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# Comparative analysis of fish sounds recorded during an early acoustic experiment in a Mediterranean seagrass meadow

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**Research Article**

In memoriam of Jean-Pierre Hermand.

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## Abstract

*Posidonia oceanica* seagrass meadows constitute an important ecosystem of the Mediterranean Sea, providing habitat for many species of invertebrates and fishes, some of which produce sounds with distinctive features. Using such sounds to monitor marine habitats is at the core of passive acoustic monitoring. In the Mediterranean, an arched frequency modulation centred around 747 Hz, which aurally sounds like */kwa/*, has been investigated as an environmental proxy. Remarkably, these sounds were already noted as a distinctive feature of the soundscape recorded during an early acoustic experiment, USTICA 99 (Ustica, Sicily, Italy), which simultaneously measured photosynthetic gas exchanges and fish migration at the scale of a *Posidonia* meadow. In this study, we revisit that dataset to describe the specific characteristics of the early recorded */kwa/* sounds and compare them with more recent field studies conducted in French *P. oceanica* meadows, approximately 500 km north of Ustica and 15 years later. Our comparative analysis confirms a high degree of homogeneity in the */kwa/* sounds, with some variations that are further examined.

## Introduction

*Posidonia oceanica* (L.) Delile, 1813 meadows are key ecosystems of the Mediterranean Sea (Boudouresque *et al.*, 2007). These underwater seagrasses are well known for their multiple and diverse ecosystem services, including coastal protection from erosion (Sánchez-González *et al.*, 2011), stabilization of the seabed (Terrados and Duarte, 2000; Gacia and Duarte, 2001), and oxygen production (Agueda Aramburu *et al.*, 2024). They also serve as important nurseries and breeding habitats for many animal species (Boudouresque *et al.*, 2007; Kalogirou *et al.*, 2010).

Among the fish inhabiting *P. oceanica* meadows, several species from different families are known to produce sounds (e.g., Gobiidae, Ophidiidae, Sciaenidae, Scorpaenidae). One of the dominant sounds in *P. oceanica* meadows is the */kwa/*, which can be over 20 times more abundant than other fish sounds (Di Iorio *et al.*, 2018; Bolgan *et al.*, 2019). These sounds are produced by *Scorpaena* spp. (Bolgan *et al.*, 2019) and have been recorded along different coasts of the Mediterranean Sea, including France (Di Iorio *et al.*, 2018; Bolgan *et al.*, 2019), Italy (Ceraulo *et al.*, 2018; La Manna *et al.*, 2021, 2024), Greece (Bolgan *et al.*, 2022), and Spain (González Correa *et al.*, 2019; Bolgan *et al.*, 2022). However, this sound is known to be highly variable, and its description has mainly been based on French meadows (Di Iorio *et al.*, 2018). A better understanding of its temporal and spatial variability will help confirm the relevance of the */kwa/* sound for monitoring *P. oceanica* meadows using passive acoustic monitoring, a technique using such sounds to monitor terrestrial and aquatic habitats (Darras *et al.*, 2025).

Ustica is a small island of 8 km$^2$ located 52 km north of Sicily (southern Italy, Figure 1). In 1986, together with Miramare (D.M. 12/11/86), it became one of the first marine protected areas established in Italy. While its terrestrial flora is not particularly luxuriant, well-developed seagrass meadows can be found along parts of its coast (Andaloro *et al.*, 1998). In 1999, an early marine acoustics experiment was conducted in Ustica (USTICA 99, for details, see Hermand, 2003) in a *P. oceanica* meadow (Agate *et al.*, 2001; Hermand, 2003). The aim of this experiment was to measure oxygen production by the meadow using active acoustics. Since the experiment also involved passive acoustic listening of the emitted chirps, Hermand (2003) noted the presence of fish sounds corresponding to the */kwa/* sounds later described from French meadows (Di Iorio *et al.*, 2018). Building on these early observations, this study aims to describe */kwa/* sounds recorded during USTICA 99 (Ustica Island; 1999) and to compare their acoustic features with those used to characterize the sound (France, 2014–2015) (Di Iorio *et al.*, 2018).


