1 **Fish acoustic community structure in Neptune seagrass meadows across the**

2 **Mediterranean basin.**

3 Marta Bolgan[1]*, Lucia Di Iorio[2], Thanos Dailianis[3], Ignacio A. Catalan[4], Pierre Lejeune[5], Marta

4 Picciulin[6], Eric Parmentier[1]

5 [1] Laboratory of Functional and Evolutionary Morphology (Freshwater and Oceanic sCience Unit of reSearch),
6 Institut de Chimie B6c, University of Liège, Liège, Belgium.
7 [2] CHORUS Institute, 115 rue des Alliés, Grenoble, France.
8 [3] Institute of Marine Biology, Biotechnology and Aquaculture (IMBBC), Hellenic Centre for Marine Research
9 (HCMR), Heraklion, Crete, Greece.
10 [4] Mediterranean Institute for Advanced Studies, IMEDEA, CSIC/UIB, Esporles, Illes Balears, Spain.
11 [5] Station de Recherches Sousmarines et Océanographiques, Pointe Revellata BP33, Calvi, France.
12 [6] Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University of Venice, Venice,
13 Italy.
14   * corresponding author: marta.bolgan@gmail.com, tel: +32 468 08 51 32

15

16

17 **Abstract**

18 1. Sound production represents an integral part of social communication in many teleost fish, however few studies
19 have investigated the structure, organisation, and variability of fish sounds at the community level.

20 2. Fish acoustic community structure was recorded simultaneously in three sites located along the Mediterranean
21 basin within the endemic habitat of *Posidonia oceanica* seagrass beds. Acoustic diversity and species-specific
22 sound features were expected to differ between locations. We predicted that, in communities characterised by
23 higher acoustic richness, fish species would specialise in their use of acoustic resources (i.e., realised acoustic
24 niche compression), while the overall allocation of resources within the community signal space would expand.

25 3. The fish acoustic communities inhabiting Posidonia beds were characterised by the same main contributors (the
26 /Kwa/, *Ophidion rochei* and *Sciaena umbra* sound types). However, their relative occurrence, abundances and use
27 of acoustic resources were site-specific. Acoustic diversity differed between geographic locations. The range of
28 spectral and temporal resources exploited by the fish acoustic community was wider in sites where acoustic
29 richness was at its highest score. *Ophidion rochei* was highly specialised in its use of temporal resources where
30 acoustic richness was higher, whilst *Sciaena umbra* appeared less efficient in specialising the use of spectral and
31 temporal resources.

32 4. By showing that the same species can exploit different acoustic resources between locations, this study supports
33 the concept of Acoustic Niche plasticity (i.e., plasticity of acoustic resources allocation within a species). Results
34 suggest that the degree of Acoustic Niche plasticity might be determined by the species-specific degree of sound-
35 producing system plasticity. In turn, different degrees of Acoustic Niche plasticity might determine different
36 species-specific levels of acoustic adaptability to changing biotic or environmental conditions.

40

41

42

43

44   **1. Introduction**

45   The high diversity of sonic mechanisms which have evolved independently in several fish lineages indicates that

46   sound production contributes to teleost fitness, represents an integral part of their social communication, and was

47   likely acquired by the independent modifications of existing body structures (Parmentier, Diogo & Fine, 2017).

48   The reliance on acoustic signals for mediating social interactions is widespread across teleosts; for example, in

49   coastal areas such as coral reefs, it has been estimated that at least half of the fish families contain vocal species

50   (Parmentier et al., 2021). In a wide range of aquatic ecosystems, ranging from inland waters to coral reefs, from

51   temperate coastal areas to underwater seamounts and canyons, fish communicative sounds constitute an integral

52   part of underwater soundscapes (*e.g.,* Tricas & Boyle, 2014; Amorim, Vasconcelos & Fonseca, 2015; Lindseth &

53   Lobel, 2018; Desiderà et al., 2019; Carriço et al., 2020; Bertucci et al., 2020; Bolgan et al., 2020; Rountree, Juanes

54   & Bolgan 2020). In the past few years, there has been growing interest in the use of environmental sounds to

55   investigate ecological and community complexity (Farina & James, 2016). In this context, fish bioacoustics is

56   shifting from single species studies to whole acoustic community monitoring (Farina & James, 2016; Bertucci et

57   al., 2020; Parmentier et al., 2021; Di Iorio et al., 2021; refer to Table 1 for acoustic terminology). While different

58   mechanisms for interference avoidance have been documented in acoustic communities of birds, mammals, and

59   frogs (Sinsch et al., 2012; Farina & James, 2016), only a few studies have focused on whole fish acoustic

60   communities (Hasting & Sirovic, 2015; Ruppé et al., 2015; Bertucci et al., 2020; Wilson et al., 2020; Di Iorio et

61   al., 2021; see also Sup. Table 1). Little is known about interference avoidance, signal divergence, and acoustic

62   plasticity in fish acoustic communities (Hasting & Sirovic, 2015; Bertucci et al., 2020; Wilson et al., 2020).

63   Different factors likely shape fish sound production in acoustic communities. Morphological, physiological, and

64   neural constraints set the boundaries for variability in fish sound types. These biological constraints, which are

65   related to tissue properties (*e.g.,* muscle abilities, bone rigidity, swim bladder elasticity, etc.) are acting in similar

66   ways in all teleosts. This explains why convergent evolution has been observed in both the morphology of fish

67   sonic apparata and in fish sound features (Fine & Parmentier, 2015). This convergence results in a relatively lower

68   range of acoustic variability in fish communicative sounds than in other taxa (*e.g.,* tetrapods) (Amorim, 2006; Fine

69   & Parmentier, 2015).

70   In aquatic habitats, environmental features such as depth, temperature, bottom type and topography can influence

71   sound propagation (Urick, 1986). Within an acoustic community, similar habitat properties would theoretically

72   result in the convergence of acoustic signals toward features that minimize signal attenuation and degradation

73   (Acoustic Adaptation Hypothesis AAH, Morton, 1975). However, evidence for the AAH was not found to be as

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

74 widespread as expected across taxa. Environment-related adjustments in acoustic signals appeared to be

75 constrained by call function in anurans and mammals (Ey & Fischer, 2009). In fish, the AAH was tested in different

76 goby species inhabiting freshwater and shallow coastal areas (Lugli, Yan & Fine, 2003; Amorim et al., 2018). In

77 both environments, gobies emitted sounds with most acoustic energy in frequencies that matched the "quiet noise

78 window" which characterised the soundscape of their preferred habitats (Lugli, Yan & Fine, 2003; Amorim et al.,

79 2018). These findings supported the AAH concept, and the authors proposed that signals might evolve to be

80 effective within local environmental constraints (Lugli, Yan & Fine, 2003; Amorim et al., 2018).

81 On the other hand, the competition for acoustic resources by different species within the same acoustic community

82 should act as a divergent force on species sound repertoires, leading toward signal diversification to minimize

83 interference (Acoustic Niche Hypothesis, Krause, 1993). Recent studies have shown that fish species tend to

84 partition their signal space by using different strategies, such as emitting sounds at different locations, time of day,

85 and/or with different spectral and temporal features (Ruppé et al., 2015; Desiderà et al., 2019; Bertucci et al., 2020;

86 Wilson et al., 2020). Species sharing the same acoustic habitat would therefore differentiate their call

87 characteristics to minimise signal overlaps, but their adaptations are restricted by phylogenetic and environmental

88 constraints (e.g., depth, bottom type, topography, noise levels) which affect signal transmission (Morton, 1975;

89 Wilkins, Seddon & Safran, 2013; Fine & Parmentier, 2015).

90 As a result, it can be hypothesized that the composition and diversity of fish acoustic communities (Table 1) change

91 between locations of the same habitat type, depending on site-specific conditions. In particular, we hypothesized

92 that in communities characterised by higher acoustic richness, fish would specialise their use of acoustic resources

93 to minimize acoustic interference within the boundaries imposed by different sonic mechanisms. We also predicted

94 that the overall allocation of acoustic resources within the community signal space would expand in communities

95 characterised by higher acoustic richness. In light of these hypotheses, this study compares fish acoustic

96 community structure recorded simultaneously in three distant locations across the Mediterranean Sea basin,

97 characterised *a priori* by the same habitat-structuring species, the endemic seagrass *Posidonia oceanica* (L.,

98 Delile). *Posidonia oceanica* meadows are considered a priority habitat for conservation under the European

99 Habitats Directive (Dir 92/43/CEE; Díaz-Almela & Duarte, 2008). Previous studies have shown that at least three

100 vocal fish taxa should be present in this habitat, namely *Ophidion rochei* (Müller, 1845), *Sciaena umbra* (Linnaeus,

101 1758) and *Scorpaena* spp. (Linnaeus, 1758) (Ceraulo et al., 2018; Di Iorio et al., 2018; Bolgan et al., 2019; Di

102 Iorio et al., 2020). *Ophidion rochei*, an endemic Mediterranean fish inhabiting sandy areas and patchy seagrass

103 meadows, presents extensive anatomical modifications related to sound production abilities (Dulčić et al., 2002;

104   Keskin, 2007; Parmentier et al., 2010; Kéver et al., 2012). *Sciaena umbra*, a small-sized, demersal sciaenid

105   inhabiting rocky bottoms and Posidonia beds, was the first fish species to be monitored by its communicative

106   sounds in the Mediterranean Sea (Bonacito et al., 2002; Also & Cabanellas-Reboredo, 2012; Picciulin et al., 2012;

107   Picciulin et al., 2013; Picciulin et al., 2020; Parmentier et al., 2018; Di Iorio et al., 2020). *Scorpaena* spp. was

108   recently identified as the genus emitting the onomatopoeically named fish sound type /Kwa/ (Di Iorio et al., 2018;

109   Bolgan et al., 2019). The /Kwa/ was found to be twenty times more abundant than any other fish sound type in

110   Posidonia beds located in the Western Mediterranean Sea (Di Iorio et al., 2018). Despite these studies and previous

111   knowledge, no study has focused on the whole fish acoustic community inhabiting Posidonia beds.

112   The specific aims of this study were to: *i)* investigate the acoustic structure of three fish acoustic communities

113   inhabiting Posidonia beds, located across a broad geographical area within the Mediterranean Sea; *ii)* compare the

114   variability between fish sound types features and *iii)* understand how different vocal fish species share the acoustic

115   space in relation with different levels of acoustic richness.

116

117   **2. Materials and methods**

118   **2.1. Data collection**

119   Fish acoustic communities were simultaneously monitored in three recording sites located across the

120   Mediterranean basin (Palma, Mallorca, Spain; Calvi, Corsica, France and Heraklion, Crete, Greece; Figure 1a,

121   Table 2). The same environmental conditions characterised the sites in terms of depth (20 m) and habitat (*P.*

122   *oceanica* meadows). High resolution water temperature data were available at each site; in Mallorca, water

123   temperature was recorded by a SBE-37 conductivity and temperature recorder (www.socib.es), while in Corsica

124   and Crete this was recorded by Onset HOBO Pro v2 Temperature loggers (Sup. Figure 1).

125   At each site, fish acoustic activity was monitored using an underwater acoustic datalogger SNAP (hydrophone

126   sensitivity; −170 dB re 1 V/μPa, frequency response 2 Hz – 30 kH, sample rate 44100 Hz, 16 bits .wav; Loggerhead

127   Instruments, Sarasota, FL, USA) moored to the sea bottom. The SNAPS were synchronised prior to deployments

128   and were set for recording 1 minute every 11 min. This duty cycle (1/11) was chosen because it should provide a

129   good estimation of both acoustic presence and call rate (Thomisch et al., 2015). Data were simultaneously collected

130   for approximately one month between June and August 2017, with some variation in duration between sites (Table

131   2). The summer month of July was chosen because previous studies have shown that fish acoustic activities peak

132   during summer months in the Mediterranean coastal areas (*e.g.,* Kéver et al., 2016; Di Iorio et al., 2020), and

133   because fish taxonomic richness, diversity, evenness and density peak in July in *P. oceanica* meadows (Deudero

134   et al., 2008).

135   **2.2. Acoustic analysis**

136   To visualise and inspect the soundscape in the fish auditory range (0-2 kHz), Long-Term spectrograms (LTs) for

137   the full recording durations from each site (Table 2) were built with routines developed in MATLAB (R2014b).

138   These were assessed at different time scales (see for example Sup. Figures 2-4) for the full recording duration. In

139   particular, hourly LTs were inspected for all nights collected at each site and provided a first, qualitative and

140   macroscopic appreciation of fish sounds patterns. Following this first qualitative screening based on data

141   visualization techniques, 5 days per site were selected for manual analysis to cover the full month and to best

142   capture fish sounds in terms of occurrence and variability. Manual analysis was carried out on five days of

143   recordings collected over the entire month in each site (4th, 9th, 16th, 23rd and 27th of July; total of 1,800 min). This

144   manual analysis was conducted by aural and visual assessment using Raven Pro 64 1.5 (Bioacoustic Research

145   Program, Cornell Laboratory of Ornithology, Ithaca, NY, USA; sound files down sampled at 4 kHz, FFT size 256

146   points, 50% overlap, Hanning window). All subsequent analyses are based on these same five days of recordings

147   processed for each site. All sound types with features similar to those characterising sounds emitted by known

148   vocal fish species were considered. Some sound types could be labelled and assigned to a species or a genus

149   previously identified (*e.g.,* Parmentier et al., 2010, Picciulin et al., 2012, Di Iorio et al., 2018, Bolgan et al., 2019).

