

1 **Spatio-temporal surveys of the brown meagre *Sciaena umbra* using passive**
2 **acoustics for management and conservation**

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4 Lucia Di Iorio^{1*}, Patrick Bonhomme², Noémie Michez³, Bruno Ferrari³, Alexandra Gigou⁴,
5 Pieraugusto Panzalis⁵, Elena Desiderà⁵, Augusto Navone⁵, Pierre Boissery⁶, Julie Lossent¹,
6 Benjamin Cadville⁷, Marie Bravo-Monin⁷, Eric Charbonnel⁷, Cédric Gervaise¹

7

8 *1 CHORUS Institute, INP Phelma Minatec, 38016 Grenoble, France*

9 *2 Parc national des Calanques, 13008 Marseille, France*

10 *3 Parc naturel marin du golfe du Lion / Office français de la biodiversité, 66700 Argelès-sur-*
11 *Mer, France*

12 *4 Délégation de façade maritime Méditerranée, Office français de la biodiversité, 13001*
13 *Marseille, France*

14 *5 Area Marina Protetta di Tavolara – Punta Coda Cavallo, 07026, Olbia, Italy*

15 *6 Agence de l'Eau Rhône Méditerranée Corse, Imm Le Noailles, 13001 Marseille, France*

16 *7 Parc marin de la Côte Bleue, 13620 Carry-le-Rouet, France*

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18 * Corresponding author: lucia.diiorio@chorusacoustics.com

19

20 **Abstract**

21 Conservation of exploited fish populations is a priority for environmental managers. Spatio-
22 temporal knowledge on reproductive sites is mandatory for species and habitat conservation but
23 is often difficult to assess, particularly over vast geographic areas. Regular and long-term
24 standardized surveys are necessary to identify reproductive sites, assess population trends and
25 their distribution. Here we emphasize the utility of Passive Acoustic Monitoring (PAM) for the
26 survey and management of a depleted vulnerable Mediterranean fish species, the brown meagre,
27 *Sciaena umbra*. Acoustic surveys of reproductive calls were conducted combining 1) spatial
28 data from standardized surveys within three MPAs and from 49 unprotected sites throughout
29 the Northwestern Mediterranean basin, as well as 2) temporal data from a two-year-long survey
30 at a presumed spawning location. The MPA surveys, which rapidly scanned ~30-50 km of the
31 rocky coastlines per MPA, unveiled maps of distribution and reproductive activity of the brown
32 meagre, including potential spawning sites. They were also effective in emphasizing effects
33 linked to management actions: Full-protection zones had a higher number of vocalizations (70%
34 of the listening sites) compared to less protected zones (30% of the sites) or sites outside MPAs
35 (45% of the sites). This was also reflected in the number of singers that was generally low (< 3
36 individuals) in less protected zones and outside MPAs, implying lower fish densities. Highest
37 calling aggregations were observed in potential spawning areas that represented only 0.04% of
38 all listening sites, and were almost all in older, fully protected MPAs, which thus play a key
39 role for fish stock recovery. The two-year survey revealed a 5-month reproductive season (from
40 May to October) with a strong positive correlation between calling activity and temperature.
41 Overall this study confirms the role of PAM as an efficient, replicable and standardized non-
42 invasive method for population management that can identify functional sites and key
43 protection zones, provide valuable information on reproduction, spatial and temporal
44 occurrence, but also on population trends and climate-driven changes.

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46

47 **Keywords:** vulnerable fish, reproductive sites, fish sounds, passive acoustic monitoring, marine
48 protected areas, Mediterranean Sea

49

50 **Highlights**

- 51 • Monitoring of threatened species and their key habitats is critical for environmental
52 managers.
- 53 • Management requires methods to assess population trends at large spatial and temporal
54 scales.
- 55 • Passive acoustics (PA) is efficient in mapping and monitoring vulnerable fish species.
- 56 • Distribution, reproductive sites and population dynamics can be assessed over vast
57 geographical areas.
- 58 • We show the utility of PA to identify key conservation zones and assess effects of
59 management actions.

60

61 1 INTRODUCTION

62 Knowledge of spawning habitats and breeding sites is essential for the conservation of exploited
63 fish stocks. Recording when and where a fish species is reproducing provides pivotal data on
64 key habitats and allows to better manage both vulnerable species and their critical habitats
65 ([Luczkovich et al., 2008b](#)). Identification, mapping and monitoring of functional fish habitats
66 is therefore a priority for environmental managers of Marine Protected Areas (MPA), in
67 particular with regard to endangered and over-exploited species ([Harmelin and Ruitton, 2006](#);
68 [Luczkovich et al., 2008a](#)). Regular and long-term surveys of target species at large spatial scales
69 are necessary to evaluate population trends, distribution, recovery, and the efficiency of
70 protection measures ([Guidetti et al., 2014a](#); [Harmelin-Vivien et al., 2015](#)). However, although
71 very effective, traditional methods based on visual surveys are logistically difficult to
72 implement at high-frequency intervals, over wide areas and for nocturnally active organisms
73 ([Harmelin-Vivien et al. 2015](#)). Management programs would therefore benefit from
74 complementary standardized and replicable methods allowing to cover long distances over
75 short time periods and to monitor key sites and key species continuously, over the long-term
76 with limited human investment.

77

78 Passive acoustic monitoring (PAM) has proven to be a powerful tool for both conservation and
79 fishery science (e.g., [Gannon, 2008](#); [Luczkovich et al., 2008a](#); [Mann et al., 2008](#)). It is a non-
80 invasive flexible listening technique that involves the use of hydrophones to record the
81 collection of sounds emanated from an environment (i.e., the soundscape). PAM exploits the
82 sounds emitted by fish mainly for communication (e.g., [Amorim, 2006](#); [Ladich, 2015](#)) to help
83 identifying species occurrence, spawning areas, cryptic species, follow reproductive activity
84 and population turnover, and to appraise diversity ([Desiderà et al., 2019](#); [Lobel, 2002](#);
85 [Luczkovich et al., 2008b](#); [Picciulin et al., 2018](#)). Despite this, and the fact that a variety of

86 commercial and vulnerable fish species produce sounds, there is a limited number of studies
87 adopting PAM for large-scale mapping of protected fish species and their critical habitats in the
88 Mediterranean Sea, and they all concern the brown meagre *Sciaena umbra* Linnaeus 1758
89 ([Bonacito et al., 2002](#); [Parmentier et al., 2018](#); [Picciulin et al., 2012](#)).

90

91 The brown meagre is an iconic demersal fish species of Mediterranean coastal habitats listed in
92 the Annexe III (Protected Fauna Species) of the Barcelona and Berne Conventions. Globally,
93 this species is classified as Near Threatened ([Chao, 2015](#)) and as vulnerable in the
94 Mediterranean Sea by the IUCN ([Abdul Malak et al., 2011](#); [Bizsel et al., 2011](#)). *S. umbra* is
95 highly vulnerable to fishing due to its aggregative behaviour and easily accessible shallow-
96 water habitat ([Lloret et al., 2008](#)). With a population decline in the Mediterranean Sea of
97 approximately 70% between 1980 and 2005 ([Bizsel et al., 2011](#)), the brown meagre falls within
98 the categories of seriously depleted and collapsed fish species. This is why in 2013, France
99 adopted a moratorium banning spear and recreational fishing of the brown meagre, which was
100 renewed in December 2018. *S. umbra* is also of high ecological and conservation value as it is
101 considered a useful bioindicator ([Mouillot et al., 2002](#)). Its presence is indicative of high
102 environmental quality and community richness ([García-Rubies et al., 2013](#); [Mouillot et al.,](#)
103 [2002](#); [Picciulin et al., 2013](#)), and it is very sensitive to the effect of protection measures ([Guidetti](#)
104 [et al., 2014b](#); [Harmelin-Vivien et al., 2015b](#); [Harmelin et al., 1995](#)). Although there is
105 conspicuous increase in its abundance in no-take integral reserves ([Francour, 1991](#); [García-](#)
106 [Rubies et al., 2013](#); [Harmelin, 2013](#)), outside most protected areas, the brown meagre is
107 frequently targeted ([Lloret et al., 2008](#); [Morales-Nin et al., 2005](#)) and found to be rare or absent
108 ([Harmelin-Vivien et al., 2015b](#); [Letourneur et al., 2003](#)). Appropriate monitoring of *S. umbra*
109 populations and their trends should involve the combination of extensive large-scale
110 observations with regular long-term monitoring of key sites within and outside MPAs

111 ([Harmelin & Ruitton, 2007](#); [Harmelin, 2013](#)). This would allow appropriate assessment of
112 species distribution as well as its spatial extension and to identify and follow functional sites
113 (e.g., feeding, reproduction, spawning).