**Figure 1.** Western Mediterranean Sea. Ustica Island is indicated in red, and the French *Posidonia oceanica* meadows studied by Di Iorio *et al.* (2018) are located along the coastline within the green box. Google Earth: data SIO, NOAA, U.S. Navy, NGA, GEBCOLandsat/Copernicus.

## Materials and methods

### *Acoustic recordings*

Sound recordings were carried out continuously between the 22nd and 25th of September 1999 in a *Posidonia oceanica* meadow off Ustica Island (Sicily, Italy; 38.70° N, 13.19° E) at a depth of 8.4 ± 0.4 m. The hydrophone was fixed on a rigid pole positioned within the meadow, 0.3 m above the seafloor. The signal was amplified and bandpass-filtered using a high-pass third-order Bessel filter ($f_{\text{-3dB}} = 500$ Hz) and a low-pass eight-order linear phase filter ($f_{\text{-3dB}} = 16.7$ kHz). Recordings were made using a portable data acquisition unit (for pictures of the deployment, see Hermand, 2003). As in the original study, artificial chirps were used to assess oxygen production in the meadow; for this study, only the inter-chirp intervals were analysed, as they are representative of the meadow's natural soundscape. Three seconds were selected each minute (1 second before and 2 seconds after each chirp), resulting in a total of 3 minutes per hour. Three nights and 4 days were analysed.

### *Acoustic analyses*

The Ustica files were subsampled at 6 kHz. Sound selections were carried out using RavenPro Sound Analysis Software 1.5 (Cornell Lab of Ornithology, USA). Acoustic features of each selected /*kwa*/ sound were extracted using custom-made Matlab® (R2012a) scripts. The extracted features were the same as the ones described in Di Iorio *et al.* (2018), which included the following: number of pulses (NP), duration ($T$), bandwidth (BW), minimum frequency ($F_{\text{min}}$), maximum frequency ($F_{\text{max}}$), peak (or dominant) frequency ($F_{\text{peak}}$), start frequency ($F_{\text{s}}$), end frequency ($F_{\text{e}}$), frequency change from end to start ($\Delta F_{\text{es}} = F_{\text{e}} - F_{\text{s}}$), from start to peak ($\Delta F_{\text{sp}} = F_{\text{s}} - F_{\text{peak}}$), from center to peak ($\Delta F_{\text{cp}} = F_{\text{c}} - F_{\text{peak}}$), and from end to peak ($\Delta F_{\text{ep}} = F_{\text{e}} - F_{\text{peak}}$). Additional features included the number of pseudo-harmonics (NbH), pseudo-harmonic interval (HI), pulse period (PP), normalized linear entropy (Entro), and the indices of the most energetic pseudo-harmonics (H1–H4) along with their ratio. The index of the most energetic pseudo-harmonic (H1) was defined relative to the principal contour ($F_{\text{peak}}$) as index 0, with the pseudo-harmonic immediately above as +1, below as −1, and so on. The energy ratio (Q3H) was calculated by comparing the energy in H1–H3 combined to the total energy in all pseudo-harmonics. Received level (RL), signal-to-noise ratio (SNR), and sound cumulative level (SCL) were not calculated in absolute terms but used in relative form for the temporal description. Detailed descriptions of these features are reported in Di Iorio *et al.*, (2018).

To compare the /*kwa*/ sounds from Ustica with those from the French littoral, we used subsamples of the data processed by Di Iorio *et al.* (2018) from the CALME acoustic network (Gervaise *et al.*, 2018). Details of the subsampling are presented in the next section.

### *Statistics analyses*

For the acoustic description, only /*kwa*/ sounds with at least four pseudo-harmonics were considered ($n = 512$). For the temporal analysis, all selected /*kwa*/ sounds were used ($n = 793$). Temporal variations in the abundance of /*kwa*/ sounds (number of sounds per minute) were graphically compared with the normalized total power variations obtained by Hermand (2003) to identify potential patterns between the two. Subsequently, the three periods of most intense /*kwa*/ soniferous activity (7 PM to midnight GMT) were compared based on the acoustic features of /kwa/ sounds. As $\text{HI} = \text{PP}^{-1}$, it was excluded from the statistical analyses, and H1 was also removed because it was too heavily influenced by extreme values. Kruskal–Wallis tests were performed for all the other acoustic features to compare them across the 3 nights.

