


ORIGINAL RESEARCH

'Posidonia meadows calling': a ubiquitous fish sound with monitoring potentialLucia Di Iorio^{1,2} , Xavier Raick^{2,3}, Eric Parmentier⁴, Pierre Boissery⁵, Cathy-Anna Valentini-Poirier⁵ & Cédric Gervaise^{1,2}¹Chorus Research Institute, Phelma Minatec, 3 parvis Louis Néel, Grenoble 38016, France²Chair Chorus, Foundation of the Grenoble Institute of Technology, 46 Rue Felix Viallet, Grenoble 38031, France³GIPSA-Lab, Grenoble INP, University Grenoble Alpes, 11 Rue des Mathématiques, Grenoble Campus, Saint Martin d'Hères 38402, France⁴Laboratory of Functional and Evolutionary Morphology, Institut de Chimie, B6c, University of Liège, Liège 4000, Belgium⁵Agence de l'Eau Rhône Méditerranée Corse, Imm Le Noailles 62 La Cannebière, Marseille 13001, France**Keywords**

Posidonia oceanica, seagrass meadows, fish sounds, passive acoustic monitoring, soundscape, habitat

Correspondence

Lucia Di Iorio, Chorus Research Institute, Phelma Minatec, 3 parvis Louis Néel, 38016 Grenoble, France. Tel: +33 (0)9 72 6193 48; E-mail: lucia.diiorio@chorusacoustics.com

Editor: Nathalie Pettorelli

Associate Editor: Nathan Merchant

Received: 16 September 2017; Revised: 12 December 2017; Accepted: 18 December 2017

doi: 10.1002/rse.2.72

Abstract

In the Mediterranean Sea, the seagrass *Posidonia oceanica* plays a key ecological role, and is protected by a range of legislation. Standard *Posidonia* monitoring programmes generally focus on the plant at different spatial and short temporal scales, without considering the organisms dependent on the ecosystem. Passive acoustic monitoring (PAM) has a high potential to non-intrusively monitor biological activities and biodiversity at high temporal resolution, and to assess ecosystem health. This is particularly relevant considering that *Posidonia* meadows host numerous sound-producing fish species. In this study, bottom-moored hydrophones were deployed in nine Western Mediterranean meadows covering a distance of more than 200 km to identify acoustic features potentially relevant to monitor this critical habitat. Among eight identified fish sound categories, we found a single type of sound (that we will refer to as /kwa/) dominating the soundscape of *Posidonia* meadows over a time span of 7 months. Compared to other low-frequency sounds, the /kwa/ presented unique characteristics that suggest it is produced by a fish via fast contracting muscles. The /kwa/ was the only sound detectable under anthropogenic noise conditions, and little affected by it. Cluster analyses performed on 13 acoustic features revealed a high degree of call diversity. /Kwa/ diversity, combined with its large-scale (all meadows), long-term (7 months) occurrence and low noise interference, make the /kwa/ a promising candidate for PAM of *Posidonia* meadows. Furthermore, variability in acoustic features suggests a central role of the /kwa/ in communication. Overall, this work sets the basis for establishing the relevance of the /kwa/ in monitoring *P. oceanica* meadows and developing PAM techniques for this critical habitat.

Introduction

Posidonia oceanica (L.) Delile, 1813 is an endemic flowering plant (Magnoliophyta) from the Mediterranean infralittoral. Although covering 1 or 2 % of the sea bottom, the multiple ecological roles of *Posidonia* make this habitat pivotal in the Mediterranean ecosystem. *Posidonia* is involved in the protection of the beaches from erosion, stabilization of the substratum, production of oxygen, reduction in bacterial pathogens and represents an important breeding and nursery habitat for many invertebrate

and fish species (e.g. Boudouresque et al. 2012; Lamb et al. 2017). *P. oceanica* is protected by EU legislation and considered as a priority habitat (Council Directive 92/43/EEC & Council Directive 2000/60/CE).

Several long-term projects currently monitor *Posidonia* meadows and follow anthropogenic impacts (Lopez y Royo et al. 2010; Holon et al. 2015a,b). The data collected essentially focus on the plant from a microscale level, that is, the *Posidonia* leaf/shoot, to a local (meadow) or macroscale level (system) (Boudouresque et al. 2000; Descamp et al. 2011; Noël et al. 2012). Only recently, a

more ecosystem-based approach has been proposed (Perronnin et al. 2014). Commonly, *P. oceanica* monitoring methods are based on scuba diving transects (e.g. Boudouresque et al. 2007; Guillén et al. 2013) and more recent techniques such as photogrammetry (Holon et al. 2015b), underwater photography and video footage (Ardizzone et al. 2006) and aerial photography (Bonacorsi et al. 2013) of *Posidonia* meadows. However, these methods do not consider the biological activities of organisms that depend on *Posidonia*, and generally require considerable human and logistic efforts in return for data of relatively low temporal resolution. There is therefore a need to identify and establish new complementary and holistic approaches to monitor at high temporal resolution this entire habitat, including organisms that live in *Posidonia* meadows. Passive Acoustic Monitoring (PAM) has a great potential to fill this gap and is receiving increasing attention as a means to acquire information on habitats, their environmental status and changes in a large range of biotopes (Rountree et al. 2006; Kinda et al. 2013; Bertucci et al. 2016). PAM offers a non-invasive and non-destructive approach that allows the study of invertebrate, fish and marine mammal diversity and activities using their sound emissions over long temporal scales (up to years) (e.g. Rountree et al. 2006; Mellinger et al. 2007; Coquerneau et al. 2016). These animal sounds may act as biological traits of the habitat highlighting species–environment relationships and serve as environmental proxies (Piccullin et al. 2013). Monitoring biogenic sounds can provide unique information on both biological and/or ecological processes and their spatio-temporal variability (Staaterman et al. 2014). For instance, acoustic diversity has been associated with ecosystem health (Sueur et al. 2008; Bertucci et al. 2016) and a recent study showed that biological sounds can also be used to monitor key species on an ocean basin level (Parmentier et al. 2017). In addition, PAM allows the investigation of the presence of cryptic species (Kéver et al. 2016), which is of particular interest in habitats where the visibility is low and/or underwater visual census are arduous to conduct such as in *Posidonia* meadows. PAM is therefore highly promising for habitat management, but in coastal habitats it also faces the challenge linked to the impact of noise from a variety of human activities.

Fish sounds, which are typically produced in the low-frequency bandwidth (<2000 Hz), are abundant in coastal environments and vary as a function of time, space and habitat (e.g. McCauley and Cato 2000; Ruppé et al. 2015). In the Mediterranean Sea, 38 fish species from 20 families have been identified to emit sounds (Table S1), and some of them (e.g. Gobiidae, Sciaenidae, Ophidiidae) are known to live in *Posidonia* meadows. However, despite the ecological importance of this biotope, the high

number of fish species present in seagrass meadows (Kalogirou et al. 2010) and the presence of many sound-producing species, PAM of *P. oceanica* meadows has not been reported to date. To be representative for habitat monitoring, acoustic features associated with biogenic sounds have to meet the following proposed criteria: (1) Occur at large geographical scales in the same habitat and (2) over long time periods (i.e. across seasons), (3) be detectable also in the presence of anthropogenic noise, and (4) show acoustic diversity, a parameter that has been linked to habitat status (cf. Farina and Gage 2017).

The aim of this study was to describe the sound production associated with fish acoustic signalling within Mediterranean *P. oceanica* meadows relevant for habitat monitoring. We recorded nine meadows covering a distance of more than 200 km of the Western Mediterranean coastline and over a temporal window of 7 months. We focussed on one particular sound that appeared to meet all criteria and evaluated its potential for monitoring *Posidonia* meadows.

Materials and Methods

Sampling

Sound recordings were carried out as part of the CALME acoustic monitoring programmes along the French Western Mediterranean coast established by the RMC Water Agency and the CHORUS Research Institute (www.medtrix.fr¹). Recordings from nine different meadows were used for this study. To allow for acoustic diversity comparisons, all recordings were made under low wind regimes (<10 kN), and only meadows in good ecosystem health were considered. Environmental status was based on PREI (*Posidonia oceanica* Rapid Easy Index, Gobert et al. 2009) index values (0.55–0.775) obtained from the *P. oceanica* surveillance programmes TEMPO (Andromède Océanologie 2015). All nine meadows were recorded in 2015, with meadow *i* also sampled in 2014 (Fig. 1 and Table 1). Because of the considerable distances between the meadows' locations (65 ± 45 km), recordings could not be conducted simultaneously. One recording was obtained at end of March, six in April, two in June, one in July and one in August (Table 1). Data were acquired using a HTI-92-WB hydrophone (High Tech Inc., Long Beach, MS, USA) with a sensitivity of -155 dB re 1 V/ μ Pa and flat frequency response from 2 Hz to 50 kHz connected to an EA-SDA14 compact autonomous recorder (RTSys[®], France). The device was

¹RMC Water Agency/Andromède Océanologie, data from the cartography platform Medtrix (www.medtrix.fr)