114

115 *S. umbra* shows strong site-fidelity particularly during the autumn and winter months ([Alós and](#)
116 [Cabanelas-Reboredo, 2012](#); [Harmelin and Ruitton, 2006](#)), but there is a lack of knowledge on
117 the reproductive movements occurring during the summer. As many other sciaenid species, the
118 brown meagre forms breeding aggregations ([Bono et al., 2001](#); [Grau et al., 2009](#); [Ragonese et](#)
119 [al., 2002](#)). Locations of aggregations and spawning sites need to be better documented in order
120 to be protected and managed ([Harmelin-Vivien et al., 2015](#)). During the spawning period, i.e.,
121 May until August ([Chauvet, 1991](#), [Grau et al., 2009](#)), *S. umbra* males produce sounds
122 ([Parmentier et al., 2017](#), [Picciulin et al., 2012](#)). In other Sciaenids, these types of vocalizations
123 have been shown to serve to aggregate individuals, attract mates to leks ([Gilmore, 2002](#); [Parsons](#)
124 [et al., 2009](#)), advertise male readiness to spawn, and synchronise gamete release ([Connaughton](#)
125 [& Taylor 1995](#), [Lobel, 1992](#)). *S. umbra* vocalizations are loud percussive sounds produced by
126 a sonic muscles associated to the males' swim bladder ([Dijkgraaf, 1947](#), [Parmentier et al.,](#)
127 [2017](#)). These percussive sounds can either be produced as irregular sounds (I-calls), or in long
128 regular stereotyped sequences of calls (R-calls) ([Picciulin et al. 2012](#)) emitted for several hours
129 at nighttime (Fig. 1). In Sciaenids these R-calls represent reproductive displays. Their
130 occurrence in high densities forms so-called choruses, which are indicative of spawning
131 aggregations ([Guest and J., 1978](#); [Picciulin et al. 2012](#), [Parsons et al., 2009](#), [Luczkovich et al.,](#)
132 [2008b](#); [Mok and Gilmore, 1983](#)). Therefore, sound production has the potential to serve 1) as a
133 proxy for *S. umbra*'s reproductive activity, 2) to identify nocturnal individual occurrence as
134 well as breeding areas and 3) to locate and monitor aggregations and spawning sites over
135 extended time periods ([Ramcharitar et al., 2006](#)). Despite the potential of PAM to fill some of

136 the knowledge gaps about the brown meagre's ecology and reproductive behaviour and a few
137 pioneering studies in the Gulf of Venice (Italy) using PAM for spatial monitoring (Bonacito et
138 al., 2002; Colla et al., 2018; Picciulin et al., 2013b), there are no studies reporting the application
139 and validation of this technique by environmental managers. The aims of this study were to
140 underline the efficiency of PAM for the survey and management of *S. umbra* and its potential
141 spawning grounds within and outside MPAs by mapping its acoustic activity 1) along the
142 coastline of three wide-ranging MPAs, 2) at large spatial scales (Northwestern Mediterranean),
143 and 3) over two years in a no-take reserve.

144

145 **2 METHODS**

146 **2.1 Spatial sampling within three MPAs**

147 **2.1.1 Study sites**

148 The study sites were three vast MPAs in the Northwestern Mediterranean Sea: The MPA of the
149 Calanques National Park (CNP), the Natural Marine Park of the Gulf of Lion (NMPGL), both
150 in France, and the MPA of Tavolara-Punta Coda Cavallo (TPCC) in Sardinia, Italy (Fig. 2).
151 The CNP is the youngest French national park established in 2012 and situated between
152 Marseille and La Ciotat (Fig. 2). The AMP comprises a 435 km² area that includes seven no-
153 take zones (NTZ, no fishing) and one reinforced protection zone (RPZ) that allows yet regulates
154 artisanal and recreational fishing activity. The NMPGL is also a young MPA, established in
155 2011 with a vast surface of 4000 km² along 100 km coastline. The NMPGL includes the Natural
156 Marine Reserve of Cerbère-Banyuls (MRCB), which is the oldest marine reserve in France
157 created in 1974, measuring 6.50 km² and consisting of a RPZ where only recreational fishing
158 and diving are allowed and regulated and a fully protected no-take and no-access zone (FPZ)
159 (Fig. 2). Finally, the TPCC MPA in Northeastern Sardinia, Italy, established in 1997 but

160 effectively managed around 2003-04, comprises 76 km of coastline and a surface area of 153.57
161 km². Three types of zones with different levels of protection have been established: (1) A zones,
162 corresponding to FPZs (i.e., no-take and no-access); (2) B zones, corresponding to RPZ, where
163 only licensed local artisanal fishing and diving are allowed; (3) C zones, corresponding to
164 general protection zones (PZ), where both artisanal and recreational fishing are authorized as
165 well as diving (Fig. 2).

166

167 2.1.2 Acoustic data acquisition and recording protocol

168 Spatial mapping of *S. umbra* based on their vocalisations has been proposed and successfully
169 adopted in the Gulf of Venice (Italy) (Bonacito et al., 2002; Colla et al., 2018; Picciulin et al.,
170 2013). In this study sound recordings were acquired using two or three simultaneously deployed
171 drifting devices equipped with an EA-SDA14 compact autonomous recorder (RTSys®, France)
172 and a HTI-92-WB (High Tech Inc.®) hydrophone with a flat sensitivity equal to -155 ± 3 dB
173 re 1 V μPa^{-1} between 5 and 50 kHz. Acoustic recordings were sampled continuously at a rate
174 of 78 kHz and a 24-bit resolution. The hydrophone was located between 5 m and 9 m below the
175 sea surface. Positions were defined based on the mean propagation range of *S. umbra* calls
176 estimated using reported source levels (Codarin et al. 2009, Parmentier et al. 2017) and
177 assuming cylindrical spreading loss. Consequently, maximal inter-recording position-distance
178 was set at 600m. Priority and secondary zones for the survey were selected by the MPA's agents
179 based on habitat, protection level and existing knowledge. Deployments were performed using
180 a standardized protocol: Along rocky coastlines, the devices were deployed within maximum
181 200m from the coast, one after the other at 200 to 600m distance, with water depths ranging
182 between 8 and 20m. After deployment of the drifting recorders at a target positions, the boat
183 moved 200 m away and stopped the engine in order to avoid noise interference. After 7 min of
184 recording, each device was recovered. At each deployment and recovery, GPS time and position

185 were noted. All drifts were conducted during the summer, from 7 p.m. to 12 p.m., which
186 includes the period of maximal vocalizing activity of the brown meagre ([Parmentier et al. 2017](#);
187 [Picciulin et al. 2013](#)) (Table 1).

188

189 2.2 Spatial sampling across the Northwestern Mediterranean basin

190 Sound recordings from 49 stations of the CALME acoustic network along the French Western
191 Mediterranean coast established by the RMC Water Agency and the CHORUS Institute
192 ([Gervaise et al. 2018](#)) were used; 22 from *Posidonia oceanica* meadows, and 25 from
193 coralligenous reefs, and two from rocky reefs obtained in summer 2016 and 2017 (Table 1).
194 The CALME network was not designed for *S. umbra* monitoring but is dedicated to key habitat
195 and noise surveillance within the scope of EU Water Framework Directive (2000/60/EC) and
196 the Marine Strategy Framework Directive (2008/56/EC). The same recording equipment
197 (hydrophones and autonomous recorders) was deployed as for the drifting devices. The
198 recorders were bottom moored with the hydrophone at 1 m from the seafloor (Fig. 3). Recorders
199 acquired sounds continuously at a 78 kHz sampling rate and 24-bit resolution. For 46 of the 50
200 recording stations, at each recording date, the recorder was submerged in the afternoon and
201 recovered the next morning for a duration of at least 14 hours. Recordings were made during
202 night-time because the brown meagre, as most temperate fishes, vocalises at night ([Parmentier
203 et al., 2017](#); [Parsons et al., 2016](#); [Picciulin et al., 2012](#)). In four sites, recordings were made
204 over more than 24h.

