, RPS, and PS4, suggesting that as day length decreases, fish may alter their vocal behavior, possibly due to changes in activity patterns. Further, the influence of moon phases on the abundance of coralligenous fish sounds was also observed, with different sound types responding both positively and negatively to changes in lunar conditions and higher total acoustic abundance observed during full moon. This finding aligns with previous studies suggesting that moon phases can influence the behavior of fish species, particularly those involved in reproductive activities (Gilmore, 1994; Monczak et al., 2017). In addition, the reduction in acoustic activity during certain moon phases could reflect different species adaptations to lunar conditions, including changes in predator-prey dynamics or environmental factors like water clarity and visibility.

The comparison of candidate models using the Akaike Information Criterion (AIC) demonstrated that the thermal descriptors (mean daily temperature, temperature variation, and heating events) were the most important drivers in explaining the abundance of coralligenous fish sounds. This supports the conclusion that the thermal environment plays a dominant role in shaping the acoustic fish community in this ecosystem. However, the final best models also included day length and moon phases, suggesting that while temperature is a key driver, these two factors should also be considered when interpreting the patterns of

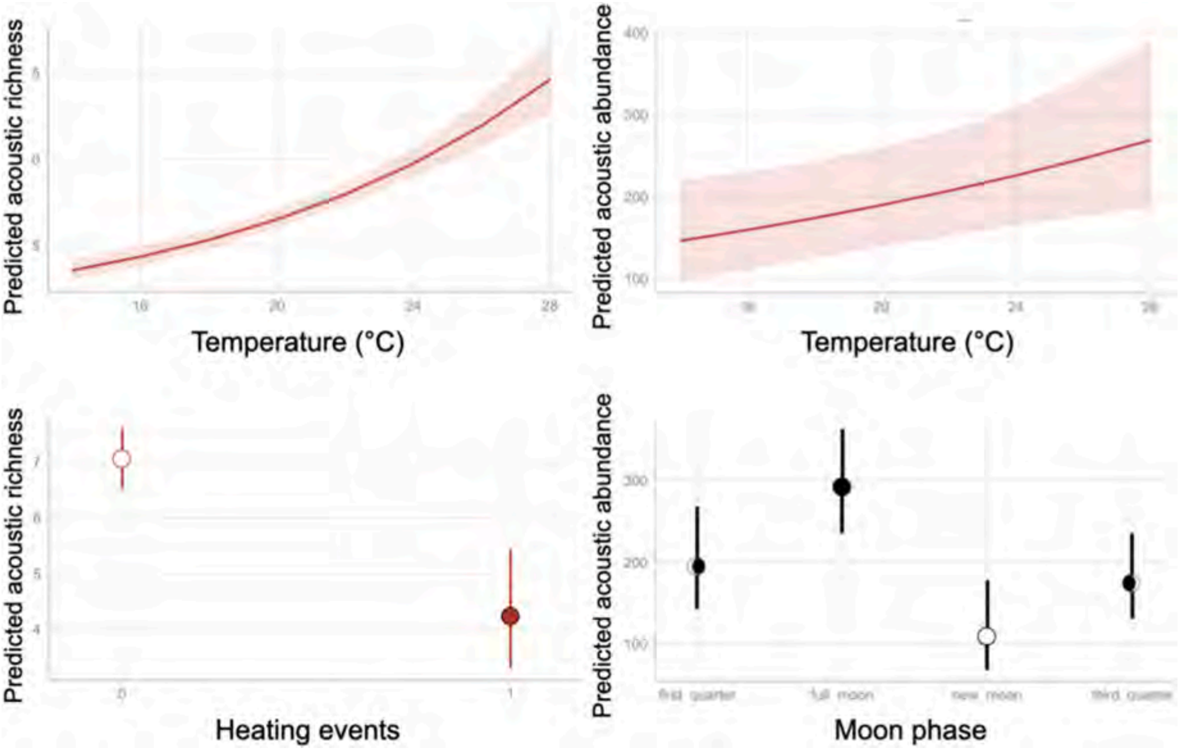

Fig. 5. Output of the GLLMs on acoustic richness and acoustic abundance (only significant explanatory variables are shown).

fish sounds in coralligenous reefs.