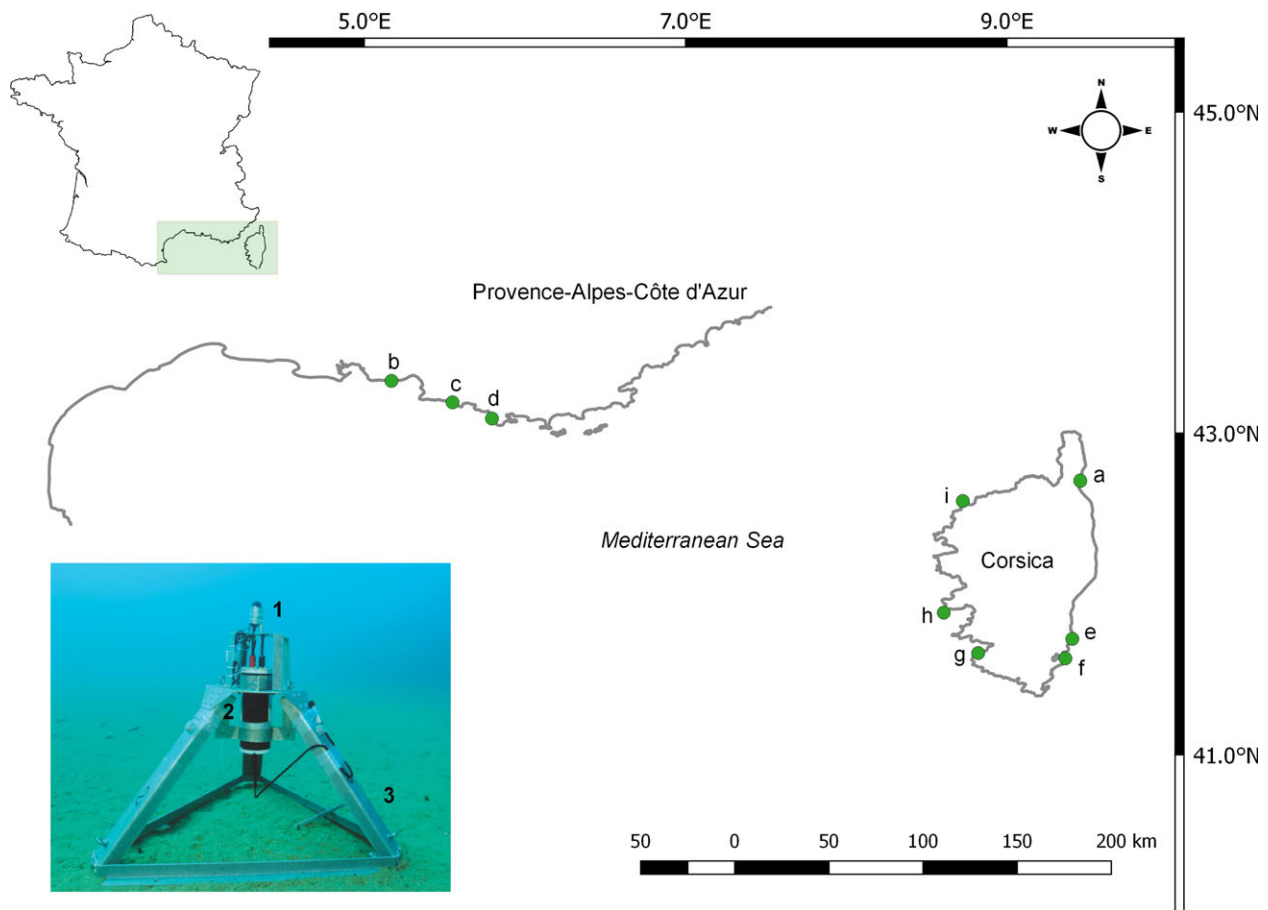


Figure 1. Locations (a-h) of the studied meadows on the French Mediterranean littoral (cf. Table 1). Photo: Recording device (EA-SDA14, RTSys[®]) with hydrophone (1), recorder (2) and structure (3) used for acoustic sampling. Photo credit: Andromède Océanologie.

bottom-moored with the hydrophone at 1 m from the seafloor (Fig. 1). It acquired sounds continuously at a 176 kHz sampling rate and 24 bit resolution. At each recording date, the recorder was submerged in the afternoon and recovered the next morning for a duration of at least 14 h. Recordings were made during the night because many temperate fishes usually vocalize and produce choruses predominantly at night (Cato 1978; McCauley and Cato 2000).

Acoustic analyses

Data diagnostics for acoustic feature identification

Long-term spectrograms of the entire night (12 h) and around dusk (5 h) were built with routines developed on Matlab[®] (R2012a) to visualize biogenic sound production. These long-term spectrograms, combined with a more detailed manual scrolling of the audio files, were used to explore *P. oceanica* soundscapes, assess the quality of the recordings and more particularly, the presence of

low-frequency noise that acoustically masks fish sounds (Radford et al. 2014). Based on these diagnostics, one particular sound, aurally sounding like a /kwa/ (Audio S1), appeared to potentially meet the criteria proposed for acoustic monitoring features. We focussed on this particular sound to assess whether it represents an appropriate candidate for PAM of *Posidonia* meadows.

Sound selection

The long-term spectrograms were used to identify the time period of highest abundance of the /kwa/ that was used as subsampling unit for manual sound selection. Sound selection was carried out using RavenPro Sound Analysis Software 1.5 (Cornell Lab of Ornithology, USA) on audio files sub-sampled at 4 kHz. Each identifiable /kwa/ during 2 h of the peak sound production period (i.e. the chorus) was manually selected in order to carefully describe sounds and their variability in detail. To validate the temporal subsampling method, the acoustic features of the /kwa/ selected during the 2-h subsampling

Table 1. Locations, recording dates and depths of the studied *Posidonia* meadows.

Meadow	Name	GPS coordinates	Date	Depth
a	Bastia	42.7052 N 9.4576 E	14/04/15	15 m
b	Côte bleue	43.3255 N 5.1697 E	09/04/15	15 m
		43.3246 N 5.1666 E	07/06/15	15 m
c	Canaille	43.1919 N 5.5499 E	03/06/15	15 m
d	Pierre plane	43.0910 N 5.7953 E	25/03/15	15 m
e	Fautea	41,7214 N 9,4079 E	05/10/15	16 m
f	Porto Vecchio	41.6000 N 9.3649 E	15/04/15	17 m
		41.6331 N 8.8218 E	16/04/15	15 m
g	Sentosa Palazzu	41.6331 N 8.8218 E	16/04/15	15 m
h	Ajaccio	41.8847 N 8.6075 E	17/04/15	15 m
i	Calvi	42.5802 N 8.7263 E	26/04/15	12 m
			08/07/15	12 m
			07/08/14	12 m

period were compared to the ones selected during the rest of the night (files from the randomly chosen meadow *e*). Paired Student’s *t*-tests with a significance level (α) of 0.05 were used to test for differences. Because of the important number of sound selections (21604 selections for the entire night, 7286 selections for the subsampling period of peak sound production) and consequently the size effect on the *P* value (Lin et al. 2013), we used Jackknife subsamples [$n_{\text{subsamples}} = 100$ (group balance not enforced) & $n_{\text{replicates}} = 1000$] to carry out the statistical tests on data subsets using R 3.1.2. [function ‘sample’, R Core Team 2014].

Sound description

Acoustic features typically used for fish sound description were extracted from the sound selections (Fig. 2). These included call duration, peak frequency (i.e. dominant

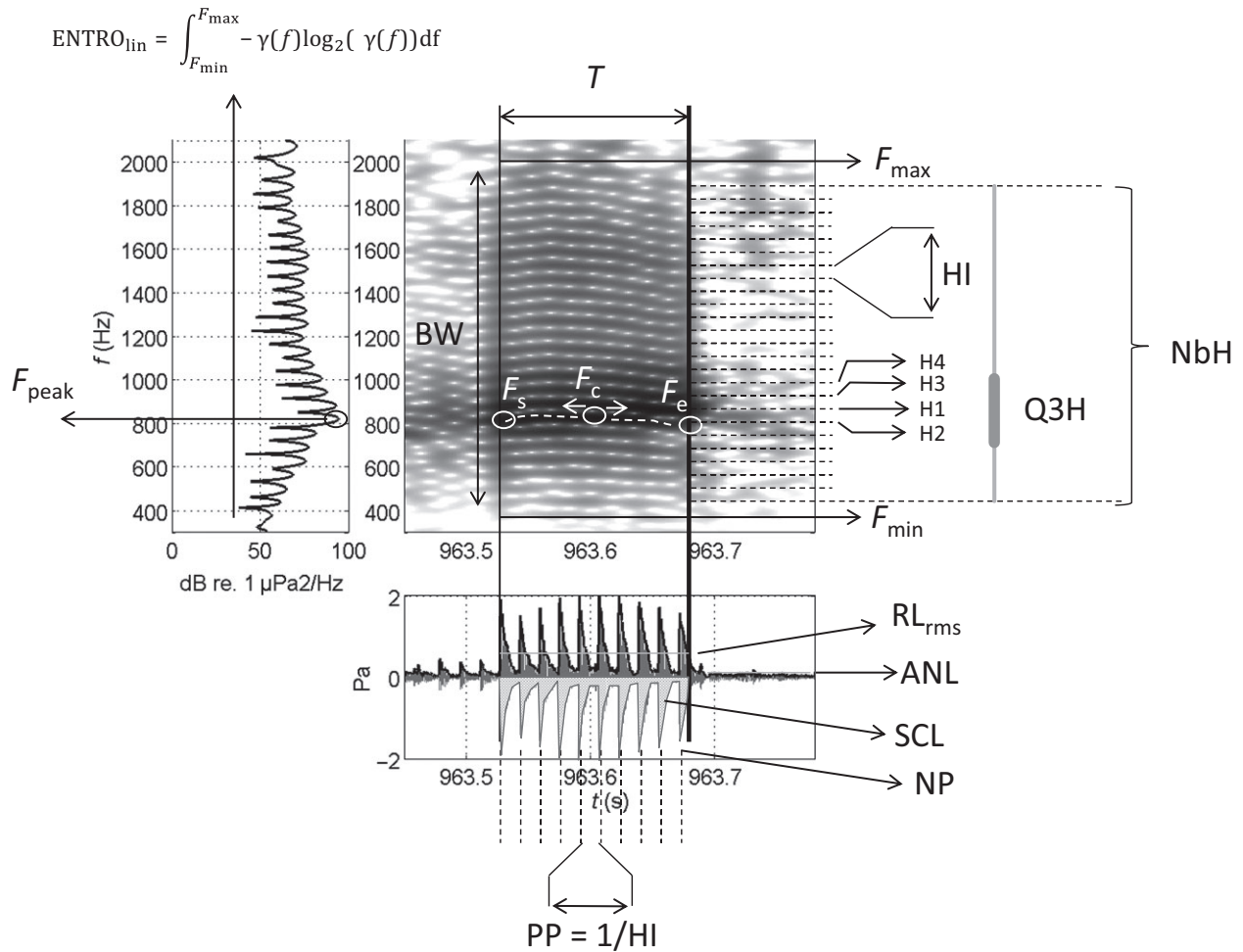


Figure 2. Acoustic representations of the */kwa/* and measured features (cf. main text for abbreviations). Centre: spectrographic view of a typical */kwa/* selection with the most energetic contour indicated as dotted white line; left: power spectrum; bottom: waveform of the sound. LFFT: 8192, sampling frequency = 15,6250 Hz, Kaiser 180 dB with 50% window overlap. Grey scale: between 50 and 95 dB re 1 $\mu\text{Pa}^2/\text{Hz}$. $1/\text{HI}$ = pulse period.