205

206 2.3 Long-term data collection

207 One long-term recording from the CALME network situated in typical *S. umbra* habitat was
208 used to assess annual trends in acoustic presence. The recording was obtained from the Réserve
209 de Couronne in the Côte Bleue Marine Park (CBMP), near Marseille, France (43° 19' 32", 5°
210 10' 11"). This reserve was created in 1996 and comprises 210 ha. It is a FPZ, where all kind of
211 fishing activities, mooring and scuba diving are prohibited. An EA-SDA14 compact
212 autonomous recorder (RTSys®, France) and an HTI-92-WB (High Tech Inc.®) with the same
213 characteristics described for the drifting device was used but equipped with an external battery
214 pack for long-term deployments. Data were recorded continuously and year-round in 2017 and
215 2018. The recorder was placed on a spawning site of seabreams (*Sparus aurata*) and seabass
216 (*Dicentrarchus labrax*) known to regularly host brown meagres. The recording site was situated
217 near an artificial reef and a natural coralligenous reef, next to a patchy *Posidonia oceanica*
218 meadow, at a depth of 25 m. Bottom temperature profiles and trends were obtained from a
219 temperature probe installed nearby by the park's agents since 1998.

220

221 2.4 Data processing

222 All data was first down-sampled to 4kHz. On the one hand, data acquired during the acoustic
223 small-scale spatial surveys within the MPAs and those obtained from the large-scale CALME
224 network were visually inspected using Raven PRO 1.5 (The Cornell Lab of Ornithology;
225 Hanning window, LFFT = 512, overlap: 50%). All recordings from the MPA surveys were
226 inspected for presence/absence of I-calls, R-calls and choruses, as the presence of these
227 different call types may indicate functional differences of sites. I-calls are characterized by
228 variable numbers of pulses with no fixed call repetition rate. In contrast, R calls are composed
229 of 5-6 pulses repeated in long regular stereotyped sequences (Picciulin et al. 2012) (Fig. 1).
230 They are mainly produced between 5 p.m. and 12 p.m. with a peak between 8 p.m. and 10 p.m.
231 and show spatial as well as temporal consistency (at least over 10 years) in their acoustic

232 features (Picciulin et al. 2012, Parmentier et al. 2017). If possible, based on signal-to-noise
233 differences of simultaneously R-calling individuals, an approximation was made on the number
234 of singers. In the presence of choruses, the abundance of calls is so high that individual call
235 sequences cannot be discriminated any more (Fig. 1).

236

237 The large-scale sampling sites across the Northwestern Mediterranean were visually inspected
238 for the presence of R-calls and choruses only, which are representative of courtship and
239 spawning behaviour. On the other hand, long-term data was processed using a custom-made
240 sound detection algorithm based on the rhythmic properties of calls and capable of discerning
241 vocalizing individuals (Le Bot et al., 2015). This rhythmic analysis algorithm is based on time
242 of arrivals of single pulses of a call within a frequency band of interest and uses a complex
243 autocorrelation function with a sliding window to build a time-rhythm representation (Le Bot
244 et al. 2015). The algorithm parameters were set to detect good-quality *S. umbra* calls that are
245 generally temporally stereotyped (i.e., R-calls with mean pulse periods of 240ms; Parmentier
246 et al. 2017) and with a minimum signal-to-noise-ratio of 6dB. Time series of the detected *S.*
247 *umbra* calls were plotted over time. When available, temperature curves were provided and
248 correlated with the acoustic activity.

249

250 **3 RESULTS**

251 3.1 Spatial distribution within MPAs

252 3.1.1 Calanques National Park

253 The three recording sessions comprised a total of 72 recording stations covering over 40km of
254 coastline and representing a surface of 20.4 km² (considering a detection range of 300 m). 40
255 recording drifts were performed within NTZs (no-take zones) of the MPA and 32 in areas with

256 a lower protection regime (RPZ) (Fig. 4). *S. umbra* R- & I-calls were recorded at 27.7% of the
257 stations, both within (55% of call detections) and outside (45%) NTZs. R-calls (reproductive
258 calls) equally occurred at 4 stations inside and 4 outside NTZ, indicating that reproductive
259 activity also takes place in less protected areas. Most I-calls were detected inside NTZs (9 out
260 of 12 stations). No choruses were detected and overall, calling activity was not abundant (only
261 one, maximum two R-calls per stations and a few single I-calls), indicating a small number of
262 vocalizing individuals.

263

264 3.1.2 Marine Natural Park of the Gulf of Lion

265 96 sites were acoustically scanned during the four night-time surveys, allowing to cover the
266 entire rocky coastline of the park (i.e., 30 km). *S. umbra* calls were present at 46 recording
267 stations (i.e., 48% of the stations); 27 were within the marine reserve (MRCB) and 19 outside
268 the reserve along the rocky coast of the marine park (Fig. 4). As the recording effort was greater
269 within the reserve than in the rest of the park, there may be a bias towards the higher number
270 of detections within the reserve. Nevertheless, the results show an effect of type and duration
271 of the protection measures. In fact, the reserve was dense in detections, with *S. umbra* calls
272 present in 77% compared to 33% of the stations in the rest of the park. Furthermore, in the
273 reserve, acoustic reproductive behaviour was intense: 21 (of 27) stations with R-calls, three
274 with choruses, and 50% of all stations with at least two singers. In the rest of the park outside
275 the reserve, R-calls were recorded at 12 stations (66%), I-calls at 6 stations and simultaneous
276 singing was detected at one station only. Overall vocal activity was therefore generally smaller
277 compared to the reserve. From 4 sites recorded both in June and August in the NMPGL, two
278 showed acoustic activity in both months, which may be indicative of site fidelity.

279

280 3.1.2 MPA of Tavolara-Punta Coda Cavallo

281 54 stations were acoustically sampled during three recording sessions covering 20 km coastline:
282 16 in the full-protection zones (no-take & no-access) A, 24 in the RPZ zones B, and 14 in the
283 less protected zone C (Fig. 4). At almost 70% of all stations, *S. umbra* calls were present.
284 Zonation, i.e., the degree of protection and enforcement level, strongly influenced the observed
285 calling behaviour: All stations in fully protected A zones showed sustained calling activity,
286 including 11 stations with R-calls, one with I-calls and 2 with choruses. 12 out of the 16 stations
287 showed elevated simultaneous singing of multiple individuals (2-4 or choruses). The B zone
288 also showed a strong vocal activity (70% of the stations) with 10 stations in which R-calls were
289 recorded, three in which I-calls occurred, three in which both R-and I-calls were present and
290 one with a chorus. Simultaneous singing activity of at least 2 individuals occurred at 5 stations.
291 The C-zone was the one with the fewest detections of *S. umbra* calls. Out of 14 stations, only 3
292 presented calling activity; one with I-calls, one with R-calls and one showing chorusing activity.
293 Moreover, the Northern part of the MPA is more exposed to anthropogenic noise of ferries and
294 other boats leaving the harbour of Olbia. Signal-to-noise ratio was overall small in N-Tavolara
295 and Capo Ceraso because of increased background noise due to vessel traffic. Masking of
296 communication signals may therefore be a cause for reduced signal production and/or detection.

297

298 3.2 Spatial sampling across the Northwestern Mediterranean basin

299 *S. umbra* was also present outside MPAs. On 23 out of 49 stations inspected, R-calls and
300 choruses were detected (Fig. 5). This corresponds to an encounter probability of 47% (Fig 4)
301 despite the fact that the recording stations were not specifically designed for *S. umbra*
302 monitoring. The comparison between sites in seagrass meadows and coralligenous reefs
303 indicates that *S. umbra* is acoustically present at 11 sites within seagrass meadows (50% of the

304 sites) and at 8 sites on coralligenous reefs (30% of the sites). Although not quantified here, the
305 number of simultaneously singing males was generally low (< 3 individuals), suggesting overall
306 low fish densities. Potential spawning sites indicated by the presence of choruses only occurred
307 at four sites; three in Corsica, and one in Sardinia. Two sites were within and two outside no-
308 take zones.

309

310 3.3 Long-term seasonal monitoring within an MPA no-take zone

311 The annual recordings in the Reserve of Couronne in CBMP highlighted an acoustic activity of
312 *S. umbra* spanning over a period of 5 months, with a strong consistency in sound production
313 from one year to the other. In 2017, the first *S. umbra* calls were present in April but singing
314 started on May 21 and stopped on October 11. In 2018 brown meagres started singing on May
315 22 and stopped on October 17 (Fig. 6). The singing period was almost identical and comprising
316 part of spring and autumn. Singing activity was most intense during the summer months (June-
317 September), and present 72% of the time (Fig. 6). Singing was also highly positively correlated
318 with water temperature ($\rho = 0.8$) (Fig. 6).