150   All unknown fish sound types were categorised using a dichotomous framework - originally proposed by Desiderà

151   et al. (2019) for coastal rocky reefs - adapted for this study (Figure 1b).

152   Data were manually analysed for acoustic richness (*i.e.,* number of sound types) and sound abundance (*i.e.,* the

153   abundance of each sound type). The abundance of each sound type was measured using a tailored ordinal scale

154   following Tellechea, Bouvier & Norbis (2011) and Picciulin et al. (2013) (Table 3). This abundance score ranged

155   from 0 (absence) to 4 (chorus: mass production of multiple sounds that are no longer discernible as discrete signals,

156   McCauley & Cato, 2000; Mooney et al., 2020). This methodology was validated on a subsample of data (Sup.

157   Figure 5). The acoustic richness and the abundance of each sound type was measured for each hour of recordings

158   (5 min per hour, duty cycle=1/11) collected at each site.

159   For all sound types, temporal features were measured from oscillograms, while spectral features were measured

160   from power spectra (for details about acoustic features, refer to Sup. Table 2) on a subsample of sounds with a

161   good Signal to Noise Ratio (SNR); descriptive statistics were calculated for each sound type (Table 4).

162   Furthermore, three sound types were present in all sites: the /Kwa/ emitted by *Scorpaena* sp. (Di Iorio et al., 2018;

163   Bolgan et al., 2019), *O. rochei* male sounds (Parmentier et al., 2010; Kéver et al., 2012) and *S. umbra* male sounds

164   (Picciulin et al., 2012; Parmentier et al., 2018). Fifty /Kwa/ and *O. rochei* sounds were selected from each site

165   (N=150 sounds per sound type). In the case of *S. umbra*, sounds from Corsica could not be considered because of

166   an overall insufficient Signal to Noise Ratio (N=4). Therefore, for this sound type only, the 150 samples were

167   taken primarily from the Mallorca and Crete datasets.

2.3. Data treatment and statistical analysis

169   For each of the three sound types recorded in all sites (/Kwa/, *O. rochei* male sound and *S. umbra* male sounds),

170   the diel pattern of acoustic activities was calculated as the mean abundance score per each hour of recording. For

171   each of these three sound types, the diel pattern of acoustic activity was compared between sites using Generalized

172   Linear Models (GLMs). GLMs for Poisson distribution and logarithmic link function were calculated using the

173   abundance score as the response variable, whereas location and time were used as explanatory variables. For *S.*

174   *umbra*, only Mallorca and Crete data were compared because of insufficient sound detection in Corsica. The

175   models were graphically validated by means of residuals plots, while the deviance statistic (residual

176   deviance/degrees of freedom) was used to assess the 'goodness of fit' of the model.

177   The inter-site variability in acoustic features of these three sound types was evaluated using Principal Component

178   Analysis (PCA). Before performing the PCA, all extracted acoustic features were inspected for correlation. Many

179   acoustic features were found to be highly correlated and, therefore, PCA was then performed using only peak

180   frequency, 5% frequency, 95% frequency, duration, and pulse period as variables (R< 0.6). The correlation matrix

181   was used to calculate the Principal Components which account for the different scales of the variables. The

182   relevance of the Principal Components was inspected through a Scree Plot. Kruskal-Wallis H and Mann Whitney

183   U tests were run on all acoustic acoustic features to further inspect the inter-site variability of these sound types.

184   Water temperature is known to influence fish sound features (Kéver et al., 2015; Ladich, 2018); the potential effect

185   of temperature on the sound features of the three abundant sound types was inspected using linear regression on

186   log10- transformed acoustic features (as these were not normally distributed). All analyses were carried out in

187   STATISTICA (version 10, Statsoft, Tulsa, OK, USA).

188   Acoustic diversity patterns, analysed as relative hourly proportions of sound types, were graphically examined and

189   compared between sites for all sound types, including the three common abundant sound types. In order to assess

190   acoustic diversity differences between sites, sound type richness was explored by building accumulation curves

191   for each site using sound types presence/ absence data. Shannon and Simpson reciprocal diversity indices, based

192   on bootstraps with 99 iterations using sound abundance score information, were calculated using EstimateS 9.1.0

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

193   (copyright R. K. Colwell: http://purl.oclc.org/estimates). Acoustic richness, Shannon and Simpson diversity

194   indexes were visualised using violin plots. As residuals were not parametric even after transformation, Kruskal–

195   Wallis tests were used to compare differences in acoustic richness as well as the Shannon and Simpson diversity

196   indexes between the three sites. Mann-Whitney U test was used for pairwise comparisons.

197   Niche analysis (Colwell & Futuyma, 1971; Sinsch et al., 2012) was conducted to evaluate the realised acoustic

198   niche of each sound type and the allocation of acoustic resources within the community signal space. The realised

199   acoustic niche is defined as a multidimensional abstraction encompassing spectral and temporal features of a sound

200   type, as well as its diel pattern of occurrence (Table 1). The realised acoustic niche corresponds to the range of

201   acoustic resources (*i.e.,* utilised resources classes) exploited by a specific sound type along three axes: *i)* diel timing

202   of calling activity, which included 24 resource classes (hours of the day, Axis I); *ii)* call spectral features, which

203   included 11 resource classes based on peak frequency intervals (width: 100 Hz, range: 80–1180 Hz, Axis II) and

204   *iii)* call temporal features, which included 17 resource classes based on the $\log_{10}$ of pulse period intervals (width:

205   0.1 $\log_{10}$ PP; range: 0.8–2.5 ms, Axis III). Data for each axis and each location were entered in a resource matrix,

206   where each row represents a sound type, and each column represents one resource class. For each sound type and

207   call axis, the number of sounds falling in each resource class was calculated and displayed with a colour scale (in

208   relative percentage). The resulting community signal space was defined as the range of acoustic resources

209   exploited by the whole fish acoustic community in the three axes (Table 1). Signal space was calculated from the

210   sum of all sound types present in each resource class of the three axes at each site. Finally, the realised acoustic

211   niche breadth (NB; Sinsch et al., 2012) was calculated as the inverse of Simpson's diversity index; the highest

212   level of resource specialization (NB= 0) occurred when only one resource class was exploited (Colwell &

213   Futuyma, 1971; Sinsch et al., 2012).

214   **3. Results**

215   A total of ten fish sound types were identified in the three locations (Mallorca, Corsica, and Crete) with different

216   relative abundances (Figure 1b, Table 4, Figure 2). Three of the sound types (the /Kwa/, *O. rochei* male sounds

217   and *S. umbra* male sounds, Table 4), were recorded in higher proportions than all other sound times at all locations

218   (Figure 2).

219   The /Kwa/ dominated the fish biophony in terms of diel pattern of occurrence and of sound abundance. The /Kwa/

220   was the most abundant sound type in all locations, and the only one recorded during daytime (Figure 2, Figure 3,

221   Table 5). Although /Kwa/ choruses were recorded in all locations, the abundance of /Kwa/ decreased from the

222   Western to the Eastern Mediterranean Sea (Figure 3, Table 5, Sup. Figure 6).

223   *Ophidion rochei* male sounds were recorded in all sites during night-time hours, although choruses were recorded

224   only in Corsica. The abundance of this sound type was greater in Corsica than in Mallorca and Crete (Figure 2,

225   Figure 3, Table 5, Sup. Figure 6).

226   *Sciaena umbra* sounds contributed to the fish biophony around sunset-hours in Mallorca and Crete, but occurred

227   on a single night in Corsica (Figure 2, Figure 3, Table 5, Sup. Figures 4 and 6). Furthermore, sounds had a low

228   signal to noise ratio in Corsica, suggesting they were produced at a greater distance from the recording device.

229   The acoustic features of the three sound types differed between locations (Table 6, Sup. Figure 7). The PCA

230   showed that the /Kwa/ recorded in Crete differed from the /Kwa/ recorded in the Western basin in terms of spectral

231   (such as peak frequency) and temporal features (such as pulse period); both these features explained 53% of the

232   variance (Figure 4a, Table 7, Sup. Figure 7). *Ophidion rochei* sounds recorded in Corsica clustered separately from

233   *O. rochei* sounds recorded in Crete and Mallorca. The acoustic features that mainly contributed to this difference

234   are temporal features (duration and pulse period). They explained 58% of the variance and were strongly related

235   to water temperature (Figure 4b, Table 7, Sup. Figures 7 & 8). No evident trend related to a specific location could

236   be observed for *S. umbra* (Figure 4c, Table 7).

237

238   In terms of relative hourly proportions of sound types, Mallorca was found to be mainly dominated a single sound

239   type, the /Kwa/. Corsica showed a strong contribution of two sound types, the /Kwa/ and *O. rochei* sounds. Crete

240   was characterised by a wider variability in the number of simultaneous sound types (Figure 2). Besides the /Kwa/,

241   *O. rochei* and *S. umbra* sounds, the fish biophony in Mallorca and Corsica included only one additional sound type

242   per site. *Pulse Series 2* (PS2) was recorded once at 4 am in Mallorca (possibly produced by the same individual),

243   while *Low Frequency Pulse Train* (LFPT) was recorded at sunset in Corsica (Figure 2). On the other hand, the

244   fish biophony in Crete included five additional sound types that occurred only at night (Figure 2, Table 4).

245   Acoustic richness and diversity were significantly different between the three locations (Figure 5; Sup. Table 3).

246   Acoustic richness showed similar cumulative trends in the Western Mediterranean Sea (Mallorca and Corsica),

247   but it was highest in Crete (Figure 5a). An increasing trend in fish acoustic diversity (Shannon and Simpsons'

248   indices) from the Western to the Eastern Mediterranean (Figure 5b-d) was matched by an increasing trend in

249   resource allocation within the community signal space (Figure 6).

250   The fish community in Crete allocated a wider range of call spectral and temporal resources (Axis II and III Figure

251   6). In Crete, the fish acoustic community used all spectral resources of the signal space (Axis II, Figure 6).

252 Furthermore, the /Kwa/ and the sound type "*Pulse Series 5*" exploited temporal resources that were not allocated

253 in the signal space of Western Mediterranean communities (Mallorca and Corsica, Axis III, Figure 6).

254 In all three sites, the rarest sound types (LFPT, FPT and all Pulse Series, Table 4, Figure 2) appeared highly

255 specialised, with low variability in all the three axes (Figure 6). Specifically in Crete, the five unknown sound

256 types exploited different spectral and/or temporal resources than those allocated by the three most abundant sound

257 types (Figure 6).

258 The /Kwa/ sound type used all diel resource classes in all sites (Axis I, Figure 6). It monopolised the 700- 900 Hz

259 band in the Western Mediterranean, while it exploited higher-band (900 –1100 Hz) spectral resources in Crete

260 (Axis II, Figure 6, Sup. Figure 7). In the Western Mediterranean Sea, the range of spectral and temporal acoustic

261 resources exploited by the /Kwa/ was wider when its abundance was highest (*i.e.,* Mallorca, Axis III Figure 6,

262 Figure 3, acoustic niche breadth= 0.28 vs 0.07 in Corsica and 0.16 in Crete).

263 *Sciaena umbra* used different diel resources across sites (Axis I, Figure 6). Furthermore, the allocation of both

264 temporal and spectral resources appeared most specialised in Corsica, where the abundance of this sound type was

265 at its lowest (Axis I and II Figure 6, Figure 3, acoustic niche breadth= 0.01). When comparing only Mallorca and

266 Crete (which show similar abundance trends for this sound type, Figure 3), it appears that *S. umbra* slightly

267 specialised its use of spectral resources at the site where acoustic diversity was highest (Crete) (Axis II Figure 6,

268 Figure 5, acoustic niche breadth=0.13 in Mallorca vs 0.10 in Crete).

269 Finally, *O. rochei* exploited different diel resources across sites (Axis I, Figure 6) and was highly specialised in

270 the use of temporal resources in Crete, where acoustic diversity was highest (Axis III, Figure 6; acoustic niche

271 breadth= 0.00 vs 0.10 in Mallorca and 0.08 in Corsica). Here, temporal features appeared restricted in comparison

272 to the other sites (Axis III Figure 6).

273 **4. Discussion**

274 **4.1. Does fish acoustic community composition change between different locations of a common**

275 **habitat?**

276 This study supports the hypotheses that i) some sound types are representative of a habitat overall, and that ii) the

277 composition, organization, and diversity of fish acoustic communities can be location-dependent within a specific

278 habitat.