To compare the data from Ustica with those from the French littoral, only /*kwa*/ sounds from the CALME recordings with an SNR ≥ 10 dB were considered ($n = 19{,}889$). The French /*kwa*/ sounds were randomly divided into five groups of 512 observations, matching the sample size in Ustica. For each group, bootstrap Wilcoxon–Mann–Whitney tests were performed on subsamples ($n_{\text{observations}} = 100$, $n_{\text{replicates}} = 100$), and the mean of the resulting $p$-values was calculated. This method was applied to avoid using datasets with highly unequal sample sizes and to limit the artificial

detection of statistically significant differences commonly associated with large datasets (Lin *et al.*, 2013). To better understand the differences between the data collected in Ustica in 1999 and the other datasets, we also examined the normalized mean (ranging from 0 to 1) and standard deviation of selected key acoustic features ($F_{peak}$, PP, BW, NP, and Entro) from all recordings available from the 2014–2015 period (Di Iorio *et al.*, 2018), adding the new data from Ustica.

All statistical analyses were performed using R version 3.6.1. (R Core Team, 2014). The significance level (α) was set at 0.05.

## Results and discussion

### *Acoustic description*

In the Ustica recordings, /*kwa*/ sounds occurred at rates from 0.3 to 47.7 per minute (mean ± SD: 5.5 ± 11.5). The Ustica /*kwa*/ sounds were pulse trains lasting 0.2 ± 0.06 s, with a peak frequency of 947.2 ± 141.6 Hz (Figure 2). Each sound comprised 13.9 ± 5.2 pulses, with an average PP of 9.3 ± 4.1 ms. Detailed acoustic characteristics are summarized in Table 1.

### *Temporal description*

During the 4 days and 3 nights of recordings, /*kwa*/ sounds were present both day and night, occurring during almost all of the analysed hours. However, their abundance showed marked diel variations (Figure 3). /*Kwa*/ sounds were most abundant at night, with a pronounced peak between 7 PM and 9 PM GMT (9–11 PM local time), corresponding to the beginning of the first peak in ambient noise observed each night (Figure 3). These 2 h represent only 8.33% of a 24-h cycle but accounted for 78.31% of all recorded sounds. A graphical comparison of /*kwa*/ sound abundance and ambient noise levels shows that the /*kwa*/ peak between 7 and 9 PM GMT coincides with the onset of the first nightly increase in overall sound levels (Figure 3).

Temporal trends were similar across nights in terms of abundance and contribution to the soundscape, consistent with findings from a previous study (Hermand, 2003). No clear differences were observed between nights regarding most acoustic features. Of the 24 features calculated, only 4 showed significant differences: relative $RL_{rms}$, relative SCL, entropy, and maximum frequency (Table 2, Kruskal–Wallis: $\chi^2 = 22.22, 20.70, 6.67$ & $6.22$; $p < 0.001, < 0.001$, 0.04, and 0.04, respectively); and all four variables are known to be highly correlated (Di Iorio *et al.*, 2018).