319

320 **DISCUSSION**

321 This study highlights the efficiency of PAM in studying and following *S. umbra* populations
322 over different spatial and temporal scales for species management. The standardized method
323 adopted to map the acoustic distribution of *S. umbra* using multiple drifting devices allowed to
324 establish maps of the acoustic presence and reproductive activity of almost the totality of the
325 MPAs' rocky coastlines (up to 50km) in only 3-4 evenings. This confirms the efficiency of the
326 method in rapidly assessing *S. umbra* distribution over vast areas (Picciulin et al., 2013).
327 Distribution maps of this kind, obtained with limited human and logistic effort, are difficult to

328 establish with traditionally used techniques. The results from these nocturnal surveys, showed
329 that in the CNP and the NMPGL (excluding the reserve) *S. umbra* was present in approximately
330 30% of the recorded sites. In the Reserve of Cerbère-Banyuls (within the NMPGL) and TPCC,
331 the probability of detecting *S. umbra* calls was between 70 and 80%, thus more than two times
332 higher than in the NMPGL and the CNP. These differences may be linked to different
333 management measures and particularly enforcement against anthropogenic pressures (i.e.,
334 fishing and diving), to the surveillance programs adopted by the different MPAs, to habitat
335 characteristics, but also to the onset of the protection measures. In fact, the CNP and the
336 NMPGL are young MPAs established approximately 7 years ago, while the MRCB and TPCC
337 have been managed for over 20 years. Moreover, within the TPCC MPA, *S. umbra* calls were
338 present in 100% of the sites within the fully protected zones A, 70% within reinforced B-zones
339 and only 21% in the partially protected C-zones. Together these results indicate an overall effect
340 of “age” of the MPA as well as a reserve-effect given by the level of protection and
341 enforcement. This is consistent with the findings of long-term visual observations in
342 Mediterranean MPAs indicating conspicuous increases in brown meagre abundance in fully
343 protected or no-take zones over the last decade and an overall slow recovery of *S. umbra*
344 populations (Francour, 1991; García-Rubies et al., 2013; Guidetti et al., 2014; Harmelin-Vivien
345 et al., 2008; 2015; Harmelin and Ruitton, 2006). The role of enforced protection is further
346 supported by the fact that almost all (8 out of 11) sites with chorusing activity, which are
347 indicative of potential spawning aggregations, occurred within fully protected zones of older
348 MPAs. Furthermore, in younger MPAs, calling activity was generally lower and the number of
349 simultaneously singing individuals per site was smaller (< 3) compared to older more enforced
350 MPA zones.

351

352 Overall, the R-call was the most abundant call type and it occurred within MPAs as well as in
353 non-protected areas of the Northwestern Mediterranean. Outside MPAs, *S. umbra* reproductive
354 calls were present in 47% of the sites, both in *Posidonia oceanica* seagrass meadows (50% of
355 the seagrass sites) and in coralligenous reefs (30% of the coralligenous reefs). However, except
356 for two chorusing sites in Corsica, the number of singers at one site was generally low, possibly
357 indicating low animal densities. Corsica showed the highest number of sites with singing brown
358 meagres (11 out of 23). On the mainland, they were mainly detected in the Eastern part of the
359 region Provence-Alpes-Côte d'Azur (PACA, stations 8-6). In Western PACA only the CBMP
360 reserve recorded brown meagre acoustic activity, while none was observed in the Languedoc-
361 Roussillon region, which was however only represented by three stations (Fig. 5). These
362 differences may be linked to the presence of suitable habitats for the species or fishing and may
363 also be due to the fact that the recording sites were not specifically chosen to monitor the brown
364 meagre. The coast of the gulf of Lion is dominated by sandy substrate with limited rocky and
365 *P. oceanica* habitats. Overall, the *P. oceanica* sites with *S. umbra* detections were characterized
366 by higher percentage of rocky substrate compared to the sites without detections (14% vs 6%
367 rock). This may partly explain the distributions observed and why this species, typically
368 associated to rocky habitats, was present in *P. oceanica* meadows. A more detailed analysis on
369 habitat characteristics may provide insights to elucidate the observed distributions. The acoustic
370 presence of *S. umbra* also outside MPAs, although generally in low densities, might be due to
371 1) the extended spatial coverage of the CALME network, 2) the presence of habitats suitable
372 for the occurrence of the study species but also 3) the long-term management measures to
373 increase water and habitat quality (EU Water Framework Directive) and 4) the ongoing
374 moratorium in France that bans spearfishing and hook-and-line recreational fishing until
375 December 2023 and thus partially protects *S. umbra* populations ([Harmelin-Vivien et al., 2015](#);
376 [Rocklin et al., 2011](#)).

377

378 Overall, these results show that, although strongly linked to habitat characteristics and
379 protection level, *S. umbra* courtship activity occurs both within and outside MPAs (at least in
380 France), and that PAM can be used to identify distribution and potential reproductive sites.
381 Within the scope of spatial planning, PAM can contribute to define protection areas around
382 functionally relevant zones (Erisman et al., 2012; Luczkovich et al., 2008b). This is particularly
383 true for sites with chorusing activity that is associated with spawning aggregations, with chorus
384 intensity being related to fish abundance and biomass in other Sciaenids (Gannon and Gannon,
385 2010; Rowell et al., 2017). Large aggregations of the brown meagre have been reported in the
386 Mediterranean Sea (Fiorentino et al., 2001; Ragonese et al., 2002). Surveys combining passive
387 and active acoustics will help confirming the link between acoustic activity and fish abundance
388 (Erisman and Rowell, 2017; Mann et al., 2008). Furthermore, in *S. umbra* it remains unknown
389 if choruses are related to egg production and spawning as in the weakfish (*Cynoscion regalis*),
390 spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), silver perch
391 (*Bairdiella chrysoura*), meagre (*Argyrosomus regius*) or the mullet (*Argyrosomus*
392 *japonicus*) (Lagardère and Mariani, 2006; Lowerre-Barbieri et al., 2008a; Luczkovich et al.,
393 1999; Parsons et al., 2006). Ichthyoplankton and adult surveys at chorusing sites are required
394 to assess the link between sound production and spawning (Luczkovich et al. 2008a). However,
395 the results of the acoustic activity of *S. umbra* reported here clearly show that chorusing is rare
396 (11 out of 271 sites) and prevails within fully protected or no-take zones in well-enforced
397 MPAs. This is particularly relevant and further underlines the importance of marine reserves in
398 protecting spawning sites and ultimately populations.

399

400 The vocal activity patterns reported here also allow to better describe reproductive movements
401 of the brown meagre and the displacement of individuals for breeding aggregations that are still

402 poorly documented (*c.f.*, [Harmelin-Vivien et al. 2015](#)). PAM offers a means to identify the sites
403 of vocal males and help assess the extent of their poorly known spatial movements and home
404 ranges. It also shows its utility to fill some of the knowledge gaps in the nocturnal behaviour of
405 this species ([Harmelin-Vivien et al. 2015](#)). *S. umbra* males in the Northwestern Mediterranean
406 predominantly vocalize during the first half of the night, with a peak about one hour after sunset.
407 This is therefore a time period at which, during the reproductive season, animals are engaged
408 in reproductive behaviours. The diel pattern described here coincides with the one reported in
409 Corsica (France), Sardinia (Italy) and in the Adriatic Sea (Italy) ([Parmentier et al. 2017](#),
410 [Picciulin et al. 2013](#)) and is commonly observed in many sciaenid species ([Fish and Cummings,](#)
411 [1972](#); [Mann and Grothues, 2009](#); [Saucier and Baltz, 1993](#)).