Table 2. List of measured acoustic features (cf. Data S1 for detailed descriptions).

Abbreviation	Definition	Description
NP	Number of pulses	Number of pulses within the temporal envelope
T	Duration (s)	
BW	Bandwidth (Hz)	Bandwidth based on the signal selection box
F_{\min} & F_{\max}	Minimal and maximal frequency (Hz)	Minimal & maximal frequency based on the signal selection box
F_{peak}	Peak or dominant frequency (Hz)	The frequency at the maximum of the power spectrum
F_s & F_e	Start frequency & end frequency (Hz)	Start and end frequency of the most energetic contour $C(t, f, f_{\text{peak}})$.
ΔF_{es}	End frequency minus start frequency (Hz)	$F_e - F_s$
ΔF_{sp}	Start frequency minus peak frequency (Hz)	$F_s - F_{\text{peak}}$
ΔF_{ep}	End frequency minus peak frequency (Hz)	$F_e - F_{\text{peak}}$
NbH	Number of pseudo-harmonics	Number of pseudo-harmonics between F_{\min} and F_{\max} .
HI	Pseudo-harmonic interval	Interval between the estimated using the complex auto-correlation function of $E(f_0)$ (Le Bot et al. 2015).
PP	Pulse period	The reciprocal of HI (i.e. $1/\text{HI}$) It is therefore redundant to include both features in the analyses.
H1, H2, H3, H4	Pseudo-harmonic index	The index of the four most energetic pseudo-harmonics.
Q3H	Pseudo-harmonic ratio	Ratio of the energy contained in H1 + H2 + H3 to the energy contained in all pseudo-harmonics between F_{\min} and F_{\max} .
Entro	Normalized linear entropy	$\text{Entro} = \frac{\int_{F_{\min}}^{F_{\max}} -\gamma(f) \log_2(\gamma(f)) df}{\log 2(\text{LEFT})}$
RL	Received Level in dB re $1 \mu\text{Pa}$	$RL = 10 \log_{10} \left\{ \frac{1}{T} \int [s_f(t)]^2 dt \right\}$. RL corresponds to the root mean square (RMS) T sound pressure level.
SNR	Signal to noise ratio in dB re $1 \mu\text{Pa}$	Signal to noise ratio with the underlying Ambient Noise Level (ANL) in dB re $1 \mu\text{Pa}$. (Kinda et al. 2013; Mathias et al. 2016).
SCL	Sound cumulative level in dB re $1 \mu\text{Pa}^2\text{s}$	The SCL quantifies the energy contained in the signal. $\text{SCL} = 10 \log_{10} \left(\int_T S_f(t) dt \right)$

frequency), pulse period and number of pulses (e.g. Amorim et al. 2008). However, these features do not allow to describe the complexity and diversity of the signal. Consequently, additional acoustic features were considered, including parameters used for characterizing harmonic or pseudo-harmonic² (Watkins 1968) sounds emitted by anurans and primates (e.g. Gerhardt 1981; Price et al. 2015) and for describing transient sounds (Tucker and Brown 2005). Some features (e.g. duration, bandwidth, minimal and maximal frequency) were calculated within the selection box using RavenPro, while most features were extracted from the selection box using custom-made Matlab[®] codes. The considered features are listed in Table 2 and described in detail in the Data S1 (cf. Fig. 2).

Only the sounds with at least four pseudo-harmonics and a SNR ≥ 0 dB were included in the analyses. This allowed to only consider high-quality sounds (23,566 out of 44,257 selections). To facilitate comprehension and interpretation, the set of 23 features was subdivided into

three subsets with increasing dependency on the sound level features:

- 1 Subset №1 {HI, ΔF_{sp} , ΔF_{es} , ΔF_{ep} , ΔF_{cp} , F_{\min} , F_{peak} , H1, H2, H3, H4, T, NP},
- 2 Subset №2 {BW, Entro, F_s , F_e , F_{\max} , NbH, Q3H},
- 3 Subset №3 {RL, SCL, SNR}

Subset №1 contains 13 features describing the spectral shape (contour) of the sound and the temporal pattern (NP (& PP, i.e. $1/\text{HI}$)), subset №2 comprises seven features, which describe the spectral shape (BW, Entro, F_s , F_e , F_{\max} , NbH) and the repartition of the relative acoustic power along the pseudo-harmonics (Q3H) and subset №3 comprises three features characterizing only the level of the sound without any information on the contour. Pearson correlations were carried out to highlight relationships between the 23 acoustic features.

Occurrence

The presence of the */kwa/* was assessed for all recordings allowing to determine the extent of spatial and temporal occurrence. The selections from meadow *e* (14 consecutive hours, from 6 P.M. to 8 A.M.) used to test acoustic differences between the */kwas/* of the period of highest

²In the spectrographic view, pulse trains with fast repetition rates are indicated by the 'pseudo-harmonic' interval (harmonic of the amplitude-modulated function).

abundance at dusk and the rest of the night were also used to illustrate night-time patterns. Because selecting each */kwa/* over 14 h (from 6 P.M. to 8 A.M.) is extremely time-consuming considering the high number of */kwas/* present (7284 selections for meadow *e*), data from only one recording were used. Furthermore, the presence of the dusk chorus is also indicative of the night-time pattern in */kwa/* abundance. To evaluate the presence and relative abundance of the */kwa/* compared to other fish calls present in meadows, the */kwas/* and all other fish sound types of one entire night were also manually selected and their night-time patterns compared to the one of the */kwa/*. Meadow *c* was randomly chosen between the three meadows in which sound detection was not masked by anthropogenic noise.

***/Kwa/*diversity**

Visual inspection during the manual selection procedure suggested the existence of different types of */kwa/*, particularly with respect to the spectral content and contour's shape (Fig. 4). Cluster analysis was conducted to quantify this signal diversity. To reduce the dimensions for cluster analysis and eliminate redundancy due to high intercorrelation of the acoustic variables Principal Component Analysis (PCA) was performed. The PCA was conducted using all acoustic features of subset N=1, because received-level dependent parameters may be linked to factors such as the distance of the vocalizing animals. The scores of the first three principal components of the PCA were used as input for the cluster analysis. Because the distribution of the PCA scores was multimodal, we considered the data to be distributed as a finite Gaussian mixture. For a given number of clusters, the maximum likelihood estimators of the mean and covariance matrix of each Gaussian component of the mixture were found using an expectation-maximization algorithm (McLachlan and Peel 2000). The minimum of the distribution of the Bayesian Inference Criteria (BIC) was used to estimate the optimal number of clusters (Penny et al. 2007). The clustering was realized using the *gmdistribution.fit* function of the Statistics Toolbox in Matlab® (R2012a).

Temporal variability

Acoustic features may change over time linked to adaptations to environmental factors (e.g. temperature, ambient noise) or morphological changes associated to specific behaviours such as reproduction (Connaughton and Taylor 1995; Ladich and Schleinzner 2014; Radford et al. 2014). Meadow recordings were ranked according to their recording date. The temporal variability in the */kwa/* was illustrated by plotting acoustic variables over time (given

the rank). To test seasonal differences, comparisons were only conducted on meadows sampled in both spring and summer of the same year and at the same or almost the same position (meadows *b* and *i*). Welch's *t*-test on Jackknife subsamples was used to test for significant differences. The significance level (α) was 0.05.

Results

Diagnostics

Six of the nine sites were subject to low-frequency anthropogenic noise also during night-time. This noise was mainly caused by distant shipping and potentially nearby harbour activity. Sound selection was therefore compromised or impaired due to acoustic masking (i.e. when the perception of one sound is affected by the presence of another sound). Only three of the nine site-recordings allowed the analysis of all types of fish sounds recorded. Consequently, fish sound diversity, which is recognized as an indicator of environmental status, was considered inappropriate for PAM of *P. oceanica* meadows.

All nine sites were dominated by one particular sound, the */kwa/* with a frequency range above the noise responsible for the masking of all other fish sounds (Fig. 3). Together, these diagnostics suggested to focus on the */kwa/* to establish its potential as an acoustic monitoring feature.

Sound description

The */kwa/* is a pulse train of 0.27 ± 0.09 sec duration, characterized by 13 ± 6 pulses and a pulse period of 13 ± 4 msec ($N = 23,566$ sounds). Its waveform is characterized by a peak or dominant frequency of 747 ± 136 Hz modulated in amplitude by a periodic envelope with $1/HI$ oscillations. In the spectrographic view, this is visible as pseudo-harmonics around a 800 Hz contour with a mean pseudo-harmonic interval (HI) of 81.2 ± 30.6 Hz and a frequency bandwidth of 723 ± 280 Hz (Fig. 2). The average frequency contour is characterized by similar start and end frequencies around 750 Hz and a 70 Hz higher centre frequency indicative of a generally arch-shaped contour. The sound has an average received level of 95 ± 10 dB re $1 \mu\text{Pa}$ (RMS) with three pseudo-harmonics comprising 85% of the signal's power. All the detailed characteristics of the sounds are summarized in Table 3. Statistical comparison between the acoustic features of */kwas/* selected across one entire night and those selected during the 2 h of peak sound production at dusk revealed no differences (Table S2). This supports the selection procedure that was restricted to 2 h of the dusk chorus.