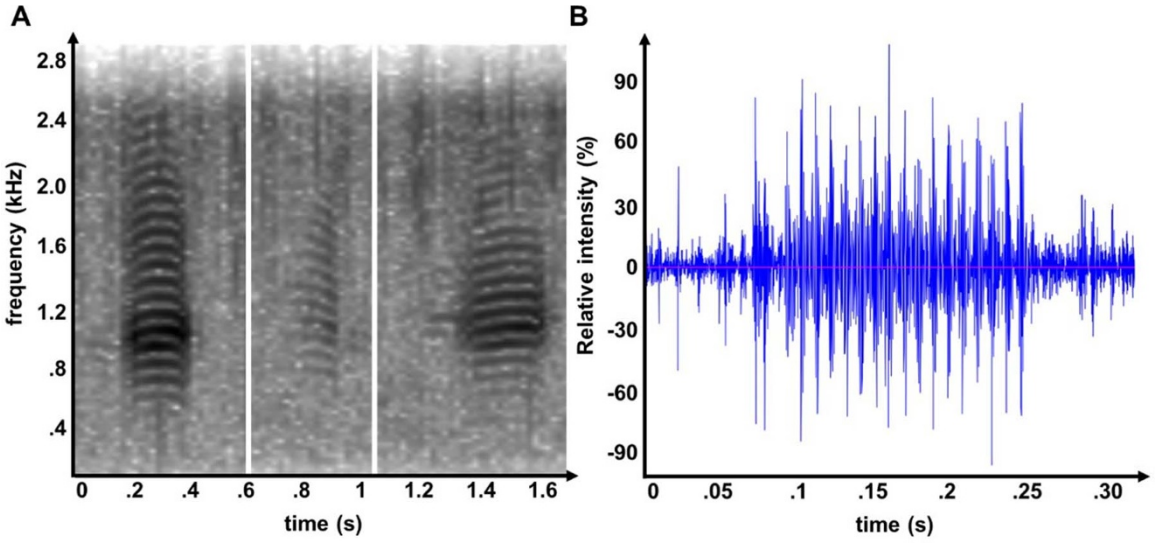


**Figure 2.** (a) Three spectrograms of /*kwa*/ sounds recorded at Ustica Island in 1999 (FFT = 256, overlap = 50%, Hann window). (b) Oscillogram of a /*kwa*/ sound recorded at Ustica Island in 1999.

**Table 1.** Summary statistics of the acoustic features of /kwa/ sounds with at least four pseudo-harmonics

| | $\bar{x}$ | SD | SE | IQR | 0% | 25% | 50% | 75% | 100% |
|---|---|---|---|---|---|---|---|---|---|
| **NP** | 13.91 | 5.24 | 0.23 | 7 | 4 | 10 | 13 | 17 | 32 |
| **PP (ms)** | 9.56 | 4.16 | 0.18 | 0.90 | 5.00 | 9.01 | 9.48 | 9.91 | 90.91 |
| **HI (Hz)** | 111.30 | 26.85 | 1.19 | 10.12 | 11.00 | 100.88 | 105.50 | 111.00 | 200.00 |
| **$\Delta F_{sp}$ (Hz)** | −6.15 | 135.23 | 5.98 | 51.00 | −715.00 | −41.00 | −12.00 | 10.00 | 867.00 |
| **$\Delta F_{es}$ (Hz)** | −1.00 | 129.95 | 5.74 | 65.50 | −874.00 | −23.00 | 6.00 | 42.50 | 520.00 |
| **$\Delta F_{ep}$ (Hz)** | −7.15 | 57.98 | 2.56 | 14.00 | −979.00 | −13.00 | −6.00 | 1.00 | 397.00 |
| **$\Delta F_{cp}$ (Hz)** | −1.01 | 24.04 | 1.06 | 7.00 | −442.00 | −3.00 | 1.00 | 4.00 | 72.00 |
| **$F_{min}$ (Hz)** | 669.53 | 142.88 | 6.31 | 166.00 | 161.00 | 592.00 | 678.00 | 758.00 | 1111.00 |

(*Continued*)