412

413 Two-year recordings in the Reserve of CBMP showed that the brown meagre is vocally active
414 from May to October. Seasonal calling activity is common in Sciaenids (e.g., [Connaughton and](#)
415 [Taylor, 1994](#); [Montie et al., 2015](#)), but this is the first description of annual calling activity and
416 natural variability in the brown meagre that may help better assess the spawning period of this
417 vulnerable specie ([Monczak et al., 2017](#)). The spawning season of *S. umbra* is suggested to be
418 from May to August, as estimated from histological examination and gonadosomatic index
419 ([Chauvet, 1991](#); [Grau et al., 2009](#)). Here we show that singing activity was sustained (i.e., 72%
420 of occurrence) from late spring to autumn, indicating that the reproductive season of *S. umbra*
421 is likely protracted, and occurring over a five-months period. Additional long-term recordings
422 at different potential spawning sites will allow to confirm this extended reproductive season.
423 The duration of the singing activity was equivalent in both years, starting on May 21 in 2017
424 and May 22 in 2018 and ending on October 11 in 2017 and October 17 in 2018. This relatively
425 abrupt onset of calling activity suggests the presence of an environmental trigger. Temperature
426 has been shown to initiate reproductive behaviour and chorusing in other sciaenid species

427 ([Mann and Grothues, 2009](#); [Monczak et al., 2017](#); [Rice et al., 2016](#)). In this study, there was a
428 strong positive correlation between water temperature and calling activity ($\rho = 0.8$), supporting
429 the temperature-related hypothesis. Furthermore, although singing was sustained throughout
430 the summer, it showed fluctuations in calling intensity (i.e., number of calls per hour). Peaks of
431 vocal activity occurred in June, July, August and September and coincided with peaks in water
432 temperature at the recording site. Similar temperature-related fluctuations in calling during the
433 spawning season have been described in other Sciaenids ([Connaughton and Taylor, 1994](#);
434 [Monczak et al., 2017](#); [Montie et al., 2015](#)) and have been related to seasonal cycles in the sonic
435 muscle of males ([Connaughton and Taylor, 1994](#)). The smaller pulse-period observed during
436 intense calling activity may be related to faster muscle twitch and contraction velocity at higher
437 temperatures ([Connaughton et al., 2002](#), [Bolgan et al. 2020](#)). An alternative explanation for the
438 observed variations in calling intensity may be the influence of the lunar cycle ([McCauley,](#)
439 [2012](#), [Monczak et al., 2017](#)). However, in this study intervals between peaks varied between 14
440 and 36 days (mean 25 days), thus indicating no clear lunar cycle pattern. In other sciaenid
441 species, changes in calling behaviour have been related to spawning events ([Lowerre-Barbieri](#)
442 [et al., 2008](#); [Mok and Gilmore, 1983](#); [Montie et al., 2017](#)). Although this remains to be
443 elucidated for the brown meagre, the species is a multiple-spawning fish and within a
444 population, females do not show synchronous ovarian maturity, which results in an extended
445 spawning season ([Grau et al. 2009](#)).

446

447 CONCLUSIONS

448 This study emphasizes the utility of PAM for the survey and conservation of exploited,
449 vulnerable Mediterranean fish species. It represents a complementary, non-invasive, low-cost,
450 standardized, replicable and efficient monitoring technique for environmental managers
451 ([Luczkovich et al., 2008a](#); [Mann et al., 2008](#); [Rountree et al., 2011](#)). Here we focussed on the

452 brown meagre, but the method can be extended to other vocal species (e.g., groupers).
453 Harmelin-Vivien and co-authors (2015) underlined the need to combine extensive observations
454 along the coast and regular long-term monitoring of favourable sites to document spatial
455 distribution and the effect of increased protection of *S. umbra*. Here we show that PAM will
456 allow to fill some of the knowledge gaps on species distribution, behaviour and reproduction
457 needed for the conservation of the species using a combination of spatial and long-term acoustic
458 recordings. Information of this kind is essential for the conservation of exploited or vulnerable
459 fish species (Erisman et al., 2017).

460

461 The importance of recurrent monitoring surveys of threatened species inside and outside MPAs
462 is critical to estimate population trends. Repeated standardized evening surveys over the season
463 and across years will also allow, with limited human and logistic effort, to study site-fidelity
464 and identify preferential sites of brown meagre populations over wide areas and help decision-
465 makers to adopt protection acts and establish management zones (Luczkovich et al., 2008b).
466 Here we showed that PAM increases our knowledge on the distribution and reproductive
467 activity of this vulnerable species in rarely surveyed areas (i.e. outside MPAs) and over large
468 geographical scales. PAM is also effective in emphasizing effects linked to management actions
469 (e.g., no-take zones). Combining the obtained findings with existing visual observations,
470 abundance estimations (e.g., using underwater visual census data or active acoustics),
471 individual telemetry tracking data (Parsons et al., 2009; Taylor et al., 2006) as well as
472 ichthyoplankton surveys on chorusing sites will provide critical information on the reproductive
473 behaviour of the species, their distribution and population trends and allow to further
474 consolidate the use of PAM for monitoring and managing this vulnerable species. Furthermore,
475 simultaneous annual recordings on chorusing or known aggregation sites will help identify
476 spawning events (e.g; Luczkovich et al., 2008b; Rice et al. 2015), trends in fish abundance via

477 the calling activity (Erisman and Rowell, 2017; Rowell et al., 2017), and shifts in reproductive
478 timelines associated with climate change (Monczak et al. 2017). Altogether, the findings
479 reported here highlight the use of PAM as a means to support managers in their efforts to
480 monitor, recover, and ultimately protect key ecological, commercial and emblematic species
481 such as the Mediterranean brown meagre.

482

483 **CRedit authorship contribution statement**

484 Lucia Di Iorio: Conceptualization, Methodology, Formal analysis, Writing – initial, review &
485 editing, Investigation, Visualization, Supervision, Project administration. Patrick Bonhomme:
486 Conceptualization, Investigation, Resources, Visualization, Funding acquisition. Noémie
487 Michez: Investigation, Resources, Writing - Review & Editing. Bruno Ferrari: Investigation,
488 Resources. Alexandra Gigou: Conceptualization, Funding acquisition. Pieraugusto Panzalis:
489 Investigation, Resources, Elena Desiderà: Investigation, Writing - Review & Editing. Augusto
490 Navone: Resources, Pierre Boissery: Resources, Writing - Review & Editing, Funding
491 acquisition. Julie Lossent: Methodology, Investigation. Benjamin Cadville: Investigation,
492 Resources. Marie Bravo-Monin: Investigation, Resources. Eric Charbonnel: Resources,
493 Writing - Review & Editing, Cédric Gervaise: Software, Methodology, Formal analysis,
494 Conceptualization, Writing – review & editing, Investigation, Supervision, Project
495 administration.

496

497 **Declaration of competing interest**

498 The authors declare that they have no known competing financial interests or personal
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500

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731 **TABLES**

732

733 **Table 1.** Summary table of the different survey types and the recording sites. For

734 precautionary reasons with regard to illegal fishing, the coordinates of the positions are not

735 provided.