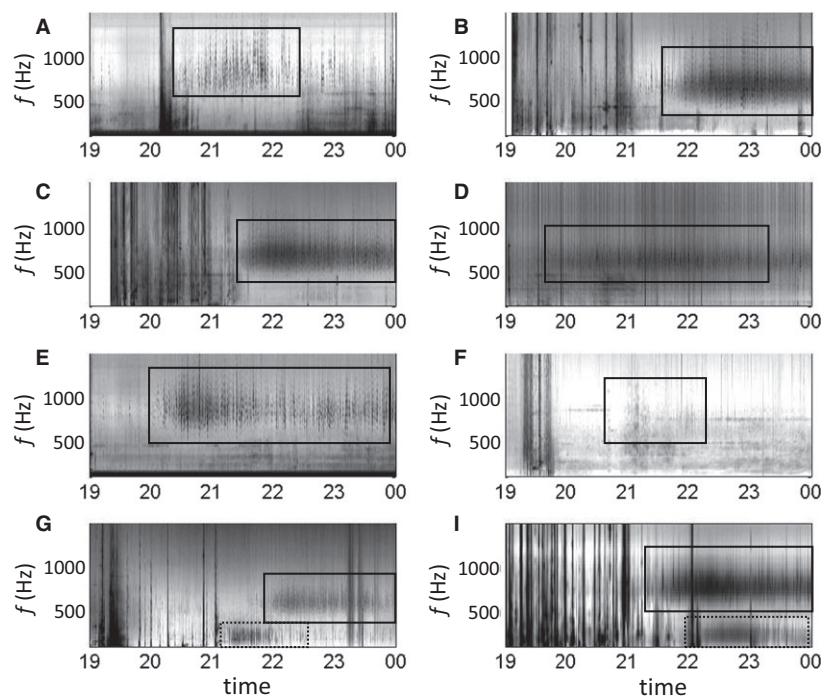


Figure 3. 5-h spectrograms (from 7 P.M. to midnight) of Western Mediterranean *Posidonia oceanica* meadows in good ecological condition (Andromède Océanologie 2015). The letters indicate different meadows (cf. Table 1). Letters correspond to the meadows as reported in Table 1. Meadow h is not represented but follows the same pattern as the other meadows. The dark vertical lines represent passing boats, and the dark clouds are mass productions of fish sounds (choruses). Solid black boxes: */kwa/* choruses; dashed boxes: *Ophidion rochei* choruses. LFFT: 8192, sampling frequency: 15,6250 Hz, Kaiser 180 dB with 50% window overlap, grey scale: between 50 and 90 dB re $1 \mu\text{Pa}^2/\text{Hz}$.

Occurrence

The */kwa/* occurred within all 12 sampling nights of the 9 sites used in this study covering a time span from April until October. Overall, 44257 */kwas/* were selected. The average number of sounds per selection period of 2 h was 3248.25 ± 2830.05 (minimum: 40 sounds per 2 h, maximum: 9521 sounds per 2 h), that is, on average more than 27 sounds per minute. The */kwa/* production varied over the course of the night, with an important peak 2 h after sunset (33.72% of all the selections, calculated on meadow *e*). This period of highest abundance lasts around 2 h and corresponds to a mass phenomenon referred to as chorus (Cato 1978), which is clearly visible on the long-term spectrograms (Figs. 3 and 4). Compared to other identified fish sound types, the */kwa/* was the only call above 500 Hz. All other fish sounds were in the low-frequency (50–500 Hz) range. Overall, eight fish sound types were identified based on their acoustic characteristics (details available in Table S3). Quantitatively, more than 95% of all the recorded fish sounds were */kwas/*. This percentage was not constant over the course of the night, as illustrated in Figure S1. After 1 A.M., the total number of fish sounds strongly decreased and the

/kwa/ was almost the only one (almost 100%) recorded until sunrise.

Sound diversity

The correlation analysis between the 23 acoustic features revealed that 31 inter-correlations had absolute magnitudes greater than 0.4 comprehending 15 features. (Table S4). PCA was thus used to reduce the dimensionality of the features for cluster analysis. The first three axes of the PCA explained 43.8% of the variance (16.7% axis 1; 27.1% axes 1 and 2). All features of subset №1 (i.e. mainly describing the contour shape of the call) produced a sensitive variation (i.e. long projection of a feature's unitary vector in the first three axes of the PCA) (Fig. S2). Their projections showed three groups of nearly collinear vectors (i.e. with a small angle between the feature's unitary vectors): (1) $\{\Delta F_{es}, \Delta F_{sp}\}$, (2) $\{T, HI \text{ (or PP)}\}$ and (3) $\{H1, H2, H3, H4\}$. Features with collinear projections act in the same way in the PCA approximation and may not account to discriminate between different classes in a classification process. Cluster analysis performed on the three first components of the PCA revealed the existence of 11

Table 3. Summary statistics of the acoustic features (cf. Table 2 for abbreviation definitions) for sounds with more than four pseudo-harmonics during the 2-h sampling units.

	\bar{x}	SD	SE	IQR	0%	25%	50%	75%	100%
NP	12.8	5.8	0.04	7	2	8	11	15	51
PP (s)	0.013	0.004	0.00003	0.005	0.005	0.011	0.014	0.017	0.041
HI (Hz)	81.23	30.61	0.16	27.5	10.5	62.5	72.5	90	200
ΔF_{sp} (Hz)	7.74	104.07	0.54	33	-1130	-22	-4	11	1067
ΔF_{es} (Hz)	-6.43	105.09	0.55	51	-1068	-20	0	31	731
ΔF_{ep} (Hz)	1.31	30.87	0.16	12	-890	-9	-3	3	649
ΔF_{cp} (Hz)	1.08	20.43	0.11	5	-878	-2	1	3	531
F_{min} (Hz)	540.71	131.83	0.69	175	85	447	518	622	1168
F_{peak} (Hz)	746.85	135.6	0.7	187.5	402.3	644.5	724.6	832	1884.8
H1	0 ¹	0 ¹	0	0	-8	0	0	0	10
H2	0 ¹	1 ¹	0.01	2	-7	-1	1	1	12
H3	1 ¹	2 ¹	0.01	3	-9	-1	1	2	12
H4	1 ¹	2 ¹	0.01	3	-10	-1	2	2	20
T (s)	0.27	0.09	0	0.11	0.07	0.2	0.25	0.32	1.09
BW (Hz)	722.82	280	1.99	386	168	506	694	892	1844
Entro	86.63	5.60	0.03	7.78	59.32	83.08	87.38	90.87	98.94
F_s (Hz)	754.59	161.82	0.84	210	294.8	637.8	734.3	847.8	1894.9
F_e (Hz)	748.17	134.87	0.7	185.5	386.3	647.3	727.7	832.8	1829
F_{max} (Hz)	1196.13	261.42	1.36	342	584	1009	1171	1351	2000
NbH	9.72	4.33	0.02	6	4	6	9	12	41
Q3H (%)	85.05	11.14	0.06	14.91	21.66	78.66	87.25	93.58	100.00
RL (dB re 1 μ Pa)	95.24	10.17	0.05	17	70	86	96	103	128
SCL (dB re 1 μ Pa ² s)	89.31	10.09	0.05	16	65	81	90	97	123
SNR (dB)	11.19	3.76	0.02	4	0	9	11	13	34

$N = 23566$. IQR, Inter Quartile Range; SD, Standard Deviation; SE, Standard Error.

¹Most probable H.

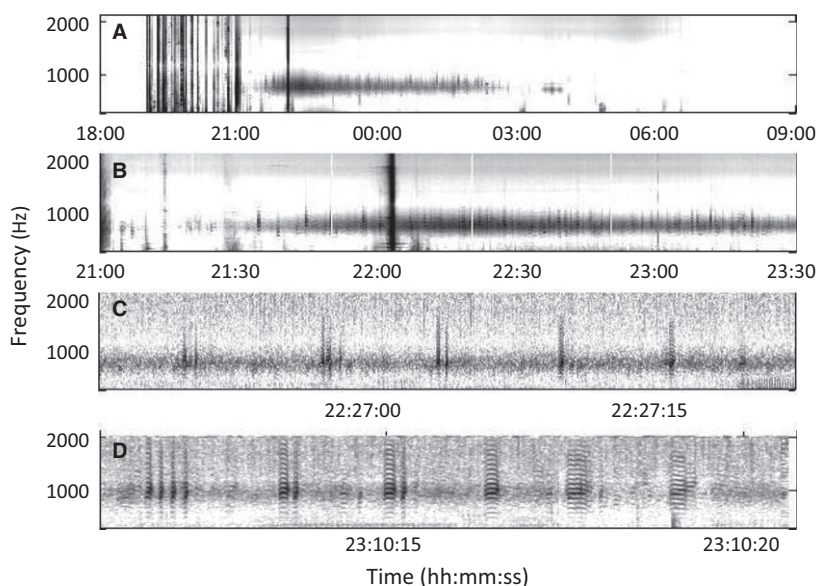


Figure 4. Spectrographic views of /kwas/ over different temporal scales. (A) Long-term spectrogram of an entire night on a *P. oceanica* meadow (meadow *i*, July 2015); (B) 3-h spectrogram showing massif /kwa/ chorus after sunset (dark horizontal band around 800 Hz); (C) spectrogram showing rhythmic repetitions of single /kwas/; (D) spectrogram showing different types of /kwa/. LFFT: 8192, sampling frequency = 156250 Hz, Kaiser 180 dB with 50% window overlap. Grey scale: between 50 and 95 dB re 1 μ Pa² Hz⁻¹.

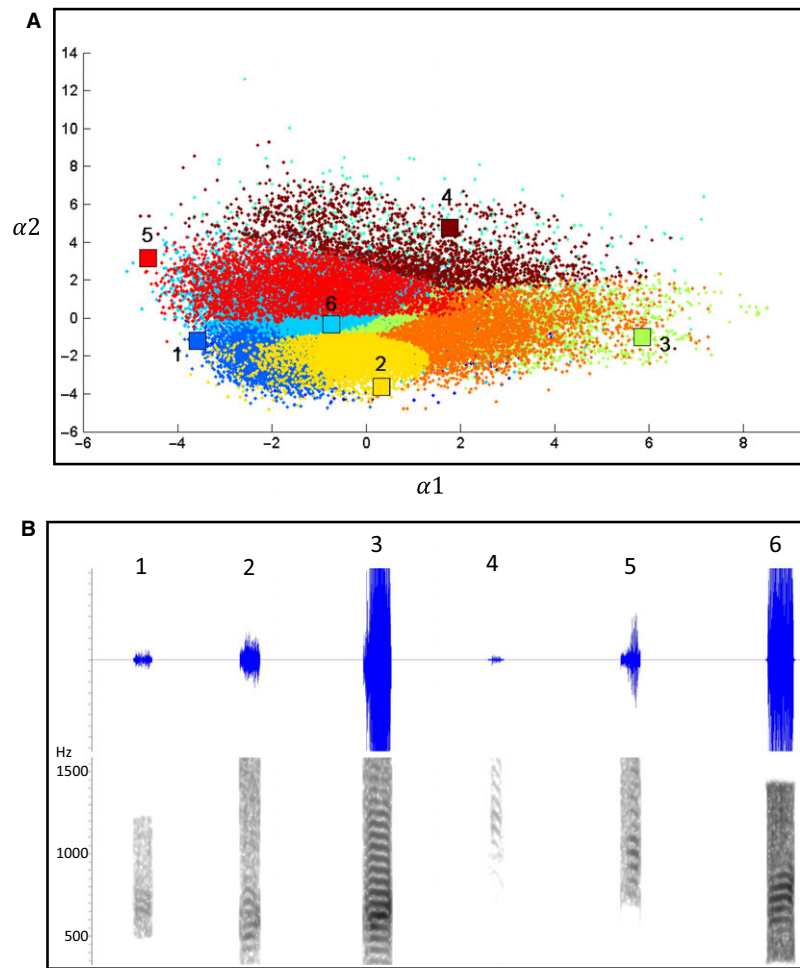


Figure 5. (A) Scatterplot of the classes given by the cluster analysis based on the first three components of the PCA performed on subset №1 acoustic features. Spectrograms represent ‘types’ of /kwas/ corresponding to distinct classes indicated by the numbers and different colours.

classes (Fig. 5), which correspond to the minimum BIC value. These results suggest that /kwas/ have a high intrinsic variability.