**Table 1.** (*Continued.*)

| | $\bar{x}$ | SD | SE | IQR | 0% | 25% | 50% | 75% | 100% |
|---|---|---|---|---|---|---|---|---|---|
| **$F_{peak}$ (Hz)** | 947.16 | 141.59 | 6.26 | 164.82 | 550.80 | 861.30 | 931.60 | 1026.12 | 2074.20 |
| **H1** | 0.03 | 0.42 | 1.88 | 0 | −3 | 0 | 0 | 0 | 6 |
| **H2** | 0.54 | 1.42 | 6.26 | 2 | −5 | −1 | 1 | 1 | 8 |
| **H3** | 1.12 | 1.84 | 0.08 | 3 | −4 | −1 | 1 | 2 | 10 |
| **H4** | 1.20 | 2.28 | 0.10 | 4 | −5 | −1 | 2 | 3 | 8 |
| ***T* (s)** | 0.19 | 0.06 | 0.003 | 0.07 | 0.08 | 0.14 | 0.18 | 0.22 | 0.52 |
| **BW (Hz)** | 867.34 | 462.95 | 20.46 | 546.75 | 246.00 | 524.75 | 729.50 | 1071.50 | 2440.00 |
| **Entro** | 0.89 | 0.06 | 0.003 | 0.071 | 0.63 | 0.86 | 0.91 | 0.93 | 0.99 |
| **$F_s$ (Hz)** | 941.02 | 169.04 | 7.47 | 186.38 | 302.30 | 840.22 | 922.30 | 1026.60 | 2064.20 |
| **$F_e$ (Hz)** | 940.01 | 128.48 | 5.68 | 161.75 | 623.00 | 858.22 | 929.45 | 1019.98 | 2064.20 |
| **$F_{max}$ (Hz)** | 1536.88 | 406.41 | 17.96 | 481.25 | 890.00 | 1242.00 | 1414.50 | 1723.25 | 2875.00 |
| **NbH** | 9.0078 | 5.017 | 0.22 | 6 | 4 | 5 | 7 | 11 | 39 |
| **Q3H (%)** | 0.84 | 0.13 | 0.006 | 0.17 | 0.30 | 0.77 | 0.87 | 0.94 | 0.9997 |

$N = 512$. IQR, interquartile range; SD, standard deviation; SE, standard error.

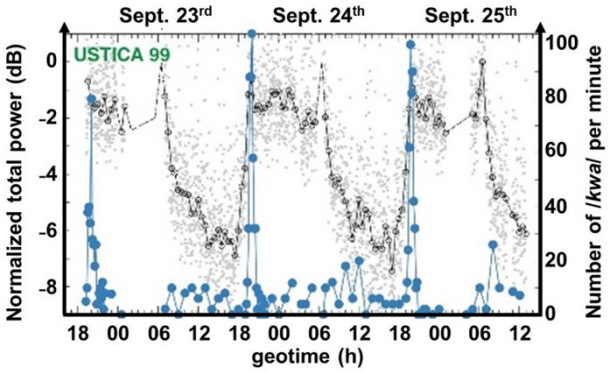


**Figure 3.** Number of /*kwa*/ sounds per minute (right axis, blue) over time (GMT), compared to the normalized total power (left axis, in dB, black). Adapted from Hermand (2003), CRC Press. Grey dots represent raw data points.

The 2-h period of high sound production begins approximately 2 h after sunset (based on sunset times for Palermo, Northern Sicily; NOAA/GML Solar Calculator). The duration of this period and its position within the day/night cycle are similar to the choruses described in southern metropolitan France (Di Iorio *et al.*, 2018), Corsica (Di Iorio *et al.*, 2018), and in Italian meadows (Ceraulo *et al.*, 2018). In winter, /*kwa*/ sounds are known to occur sporadically, with no choruses being recorded (Ceraulo *et al.*, 2018). This period and duration are also similar to those observed for *kwa*-like sounds from tropical reefs (Raick *et al.*, 2023, 2025).

Both RL and SCL, which represent the intensity levels of sound emission, differed significantly between nights. The fact that only this subset of features varies, while all others remain consistent, indicates that the /*kwa*/ sounds are essentially similar across nights in terms of duration, frequency, and shape, but differ in intensity. This finding aligns with observations of French /*kwa*/ choruses, where intensity varies from night to night (Di Iorio *et al.*, 2018). At a broader time scale, RL is known to peak in July, being higher in summer than in spring. However, more data are needed to better understand not only potential seasonal variations but also those occurring over shorter time frames.