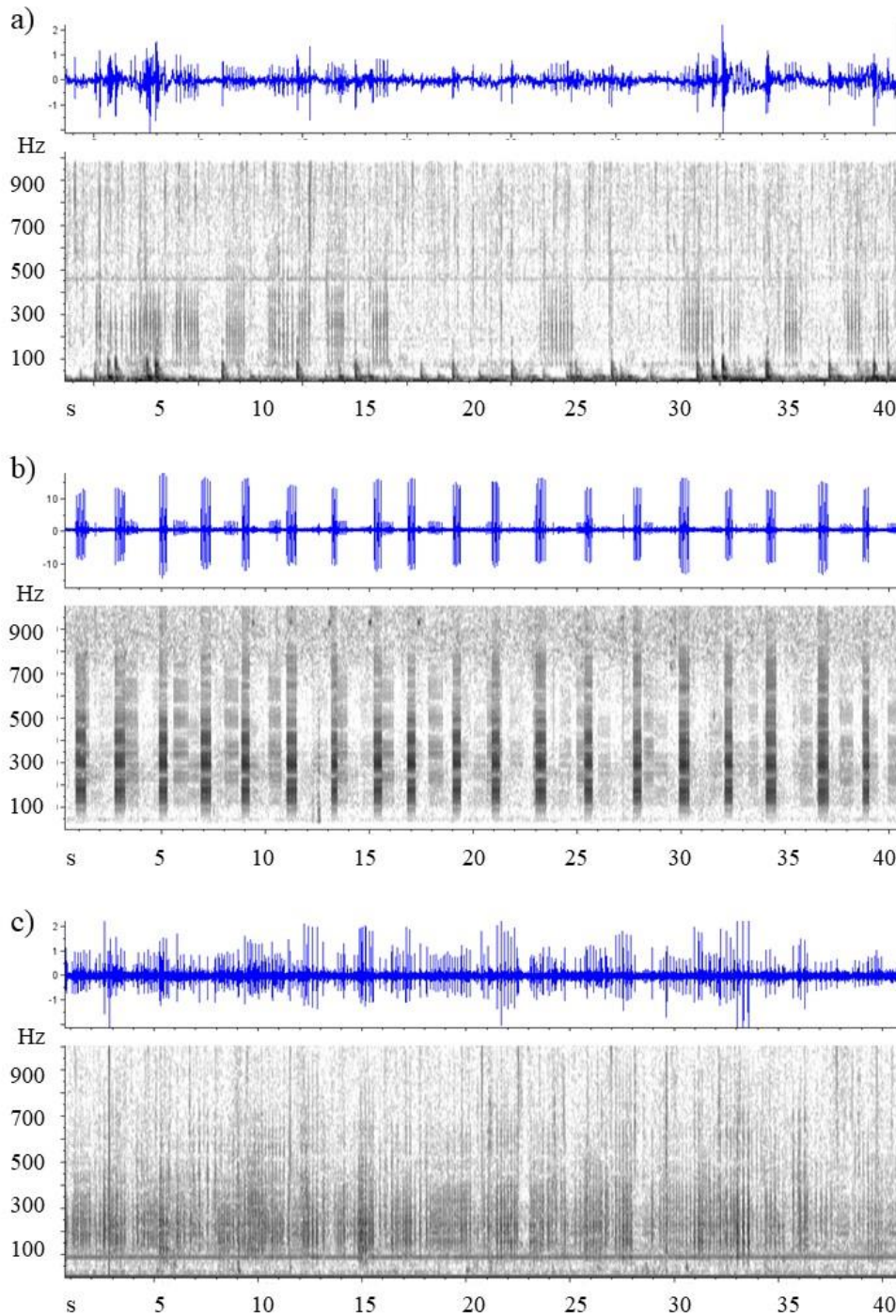
ID	Site	Habitat	Survey	Survey dates	Year	<i>S. umbra</i>	Recorders	Recorder support	Recording stations
	CNP	rock	MPA	26-28/06/2018	2018	1	3	floating device	72
	NMPGL	rock	MPA	24-27/06 & 29/08/2019	2019	1	3	floating device	96
	TPCC	rock	MPA	22-24/07/2019	2019	1	2	floating device	54
1	Banuyls	coralligenous	NW Med Sea	2016/06/21	2016	0	1	bottom mooring	1
1	Banuyls	seagrass	NW Med Sea	2016/06/21	2016	1	1	bottom mooring	1
2	Agde	coralligenous	NW Med Sea	2016/06/20	2016	1	1	bottom mooring	1
3	Grand Travers	coralligenous	NW Med Sea	2016/06/17	2016	0	1	bottom mooring	1
4	Ciotat	seagrass	NW Med Sea	2016/06/02	2016	0	1	bottom mooring	1
4	Ciotat	coralligenous	NW Med Sea	2016/06/02	2016	1	1	bottom mooring	1
5	Sicie	seagrass	NW Med Sea	2016/06/03	2016	0	1	bottom mooring	1
5	Sicie	coralligenous	NW Med Sea	2016/06/03	2016	1	1	bottom mooring	1
6	Giens	coralligenous	NW Med Sea	2016/06/04	2016	1	1	bottom mooring	1
7	Ribaud	seagrass	NW Med Sea	2016/06/04	2016	1	1	bottom mooring	1
8	Bornes	coralligenous	NW Med Sea	2016/06/05	2016	0	1	bottom mooring	1
8	Bornes	seagrass	NW Med Sea	2016/06/05	2016	1	1	bottom mooring	1
9	Cap Lardier	coralligenous	NW Med Sea	2016/06/06	2016	0	1	bottom mooring	1
9	Cap Lardier	seagrass	NW Med Sea	2016/06/06	2016	1	1	bottom mooring	1
10	Bonneau	seagrass	NW Med Sea	2016/06/08	2016	1	1	bottom mooring	1
10	Bonneau	coralligenous	NW Med Sea	2016/06/08	2016	1	1	bottom mooring	1
11	Cap Roux	seagrass	NW Med Sea	2016/06/09	2016	0	1	bottom mooring	1
11	Cap Roux	coralligenous	NW Med Sea	2016/06/09	2016	0	1	bottom mooring	1
12	Golfe Juan	seagrass	NW Med Sea	2016/06/10	2016	0	1	bottom mooring	1
12	Golfe Juan	coralligenous	NW Med Sea	2016/06/10	2016	0	1	bottom mooring	1
13	Bacon	coralligenous	NW Med Sea	2016/06/11	2016	0	1	bottom mooring	1
13	Bacon	seagrass	NW Med Sea	2016/06/11	2016	0	1	bottom mooring	1
14	Nice	coralligenous	NW Med Sea	2016/06/12	2016	0	1	bottom mooring	1
14	Nice	seagrass	NW Med Sea	2016/06/13	2016	1	1	bottom mooring	1
15	Eze	coralligenous	NW Med Sea	2016/06/13	2016	0	1	bottom mooring	1
16	Cap Martin	coralligenous	NW Med Sea	2016/06/15	2016	0	1	bottom mooring	1
17	Maccinagio	seagrass	NW Med Sea	2017/06/02	2017	1	1	bottom mooring	1
17	Maccinagio	coralligenous	NW Med Sea	2017/06/02	2017	1	1	bottom mooring	1
18	Bastia	coralligenous	NW Med Sea	2017/05/31	2017	0	1	bottom mooring	1
18	Bastia	seagrass	NW Med Sea	2017/05/31	2017	0	1	bottom mooring	1
19	Tarco	coralligenous	NW Med Sea	2017/05/30	2017	0	1	bottom mooring	1
19	Tarco	seagrass	NW Med Sea	2017/05/30	2017	1	1	bottom mooring	1
20	Rondinara	coralligenous	NW Med Sea	2017/05/29	2017	0	1	bottom mooring	1
20	Rondinara	seagrass	NW Med Sea	2017/05/29	2017	1	1	bottom mooring	1
21	Murtoli	seagrass	NW Med Sea	2017/05/27	2017	1	1	bottom mooring	1
22	Parata	seagrass	NW Med Sea	2017/06/12	2017	1	1	bottom mooring	1
22	Parata	coralligenous	NW Med Sea	2017/06/12	2017	1	1	bottom mooring	1
23	Cappo Rossu	seagrass	NW Med Sea	2017/06/10	2017	1	1	bottom mooring	1
23	Cappo Rossu	coralligenous	NW Med Sea	2017/06/10	2017	0	1	bottom mooring	1
24	Focolara	coralligenous	NW Med Sea	2017/06/09	2017	0	1	bottom mooring	1
24	Focolara	seagrass	NW Med Sea	2017/06/09	2017	1	1	bottom mooring	1
25	Calvi	seagrass	NW Med Sea	2017/06/05	2017	1	1	bottom mooring	1
25	Calvi	coralligenous	NW Med Sea	2017/06/05	2017	1	1	bottom mooring	1
26	Agriates	coralligenous	NW Med Sea	2017/06/03	2017	0	1	bottom mooring	1
26	Agriates	seagrass	NW Med Sea	2017/06/03	2017	1	1	bottom mooring	1
CBMP	Côte Bleue	seagrass	NW Med Sea	2016/05/30	2016	0	1	bottom mooring	1
27	Cala Gonone	rock	NW Med Sea	several months	2017	1	1	bottom mooring	1
CBMP	Côte Bleue	rock	NW Med Sea	yearround	2017/2018	1	1	bottom mooring	1
TPCC	Tavolara	coralligenous	NW Med Sea	several months	2017	1	1	bottom mooring	1