Temporal variability

RL, Entro, PP, NP, BW and the frequency features (F_{\min} , F_{peak} , F_s and F_e) varied over time. RL showed a maximum in July, while the entropy showed an opposite trend with a minimum in June. BW and NP also peaked in June but the number of pulses decreased more rapidly than the bandwidth, which was almost constant until October. Peak frequency and pulse period showed opposite trends, with F_{peak} increasing during the summer months and PP decreasing (minimum in August) (Fig. 6). To avoid effects linked to spatial variability, the seasonal variability in two specific meadows, for which both spring and summer data were available (meadows *b* and *i*), was

analysed separately. The same trends were confirmed: the RL was significantly higher in summer than in spring, while the linear entropy followed an opposite trend (Table 4, Table S5, Fig. 7). PP significantly decreased in summer compared to spring, with August showing the smallest values (in meadow *i*, Table 4 & Table S5). Seasonal peak frequency comparison in meadows *b* and *i* resulted in overall greater values in summer than in spring. F_{\min} , F_s and F_e showed the same behaviour as F_{peak} . Although preliminary, these results indicate a potential seasonal effect on the acoustic structure of the /kwa/. During the summer, fish appear to produce more powerful and spectrally structured sounds with a greater bandwidth (and thus more pseudo-harmonics), higher dominant frequencies and smaller pulse periods. Because the sampling campaign was not designed to study seasonal acoustic variation, these results need to be confirmed with appropriate long-term data.

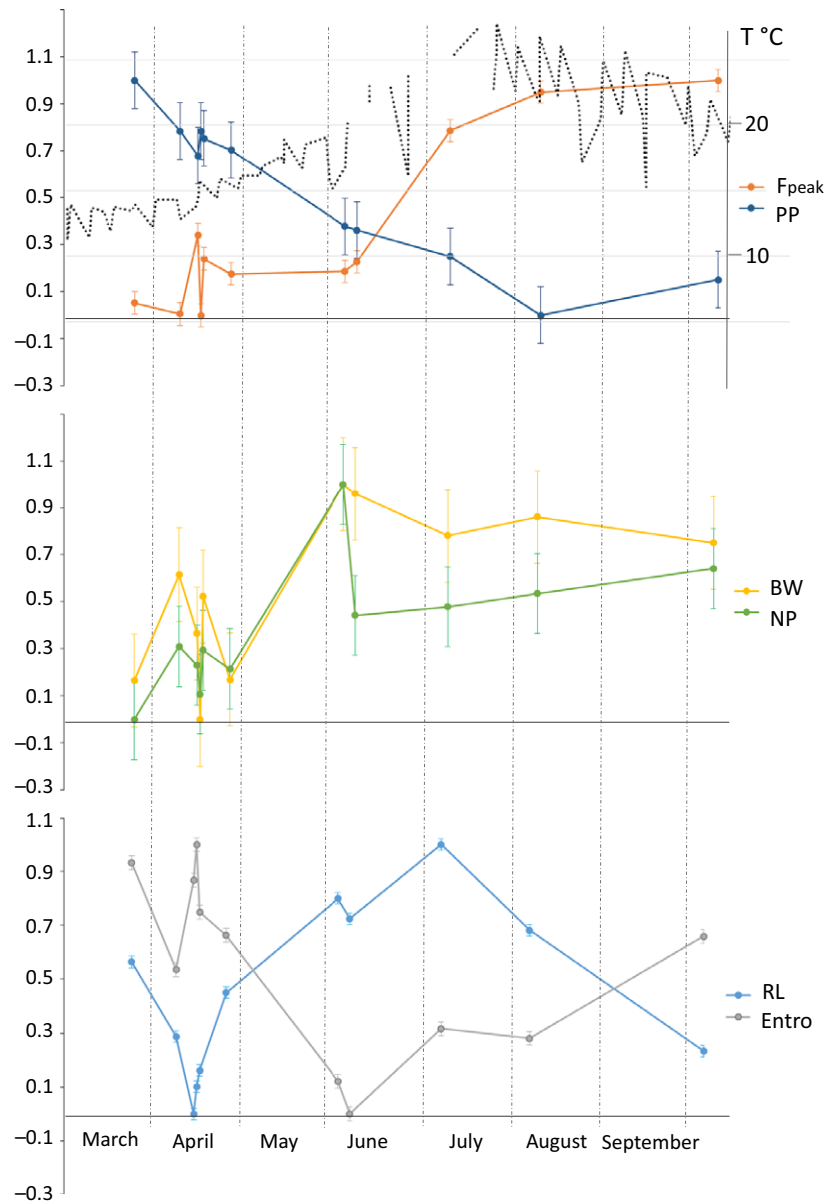


Figure 6. Normalized mean (between 0 and 1) and standard deviation of acoustic features as a function of time: the entropy (grey) and the received level (light blue) at the bottom, the bandwidth (yellow) and the number of pulses (green) in the centre, and peak frequency (orange) and pulse period (dark blue) at the top. Each dot represents a single night-time recording. The dotted black curve in the top panel represents the Mediterranean surface temperature trend during the same time period measured at three stations (data provided by 'Service d'Observation en Milieu Littoral, INSU-CNRS').

Discussion

Acoustic features for *P. oceanica* monitoring

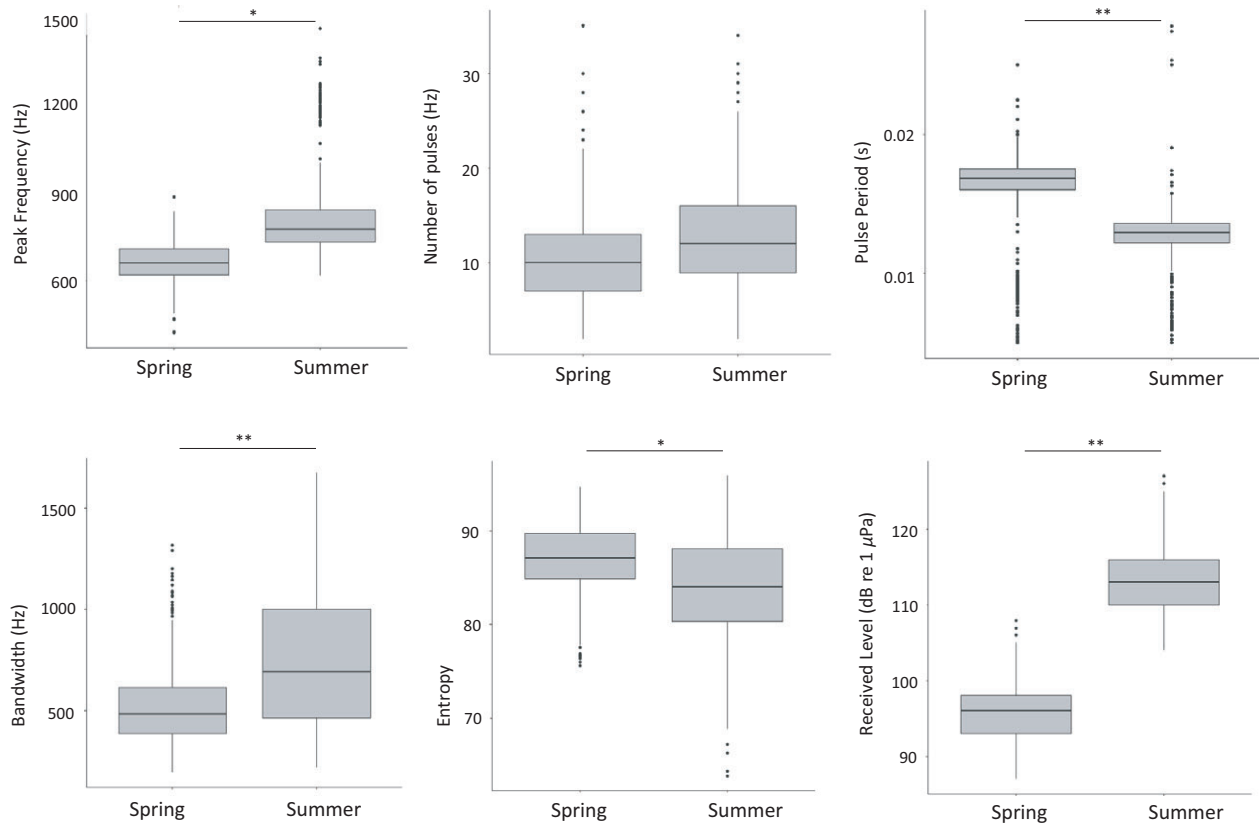
Our study identified and characterized an acoustic feature potentially relevant for monitoring *P. oceanica* meadows, a key habitat protected by numerous legislations. According to the proposed criteria such an acoustic feature has to: (1) be measurable over large geographical scales in the

same habitat; (2) occur across seasons, so independent of time-specific behaviours such as reproduction of the sound emitter (e.g. Amorim et al. 2006); (3) be poorly affected by noise interference, (4) show acoustic diversity that can be influenced by the ecological status of the habitat.