### *Comparison with /kwa/ sounds from French meadows*

When comparing /*kwa*/ sounds from Ustica and the French littoral, several differences were observed. First, all the frequency-related features ($F_{min}$, $F_{peak}$, $F_{max}$, $F_s$, $F_e$) were significantly different (Table 2), with /*kwa*/ frequencies in Ustica being higher than those in France. All other features were equivalent, except for duration ($T$), entropy (Entro), and PP. The PP of /*kwa*/ in Ustica was shorter than in France (9.56 ± 4.16 ms compared to 13 ± 4 ms). The same was observed for $T$ (0.19 ± 0.064 s vs. 0.27 ± 0.09 s) and the contrary for Entro (89.1 ± 6.1 vs. 86.6 ± 5.6). Notably, Ustica /*kwa*/ sounds exhibited the highest $F_{peak}$ values and the shortest durations. Entropy, duration, and frequency features (such as $F_{peak}$) in Ustica /*kwa*/ were similar to those recorded at an equivalent period in the French meadows (Figure 4).

The frequencies of Ustica /*kwa*/ sounds were higher than those recorded in the French datasets, a pattern also observed for PP. Variability in both $F_{peak}$ and PP has already been reported for French /*kwa*/ sounds (Di Iorio *et al.*, 2018), with $F_{peak}$ tending to be higher in summer than in spring, while the opposite trend was observed for PP. This seasonal variation was demonstrated in specific meadows in the South of France (Parc Marin de la Côte Bleue) and Corsica (Calvi), as well as through comparisons between different meadows. The peak frequency of the Ustica /*kwa*/ sounds was more than 100 Hz higher than that reported by Ceraulo *et al.* (2018) for the corresponding 'MF-fish sounds' (mean ± SE: 840 ± 75.37) (Ceraulo *et al.*, 2018); however, their data were collected over several months, which may have averaged out $F_{peak}$ values. The difference in $F_{peak}$ was smaller when compared with croak sounds recorded in Spain (González Correa *et al.*, 2019) (mean ± SE: 900 ± 145.7 Hz), which are now considered synonymous with the /kwa/ sound type (Bolgan *et al.*, 2019). It has also been shown that /kwa/ sounds recorded in Crete differ from those recorded in the western basin (Corsica and Mallorca) in terms of frequency characteristics (e.g., peak frequency) and temporal features (e.g., PP) (Bolgan *et al.*, 2022). While this sound dominated the 700–900 Hz range at western sites, it was most frequently observed between 900 and 1100 Hz in Crete (Bolgan *et al.*, 2022).