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739 **FIGURES**



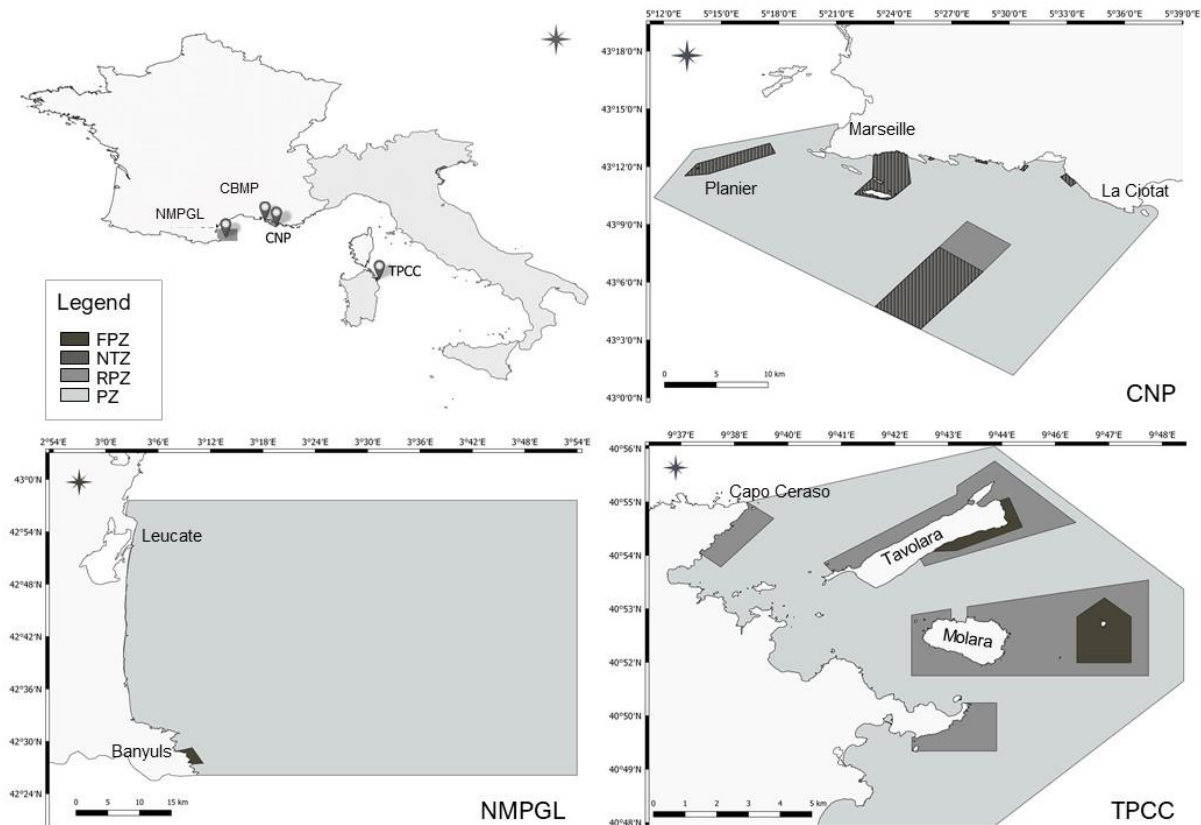
740

741 **Figure 1.** Oscillograms (top) and spectrograms (bottom) of *S. umbra* call categories. a) Irregular

742 I-calls, b) series of stereotyped R-calls, and c) choruses, as described by Picciulin et al. 2012.

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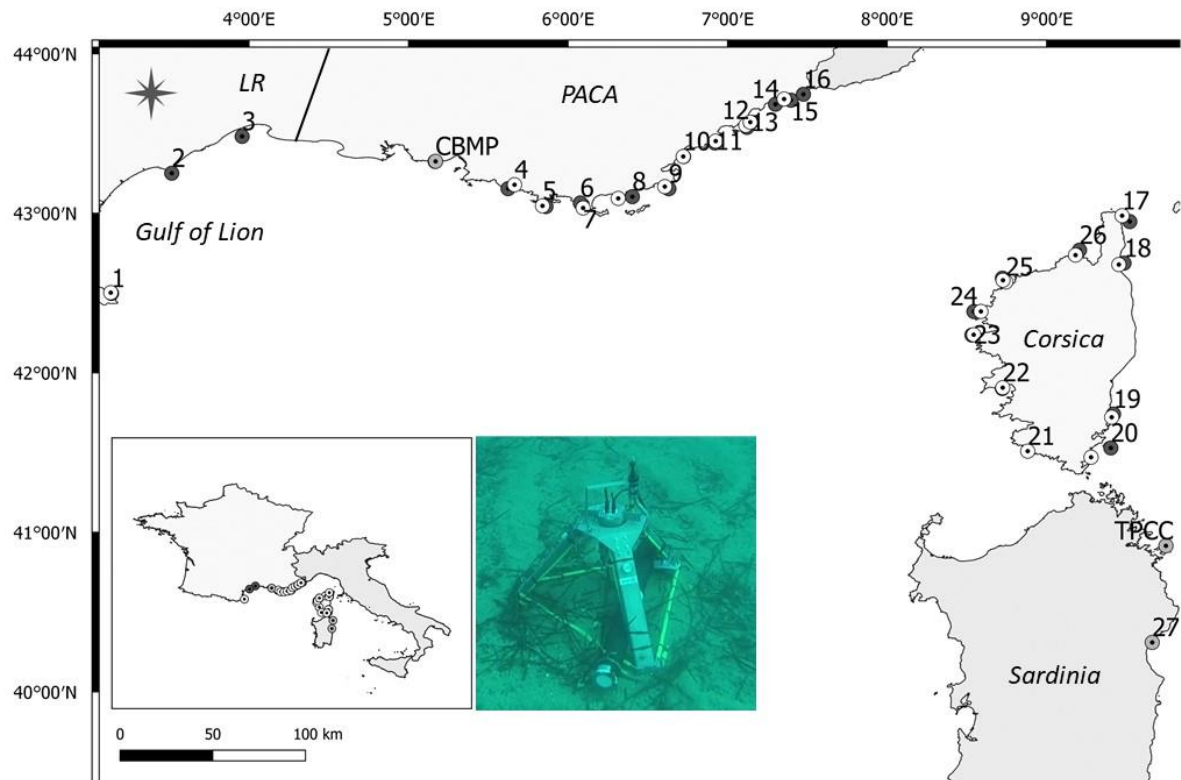
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747 **Figure 2.** Maps of the MPAs where drifting surveys were conducted. Top left panel: France
748 and Italy with the locations of the four MPAs. Other panels: Maps of the three MPAs in which
749 *S. umbra* distribution was assessed using drifting devices. The different protection levels are
750 indicated by different colours described in the legend: FPZ = Full Protection Zone (=Reserve =
751 A zone), NTZ = No-Take-Zone (only in PNC), RPZ = Reinforced Protection Zone (= B zone),
752 PZ = Protection Zone (= C zone). CNP: Calanques National Park, NMPGL: Natural Marine
753 Park of the Gulf of Lion with the Marine Reserve of Cerbère-Banyuls (dark grey), TPCC:
754 MPA of Tavolara-Punta Coda Cavallo.

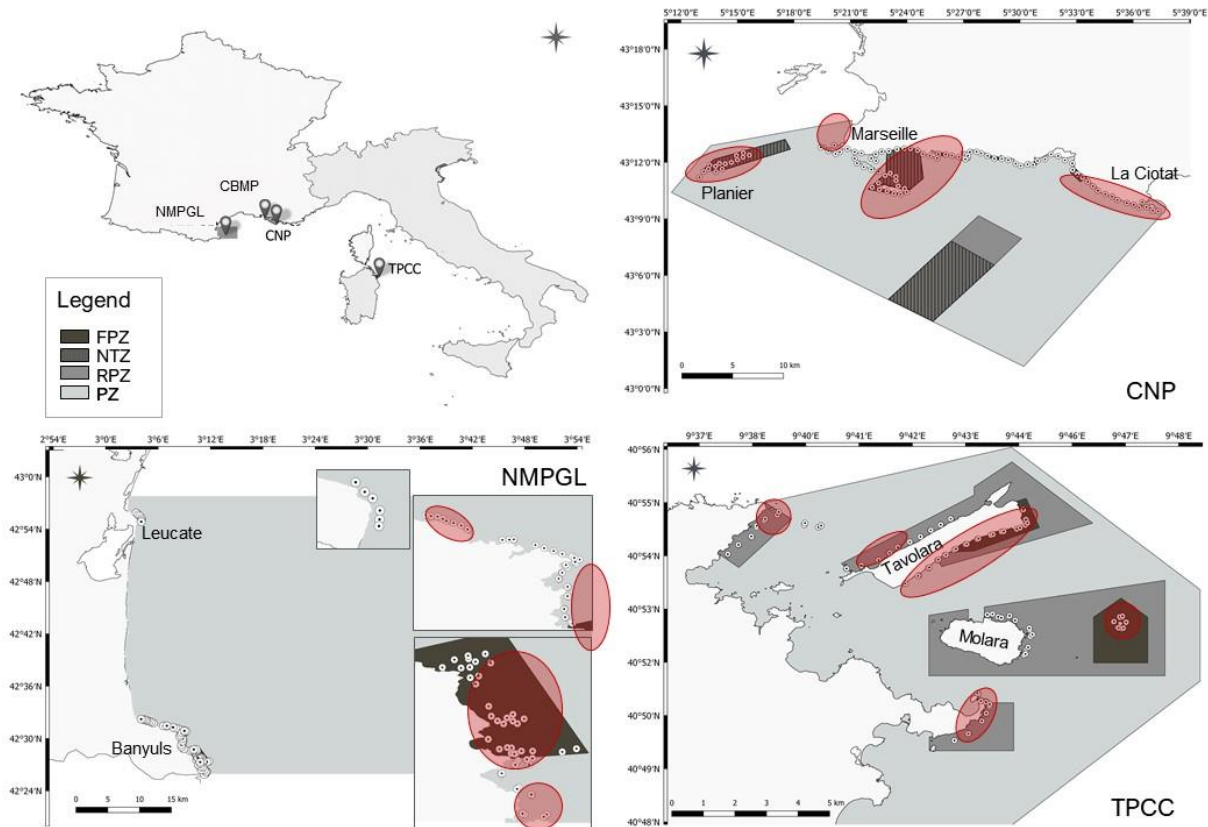
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755