279 All sites were characterised by the same main sound contributors, namely the /Kwa/, *O. rochei* and *S. umbra* sound

280 types. These three most abundant sound types - which differed in their relative abundances and allocation of

281 acoustic resources between locations - could be considered as a potential proxy for habitat monitoring in *P.*

282   *oceanica* meadows. This observation is in agreement with previous studies (Ceraulo et al., 2018; Di Iorio et al.,

283   2018). Two of these sound types (/Kwa/ and *O. rochei* sounds) are produced by behaviourally cryptic taxa that are

284   difficult to monitor using traditional surveying techniques (*e.g.,* visual census; La Mesa, Muccio & Vacchi, 2005).

285   The use of PAM can enhance the resolution of fish population monitoring and therefore provide information for

286   conservation programs (*sensu* Picciulin et al., 2019). *Ophidion rochei*, in particular, is a nocturnal predator that

287   hides during daylight hours in the sandy bottom; as a result of this cryptic behaviour, *O. rochei* has been described

288   as uncommon and rare (e.g., Pallaoro & Jardas, 1996; Nielsen et al., 1999). This study strongly suggests that *O.*

289   *rochei* populations are likely ubiquitous and abundant in *P. oceanica* meadows across the Mediterranean Sea. In

290   particular, the abundance of this species can be high enough to generate choruses, such as those recorded in

291   Corsica. Furthermore, and in contrast with current knowledge, the simultaneous and ubiquitous sound production

292   by more than one individual during *O. rochei* reproductive season suggests that *P. oceanica* meadows might

293   represent important spawning grounds for this species.

294   In regard to the overall acoustic community, the set of sound types recorded at each site, their relative proportion

295   as well as their allocation of acoustic resources differed between locations.

296   Acoustic diversity increased along a West-to-East longitudinal gradient in the Mediterranean, with the highest

297   values recorded in Crete. In accordance with the study of Desiderà et al. (2019), the sound types that mainly

298   contributed to acoustic diversity were emitted by unidentified fish species, occurred in isolated bouts, and in small

299   numbers. Acoustic diversity has been shown to correlate to the taxonomic diversity of fish assemblages (Desiderà

300   et al., 2019; Carriço et al., 2020). According to our acoustic data, species diversity should therefore be more

301   important in Crete. Using different kinds of taxonomic indexes, many studies have argued for a longitudinal

302   decreasing western/eastern gradient of taxonomic diversity (Quignard & Tomasini, 2000; Bianchi & Morri, 2002;

303   Arvanitidis et al., 2002; Lasram et al., 2009; Coll et al., 2010; Mouillot et al., 2011). However, two studies on

304   demersal fish assemblages support that there is no such gradient but rather various biodiversity hotspots (Gaertner

305   et al., 2007; Granger et al., 2015). This observation, together with the results of our study, supports that micro-

306   scale effects related to the location and its specific characteristics (*e.g.,* presence or absence of rocks nearby,

307   seagrass density, size of seagrass meadow, etc.) might influence community composition within the same habitat

308   type. However, this study included a limited number of sites and analyzed days, thus not allowing to draw general

309   conclusions. Further studies are needed to better understand the variability in community composition at different

310   spatial and temporal scales. These studies should be combined with additional information on habitat

311   characteristics (*e.g.,* percentage of *P. ocenica* cover, patchiness, seagrass density, etc.) which are likely to influence

312   fish assemblages and associated acoustic communities. In particular, it would be interesting to compare community

313   composition and dynamics over a smaller geographical scale than which was considered in this study by comparing

314   multiple, closely located recording points between distant locations of the same habitat type. Finally, the possibility

315   that the higher acoustic diversity recorded in Crete results from Lessepsian migrations *(i.e.,* the migration of marine

316   species across the Suez Canal, usually from the Red Sea to the Mediterranean Sea) cannot be excluded

317   (Katsanevakis et al., 2013). For example, the common lionfish *Pterois miles* (and similar sister species) which has

318   rapidly spread across the Eastern Mediterranean Sea (Poursanidis et al., 2020; Kleitou et al., 2021) is a vocal

319   species (Schärer-Umpierre et al., 2019). If invasive species are behaviourally or taxonomically cryptic, PAM might

320   represent the most efficient tool to monitor the biological invasion, as well as to promptly inform managers and

321   regulators (Rountree & Juanes, 2016; Juanes, 2018; Ceraulo et al., 2018; Picciulin et al., 2019; Raick et al., 2020).

322   **4.2. Which range of sound feature variability can be found in fish acoustic communities?**

323   The acoustic features characterising the sound types recorded in all locations differed between sites. Fish-

324   dependent factors ranging from characteristics of the sonic apparatus to fish size, age, and spawning motivation,

325   as well as environmental-dependent factors, including features influencing sound propagation and water

326   temperature, can explain these results.

327   In the PCA, the /Kwa/ recorded in Crete clustered separately from the recordings in the Western Mediterranean

328   Sea. The main features contributing to this differentiation were peak frequency and pulse period. The /Kwa/ is an

329   onomatopoeia for a sound type having an extreme acoustic variability most probably emitted by species from the

330   *Scorpaena* genus (Di Iorio et al., 2018; Bolgan et al., 2019). All observed *Scorpaena* spp. (*S. porcus*, *S. scrofa* and

331   *S. notata*) share the same sonic apparatus. This apparatus, present in both males and females, consists of 3

332   bilaterally symmetrical muscular bundles with 3–5 long tendons inserted on ventral bony apophyses of the

333   vertebral bodies (Bolgan et al., 2019). In *Scorpaena* spp., the number and length of tendons are variable both

334   within and between species, which could explain the large diversity of /Kwa/ acoustic features. As this sound type

335   could be produced by different species, differences in acoustic features could reflect variation in taxonomic

336   composition of this genus. An increased abundance of *S. maderensis*, which is commonly found in the Eastern

337   Mediterranean and the Aegean Sea (De Raedemaecker, Miliou & Perkins, 2010) but reported sporadically in the

338   Western basin (Encarnação et al., 2019), could impact /Kwa/ acoustic features in Crete. On the other hand, high

339   plasticity at the level of the sonic mechanism might allow species of this genus to adapt the temporal and spectral

340   features of their call when in sites characterised by higher acoustic richness. Further studies are required to shed

341   light on these two hypotheses.

342   *Ophidion rochei* sounds recorded in Corsica were clustered separately in the PCA, mainly because their pulse

343   periods were longer than in Mallorca and Crete (Sup Figure 1, Sup. Figure 7). This difference is probably

344   physiological and related to colder temperatures in Corsican waters that will directly impact the muscle contraction

345   rate (Kéver et al., 2015, Sup Fig 1., Sup Figure 8).

346   On the other hand, a high level of overlap in the PCA was observed for *S. umbra* sounds, suggesting a reduced

347   inter-site variability between the Western and Eastern basins. The reduced site-specificity in *S. umbra* sound

348   features highlighted in this study is consistent with previous data collected over a 17 years-time span in the Western

349   basin (Parmentier et al., 2018). The authors argued that the geographical and temporal consistency of *S. umbra*

350   sound features results from constraints associated with its sound-producing mechanism (Parmentier et al., 2018).

351   The high mobility within the water column of this species, which can swim closer to the surface where waters are

352   warmer, could contribute to the homogeneity of sound-producing muscles and, consequently, sound features

353   between locations. This is on the contrary to what was obsvered for *O. rochei*. We suggest that differences in sonic

354   apparata (at the morphological, physiological and neurological level) might result in different levels of acoustic

355   plasticity between species in a fish community, and therefore in different extents of variability in acoustic features.

356

357   **4.3 Is acoustic diversity related with acoustic resource allocation in fish acoustic communities?**

358   This is the first instance in which the allocation of acoustic resources within the community signal space, and the

359   realised acoustic niches of different fish sound types, were estimated in relation to fish acoustic richness on a broad

360   geographical scale. The range of spectral and temporal resources exploited by the fish acoustic community was

361   broader where acoustic richness was at its highest score. Furthermore, different species showed a different extent

362   of acoustic niche compression in relation to acoustic richness. In Crete, all resources in the call spectral axis of the

363   signal space were allocated; furthermore, more extreme call temporal resources were exploited by different sound

364   types. This broad allocation of acoustic resources might be related to higher levels of acoustic competition,

365   enhanced by a greater number of sound types (and potentially more acoustic species). In Crete, the realised acoustic

366   niches of the additional sound types contributing to acoustic diversity were highly specialised, with the exploitation

367   of only one resource class in each axis.

368   *Ophidion rochei* and *S. umbra* sounds showed differences in the realised acoustic niche depending on the locations.

369   This statement cannot be extended to the /Kwa/ sound, since different species likely emit this sound type. Both *O.*

370   *rochei* and *S. umbra* exploited different diel resources between sites. *Ophidion rochei* was highly specialised in its

371   use of temporal resources where acoustic richness was highest. In Crete, this sound type exploited only one class

372 of resources in the call temporal axis (*vs* three to four in the Western Mediterranean Sea). *Sciaena umbra* appeared

373 less specialised in the use of temporal resources, as this sound type exploited three temporal resource classes in

374 both Mallorca and Crete. The sonic system in *O. rochei* is characterised by six sonic muscles and additional

375 morphological adaptations (*e.g.,* presence of modified epineural and ribs, see Parmentier et al., 2010; Kéver et al.,

376 2012). This high complexity could explain better adaptive abilities than *S. umbra*, who only possess a pair of sonic

377 muscles (Parmentier et al., 2018).

378 The degree of specialisation in acoustic resource allocation might be linked with sound abundances, since the

379 reduced abundance of a sound type can result in a limited variability of its call spectral and temporal features. This

380 could be the case for the additional sound types that mainly contributed to acoustic diversity, including *S. umbra*

381 sounds recorded in Corsica. An inverse relationship between the realised acoustic niche of a sound type and its

382 abundance was not observed for *O. rochei. Ophidion rochei* sound type was most abundant in Corsica, but the

383 widest use of spectral resources was recorded in Mallorca. Overall, these results support the hypothesis formulated

384 in section 4.2, which suggests that different levels of sonic system plasticity might result in different capabilities

385 and strategies for acoustic resource allocation.

386 The potential modifications in realised acoustic niche features, combined with the ability of a fish community to

387 make efficient use of the acoustic space, support the hypothesis that species are constrained in sharing their signal

388 space to avoid or reduce acoustic competition (Ruppé et al., 2015; Bertucci et al., 2020). In addition, we observed

389 partial niche overlap between sound types recorded in the same location. While the realised acoustic niche of

390 different sound types recorded in Crete (*e.g.,* Fast Pulse Series, Pulse series 1 and Pulse Series 5) did not overlap

391 with that of *O. rochei* and *S. umbra* sounds in two or three axes, one sound type (Pulse series 3) overlapped with

392 *S. umbra* and *O. rochei* sounds in two axes. The realised acoustic niche of *O. rochei* and *S. umbra* overlapped in

393 one or more axes, suggesting a potential for interference. A similar interference potential was also suggested in a

394 multi-species spawning site off the Cayman Islands (Wilson et al., 2020); in this work, the separation of calls in

395 time and space, and the emission of sounds at different frequencies, was observed but did not always occur. The

396 observed differences in call temporal features were suggested to aid species discrimination (Wilson et al., 2020).

397 Such studies provide important baselines required to elucidate on the drivers of acoustic similarities and divergence

398 in fish acoustic communities, a poorly studied topic. In terrestrial habitats, a recent study on tropical anuran showed

399 that acoustic partitioning and acoustic adaptation play a minor role in shaping acoustic assemblages, whereas

400 phylogenetic niche conservatism seem to play a major role (Sugai et al., 2021). This study also underscored the

401 importance of including the ecological context of communities to understand drivers of acoustic divergence (Sugai

402   et al., 2021). Similar studies are not yet available for fish acoustic communities, nevertheless it cannot be excluded

403   that these are similarly shaped by multiple drivers. In this context, we would like to raise two final unanswered

404   questions which deserve further research. These are (1) what are the boundaries of an acoustic fish community,

405   and (2) how do these relate with species hearing capabilities and ecological niches?

406   Sound travels very efficiently in water, and some fish species can emit loud sounds that propagate over relatively

407   long distances. In such cases, propagation might overcome habitat boundaries, and therefore, the "boundaries" of

408   the acoustic community might differ from those of the habitat. Furthermore, competition occurs only for resources

409   that can be accessed; if the resource is a portion of the signal space, this means that fish compete only for what

410   they can hear and discriminate. In the case of *S. umbra* and *O. rochei*, audiograms are available (Codarin et al.,

411   2009; Kéver et al., 2014). *Sciaena umbra* has a broader hearing bandwidth (100-3000 Hz *vs* 150- 2100 Hz) and

412   overall higher sensitivity than *O. rochei* (*S. umbra* hearing thresholds range from 82 to 131 dB re 1 Pa while *O.*

413   *rochei* range from 100 to 140 dB re 1 Pa); furthermore, the lowest hearing thresholds were measured for signals

414   at 300 Hz in *S. umbra* and 600 Hz in *O. rochei* (Codarin et al., 2009; Kéver et al., 2014). While the hearing

415   sensitivity of *S. umbra* seems finely tuned on the peak frequency of conspecific sounds, that of *O. rochei* is

416   enhanced to the higher-frequency components of conspecific sounds (Codarin et al., 2009; Kéver et al., 2014).