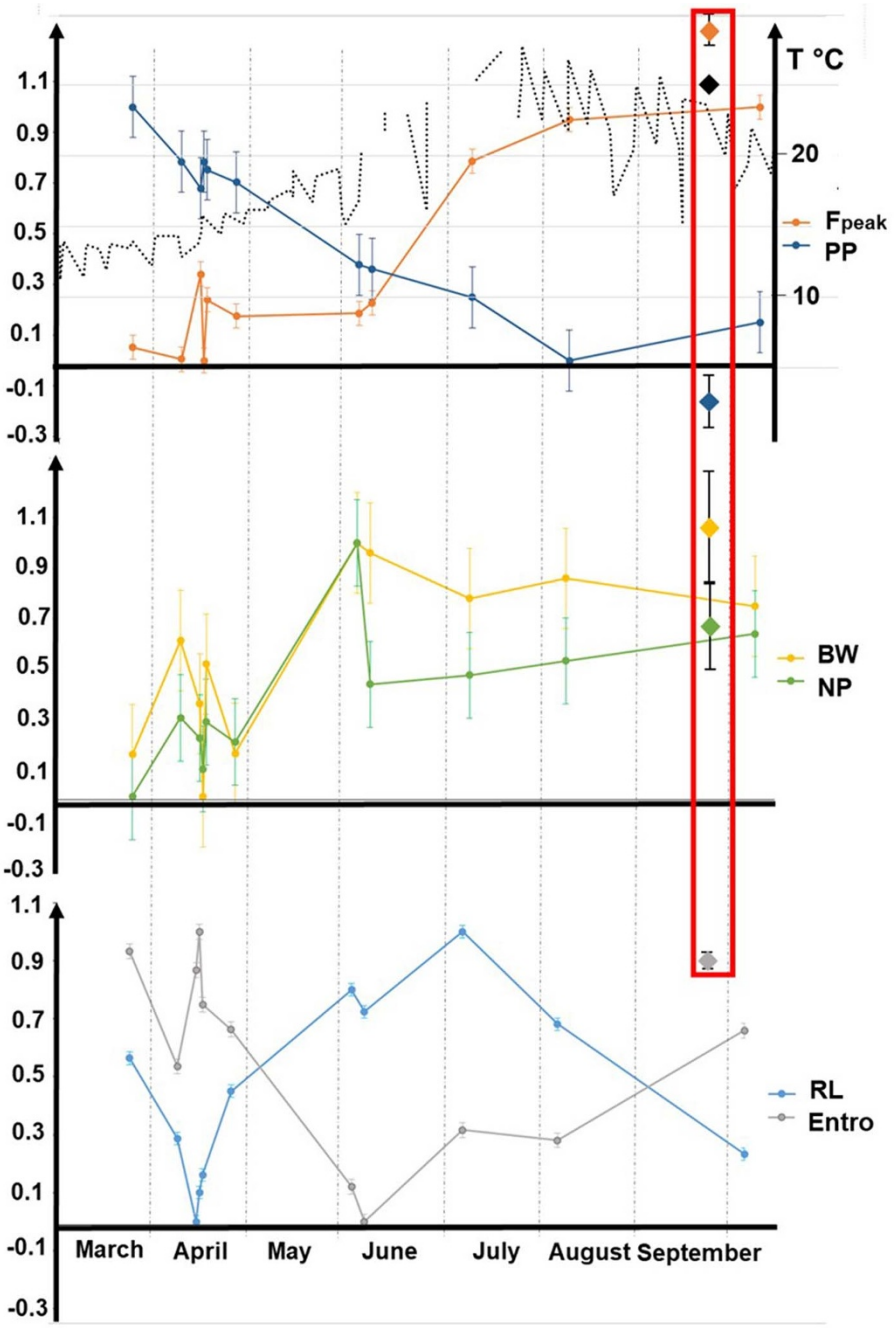


**Figure 4.** Normalized mean (ranging from 0 to 1) and standard deviation of selected key acoustic features from the French littoral as a function of time (adapted from Di Iorio *et al.* (2018): $F_{peak}$ in orange, PP in blue, BW in yellow, NP in green, and Entropy in grey. The red box highlights the Ustica data.

The previously mentioned features are influenced by the temperature [4]; as temperature increases, both the velocity and activation rate of fish muscles also increase. In Ustica, water temperatures in September are typically higher than those recorded at all French sites, including during the warmest months. Consequently, it is expected that temperature-dependent features would increase ($F_{peak}$) or decrease (PP) in the Ustica recording. However, the difference in PP between Ustica and the French data is so substantial that it may also indicate an intrinsic difference. It is possible that, due to spatial separation, the populations of fish producing /*kwa*/ sounds are different, either two closely related species or distinct populations of the same species (Bolgan *et al.*, 2022). One of these species is *Scorpaena maderensis*, a subtropical species from the eastern Atlantic and parts of the Mediterranean Sea, including areas such as Greece, Spain, and Sicily (Hureau and Litvinenko, 1986; La Mesa *et al.*, 2004). In 2001, *S. maderensis* was the most abundant cryptobenthic fish species off northern Sicily, far exceeding the abundance of species such as *S. porcus* (La Mesa *et al.*, 2004). Off Corsica, where a significant portion of the comparative data used in this study originates, this species was first documented in 2003. By 2018, it had become the most prevalent Scorpaenidae species observed along the region's rocky coast (Astruch *et al.*, 2022).