4.1. *Study limitations*

This study highlights the effect of different drivers—especially those related to the thermal environment—on the fish acoustic community for the first time in the Mediterranean coralligenous ecosystem. However, some study limitation should be considered to address future research. First, the study focused on a two-month period (mid-June to mid-August 2023), selected because it corresponds to the season when most fish produce sounds in the Mediterranean Sea (Buscaino et al., 2016). However, this duration is relatively short in the context of long-term ecological processes. Coralligenous reefs and the fish communities they support can exhibit seasonal and yearly variations in abundance, which cannot be fully captured by a single sampling period. Since, it is unclear whether the observed relationships hold over longer periods, long-term monitoring across multiple years would be needed to fully understand how the coralligenous fish acoustic community responds to changing environmental conditions over time. Second, the study focused on two coralligenous reefs in Sardinian MPAs, which, while providing valuable data representative of the Western Mediterranean Sea, may not be fully representative of all coralligenous reefs, characterized by profound spatial variability (Piazzi et al., 2016). Thus, future studies could expand to other reef sites to test the robustness and transferability of the present results. Finally, the incomplete identification of fish species emitting sounds can potentially hinder the ecological understanding of the fish communities at the reefs. In fact, at present, the acoustic repertoires of many species remain still undescribed. For this reason, we could not directly translate the 17 distinct sound types we detected into an exact number of species. Future efforts to improve sound classification through advanced acoustic analysis methods (e.g., automatic detection by AI) and more precise species identification may enhance the accuracy of such research.

4.2. *Conclusion*

As marine ecosystems experience more frequent temperature fluctuations due to climate change, understanding the impact of temperature variation on acoustic community becomes increasingly important. It is crucial to consider how climate-driven changes in temperature variability might alter the acoustic ecology of coralligenous reefs and the species that depend on them.

This study highlights the complex interactions between the thermal environment, day length, and moon phases in shaping the acoustic community of coralligenous fish. The findings suggest that temperature is a primary driver of fish vocal activity. However, the response to temperature variation and heating events was species-specific, indicating that fish species may have different tolerance and adaptations to environmental stressors. The study also emphasizes the role of day length and moon phases in influencing the temporal patterns of fish sounds. These results contribute to understanding how environmental factors shape the acoustic ecology of coralligenous reefs, which is critical for the effective monitoring and conservation of these vulnerable ecosystems.

Given the high sensitivity of coralligenous biodiversity to thermal anomalies, it is crucial to further investigate the mechanisms underlying the observed impact on fish communities. Future research should explore whether the observed decrease in calling activity among most species in response to the thermal environment is due to physiological mechanisms, such as reduced sonic muscle activity from thermal stress (Amorim, 2006), behavioral changes (e.g., modifications in agonistic, reproductive, and acoustic behaviors; Connaughton et al., 2000; Papes and Ladich, 2011; Vieira et al., 2022), or shifts in vertical distribution to avoid adverse thermal conditions (Munday et al., 2008; Ladich, 2018). Understanding these mechanisms would be vital for predicting the broader ecological consequences of climate change on this marine ecosystem. In fact, behavioral and distributional changes can cascade through food webs, affecting predator-prey relationships (Ockendon et al., 2014; Allan et al., 2015), competition for habitat, habitat selection (Matis et al., 2018) and, ultimately, influencing the services provided by fish (Nagelkerken and Munday, 2016; 2020).

CRediT authorship contribution statement

Gabriella La Manna: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Mariangela Moro Merella:** Investigation. **Riccardo Vargiu:** Investigation. **Giuseppe Morello:** Investigation. **Gianluca Sarà:** Writing – original draft, Supervision, Funding acquisition. **Giulia Ceccherelli:** Writing – original draft, Supervision, Funding acquisition, Conceptualization.

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Declaration of competing interest

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Data availability

Data will be made available on request.

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