417   The hearing sensitivity of *S. umbra* and *O. rochei* is therefore tuned to different spectral resources. This suggests

418   that acoustic competition between these two species might be less intense than predicted by the overlap of their

419   realised acoustic niches. Finally, it should be considered that the concept of acoustic niche should be evaluated in

420   relation to the concept of ecological niches. *Sciaena umbra* and *O. rochei* exploit different feeding and habitat

421   resources; *S. umbra* is a demersal feeding specialist, feeding mainly on decapods and amphipods, while *O. rochei*

422   is a sand-dwelling carnivorous species, feeding mainly on decapods and small teleosts (Dulčić et al., 2004; Fabi

423   et al., 2006; Chao, 2015). The demersal *vs* sand-dwelling preferences of these two species might result in a reduced

424   acoustic competition if they are capable of discriminating sounds emitted in the water column (*S. umbra*) or on the

425   bottom (*O. rochei*). Further studies are needed to better define the "concept" of fish acoustic community and its

426   boundaries. If we define acoustic communities not as mere co-occurrence of species but as closely-knit

427   assemblages, which interact and compete between one another for acoustic resources, we might need to shift our

428   paradigm from a "habitat-based" community definition to the incorporation of *i)* animal perception, *ii)* propagation

429   dynamics and *iii)* ecological niche into the definition of acoustic communities.

430

431   **5. Conclusions; a conservation perspective.**

432   Acoustic data provides information on the organization, diversity and dynamics of a community, and thus enable

433   the study of ecological changes and turnover in a non-intrusive way (Sugai & Lluisa, 2019; Mooney et al. 2020;

434   Chhaya et al., 2021). This is particularly important considering the current extinction crisis, and the urgent need

435   to document biodiversity worldwide (Sugai & Lluisa, 2019). Recent software and hardware advancements have

436   allowed the monitoring of acoustic community composition, structure and dynamics over large spatial scales in

437   terrestrial habitats, along with the application of the acoustic community paradigm to environmental and

438   community assessment, and conservation (Farina & James, 2016; Mullet, Farina & Cage, 2017). In aquatic

439   habitats, the study of fish acoustic communities, their structure, organization, and variability represent an emerging

440   field known as fish acoustic community ecology. This emerging field is already showing a strong conservation

441   potential, as it provides high-resolution information from the community down to the species level in a completely

442   non-invasive way, and over different spatial and geographical scales. Passive acoustic monitoring of multi-species

443   assemblages has revealed important information about habitat use and preference, allowing spawning locations to

444   be pinpointed, and informing on populations structure and status (Wilson et al., 2020). The diversity of fish

445   acoustic communities reflects status and protection in Marine Protected Areas (Desiderà et al., 2019), similar to

446   what happens in terrestrial habitats, where acoustic diversity patterns are linked to community stability and habitat

447   quality (Sueur et al., 2008). The structure and organization of acoustic fish communities has been shown to provide

448   multi-level information on biodiversity, environmental status, and functional aspects of the habitat (Di Iorio et al.,

449   2021). In this study, we propose a frame to visualise the allocation of acoustic resources within a fish community.

450   Despite the need for additional investigations on larger temporal and spatial scales, this study sets promising basis

451   and opens new perspectives in the the study of acoustic fish communities using resource allocation. Monitoring

452   acoustic resource allocation in the same area over long-time periods might for instance inform on sudden changes

453   in community composition, such as the arrival of invasive vocal fish species. Under this framework, the arrival of

454   an invasive vocal species could be identified by the sudden allocation of acoustic resources that were not previously

455   exploited. This could lead to a cascade of effects over acoustic resource allocation within the community, which

456   would be detectable even if sound type identity is yet to be ascertained, thus helping to promptly inform managers

457   and conservation plans. Finally, we have shown that the allocation of acoustic resources is not fixed within a fish

458   species, as the same species can adapt its use of acoustic resources. In this sense, this study supports the concept

459   of Acoustic Niche plasticity. We have suggested that the degree of Acoustic Niche plasticity might be determined

460   by the species-specific degree of plasticity in fish sonic mechanisms. In terrestrial habitats, the range of acoustic

461   resources used by a species determines the geographical area it can occupy and its vulnerability to environmental

462   changes (e.g., habitat loss and climate changes, see Slatyer, Hirst & Sexton, 2013). Additional studies are needed

463   to shed light on the relationship between sound-producing mechanisms and acoustic Niche plasticity across

464   different teleosts species. Furthermore, there is a need to verify if the range of acoustic resources used by a fish

465   species determines the geographical area it can occupy and its vulnerability to environmental changes in our

466   quickly changing seas.

467

475   **7. References**

476   Alós, J. & Cabanellas-Reboredo, M. (2012). Experimental acoustic telemetry experiment reveals strong site

477   fidelity during the sexual resting period of wild brown meagre, *Sciaena umbra*. *Journal of Applied*

478   *Ichthyology*, 28(4), 606-611. https://doi.org/10.1111/j.1439-0426.2012.01955.x

479   Amorim, M.C.P. (2006). Diversity of sound production in fish. In: F. Ladich, S.P. Collin, P. Moller, B.G. Kapoor

480   (Eds.) *Communication in fishes*. Enfield, NH: Science Publishers, pp.71-104.

481   https://doi.org/10.1007/978-3-7091-1846-7

482   Amorim, M.C.P., Vasconcelos, R.O. & Fonseca, P.J. (2015). Fish sounds and mate choice. In: F. Ladich (Eds.)

483   *Sound communication in fishes*. Vienna, AT: Springer, pp. 1-33. https://doi.org/10.1007/978-3-7091-

484   1846-7_1

485   Amorim, M.C.P., Vasconcelos, R.O., Bolgan, M., Pedroso, S.S. & Fonseca, P. J. (2018). Acoustic communication

486   in marine shallow waters: testing the acoustic adaptive hypothesis in sand gobies. *Journal of*

487   *Experimental Biology*, 221(22), jeb183681. https://doi.org/10.1242/jeb.183681

488   Arvanitidis, C., Bellan, G., Drakopoulos, P., Valanavis, V., Dounas, C., Koukouras, A. et al. (2002). Seascape

489   biodiversity patterns along the Mediterranean and the Black Sea: lessons from the biogeography of

490   benthic polychaetes. *Marine Ecology Progress Series*, 244, 139–152.

491   https://doi.org/10.3354/meps244139

492   Bertucci, F., Maratrat, K., Berthe, C., Besson, M., Guerra, A. S., Raick, X. et al. (2020). Local sonic activity reveals

493   potential partitioning in a coral reef fish community. *Oecologia*, 193(1), 125-134.

494   https://doi.org/10.1007/s00442-020-04647-3

495   Bianchi, C.N. & Morri, C. (2000). Marine biodiversity of the Mediterranean Sea: situation, problems and prospects

496   for future research. *Marine Pollution Bulletin*, 40, 367–376. https://doi.org/10.1016/S0025-

497   326X(00)00027-8

498   Bolgan, M., Soulard, J., Di Iorio, L., Gervaise, C., Lejeune, P., Gobert, S. et al. (2019). Sea chordophones make

499   the mysterious / Kwa / sound : identification of the emitter of the dominant fish sound in Mediterranean

500   seagrass meadows. *Journal of Experimental Biology*, 222(11), jeb196931.

501   https://doi.org/10.1242/jeb.196931

502   Bolgan, M., Gervaise, C., Di Iorio, L., Lossent, J., Lejeune, P., Raick, X. et al. (2020). Fish biophony in a

503   Mediterranean submarine canyon. *The Journal of the Acoustical Society of America*, 147(4), 2466-2477.

504   https://doi.org/10.1121/10.0001101

505   Bonacito, C., Costantini, M., Picciulin, M., Ferrero, E.A. & Hawkins, A.D. (2002). Passive hydrophone census of

506   *Sciaena umbra* (Sciaenidae) in the Gulf of Trieste (Northern Adriatic sea, Italy). *Bioacoustics*, 12, 292–

507   294. https://doi.org/10.1080/09524622.2002.9753726

508   Carriço, R., Silva, M.A., Menezes, G.M., Vieira, M., Bolgan, M., Fonseca, P.J. et al. (2020). Temporal dynamics

509   in diversity patterns of fish sound production in the Condor seamount (Azores, NE Atlantic). *Deep Sea

510   Research Part I: Oceanographic Research Papers*, 164, 103357.

511   https://doi.org/10.1016/j.dsr.2020.103357

512   Ceraulo, M., Papale, E., Caruso, F., Filiciotto, F., Grammauta, R., Parisi, I. et al. (2018). Acoustic comparison of

513   a patchy Mediterranean shallow water seascape: *Posidonia oceanica* meadow and sandy bottom habitats.

514   *Ecological Indicators*, 85, 1030-1043. https://doi.org/10.1016/j.ecolind.2017.08.066

515   Chhaya, V., Lahiri, S., Jagan, M.A., Mohan, R., Pathaw, N.A. & Krishnan, A. (2021). Community Bioacoustics:

516   Studying acoustic community structure for ecological and conservation insights. *Frontiers in Ecology

517   and Evolution*, 488. https://doi.org/10.3389/fevo.2021.706445

518   Chao, L. (2015). *Sciaena umbra*. *The IUCN Red List of Threatened Species*. e.T198707A83232286.

519   https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T198707A83232286.en.

520 Codarin, A., Wysocki, L.E., Ladich, F. & Picciulin, M. (2009). Effects of ambient and boat noise on hearing and
521   communication in three fish species living in a marine protected area (Miramare, Italy). *Marine pollution*
522   *bulletin*, 58(12), 1880-1887. https://doi.org/10.1016/j.marpolbul.2009.07.011

523 Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B.R., Aguzzi, J. et al. (2010). The biodiversity of the
524   Mediterranean   Sea: estimates,   patterns,   and   threats.   *PloS   one*,   5(8),   e11842.
525   https://doi.org/10.1371/journal.pone.0011842

526 Colwell, R.K. & Futuyma, D.J. (1971). On the measurement of niche breadth and overlap. *Ecology*, 52, 567–576.
527   https://doi.org/10.2307/1934144

528 De Raedemaecker, F., Miliou, A. & Perkins, R. (2010) Fish community structure on littoral rocky shores in the
529   Eastern Aegean Sea: Effects of exposure and substratum. *Estuarine, Coastal and Shelf Science*, 90, 35–
530   44. https://doi.org/10.1016/j.ecss.2010.08.007

531 Desiderà, E., Guidetti, P., Panzalis, P., Navone, A., Valentini-Poirrier, C.A., Boissery, P. et al. (2019). Fish
532   acoustic communities: sound diversity of rocky habitats reflects fish species diversity. *Marine Ecology*
533   *Progress Series*, 608, 183-197. https://doi.org/10.3354/meps12812

534 Deudero, S., Morey, G., Frau, A., Moranta, J. & Moreno, I. (2008). Temporal trends of littoral fishes at deep
535   Posidonia oceanica seagrass meadows in a temperate coastal zone. *Journal of Marine Systems*, 70(1-2),
536   182-195. https://doi.org/10.1016/j.jmarsys.2007.05.001

537 Díaz-Almela, E. & Duarte, C.M. (2008). *Management of Natura 2000 habitats; 1120, Posidonia beds (Posidonia*
538   *oceanica)*. Brussels, BE: European Commission Press.

539 Di Iorio, L., Raick, X., Parmentier, E., Boissery, P., Valentini-Poirrier, C.A. & Gervaise, C. (2018). 'Posidonia
540   meadows calling': a ubiquitous fish sound with monitoring potential. *Remote Sensing in Ecology and*
541   *Conservation*, 4(3), 248-263. https://doi.org/10.1002/rse2.72

542 Di Iorio, L., Bonhomme, P., Michez, N., Ferrari, B., Gigou, A., Panzalis, P. et al. (2020). Spatio-temporal surveys
543   of the brown meagre *Sciaena umbra* using passive acoustics for management and conservation. *BioRxiv*,
544   https://doi.org/10.1101/2020.06.03.131326

545 Di Iorio, L., Audax, M., Deter, J., Holon, F., Lossent, J., Gervaise, C. et al. (2021). Biogeography of acoustic
546   biodiversity   of   NW   Mediterranean   coralligenous   reefs.   *Scientific   Reports*,   11(1),   1-10.
547   https://doi.org/10.1038/s41598-021-96378-5

548   Dulčić, J., Matíc-Skoko, S., Kraljevic, M., Franicevic, M. & Lipej, L. (2002). New data on the cuskeel, *Ophidion*

549   *rochei* (Osteichthyes: Ophidiidae), from the eastern Adriatic. *Journal of the Marine Biological*

550   *Association of the United Kingdom*, 82, 1045-1046. https://doi.org/10.1017/S0025315402006665

551   Dulčić, J., Fencil, M., Matíc -Skoko, S., Kraljevic, M. & Glamuzina, B. (2004). Diel catch variations in a shallow-

552   water fish assemblage at Duce Glava, eastern Adriatic (Croatian Coast). *Journal of the Marine Biological*

553   *Association of the United Kingdom*, 84, 659-664. https://doi.org/10.1017/S0025315404009701h

554   Encarnação, J., Morais, P., Baptista, V., Cruz, J. & Teodósio, M.A. (2019). New Evidence of Marine Fauna

555   Tropicalization off the Southwestern Iberian Peninsula (Southwest Europe). *Diversity*, 2019, 11(4): 48.

556   https://doi.org/10.3390/d11040048

557   Ey, E. & Fischer, J. (2009). The "acoustic adaptation hypothesis"—a review of the evidence from birds, anurans

558   and mammals. *Bioacoustics*, 19(1-2), 21-48. https://doi.org/10.1080/09524622.2009.9753613

559   Fabi, G., Manoukian, S. & Spagnolo, A. (2006). Feeding behavior of three common fishes at an artificial reef in

560   the northern Adriatic Sea. *Bulletin of Marine Science*, 78(1), 39-56.