The higher peak frequencies and smaller PPs found in Ustica may therefore linked either to higher temperatures or to species/population differences compared to other Mediterranean sites. To differentiate between the two, more research is needed. First, to better understand the source of /kwa/ sounds at a fine

**Table 2.** Comparisons of /*kwa*/ acoustic features between the 3 nights ('temporal' column, Kruskal–Wallis tests, $df = 2$) and between Ustica and French /*kwa*/ sounds ('spatial' column, Wilcoxon–Mann–Whitney tests)

| | Temporal | | Spatial | |
|---|---|---|---|---|
| | $n = 182$, 243, and 239 | | $n = 512$ and 5 groups of 512 | |
| Feature | $\chi^2$ | *p*-value | Mean *W* | Mean *p*-value |
| $F_{peak}$ | 2.03 | 0.36 | 286.24 | **<0.001** |
| NP | 4.74 | 0.09 | 975.96 | 0.19 |
| PP | 2.88 | 0.24 | 2171.20 | **<0.001** |
| $\Delta F_{sp}$ | 1.69 | 0.43 | 1408.66 | 0.32 |
| $\Delta F_{es}$ | 0.95 | 0.62 | 1128.74 | 0.44 |
| $\Delta F_{ep}$ | 0.72 | 0.70 | 1433.36 | 0.27 |
| $\Delta F_{cp}$ | 2.01 | 0.37 | 1206.30 | 0.52 |
| $F_{min}$ | 2.91 | 0.23 | 544.90 | **<0.001** |
| H2 | 0.21 | 0.90 | 1164.96 | 0.46 |
| H3 | 2.60 | 0.27 | 1099.26 | 0.34 |
| H4 | 0.40 | 0.82 | 1252.46 | 0.50 |
| *T* | 4.07 | 0.13 | 1942.00 | **<0.001** |
| BW | 2.00 | 0.37 | 1070.50 | 0.33 |
| Entro | 6.67 | **0.04** | 701.48 | **0.004** |
| $F_s$ | 1.17 | 0.56 | 403.56 | **< 0.001** |
| $F_e$ | 2.45 | 0.29 | 290.40 | **<0.001** |
| $F_{max}$ | 6.22 | **0.04** | 708.80 | **0.01** |
| NbH | 1.25 | 0.53 | 1542.00 | 0.13 |
| Q3H | 0.52 | 0.77 | 1227 | 0.53 |
| Relative $RL_{rms}$ | 27.22 | **<0.001** | / | / |
| Relative SCL | 20.70 | **<0.001** | / | / |
| Relative SNR | 5.70 | 0.06 | / | / |

For the between-nights comparison, only data recorded between 7 PM and midnight GMT have been used. For the spatial comparison, five groups of 512 observations from both French and Ustica datasets were compared using bootstrap Wilcoxon–Mann–Whitney tests. *p*-values $<0.05$ are indicated in bold.

species and population level within Scorpaenidae. Second, to better understand the seasonality of /kwa/ sounds in relation to temperature. These two lines of investigation are not independent and may potentially reveal a dual effect of global change on the biophony of *P. oceanica* meadows. Rising temperatures may impact sonic mechanisms at the physiological level, leading to increases in peak frequencies. A previous study found that when the abundance of the */kwa/* was higher, the range of spectral and temporal acoustic resources it exploited was also broader (Bolgan *et al.*, 2022). However, it remains unclear whether the sonic system possesses sufficient plasticity to accommodate higher frequencies. On the other hand, increasing temperatures are known to alter the relative abundance of *Scorpaena* species in shallow fish assemblages, which may further affect biophony, especially if all species within the genus produce this sound type. The two research directions highlighted above – the relationship between species differences in *Scorpaena* and the variability of /kwa/ sounds, and the influence of water temperature on the acoustic characteristics of /kwa/ sounds – are crucial for understanding potential modifications of soundscapes in the context of global change.

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**Author contributions.** X.R. and J.-P.H. conceived the study. X.R. performed the acoustic and statistical analyses under the supervision of L.D.I. X.R. wrote the manuscript. Both L.D.I. and J.-P.H. contributed to the final version of the manuscript. All authors provided critical feedback and helped shape the research, analysis, and manuscript. X.R. supervised the project.

**Declaration of interest.** The authors declare that they have no conflicts of interest.

**Data availability statement.** The data supporting the findings of this study are available in Hermand (2003) and Di Iorio *et al.* (2018). Additional data are available from the corresponding author upon reasonable request.

**Ethics and approach.** No ethical approval was required for this study, as passive acoustic monitoring is a non-invasive method and did not involve direct interaction with animals or humans.

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