The /kwa/ occurred in all analysed *P. oceanica* meadows along 200 km of the Western Mediterranean littoral, supporting a strong relationship with this habitat. /Kwas/

Table 4. Mean values \pm SD of some acoustic features for separated sites and months, SNR \geq 10 and NbH \geq 4.

Meadow	Month	<i>N</i>	RL (dB re 1 μ Pa)	Entro	F_{peak} (Hz)	BW (Hz)	HI (Hz)	PP (s)	NP
<i>b</i>	April	1843	91 \pm 5	85.9 \pm 3.6	621 \pm 61	691 \pm 199	70.8 \pm 38.9	0.017 \pm 0.005	11.4 \pm 5.6
	June	4876	105 \pm 5	81.2 \pm 4.7	677 \pm 66	824 \pm 231	78.8 \pm 27.1	0.016 \pm 0.002	12.3 \pm 5.3
<i>i</i>	April	842	96 \pm 4	89.9 \pm 3.6	664 \pm 68	520 \pm 189	65.9 \pm 23.2	0.016 \pm 0.003	10.8 \pm 4.7
	July	827	113 \pm 4	83.9 \pm 5.6	816 \pm 146	755 \pm 332	81.9 \pm 19.9	0.013 \pm 0.002	12.6 \pm 5.2
	August	2899	103 \pm 7	83.6 \pm 5.5	856 \pm 137	786 \pm 316	95.7 \pm 20.4	0.01 \pm 0.002	13 \pm 5.4

**Figure 7.** Feature comparisons of */kwas/* between spring (left) and summer (right) from meadow *i* and *b*, for which data across seasons were available from the same recording positions. Two night-time recordings were used for each season (09/04/15 and 26/04/15; 07/08/15 and 07/06/15). * $P < 0.01$, ** $P < 0.001$.

were present across seasons, over a time span of 7 months (April until October) and dominated the fish sound production in meadows with water depths around 15 m. Overall, there were over 20 times more */kwas/* than all other fish calls combined in the analysed recordings. */Kwas/* were present during the whole night, with a peak production 2 h after sunset (33.72% of all night-time selections) corresponding to a chorus of at least 2 h duration. Furthermore, the */kwa/* occupies a frequency window (747 ± 136 Hz) that is at least three times higher than the one of the majority of Mediterranean fish sounds recorded to date (cf. Table S2). Consequently, compared

to all the fish sounds identified in this study, the */kwa/* was the only low-frequency sound that showed poor anthropogenic noise interference. This is particularly relevant considering that *P. oceanica* monitoring programmes include meadows affected by human activities (e.g. fishing, recreational navigation) that can acoustically mask low-frequency animal sounds (e.g. most fish sounds) (e.g. Radford et al. 2014). In fact, 67% of the recorded *Posidonia* meadows presented low-frequency noise also at night, mainly related to shipping that impaired the selection of all fish sounds, except for the */kwa/*. Finally, */kwas/* also present a high diversity, as revealed by the cluster

analysis. Although it remains to be tested, differences in /*kwa*/ diversity could be relevant to depict habitat differences and underline environmental status. In terrestrial animals, such as birds or anurans it has been shown that acoustic diversity decreases with poor habitat quality (i.e. urbanization, habitat loss, degradation, fragmentation) (Laiolo and Tella 2007; Laiolo et al. 2008; Pillsbury and Miller 2008) and that condition-dependent traits in male songs, relevant for reproduction, are reduced at the level of the population (McGregor 2005; Grava 2006). Although temporal signal variation remains to be fully validated, it has to be taken under consideration when performing diversity comparisons across seasons, as it may affect /*kwa*/ diversity at the population level (e.g. Connaughton et al. 2002). Together, these results indicate that the /*kwa*/ meets all criteria relevant for PAM of *P. oceanica* meadows. Whether it actually reflects differences associated to habitat quality for application in monitoring programmes, remains to be tested.

The /*kwa*/, its origin and potential role

/*Kwas*/ are composed of 13 ± 6 pulses separated by 13 ± 4 msec intervals and have a mean dominant frequency of 747 ± 136 Hz. The acoustic structure of the /*kwa*/ shares similarities with other fish sounds. Pulses are emitted at a regular frequency of 81 Hz, implying that each single pulse corresponds to a unit of muscle activity that takes place every 12 msec. This information clearly supports the use of fast contracting muscles for sound production. In species with similar contraction periods, sounds produced by drumming muscles are characterized by a relatively low fundamental frequency (<300 Hz) (Parmentier et al. 2013; Boyle et al. 2015) that generally corresponds to the contraction rate of the sonic muscle (Zelick et al. 1999). In the /*kwa*/, the pulse period of 81 Hz is not responsible for the dominant frequency of the call, which ranges between 700 and 1000 Hz. This dominant frequency appears to correspond to one of the harmonics of the pulse period as reported in various fish families (Amorim et al. 2004; Rice and Bass 2009; Parmentier et al. 2016). Within the call, each pulse consists of different peaks with the peak period corresponding to the dominant frequency of the call. Each muscle twitch produces multiple vibrations causing the radiated sound to have a different dominant frequency than the muscle contraction rate. The tension that increases in the contracting muscles makes it oscillate like a guitar string (Sprague 2000). This muscle vibration provides the dominant frequency of the sound. Scorpaeniformes comprise species capable of producing harmonic sounds with fast contracting muscles (Amorim et al. 2004; Connaughton 2004) thus representing good candidates as the source of

the /*kwa*/. In Mediterranean *Posidonia* meadows, the most abundant and nocturnal species of this order are from the Scorpaenidae family (Kalogirou et al. 2010).

/*Kwas*/ form a specific sound category that can easily be distinguished from other fish calls. The /*kwa*/ appears to occupy an exclusive frequency-niche that reduces masking interference by other fish sounds and promotes intraspecific communication (McCauley and Cato 2000; Hastings and Širović 2015). /*Kwas*/ also present a high diversity in spectral shape and temporal pattern (subset №1 features) as revealed by cluster analysis. The factors responsible for this high signal variability remain to be elucidated, but these findings suggest the transmission of multiple messages, and/or a link to different species, as observed in Sciaenidae (Picciulin et al. 2016) and Gobiidae (Pedroso et al. 2012; Blom et al. 2016), and/or inter-individual differences. For instance, across taxa, differences in the number of harmonics as well as in the energetic distribution across harmonics have been attributed to individual differences (e.g. penguins: Searby et al. 2004; toadfish: Amorim and Vasconcelos 2008; monkeys: Price et al. 2015), and/or allow individuals to occupy a greater frequency window and thus enhance signal transmission (Brumm and Naguib 2009; Radford et al. 2014). Combined with the presence of stereotyped, rhythmic sequences, sometimes involving different types of /*kwas*/, our findings support a communicative function of this fish call.

/*Kwas*/ showed temporal differences in frequency features (BW, F_{\min} , F_{peak} , F_s and F_e), temporal features (NP, PP) and amplitude-related features (RL, Entro). Hydrophone position, distance and number of calling fishes, environmental factors such as lunar cycle, or ambient noise (Connaughton and Taylor 1995; Radford et al. 2014) may contribute to the observed temporal variations. However, the interplay between the changes in acoustic features shows similarities to the one observed in other temperate fish species that have been attributed to physiological or morphological changes during the reproductive season. For instance, similar to many different fish species, peak frequency and water temperature increased over the course of the months and call amplitude was 14 to 17 dB higher in summer than in spring. A rise in temperature is known to increase the activation rate and the velocity of the sonic muscle (e.g. Connaughton et al. 2002; Ladich and Schleizer 2014; Kéver et al. 2015), while an increase in call amplitude has been reported as a result of sonic muscle hypertrophy during the spawning period (Connaughton et al. 2002; Rowe and Hutchings 2004; Nguyen et al. 2008). The identification of the /*kwa*-producing species combined with long-term data acquired within the same *Posidonia* meadow will allow to verify the here observed seasonal trends in acoustic features and evaluate their potential role.

Conclusions

This work is foundational in describing a ubiquitous Mediterranean coastal fish sound that meets the proposed criteria relevant for PAM of *P. oceanica* seagrass meadows. It sets the bases for future studies aiming at revealing if the /kwa/ can be used as an environmental proxy for habitat monitoring. Fish sounds are used in communication; they reflect an organism's activity and play a role in the species survival (Ladich 2015). Across taxa, there is evidence that environmental disturbance and habitat quality are reflected in the acoustic behaviour and variation in animal communities and populations (Riede 1998; van Oort et al. 2006; Pillsbury and Miller 2008; Laiolo 2010; Rosenthal and Stuart-Fox 2012). The next step to further evaluate if the /kwa/ is valuable for PAM of *P. oceanica* meadows would be to test /kwa/ diversity, chorus output and calling activity in relation to environmental variables and the status of *P. oceanica* seagrass meadows, characterized by different quality index values (e.g. BiPo, PREI, EBQI). Besides identifying a possible environmental proxy of a key habitat, this work also describes a sound with unique features compared to other known Mediterranean fish vocalizations that is potentially significant in the study of fish communication. Future studies need to be designed to further elucidate the source of the sound, the communicative role of the /kwa/ and its diversity.

Acknowledgments

We particularly thank F. Holon and Andromède Océanologie for the logistics and for sharing their habitat maps and information on the meadows studied. We also thank STARESO (Corsica, France) and its programme STARECAPMED for field work support in Calvi. We thank J. Decelle, M. Bolgan and anonymous reviewers for constructive comments on previous drafts. Thanks to 'The Clash' for the song 'London calling' that inspired the title. XR was financially supported by an 'Erasmus +' grant of the European Commission. L. Di Iorio and X. Raick equally contributed to the realization of this work.

Conflict of Interest

All authors declare that they have no conflict of interest.

References

Amorim, M. C. P., and R. O. Vasconcelos. 2008. Variability in the mating calls of the Lusitanian toadfish *Halobatrachus didactylus*: cues for potential individual recognition. *J. Fish Biol.* **73**, 1267–1283. <https://doi.org/10.1111/j.1095-8649.2008.01974.x>.