561   Farina, A. & James, P. (2016). The acoustic communities: Definition, description and ecological role. *Biosystems*,

562   147, 11–20. https://doi.org/10.1016/j.biosystems.2016.05.011

563   Fine, M. L., & Parmentier, E. (2015). Mechanisms of fish sound production. In: F. Ladich (Eds.) *Sound*

564   *communication in fishes*. Vienna, AT: Springer, pp. 77-126. https://doi.org/10.1007/978-3-7091-1846-

565   7_3

566   Gaertner, J.C., Bertrand, J.A., Relini, G., Papaconstantinou, C., Mazouni, N., De Sola, L.G. et al. (2007). Spatial

567   pattern in species richness of demersal fish assemblages on the continental shelf of the northern

568   Mediterranean Sea: a multiscale analysis. *Marine Ecology Progress Series*, 341, 191-203.

569   https://doi.org/10.3354/meps341191

570   Granger, V., Fromentin, J.M., Bez, N., Relini, G., Meynard, C.N., Gaertner, J.C. et al. (2015). Large-scale spatio-

571   temporal monitoring highlights hotspots of demersal fish diversity in the Mediterranean Sea. *Progress in*

572   *oceanography*, 130, 65-74. https://doi.org/10.1016/j.pocean.2014.10.002

573   Hastings, P.A. & Širović, A. (2015). Soundscapes offer unique opportunities for studies of fish communities.

574   *Proceedings of the National Academy of Sciences*, 112(19), 5866-5867.

575   https://doi.org/10.1073/pnas.1505897112

576   Juanes, F. (2018). Visual and acoustic sensor for early detection of biological invasions: Current uses and future

577   potential. *Journal for Nature Conservation*, 42, 7–11. https://doi.org/10.1016/j.jnc.2018.01.003

578 Katsanevakis, S., Zenetos, A., Belchior, C. & Cardoso, A.C. (2013). Invading European Seas: assessing pathways

579   of introduction of marine aliens. *Ocean and Coastal Management*, 76, 64–74.

580   https://doi.org/10.1016/j.ocecoaman.2013.02.024

581 Keskin, C. (2007). Temporal Variation of Fish Assemblages in Different Shallow-water Habitats in Erdek Bay,

582   Marmara Sea, Turkey. *Journal of the Black Sea/Mediterranean Environment*, 13(3), 215-234.

583 Kéver, L., Boyle, K.S., Dragičević, B., Dulčić, J., Casadevall, M. & Parmentier, E. (2012). Sexual dimorphism of

584   sonic apparatus and extreme intersexual variation of sounds in *Ophidion rochei* (Ophidiidae): first

585   evidence of a tight relationship between morphology and sound characteristics in Ophidiidae. *Frontiers*

586   *in Zoology*, 9(1), 1-16. https://doi.org/10.1186/1742-9994-9-34

587 Kéver, L., Colleye, O., Herrel, A., Romans, P. & Parmentier, E. (2014). Hearing capacities and otolith size in two

588   ophidiiform species (*Ophidion rochei* and *Carapus acus*). *Journal of Experimental Biology*, 217(14),

589   2517-2525. https://doi.org/10.1242/jeb.105254

590 Kéver, L., Boyle, K.S. & Parmentier, E. (2015) Effects of seawater temperature on sound characteristics in

591   *Ophidion rochei* (Ophidiidae). *Journal of Fish Biology*, 87(2), 502-509. https://doi.org/10.1111/jfb.12730

592 Kéver, L., Lejeune, P., Michel, L.N. & Parmentier, E. (2016). Passive acoustic recording of *Ophidion rochei*

593   calling activity in Calvi Bay (France). *Marine Ecology*, 37(6), 1315–1324.

594   https://doi.org/10.1111/maec.12341

595 Kleitou, P., Hall-Spencer, J. M., Savva, I., Kletou, D., Hadjistylli, M., Azzurro, E. et al. (2021) The case of Lionfish

596   (*Pterois miles*) in the Mediterranean Sea demonstrates limitations in EU Legislation to address marine

597   biological invasions. *Journal of Marine Science and Engineering*, 9(3), 325.

598   https://doi.org/10.3390/jmse9030325

599 Krause, B.L. (1993). The niche hypothesis: a virtual symphony of animal sounds, the origins of musical expression

600   and the health of habitats. *Soundscape Newsletter*, 6, 6–10.

601 La Mesa, G.L., Muccio, S.D. & Vacchi, M. (2005). Structure of a Mediterranean cryptobenthic fish community

602   and its relationships with habitat characteristics. *Marine Biology*, 149, 149–167.

603   https://doi.org/10.1007/s00227-005-0194-z

604 Ladich, F. (2018). Acoustic communication in fishes: temperature plays a role. Fish and Fisheries, 19(4), 598-612.

605   https://doi.org/10.1111/faf.12277

606   Lasram, F.B.R., Guilhaumon, F. & Mouillot, D. (2009). Fish diversity patterns in the Mediterranean Sea:
607   deviations from a mid-domain model. *Marine Ecology Progress Series*, 376, 253-267.
608   https://doi.org/10.3354/meps07786

609   Lindseth, A.V. & Lobel, P.S. (2018). Underwater soundscape monitoring and fish bioacoustics: a review. *Fishes,*
610   3(3), 36. https://doi.org/10.3390/fishes3030036

611   Lugli, M., Yan, H.Y. & Fine, M. L. (2003). Acoustic communication in two freshwater gobies: the relationship
612   between ambient noise, hearing thresholds and sound spectrum. *Journal of Comparative Physiology A*,
613   189(4), 309-320. https://doi.org/10.1007/s00359-003-0404-4

614   McCauley, R.D. & Cato, D.H. (2000). Patterns of fish calling in a nearshore environment in the Great Barrier
615   Reef. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*,
616   355(1401), 1289-1293. https://doi.org/10.1098/rstb.2000.0686

617   Mönkkönen, M., Helle, P. & Soppela, K. (1990). Numerical and behavioral responses of migrant passerines
618   tomexperimental manipulation of resident tits (Parus spp): Heterospecific attraction in northern breeding
619   communities. *Oecologia*, 85, 218–225.

620   Mooney, T.A., Di Iorio, L., Lammers, M., Lin, T.H., Nedelec, S.L., Parsons, M. et al. (2020). Listening forward:
621   approaching marine biodiversity assessments using acoustic methods. *Royal Society open science*, 7(8),
622   201287. https://doi.org/10.1098/rsos.201287

623   Morton, E.S. (1975). Ecological sources of selection on avian sounds. *American Naturalist*, 109, 17–34.
624   https://doi.org/10.1086/282971

625   Mouillot, D., Albouy, C., Guilhaumon, F., Lasram, F.B.R., Coll, M., Devictor, V. et al. (2011). Protected and
626   threatened components of fish biodiversity in the Mediterranean Sea. *Current Biology*, 21(12), 1044-
627   1050. https://doi.org/10.1016/j.cub.2011.05.005

628   Mullet, T.C., Farina, A. & Gage, S. H. (2017). The acoustic habitat hypothesis: An ecoacoustics perspective on
629   species habitat selection. *Biosemiotics*, 10(3), 319-336. https://doi.org/10.1007/s12304-017-9288-5

630   Nielsen, J.G., Cohen, D.M., Markle, D.F. & Robins, C.R. (1999). Ophidiiform fishes of the world (Order
631   Ophidiiformes). An annotated and illustrated catalogue of pearlfishes, cusk-eels, brotulas and other
632   ophidiiform fishes known to date. FAO species catalogue, vol. 18. *FAO Fisheries Synopsis 125*: 18.
633   Rome, Italy.

634   Pallaoro, A. & Jardas, I. (1996). Ichthyological collection of the Institute of Oceanography and Fisheries in Split
635   (Croatia). *Natura Croatica,* 3, 177–219.

636   Parmentier, E., Bouillac, G., Dragičević, B., Dulčić, J. & Fine, M. (2010). Call properties and morphology of the

637   sound-producing organ in *Ophidion rochei* (Ophidiidae). *Journal of Experimental Biology*, 213(18),

638   3230-3236. https://doi.org/10.1242/jeb.044701

639   Parmentier, E., Diogo, R. & Fine, M. L. (2017). Multiple exaptations leading to fish sound production. *Fish and

640   fisheries*, 18(5), 958-966. https://doi.org/10.1111/faf.12217

641   Parmentier, E., Di Iorio, L., Picciulin, M., Malavasi, S., Lagardère, J.P. & Bertucci, F. (2018). Consistency of

642   spatiotemporal sound features supports the use of passive acoustics for long-term monitoring. *Animal

643   Conservation*, 21(3), 211-220. https://doi.org/10.1111/acv.12362

644   Parmentier, E., Bertucci, F., Bolgan, M. & Lecchini, D. (2021). How many fish could be vocal? An estimation

645   from a coral reef (Moorea Island). *Belgian Journal of Zoology*, 151, 1-29.

646   https://doi.org/10.26496/bjz.2021.82

647   Picciulin, M., Calcagno, G., Sebastianutto, L., Bonacito, C., Codarin, A., Costantini, M. et al. (2012). Diagnostics

648   of nocturnal calls of *Sciaena umbra* (L., fam. Sciaenidae) in a nearshore Mediterranean marine reserve.

649   *Bioacoustics*, 22(2), 109-120. https://doi.org/10.1080/09524622.2012.727277

650   Picciulin, M., Bolgan, M., Codarin, A., Fiorin, R., Zucchetta, M. & Malavasi, S. (2013). Passive acoustic

651   monitoring of *Sciaena umbra* on rocky habitats in the Venetian littoral zone. *Fisheries Research*, 145,

652   76–81. https://doi.org/10.1016/j.fishres.2013.02.008

653   Picciulin, M., Kéver, L., Parmentier, E. & Bolgan, M. (2019). Listening to the unseen: Passive acoustic monitoring

654   reveals the presence of a cryptic fish species. *Aquatic Conservation: Marine and Freshwater Ecosystems*,

655   29(2), 202–210. https://doi.org/10.1002/aqc.2973

656   Picciulin, M., Fiorin, R., Facca, C. & Malavasi, S. (2020). Sound features and acoustic rhythms as a proxy for

657   locating the spawning ground of *Sciaena umbra* in the wild. *Aquatic Conservation: Marine and

658   Freshwater Ecosystems*, 30(7), 1299-1312. https://doi.org/10.1002/aqc.3340

659   Poursanidis, D., Kalogirou, S., Azzurro, E., Parravicini, V., Bariche, M. & Zu Dohna, H. (2020). Habitat

660   suitability, niche unfilling and the potential spread of *Pterois miles* in the Mediterranean Sea. *Marine

661   Pollution Bulletin*, 154, 111054. https://doi.org/10.1016/j.marpolbul.2020.111054

662   Quignard, J.P. & Tomasini, J.A. (2000). Mediterranean fish biodiversity. *Biologia Marina Mediterranea*, 7, 1–66.

663   Raick, X., Huby, A., Kurchevski, G., Godinho, A.L. & Parmentier, E. (2020). Use of bioacoustics in species

664   identification: Piranhas from genus Pygocentrus (Teleostei: Serrasalmidae) as a case study. *PloS one*,

665   15(10), e0241316. https://doi.org/10.1371/journal.pone.0241316

666   Rountree, R.A. & Juanes, F. (2016). Potential of passive acoustic recording for monitoring invasive species:

667   freshwater drum invasion of the Hudson River via the New York Canal System. *Biological Invasions*, 19,

668   2075-2088. https://doi.org/10.1007/s10530-017-1419-z

669   Rountree, R.A., Juanes, F. & Bolgan, M. (2020). Temperate freshwater soundscapes: A cacophony of undescribed

670   biological sounds now threatened by anthropogenic noise. *PloS one*, 15(3), e0221842.

671   https://doi.org/10.1371/journal.pone.0221842

672   Ruppé, L., Clément, G., Herrel, A., Ballesta, L., Décamps, T., Kéver, L. et al. (2015). Environmental constraints

673   drive the partitioning of the soundscape in fishes. *Proceedings of the National Academy of Sciences*,

674   112(19), 6092-6097. https://doi.org/10.1073/pnas.1424667112

675   Schärer-Umpierre, M.T., Zayas, C., Appeldoorn, R.S., Tuohy, E., Olson, J.C., Keller, J.A. et al. (2019). The Purr

676   of the Lionfish: Sound and Behavioral Context of Wild Lionfish in the Greater Caribbean. *Gulf and*

677   *Caribbean Research*, 30(1), GCFI15-GCFI19. https://doi.org/10.18785/gcr.3001.17

678   Sinsch, U., Lümkemann, K., Rosar, K., Schwarz, C. & Dehling, M. (2012). Acoustic niche partitioning in an

679   anuran community inhabiting an Afromontane wetland (Butare, Rwanda). *African Zoology*, 47(1), 60-73.