756 **Figure 3.** Map of the 49 recording sites of the large-scale monitoring program CALME and the
757 long-term recording site in the Côte Bleue Marine Park (CBMP). Dark grey circles indicate
758 coralligenous reef recording sites, bright grey circle indicate rocky long-term recording stations,
759 white circles are seagrass meadow recording sites. The picture illustrates the mooring system
760 with the recording device. The locations corresponding to the numbers are listed in table 1.
761 *PACA*: Provence Alpes Côte d'Azur region, *LR*: Languedoc-Roussillon region.

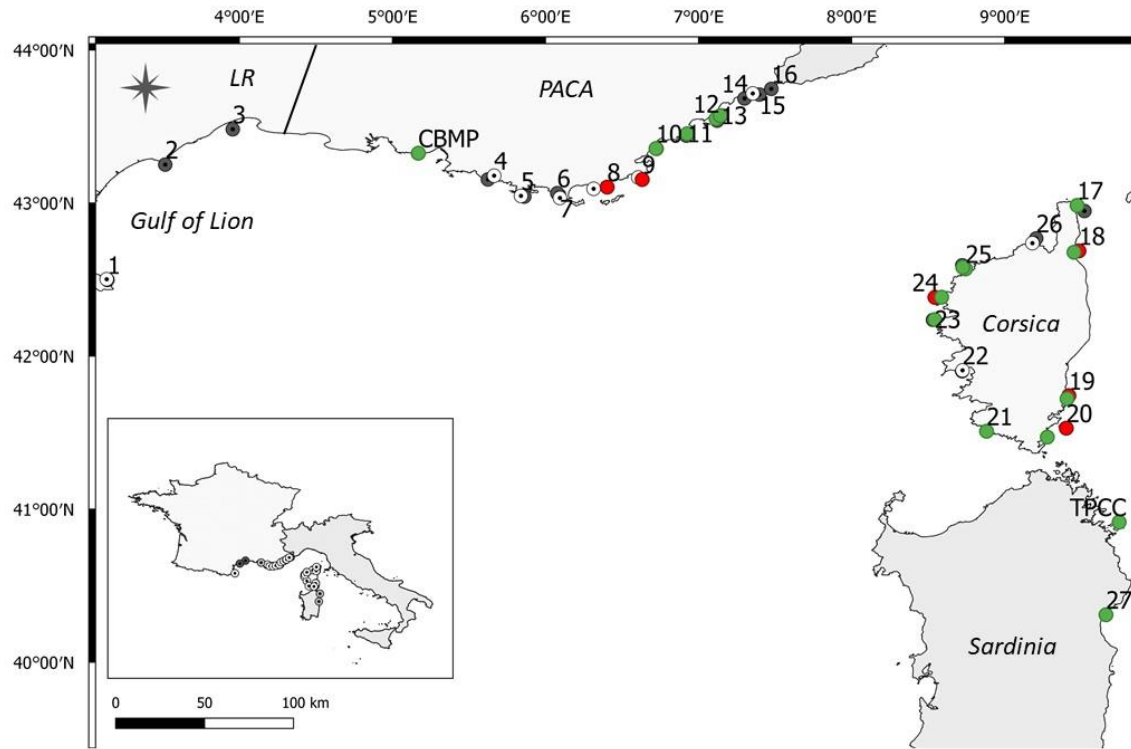
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763

764 **Figure 4.** Maps of the drifting surveys and *S. umbra* detections within the MPAs. Top left
765 panel: France and Italy with the locations of the four MPAs. Other panels: Maps of the three
766 MPAs illustrating all the recording positions (white circles). Zones of *S. umbra* call detections
767 are highlighted in red. Because of management and precautionary reasons with regard to
768 illegal fishing, more detailed detection positions are not shown here. The different protection
769 levels are indicated by different colours described in the legend: FPZ = Full Protection Zone
770 (=Reserve = A zone), NTZ = No-Take-Zone (only in PNC), RPZ = Reinforced Protection
771 Zone (= B zone), PZ = Protection Zone (= C zone). CNP: Calanques National Park, NMPGL:
772 Natural Marine Park of the Gulf of Lion, TPCC: MPA of Tavolara-Punta Coda Cavallo.

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774

775 **Figure 5.** Map of the *S. umbra* detections within the acoustic monitoring network CALME.

776 Green circles indicate *S. umbra* acoustic presence in the seagrass meadow and long-term

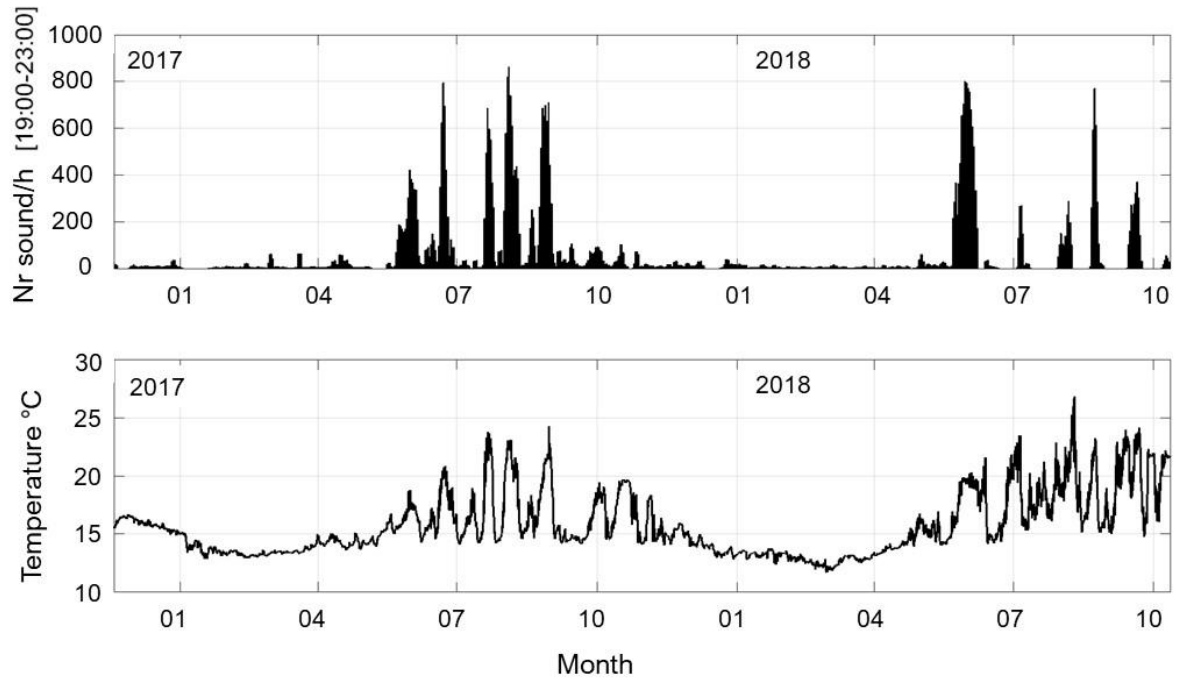
777 recording sites, red circles indicate in the coralligenous reef sites. Dark grey circles indicate

778 coralligenous reef recording sites without detections, and white circles are seagrass meadow

779 recording sites without detections. CBMP : Côte Bleue Marine Park. PACA: Provence Alpes

780 Côte d'Azur region, LR: Languedoc-Roussillon region.

781



782

783 **Figure 6.** Biannual series of *S. umbra* calls in the Côte Bleue Marine Park, no-take Reserve of
784 Couronne (top panel) and temperature profile at the recording site (bottom panel). Call
785 production and temperature show strong correlations ($\rho = 0.8$).

786

787