- Amorim, M. C. P., Y. Stratoudakis, and A. D. Hawkins. 2004. Sound production during competitive feeding in the grey gurnard. *J. Fish Biol.* **65**, 182–194. <https://doi.org/10.1111/j.0022-1112.2004.00443.x>.
- Amorim, M. C. P., R. O. Vasconcelos, J. F. Marques, and F. Almada. 2006. Seasonal variation of sound production in the Lusitanian toadfish, *Halobatrachus didactylus*. *J. Fish Biol.* **69**, 1892–1899. <https://doi.org/10.1111/j.1095-8649.2006.01247.x>.
- Amorim, M. C. P., J. M. Simões, and P. J. Fonseca. 2008. Acoustic communication in the Lusitanian toadfish, *Halobatrachus didactylus*: evidence for an unusual large vocal repertoire. *J. Mar. Biol. Assoc. U.K.* **88**, 1069–1073. <https://doi.org/10.1017/S0025315408001677>
- Andromède Océanologie (2015). Plaque de présentation de TEMPO, un réseau de surveillance des herbiers de posidonie en mer Méditerranée (Andromède & Agence de l'eau RMC, Eds.). <http://www.observatoire-mer.fr/img/tempo.pdf>
- Arduzzone, G., A. Belluscio, and L. Maiorano. 2006. Long-term change in the structure of a *Posidonia oceanica* landscape and its reference for a monitoring plan. *Mar. Ecol.* **27**, 299–309. <https://doi.org/10.1111/j.1439-0485.2006.00128.x>.
- Bertucci, F., E. Parmentier, G. Lecellier, A. D. Hawkins, and D. Lecchini. 2016. Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. *Sci. Rep.* **6**, 33326. <https://doi.org/10.1038/srep33326>.
- Blom, E. L., I. Mück, K. Heubel, and O. Svensson. 2016. Acoustic and visual courtship traits in two sympatric marine Gobiidae species – *Pomatoschistus microps* and *Pomatoschistus minutus*. *Environ. Biol. Fishes* **99**, 999–1007. <https://doi.org/10.1007/s10641-016-0550-5>.
- Bonacorsi, M., C. Pergent-Martini, N. Breand, and G. Pergent. 2013. Is *Posidonia oceanica* regression a general feature in the Mediterranean Sea? *Mediterr. Mar. Sci.* **14**, 193–203.
- Boudouresque, C. F., E. Charbonel, A. Meinesz, G. Pergent, C. Pergent-Martini, G. Cadiou, et al. 2000. A monitoring network based on the seagrass *Posidonia oceanica* in the Northwestern Mediterranean Sea. *Biol. Mar. Mediterr.* **7**, 328–331.
- Boudouresque, C. F., G. Bernad, P. Bonhomme, E. Charbonnel, L. Le Diréach, and S. Ruitton. 2007. Monitoring methods for *Posidonia oceanica* seagrass meadows in Provence and the French Riviera. *Sci. Rep. Port-Cros Natl. Park* **22**, 17–38.
- Boudouresque, C.-F., G. Bernard, P. Bonhomme, E. Charbonnel, G. Diviacco, A. Meinesz, et al. 2012. Pp. 1–202. *Protection and conservation of Posidonia oceanica meadows*. RAMOGE and RAC/SPA publisher, Tunis.
- Boyle, K. S., S. Riepe, G. Bolen, and E. Parmentier. 2015. Variation in swim bladder drumming sounds from three doradid catfish species with similar sonic morphologies. *J. Exp. Biol.* <https://doi.org/10.1242/jeb.123414>. 10.1242/jeb.123414.

- Brumm, H., and M. Naguib. 2009. Chapter 1 Environmental Acoustics and the Evolution of Bird Song. Vol 40, Pp. 1–33. *Advances in the Study of Behavior*. Academic Press, London.
- Cato, D. H. 1978. Marine biological choruses observed in tropical waters near Australia. *J. Acoust. Soc. Am.* **64**, 736. <https://doi.org/10.1121/1.382038>.
- Connaughton, M. A. 2004. Sound generation in the searobin (*Prionotus carolinus*), a fish with alternate sonic muscle contraction. *J. Exp. Biol.* **207**, 1643–1654. <https://doi.org/10.1242/jeb.00928>.
- Connaughton, M. A., and M. Taylor. 1995. Seasonal and daily cycles in sound production associated with spawning in the weakfish, *Cynoscion regalis*. *Environ. Biol. Fishes* **42**, 233–240. <https://doi.org/10.1007/BF00004916>.
- Connaughton, M. A., M. L. Fine, and M. H. Taylor. 2002. Review. Weakfish sonic muscle: influence of size, temperature and season. *J. Exp. Biol.* **205**, 2183–2188.
- Coquereau, L., J. Grall, L. Chauvaud, C. Gervaise, J. Clavier, A. Jolivet, et al. 2016. Sound production and associated behaviors of benthic invertebrates from a coastal habitat in the north-east Atlantic. *Mar. Biol.* **163**, 127. <https://doi.org/10.1007/s00227-016-2902-2>.
- Descamp, P., F. Holon, L. Ballesta, A. Guilbert, M. Guillot, P. Boissery, et al. 2011. Fast and easy method for seagrass monitoring: Application of acoustic telemetry to precision mapping of *Posidonia oceanica* beds. *Mar. Pollut. Bull.* **62**, 284–292. <https://doi.org/10.1016/j.marpolbul.2010.10.012>.
- Farina, A., and S. H. Gage. 2017. *Ecoacoustics: The Ecological Role of Sounds*. in A. Farina S. H. Gage, eds. John Wiley & Sons, Ltd, Oxford.
- Gerhardt, H. C. 1981. Mating call recognition in the green treefrog (*Hyla cinerea*): importance of two frequency bands as a function of sound pressure level. *J. Comp. Physiol. A.* **144**, 9–16. <https://doi.org/10.1007/BF00612792>.
- Gobert, S., S. Sartoretto, V. Rico-Raimondino, B. Andral, A. Chery, P. Lejeune, et al. 2009. Assessment of the ecological status of Mediterranean French coastal waters as required by the water framework directive using the *Posidonia oceanica* rapid easy index: PREI. *Mar. Pollut. Bull.* **58**, 1727–1733. <https://doi.org/10.1016/J.MARPOLBUL.2009.06.012>.
- Grava, T. 2006. Effect of habitat quality on communication and signalling in the black-capped chickadee. Thesis at the University of Northern British Columbia. Accessed from <https://www.unbc.ca/sites/default/files/sections/ken-otter/phd-thesis-thibaultgravafinal.pdf>
- Guillén, J. E., J. L. Sanchez Lizaso, S. Jiménez, J. Martínez, A. Codina, M. Montero, et al. 2013. Evolution of *Posidonia oceanica* seagrass meadows and its implications for management. *J. Sea Res.* **83**, 65–71. <https://doi.org/10.1016/j.seares.2013.04.012>.
- Hastings, P., and A. Širović. 2015. Soundscapes offer unique opportunities for studies of fish communities. *Proc. Natl Acad. Sci. USA* **112**, 5866–5867.
- Holon, F., P. Boissery, A. Guilbert, E. Freschet, and J. Deter. 2015a. The impact of 85 years of coastal development on shallow seagrass beds (*Posidonia oceanica* L. (Delile)) in South Eastern France: a slow but steady loss without recovery. *Estuar. Coast. Shelf Sci.* **165**, 204–212. <https://doi.org/10.1016/j.ecss.2015.05.017>.
- Holon, F., N. Mouquet, P. Boissery, M. Bouchoucha, G. Delaruelle, A. S. Tribot, et al. 2015b. Fine-scale cartography of human impacts along French Mediterranean coasts: a relevant map for the management of marine ecosystems. *PLoS ONE* **10**, e0135473. <https://doi.org/10.1371/journal.pone.0135473>.
- Kalogirou, S., M. Corsini-Foka, A. Sioulas, H. Wennhage, and L. Pihl. 2010. Diversity, structure and function of fish assemblages associated with *Posidonia oceanica* beds in a biodiversity enrichment in a diverse world area of the eastern Mediterranean Sea and the role of non-indigenous species. *J. Fish Biol.* **77**, 2338–2357. <https://doi.org/10.1111/j.1095-8649.2010.02817.x>.
- Kéver, L., K. S. Boyle, and E. Parmentier. 2015. Effects of seawater temperature on sound characteristics in *Ophidion rochei* (Ophidiidae). *J. Fish Biol.* **87**, 502–509. <https://doi.org/10.1111/jfb.12730>.
- Kéver, L., P. Lejeune, L. N. Michel, and E. Parmentier. 2016. Passive acoustic recording of *Ophidion rochei* calling activity in Calvi Bay (France). *Mar. Ecol.* **37**, 1315–1324. <https://doi.org/10.1111/maec.12341>.
- Kinda, G. B., Y. Simard, C. Gervaise, J. I. Mars, and L. Fortier. 2013. Under-ice ambient noise in Eastern Beaufort Sea, Canadian Arctic, and its relation to environmental forcing. *J. Acoust. Soc. Am.* **134**(1), 77–87. <https://doi.org/10.1121/1.4808330>.
- Ladich, F. 2015. *Sound communication in fishes*. in F. Ladich, ed. Springer-Verlag, Wien.
- Ladich, F., and G. Schleinzner. 2014. Effect of temperature on acoustic communication: sound production in the croaking gourami (labyrinth fishes). *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **182**, 8–13. <https://doi.org/10.1016/j.cbpa.2014.11.013>.
- Laiolo, P. 2010. The emerging significance of bioacoustics in animal species conservation. *Biol. Cons.* **143**, 1635–1645. <https://doi.org/10.1016/J.BIOCON.2010.03.025>.
- Laiolo, P., and J. L. Tella. 2007. Erosion of animal cultures in fragmented landscapes. *Front. Ecol. Environ.* **5**, 68–72. [https://doi.org/10.1890/1540-9295\(2007\)5\[68:EOACIF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[68:EOACIF]2.0.CO;2).
- Laiolo, P., M. Vögeli, D. Serrano, and J. L. Tella. 2008. Song diversity predicts the viability of fragmented bird populations. *PLoS ONE* **3**, e1822. <https://doi.org/10.1371/journal.pone.0001822>.
- Lamb, J. B., van de Water J. A. J. M., D. G. Bourne, C. Altier, M. Y. Hein, E. A. Fiorenza, et al. 2017. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. *Science* **355**: 731–733. <https://doi.org/10.1126/science.aal1956>