680   https://doi.org/10.1080/15627020.2012.11407524

681   Slatyer, R.A., Hirst, M. & Sexton, J. P. (2013). Niche breadth predicts geographical range size: a general ecological

682   pattern. *Ecology letters*, 16(8), 1104-1114. https://doi.org/10.1111/ele.12140

683   Sueur, J., Pavoine, S., Hamerlynck, O. & Duvail, S. (2008). Rapid acoustic survey for biodiversity appraisal. *PloS*

684   *one*, 3(12), e4065. https://doi.org/10.1371/journal.pone.0004065

685   Sugai, L.S.M. & Llusia, D. (2019). Bioacoustic time capsules: Using acoustic monitoring to document

686   biodiversity. *Ecological indicators*, 99, 149-152. https://doi.org/10.1016/j.ecolind.2018.12.021

687   Sugai, L.S.M., Llusia, D., Siqueira, T. & Silva, T.S. (2021). Revisiting the drivers of acoustic similarities in tropical

688   anuran assemblages. *Ecology,* e03380. https://doi.org/10.1002/ecy.3380

689   Tellechea, J. S., Bouvier, D. & Norbis, W. (2011). Spawning sounds in whitemouth croaker (Sciaenidae): seasonal

690   and daily cycles. *Bioacoustics*, 20(2), 159-168. https://doi.org/10.1080/09524622.2011.9753641

691   Thomisch, K., Boebel, O., Zitterbart, D.P., Samaran, F., Van Parijs, S. & Van Opzeeland, I. (2015). Effects of

692   subsampling of passive acoustic recordings on acoustic metrics. *The Journal of the Acoustical Society of*

693   *America*, 138(1), 267-278. https://doi.org/10.1121/1.4922703

694   Tricas, T. C. & Boyle, K. S. (2014). Acoustic behaviors in Hawaiian coral reef fish communities. *Marine Ecology*

695   *Progress Series*, 511, 1-16. https://doi.org/10.3354/meps10930

696   Urick, R.J. (1986) *Ambient noise in the sea*. Los Altos, CA: Peninsula Publishing.

697   Wilkins, M.R., Seddon, N. & Safran, R.J. (2013). Evolutionary divergence in acoustic signals: causes and

698   consequences. *Trends in ecology & evolution*, 28(3), 156-166. https://doi.org/10.1016/j.tree.2012.10.002

699   Wilson, K.C., Semmens, B.X., Pattengill-Semmens, C.V., McCoy, C. & Širović, A. (2020). Potential for grouper

700   acoustic competition and partitioning at a multispecies spawning site off Little Cayman, Cayman Islands.

701   *Marine Ecology Progress Series*, 634, 127-146. https://doi.org/10.3354/meps13181

702

703

704

705

706

707

708

709

710

711

712

713

714

8. Tables

Table 1 Glossary

Acoustic community	Aggregation of species that produces sounds for communication and compete for the allocation of acoustic resources in a specific habitat (Mönkkönen, Helle & Soppela, 1990; Farina & James, 2016). As with an ecological community, acoustic communities may be defined at different spatial and taxonomic scales (Chhaya et al. 2021)
Acoustic diversity	Concept adapted from traditional ecology; number and relative abundance of sound types found in a given biological organisation. Acoustic diversity can be measured by applying traditional diversity indexes (e.g. Shannon, Simpson, richness etc) to acoustic data.
Acoustic richness	Simplest measure of acoustic diversity; number of sound types in a given area or community.
Acoustic community composition	Relative occurrence of each sound type in a given area or community.
Acoustic community structure	The organization of an acoustic community, including species composition, distribution of species in the signal space and spatial and temporal organization of signalling species (Chhaya et al. 2021)
Acoustic resources	Resource partitioning, in traditional ecology, is the division of limited resources by species to help avoid competition. In acoustic communities, acoustic resources refers to) diel timing of calling activity; ii) call spectral features, and iii) call temporal features.
Acoustic niche	Multidimensional abstraction encompassing spectral and temporal features of a sound type, as well as its diel pattern of occurrence. The realised acoustic niche corresponds to the range of acoustic resources (i.e., utilised resources classes) exploited by a specific sound type along three axes: i) diel timing of calling activity; ii) call spectral features, and iii) call temporal features.
Acoustic niche specialisation	Acoustic niche compression: the highest level of resource specialization occurs when only one resource class is exploited (Colwell & Futuyma, 1971; Sinsch et al., 2012).
Biophony	All sounds that vocalizing non-human animals emit in each given environment.
Signal divergence	Signal divergence minimizes competitive overlap along multiple axes. This can include *i)* divergent signal parameters; *ii)* temporal and *iii)* spatial segregation in signalling activity (Chhaya et al. 2021)
Signal space	The range of acoustic resources exploited by the whole acoustic community, where each species occupies a specific volume (Chhaya et al. 2021).

Table 2 Recording sites, geographical coordinates and depth, deployment and retrieval dates and chosen duty cycle (listening periods/cycle period)

Site	Site specifications	Lat	Long	Depth (m)	Deployment day	Retrieval day	Duty cycle
Mallorca	Palma Bay Marine Reserve	N 39° 27.885	E 002° 43.331	20	22-Jun-2017	18-Aug-2017	1/11
Corsica	Calvi: STARESO research station	N 42° 34.809	E 008° 43.566	20	01-Jun-2017	15-Aug-2017	1/11
Crete	Underwater Biotechnological Park of Crete	N 35° 20.749	E 025° 16.722	20	04-Jul-2017	28-Jul-2017	1/11

Table 3 Detailed explanation of the ordinal scale used to estimate the relative abundance of each sound type **(**chorus=mass production of sounds in which single sounds are not distinguishable)

Relative abundance	*Sciaena umbra* sounds	/Kwa/ sounds	*Ophidion rochei* and all other sound types
0	No sound production	No sound production	No sound production
1	< 7 sounds $\times min^{-1}$	$< 10 \times min^{-1}$	1 sound $\times min^{-1}$
2	$7 <$ sounds $< 15 \times min^{-1}$	$10 <$ sounds $< 50 \times min^{-1}$	2 to 4 sounds $\times min^{-1}$
3	> 15 sounds $\times min^{-1}$	Mass production of sounds in which the single sounds are still distinguishable.	> 4 sounds $\times min^{-1}$
4	Chorus	Chorus	Chorus

Table 4 Sound types: qualitative description and descriptive statistics. Pf= peak frequency (Hz), BW= bandwidth (Hz), Freq 5%= 5% Frequency (Hz), Freq 95%= 95% Frequency (Hz), DUR= duration (ms), NP= number of pulses and PP= Pulse period (ms). Sd= Standard Deviation, na= not available. For measured acoustic features definition, refer to Sup. Table 2.

Sound type name	Sound type general description	Sites	N		Spectral features				Temporal features				
					Pf	BW	Freq 5%	Freq 95%	Dur	NP	PP	long PP *	short PP *
/Kwa/	Pulsed sound with short pulse periods. Amplitude modulated waveform (periodic envelope), visible in the spectrogram as pseudo-harmonics around a 800 Hz contour. Arched-shaped frequency contour, with similar start and end frequencies and ca. 70 Hz higher centre frequency (Di Iorio et al. 2018)	All sites	150	Mean	887	572	774	1249	158	12	11		
				Sd	128	454	115	417	83	6	2		
				Min	688	149	586	869	50	3	8		
				Max	1177	2082	1048	2756	424	30	14		
***Ophidion rochei* sound**	Pulse period and amplitude increase gradually during the first pulses, separating the call into two parts. The pulse period in call part 2 alternates between short and long periods (Parmentier et al. 2010)	All sites	150	Mean	328	327	136	461	3896	40	na	111	93
				Sd	95	93	32	73	1741	12	na	21	20
				Min	195	172	63	344	1089	13	na	83	65
				Max	595	611	201	611	1912	89	na	159	134
***Sciaena umbra* sounds**	Pulse series with main energy content below 1 kHz and mean peak frequency below 350 Hz, lasting approximately 500 ms and made of 4 pulses on average (2 to 12 pulses range) (Picciulin et al. 2013)	All sites	150	Mean	346	369	112	482	526	6	93		
				Sd	92	53	29	37	157	2	18		
				Min	70	273	70	445	243	2	70		
				Max	587	493	172	595	859	13	130		
LFPT **Low-frequency Fast Pulse Train**	Pulse train with very short, aurally undetectable pulse periods, with peak frequency below 200 Hz (Desiderà et al. 2019)	Corsica	5	Mean	128	831	135	966	98	16	7		
				Sd	4	211	25	189	25	6	1		
				Min	125	594	117	758	77	10	6		
				Max	133	1000	164	1125	126	21	8		
	Pulse train with very short, aurally undetectable pulse periods, with		5	Mean	447	452	141	602	71	11	7		

Type	Description	Location	N	Stat								
FPT **Fast Pulse Train**	peak frequency above 200 Hz (Desiderà et al. 2019)	Crete		*Sd*	15	80	16	79	1	1	0.5		
				Min	420	327	120	503	70	10	7		
				Max	455	549	164	725	72	11	8		
PS1 **Pulse Series 1**	Sequence of similar pulses (at least 3) with pulse period above 80 ms and peak frequency above 600 Hz	Crete	5	*Mean*	791	885	251	1135	448	4	140		
				Sd	0	0	0	0	7	0	10		
				Min	791	885	251	1135	440	4	125		
				Max	791	885	251	1135	454	4	148		
PS2 **Pulse Series 2**	Sequence of similar pulses (at least 3) with pulse period below 60 ms and peak frequency above 300 Hz	Mallorca	3	*Mean*	368	336	70	407	265	10	54		
				Sd	0	0	0	0	0	0	0		
				Min	368	336	70	407	265	10	54		
				Max	368	336	70	407	265	10	54		
PS3 **Pulse Series 3**	Sequence of similar pulses (at least 3) with pulse period above 80 ms and peak frequency below 400 Hz	Crete	12	*Mean*	367	389	187	576	648	10	86		
				Sd	8	102	54	66	181	2	2		
				Min	359	316	57	502	331	6	83		
				Max	373	646	258	703	952	13	89		
PS4 **Pulse Series 4**	Sequence of similar pulses (at least 3) with quick pulse period (below 22 ms) and peak frequency above 900 Hz	Crete	5	*Mean*	909	2316	255	2603	118	12	17		
				Sd	231	912	216	726	8	5	5		
				Min	646	1263	104	1766	109	7	12		
				Max	1077	2842	502	3043	123	16	22		
PS5 **Pulse Series 5**	Sequence of similar pulses (at least 3) with pulse period above 200 ms and peak frequency between 400 and 600 Hz	Crete	5	*Mean*	496	1203	162	1365	1691	7	280		
				Sd	18	76	5	75	9	1	3		
				Min	486	1120	157	1284	1683	7	278		
				Max	517	1269	164	1433	1701	8	284		

Table 5 Generalized Linear Model results for testing site effect on call abundance of the three most common sound types,

/Kwa/, *Ophidion rochei* and *Sciaena umbra* sounds. Statistical significance is depicted (*).

	Intercept	Standard error	Wald statistic	P
/Kwa/	0.47	0.1	33.2	< 0.001*
O.rochei	1.44	0.1	198.2	< 0.001*
S.umbra	-0.59	1.1	0.3	0.588717

Table 6 Sound features comparison between sites of the three most common sound types, i.e. /Kwa/, *Ophidion rochei* and *Sciaena umbra* sounds (*N=150 sounds per sound type*). Pf= peak frequency (Hz), BW= bandwidth (Hz), Freq 5%= 5% Frequency (Hz), Freq 95%= 95% Frequency (Hz), DUR= duration (ms), NP= number of pulses and PP= Pulse period (ms). For *Ophidion rochei* only, pulse period was measured as short and long pulse period. H: Kruskal–Wallis; U: Mann-Whitney, statistical significances are depicted (*< 0.5; ** ≤ 0.001).

		Pf	BW	Freq 5%	Freq 95%	DUR	NP	PP	Short PP	Long PP
						Sound features				
/Kwa/	**H**	73	39	71	88	49	19	101	*n.a.*	*n.a.*
	p	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	0.001**	<0.001**	*n.a.*	*n.a.*
	U	779	431	974	500	601	802	401	*n.a.*	*n.a.*
	p	0.001**	<0.001**	0.07	<0.001**	<0.001**	<0.001**	<0.001**	*n.a.*	*n.a.*
	U	205	532	212	161	342	696	85	*n.a.*	*n.a.*
	p	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	<0.001**	*n.a.*	*n.a.*
	U	296	1282	256	199	787	1067	126	*n.a.*	*n.a.*
	p	<0.001**	0.91	<0.001**	<0.001**	<0.001**	0.12	<0.001**	*n.a.*	*n.a.*
O. rochei	**H**	81	83	4	90	104	73	*n.a.*	101	101
	p	<0.001**	<0.001**	0.1	<0.001**	<0.001**	<0.001**	*n.a.*	<0.001**	<0.001**
	U	283	149	*n.a.*	128	65	364	*n.a.*	75	53
	p	<0.001**	<0.001**	*n.a.*	<0.001**	<0.001**	<0.001**	*n.a.*	<0.001**	<0.001**
	U	743	593	*n.a.*	614	673	918	*n.a.*	661	631
	p	0.119	0.004*	*n.a.*	0.07	0.03*	0.952	*n.a.*	0.02*	0.02*
	U	102	208	*n.a.*	164	14	134	*n.a.*	43	37
	p	<0.001**	<0.001**	*n.a.*	<0.001**	<0.001**	<0.001**	*n.a.*	<0.001**	<0.001**
S.umbra	**U**	2316	1436	1873	1494	2273	1221	466	*n.a.*	*n.a.*
	p	0.141	<0.001**	<0.001**	<0.001**	0.101	<0.001**	<0.001**	*n.a.*	*n.a.*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Table 7 Principal Component Analysis (PCA) loadings on sound features of the three most abundant sound types, i.e. /Kwa/, *Ophidion rochei* and *Sciaena umbra* sounds; relevant coefficients, eigenvalues, percentage of the variance and cumulative percentage of the variance explained by the first five PCs. Pf= peak frequency (Hz), 5% Freq= 5% frequency; 95% Freq= 95% frequency DUR= duration (ms) and PP= Pulse period (ms; For *Ophidion rochei* only, short pulse period). The main contributors to the first two components (selected through Scree Plot) are highlighted.

Sound origin	Variable	PC1	PC2	PC3	PC4	PC5
/Kwa/	Pf	**0.500**	0.314	0.292	0.512	-0.552
	5% Freq	0.295	**0.788**	0.011	-0.442	0.310
	95% Freq	0.454	-0.171	-0.769	-0.254	-0.330
	DUR	-0.411	0.437	-0.565	0.558	0.094
	PP	**-0.537**	0.244	0.061	-0.408	-0.694
	Eigenvalue	2.556	1.059	0.651	0.496	0.236
	Percentage	51%	21%	13%	10%	5%
	Cumulative %	51%	72%	85%	95%	100%
Ophidion rochei	Pf	-0.451	-0.044	-0.872	0.031	-0.183
	5% Freq	-0.524	-0.272	0.117	-0.267	0.753
	95% Freq	0.239	**0.808**	-0.263	-0.172	0.438
	DUR	**0.484**	-0.368	-0.307	0.574	0.455
	Short PP	**0.481**	-0.369	-0.251	-0.754	-0.028
	Eigenvalue	2.880	1.161	0.534	0.248	0.174
	Percentage	58%	23%	10%	5%	4%
	Cumulative %	58%	81%	91%	96%	100%
Sciaena umbra	Pf	-0.206	**-0.500**	-0.813	0.121	-0.181
	5% Freq	0.500	-0.480	0.069	0.301	0.651
	95% Freq	**-0.622**	0.128	-0.121	-0.275	0.712
	DUR	0.165	**0.682**	-0.415	0.555	0.165
	PP	**0.542**	0.193	-0.384	-0.716	0.097
	Eigenvalue	2.156	1.464	0.804	0.375	0.201
	Percentage	43%	29%	16%	8%	4%
	Cumulative %	43%	72%	88%	96%	100%

9. Figures legend

Figure 1 Materials and methods; a) recording locations and b) dichotomous framework used for categorising fish sound types encountered in this study. Spectrograms were generated using Hanning window, FFT 512, 50% overlap, sample rate 4 kHz (frequency resolution 7.8 Hz).

Figure 2 Community composition in the three recording sites a) Mallorca, b) Corsica, c) Crete; temporal variation expressed as the percentage of different sound types assessed per clock hour. For the sound types abbreviation, refer to Table 4

Figure 3 Diel pattern of sound production (mean + standard deviation, SD) of the three most common sound types: /Kwa/= blue, *Ophidion rochei*= red and *Sciaena umbra*=green in the three recording locations (a= Mallorca, b=Corsica and c=Crete). See Sup. Figure 6 for a different visualization.

Figure 4 Score plot of the Principal Component Analysis (PCA, first and second component) carried out on the three most common sound types (a= /Kwa/, b= *Ophidion rochei* and c= *Sciaena umbra*, N=150 sounds per sound type) recorded in the three locations (Mallorca= dark blue, Corsica= pink and Crete=light blue). Variables included in the PCA: peak frequency, 5% frequency, 95% frequency, duration and pulse period (correlation matrix, see Table 7)

Figure 5 Fish acoustic community diversity across sites; a) Sample-based accumulation curves for sound types (mean number of new sound types observed for each sampling unit accumulated up to the total sample size); b) acoustic richness; c) Shannon index calculated on sound types and d) Simpson reciprocal diversity index calculated on sound types (Mallorca= dark blue, Corsica= pink and Crete=light blue)

Figure 6 Sound types realised acoustic niche and community signal space across sites. Each vertical panel represents one resource axis (Axis I= diel timing of calling activity, 24 resource classes; Axis II= call spectral features, 11 resource classes and Axis III= call temporal features, 17 resource classes). Each horizontal panel represents one location (Mallorca= dark blue, Corsica= pink and Crete=light blue). Data for each axis and for each location were entered in a resource matrix, where each row represents a sound type (visible on the right, for sound type abbreviation refer to Table 4), and each column represents one resource class. For each sound type and for all axes, the number of sounds falling in each resource class is displayed with a colour scale (in relative percentage). The realised acoustic niche of a sound type is given by the range of acoustic resources (i.e. utilised resources classes) exploited by that sound type along three axes (multidimensional abstraction). Similarly, the community signal space is given by the range of acoustic resources exploited by the whole community along the three axes.
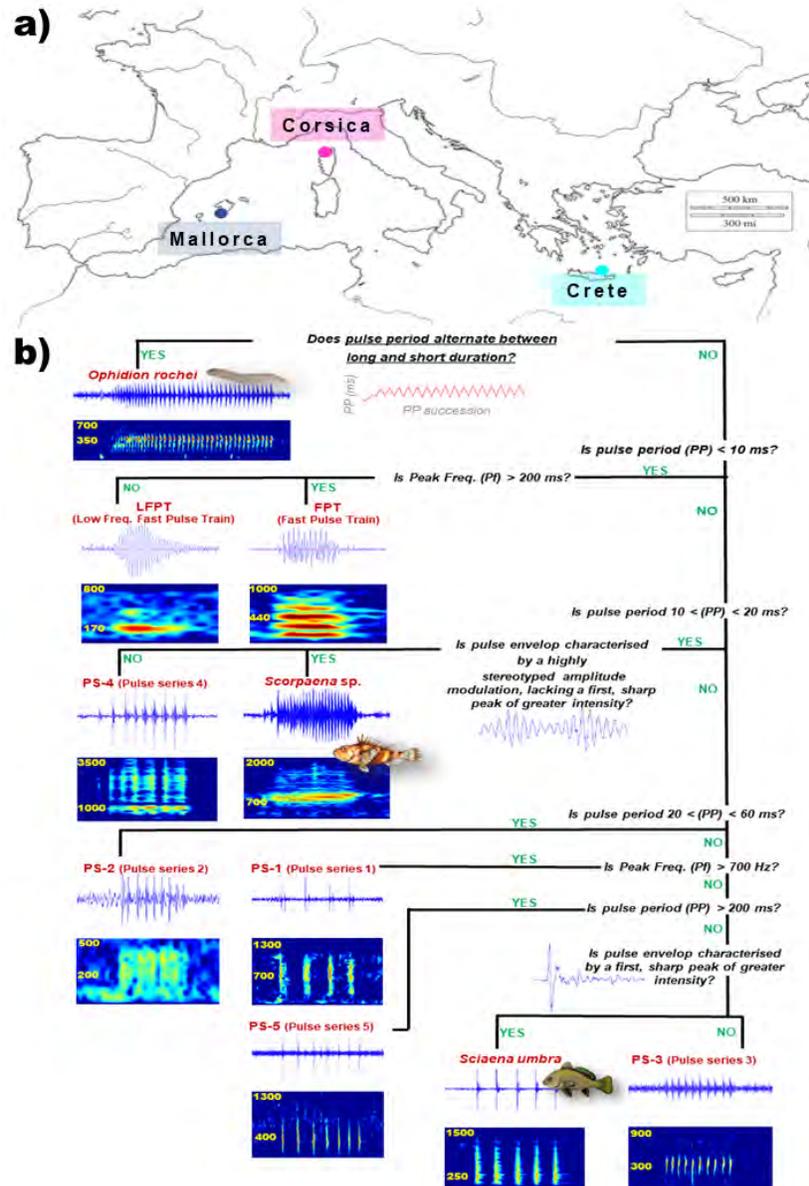
Figure 1 Materials and methods; a) recording locations and b) dichotomous framework used for categorising fish sound types encountered in this study