- Le Bot, O., J. I. Mars, C. Gervaise, and Y. Simard. 2015. Rhythmic analysis for click train detection and source separation with examples on beluga whales. *Appl. Acoust.* **95**, 37–49. <https://doi.org/10.1016/j.apacoust.2015.02.005>.
- Lin, M., H. C. J. Lucas, and G. Shmueli. 2013. Too big to fail: large samples and the *p*-value problem. *Inf. Syst. Res.* **24**, 906–917. <https://doi.org/10.1287/isre.2013.0480>.
- Lopez y Royo, C., G. Pergent, C. Pergent-Martini, and G. Casazza. 2010. Seagrass (*Posidonia oceanica*) monitoring in western Mediterranean: implications for management and conservation. *Environ. Monit. Assess.* **171**(1–4), 365–380.
- Mathias, D., C. Gervaise, and L. Di Iorio. 2016. Wind dependence of ambient noise in a biologically rich coastal area. *J. Acoust. Soc. Am.* **139**, 839–850. <https://doi.org/10.1121/1.4941917>.
- McCaughey, R. D., and D. H. Cato. 2000. Patterns of fish calling in a nearshore environment in the Great Barrier Reef. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **355**, 1289–93. <https://doi.org/10.1098/rstb.2000.0686>.
- McGregor, P. K. 2005. *Animal Communication Networks*. PK McGregor, eds. Cambridge University Press, Cambridge.
- McLachlan, G, Peel, D. 2000. *Finite Mixture Models*. John Wiley & Sons, Inc: Hoboken, NJ.
- Mellinger, D., K. Stafford, S. Moore, R. Dziak, and H. Matsumoto. 2007. An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography* **20**, 36–45. <https://doi.org/10.5670/oceanog.2007.03>
- Nguyen, T. K., H. Lin, E. Parmentier, and M. L. Fine. 2008. Seasonal variation in sonic muscles in the fawn cusk-eel *Lepophidium profundorum*. *Biol. Lett.* **4**, 707–710. <https://doi.org/10.1098/rsbl.2008.0383>.
- Noël, C., P. Boissery, N. Quelin, and V. Raimondino. 2012. *Cahier Technique du Gestionnaire: analyse comparée des méthodes de surveillance des herbiers de posidonies*, Pp. 96 CartOcean. Dreal PACA, France, Agence de l'eau RMC.
- van Oort, H., K. A. Otter, K. T. Fort, and C. I. Holschuh. 2006. Habitat quality, social dominance and dawn chorus song output in black-capped chickadees. *Ethology* **112**, 772–778. <https://doi.org/10.1111/j.1439-0310.2006.01228.x>.
- Parmentier, E., L. Kéver, K. Boyle, Y. E. Corbisier, L. Sawelew, and S. Malavasi. 2013. Sound production mechanism in *Gobius paganellus* (Gobiidae). *J. Exp. Biol.* **216**, 3189–3199. <https://doi.org/10.1242/jeb.087205>.
- Parmentier, E., M. L. Fine, and H. K. Mok. 2016. Sound production by a recoiling system in the Pempheridae and Terapontidae. *J. Morphol.* **277**, 717–724. <https://doi.org/10.1002/jmor.20529>.
- Parmentier, E., L. Di Iorio, M. Picciulin, S. Malavasi, J. P. Lagardère, and F. Bertucci. 2017. Consistency of spatiotemporal sound features supports the use of passive acoustics for long-term monitoring. *Anim. Conserv.* <https://doi.org/10.1111/acv.12362>.
- Pedroso, S. S., M. Bolgan, J. M. Jordão, P. J. Fonseca, and M. C. P. Amorim. 2012. Acoustic communication in *Pomatoschistus* spp.: a comparison between closely related species. Pp. 113–115. *The Effects of Noise on Aquatic Life*. Springer, New York, NY. doi.org/10.1007/978-1-4419-7311-5_25
- Penny, W. D., J. Mattout, and N. Trujillo-Barreto. 2007. Bayesian model selection and averaging. In *Statistical Parametric Mapping*. Pp. 454–467. Elsevier, London.
- Personnic, S., C. F. Boudouresque, P. Astruch, E. Ballesteros, S. Blouet, D. Bellan-Santini, et al. 2014. An Ecosystem-Based Approach to Assess the Status of a Mediterranean Ecosystem, the *Posidonia oceanica* Seagrass Meadow. *PLoS ONE* **9**, e98994. <https://doi.org/10.1371/journal.pone.0098994>.
- Picciulin, M., M. Bolgan, A. Codarin, R. Fiorin, M. Zucchetta, and S. Malavasi. 2013. Passive acoustic monitoring of *Sciaena umbra* on rocky habitats in the Venetian littoral zone. *Fish. Res.* **145**, 76–81. <https://doi.org/10.1016/j.fishres.2013.02.008>.
- Picciulin, M., M. Bolgan, A. B. Corò, G. Calcagno, and S. Malavasi. 2016. Sound production by the Shi drum *Umbrina cirrosa* and comparison with the brown meagre *Sciaena umbra*: a passive acoustic monitoring perspective. *J. Fish Biol.* **88**, 1655–1660. <https://doi.org/10.1111/jfb.12926>.
- Pillsbury, F. C., and J. R. Miller. 2008. Habitat and landscape characteristics underlying anuran community structure along an urban-rural gradient. *Ecol. Appl.* **18**, 1107–1118. <https://doi.org/10.1890/07-1899.1>.
- Price, T., P. Wadewitz, D. L. Cheney, R. M. Seyfarth, K. Hammerschmidt, and J. Fischer. 2015. Vervets revisited: a quantitative analysis of alarm call structure and context specificity. *Sci. Rep.* **5**, 1–11. <https://doi.org/10.1038/srep13220>.
- Radford, A. N., E. Kerridge, and D. Simpson. 2014. Acoustic communication in a noisy world: can fish compete with anthropogenic noise? *Behav. Ecol.* **25**, 1022–1030. <https://doi.org/10.1093/beheco/aru029>.
- Rice, A. N., and A. H. Bass. 2009. Novel vocal repertoire and paired swimbladders of the three-spined toadfish, *Batrachomoeus trispinosus*: insights into the diversity of the Batrachoididae. *J. Exp. Biol.* **212**, 1377–1391. <https://doi.org/10.1242/jeb.028506>.
- Riede, K. 1998. Acoustic monitoring of Orthoptera and its potential for conservation. *J. Insect Conserv.* **2**(3/4), 217–223. <https://doi.org/10.1023/A:1009695813606>.
- Rosenthal, G. G., and D. Stuart-Fox. 2012. Environmental disturbance and animal communication. Pp. 16–31 in U. Candolin and B. B. M. Wong, eds. *Behavioural Responses to a Changing World*. Oxford University Press, Oxford.
- Rountree, R. A., R. G. Gilmore, C. A. Goudey, A. D. Hawkins, J. J. Luczkovich, and D. A. Mann. 2006. Listening to fish: applications of passive acoustics to fisheries science. *Fisheries* **31**, 443–446. [https://doi.org/10.1577/1548-8446\(2006\)31\[433:LTF\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2006)31[433:LTF]2.0.CO;2)

- Rowe, S., and J. A. Hutchings. 2004. The function of sound production by Atlantic cod as inferred from patterns of variation in drumming muscle mass. *Revue canadienne de zoologie* **82**, 1391–1398. <https://doi.org/10.1139/z04-119>.
- Ruppé, L., G. Clément, A. Herrel, L. Ballesta, T. Décamps, L. Kéver, et al. 2015. Environmental constraints drive the partitioning of the soundscape in fishes. *Proc. Natl Acad. Sci. USA* **112**, 6092–7. <https://doi.org/10.1073/pnas.1424667112>.
- Searby, A., P. Jouventin, and T. Aubin. 2004. Acoustic recognition in macaroni penguins: an original signature system. *Anim. Behav.* **67**, 615–625. <https://doi.org/10.1016/j.anbehav.2003.03.012>.
- Sprague, M. W. 2000. The single sonic muscle twitch model for the sound-production mechanism in the weakfish, *Cynoscion regalis*. *J. Acoust. Soc. Am.* **108**, 2430–2437.
- Staaterman, E., C. B. Paris, H. A. DeFerrari, D. A. Mann, A. N. Rice, and E. K. D'Alessandro. 2014. Celestial patterns in marine soundscapes. *Mar. Ecol. Prog. Ser.* **508**, 17–32. <https://doi.org/10.3354/meps10911>.
- Sueur, J., S. Pavoine, O. Hamerlynck, S. Duvail, and J. Fjeldså. 2008. Rapid acoustic survey for biodiversity appraisal. *PLoS ONE* **3**, e4065. <https://doi.org/10.1371/journal.pone.0004065>.
- Tucker, S., and G. J. Brown. 2005. Classification of transient sonar sounds using perceptually motivated features. *IEEE J. Ocean Eng.* **30**, 588–600. <https://doi.org/10.1109/JOE.2005.850910>.
- Watkins, W. A. 1968. *The harmonic interval: fact or artefact in spectral analysis of pulse trains*. Woods Hole Oceanographic Institution, Woods Hole, MA.
- Zelick, R., D. A. Mann, and A. N. Popper. 1999. Acoustic communication in fishes and frogs. in R. R. Fay and A. N. Popper, eds. *Comparative hearing: fish and amphibians*. Springer, New-York.

Supporting Information

Additional supporting information may be found online in the supporting information tab for this article.

Figure S1. Number of fish sounds selected over the course of one night (meadow *c*).

Figure S2. Two views of the projections of the unitary vectors of the subset №1 features on the first three axes of the PCA, thick lines: black: single features whose projections are not collinear, blue, green and red: three sets of features whose projections are nearly collinear.

Table S1. Alphabetic list of known sound-producing fish families of the Mediterranean Sea, for which at least one reference was found in literature. The reference list is likely incomplete. Gobiidae of brackish Adriatic waters excluded.

Table S2. Comparison of the */kwa/* features during the subsampling period (i.e. the 2 h of peak production) versus the rest of the night.

Table S3. Fish sound categories present in the entirely analysed meadow recording.

Table S4. Pearson correlations for each studied feature for the sounds with ≥ 4 pseudo-harmonics during the 2 h of peak */kwa/* emission. $N = 23,566$.

Table S5. Summary table of seasonal feature differences represented as means (top row) and medians (bottom row) for 1000 *P*-values.

Audio S1. Example of typical */kwas/* recorded in Corsica, France.

Data S1. Description of the acoustic features used for sound description.