190x275mm (96 x 96 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
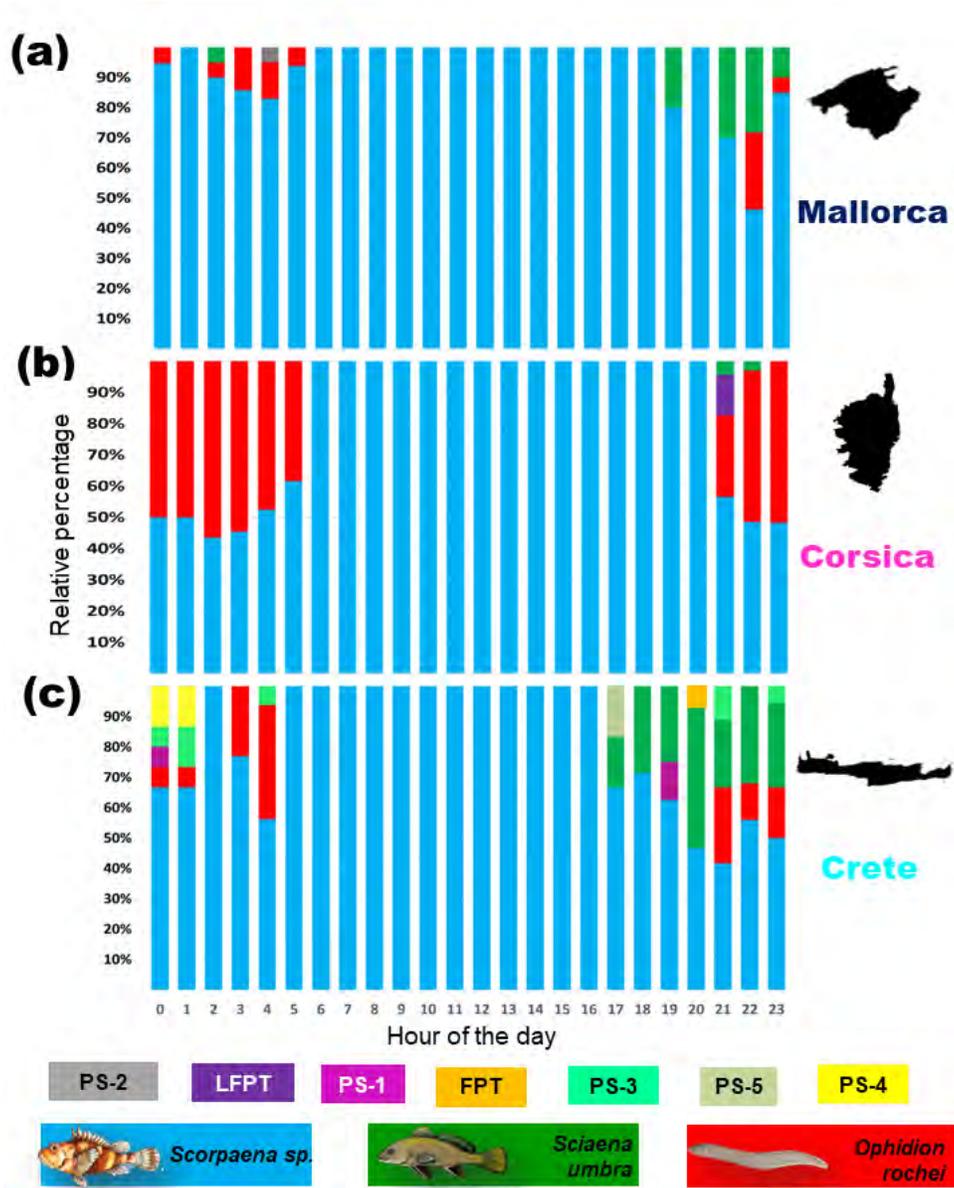43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Fig. 2 Community composition in the three recording sites a) Mallorca, b) Corsica, c) Crete; temporal variation expressed as the percentage of different sound types assessed per clock hour. For the sound types abbreviation, refer to Table 3
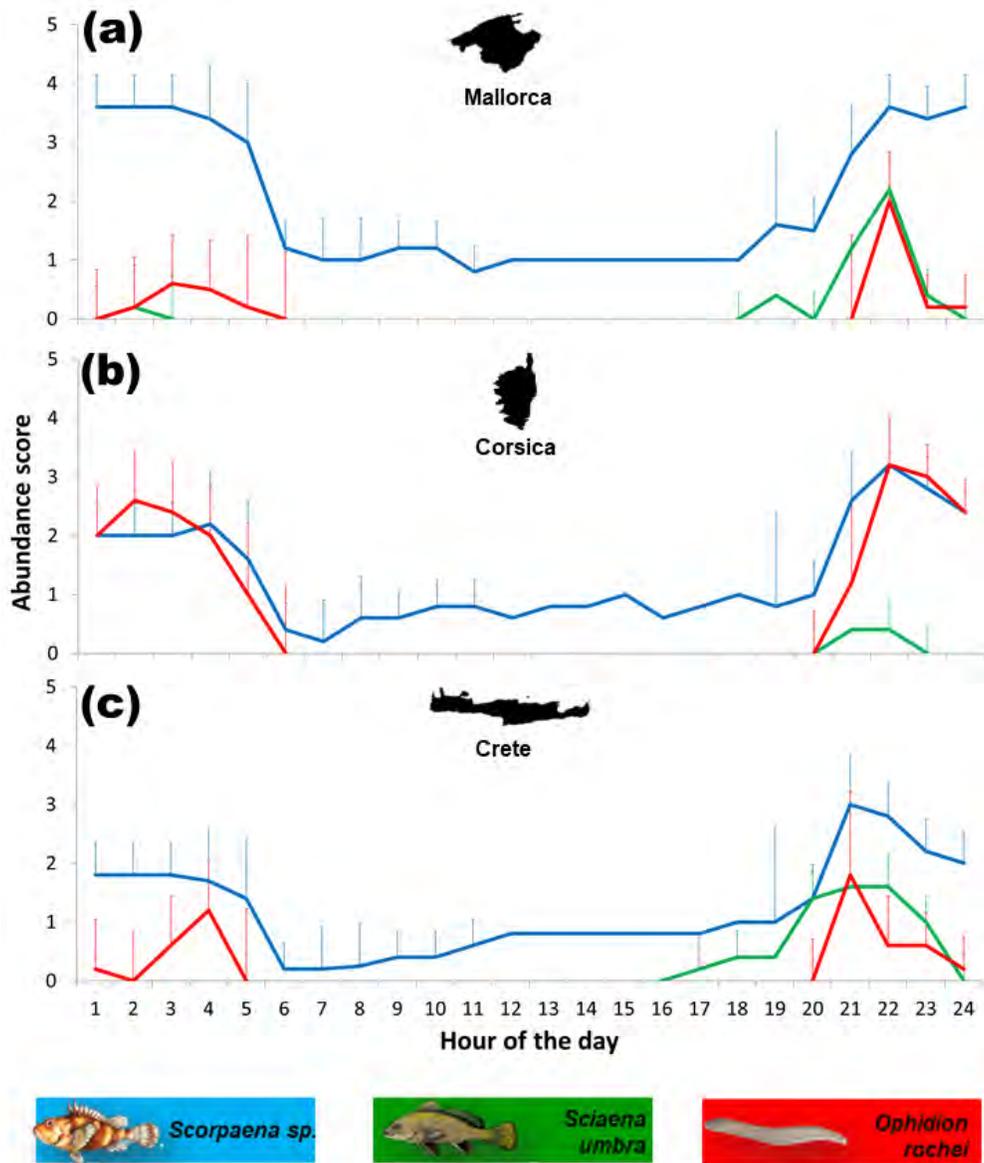
190x236mm (96 x 96 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Fig. 3 Diel pattern of sound production (mean +SD) of the three most common sound types (i.e. /Kwa/= blue, Ophidion rochei= red and Sciaena umbra=green) in the three recording locations (a= Mallorca, b=Corsica and c=Crete)

190x229mm (96 x 96 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
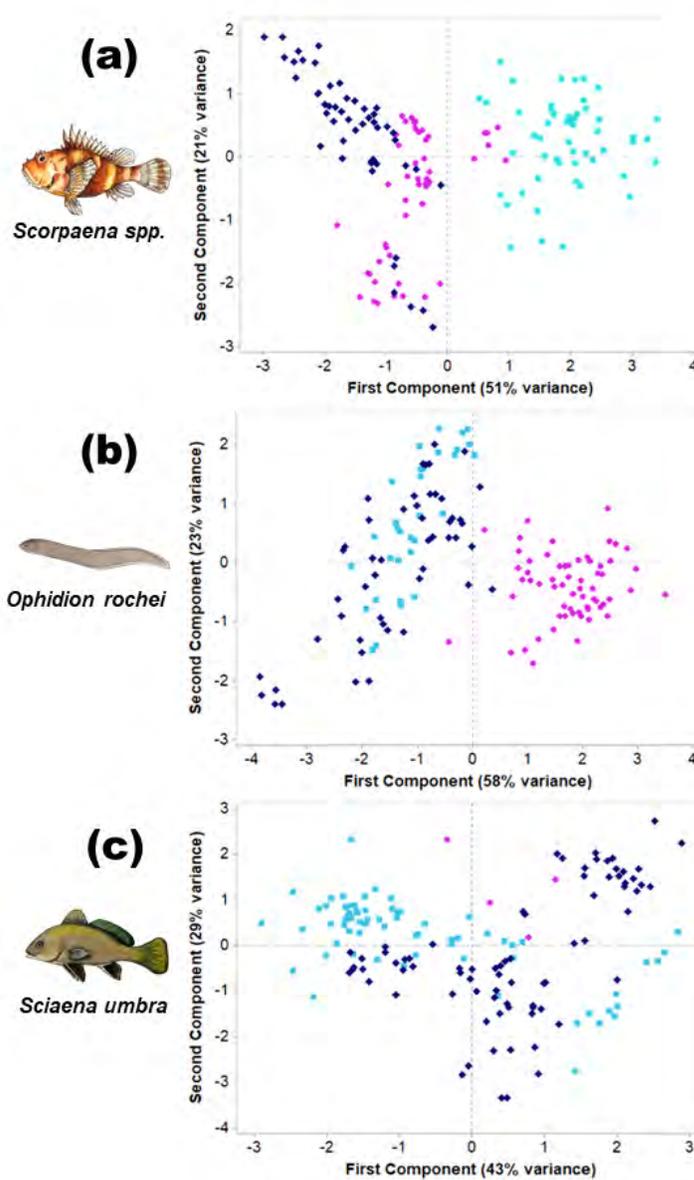42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Fig. 4 Score plot of the Principal Component Analysis (PC1 and PC2) carried out on the three most common sound types (a= /Kwa/, b= Ophidion rochei and c= Sciaena umbra, N=150 sounds per sound type) recorded in the three locations (Mallorca= dark blue, Corsica= pink and Crete=light blue). Variables included in the PCA: peak frequency, 5% frequency, 95% frequency, duration and pulse period (correlation matrix, see Table 6)

156x241mm (96 x 96 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
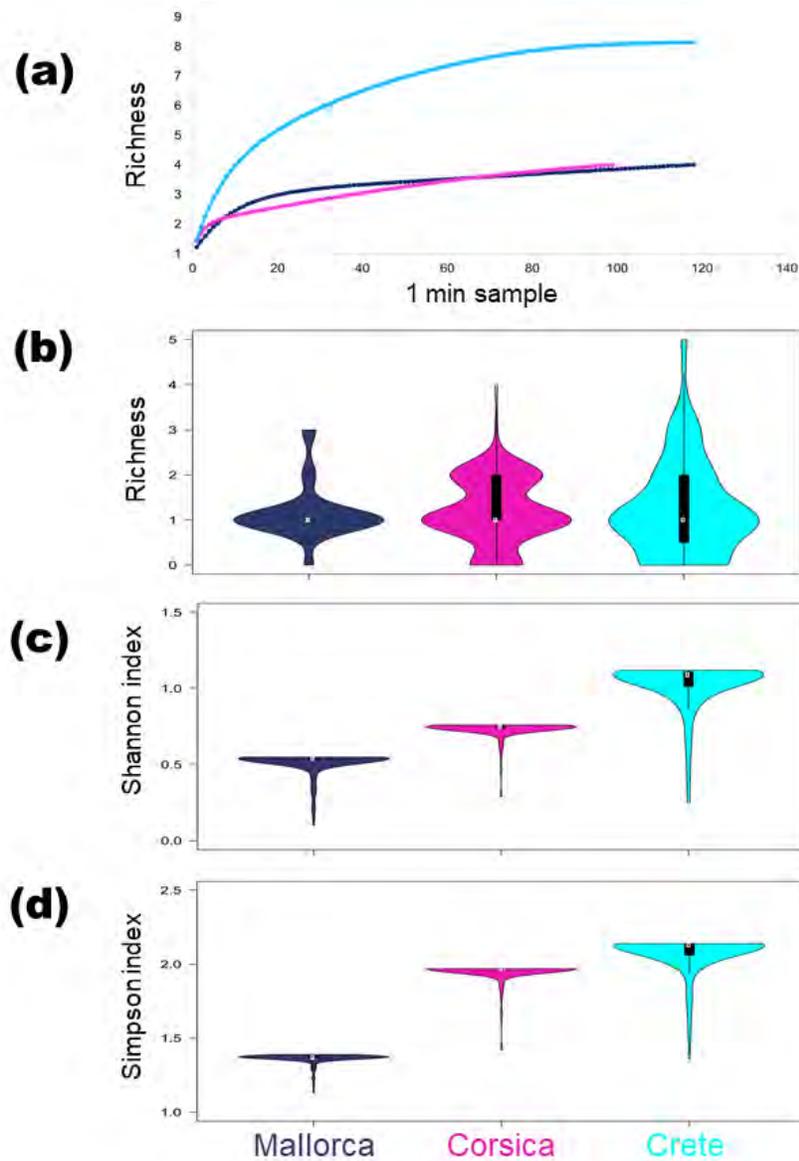43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Fig 5 Fish acoustic community diversity across sites; a) Sample-based accumulation curves for sound types; b) acoustic richness; c) Shannon index calculated on sound types and d) Simpson index calculated on sound types (Mallorca= dark blue, Corsica= pink and Crete=light blue)

167x233mm (96 x 96 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
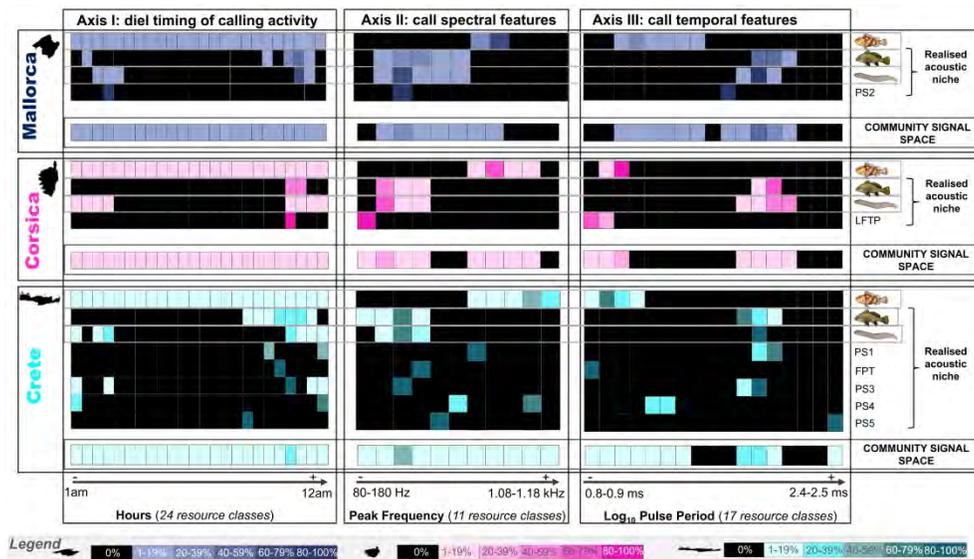22
23
24
25
26
27
28
29
30

Fig 6 Sound types realised acoustic niche and community signal space across sites. Each vertical panel represents one resource axis (Axis I= diel timing of calling activity, 24 resource classes; Axis II= call spectral features, 11 resource classes and Axis III= call temporal features, 17 resource classes). Each horizontal panel represents one location (Mallorca= dark blue, Corsica= pink and Crete=light blue). Data for each axis and for each location were entered in a resource matrix, where each row represents a sound type (visible on the right, for sound type abbreviation refer to Table 3), and each column represents one resource class. For each sound type and for all axes, the number of sounds falling in each resource class is displayed with a colour scale (in relative percentage). The realised acoustic niche of a sound type is given by the range of acoustic resources (i.e. utilised resources classes) exploited by that sound type along three axes (multidimensional abstraction). Similarly, the community signal space is given by the range of acoustic resources exploited by the whole community along the three axes.

861x484mm (118 x 118 DPI)

31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60