Sound features and vocal rhythms as a proxy for locating the spawning ground of *Sciaena umbra* in the wild

Marta Picciulin1 | Riccardo Fiorin2 | Chiara Facca1 | Stefano Malavasi1

1Department of Environmental Sciences, Informatics and Statistics, Ca’ Foscari University of Venice, Venice, Italy
2Laguna Project SNC, Venice, Italy

**Abstract**

1. The brown meagre (*Sciaena umbra*) is a demersal sciaenid fish recognized as indicative of good environmental quality and is defined as an umbrella species for the ecological community of rocky coastal habitats. *Sciaena umbra* is classified as a Vulnerable fish species by the International Union for Conservation of Nature (IUCN) and knowledge on the distribution of its spawning habitats is essential for its conservation.

2. Passive acoustic monitoring (PAM) is a suitable tool to monitor *S. umbra* distribution because of the high consistency, over space and time, of the communication sounds that this species emits during the reproductive period, with irregular or regular rhythms, or with calls merging into a chorus.

3. During the summer of 2019, the presence of this species was investigated acoustically at 40 listening points distributed along the tidal inlets that connect the Venice lagoon with the open sea.

4. Longer sounds, comprising a higher number of faster repeated pulses, were found during the chorus and were used as a proxy of spawning activity; similar sound features have been recorded in different captive Sciaenids during spawning.

5. The three inlets were classified as more or less suitable for spawning on the basis of the vocal rhythms identified, demonstrating a clear preference along a north–south gradient and indicating higher spawning activity in the internal-facing areas of the inlets, compared with the seaward-facing areas. The chorus occurred in localized areas consistently throughout the breeding season, suggesting that spawning is concentrated in preferred areas.

6. For the first time a relationship between the sound features and vocal rhythms of fish has been highlighted by an in situ study. This validates the use of the chorus as a reliable natural indicator of *S. umbra* breeding sites, and in turn suggests a potential non-invasive approach based on PAM for mapping the key reproductive areas of this vulnerable species in the Mediterranean Sea.

**Keywords**

brown meagre, coastal areas, fish, fishing, monitoring, protected species, reproduction
1 | INTRODUCTION

Passive acoustic monitoring (PAM) is a successful method to detect, record, and analyse biological sounds (Sousa-Lima, Norris, Oswald, & Fernandes, 2013). Mainly used for studying marine mammals (Mellinger, Stafford, Moore, Dziak, & Matsumoto, 2007), PAM has been more recently applied to fish monitoring (Connaughton & Taylor, 1995; Gannon, 2008; Lobel, Kaatz, & Rice, 2010; Locascio & Mann, 2008; Luzckovich, Pullinger, Johnson, & Sprague, 2008; Mok & Gilmore, 1983; Mok, Yu, Ueng, & Wei, 2009; Nelson, Koenig, Coleman, & Mann, 2011; Saucier & Bultz, 1993), as there are over 800 species of fishes worldwide that emit sounds, thanks to diverse sound-producing mechanisms (Ladich & Fine, 2006). Passive acoustic techniques have been used to identify essential fish habitats (Lobel, 2002; Lobel et al., 2010; Locascio & Mann, 2011; Luzckovich et al., 2008; Luzckovich, Sprague, Johnson, & Pullinger, 1999; Mann & Lobel, 1995), to locate fish concentrations during their vulnerable spawning stage (Casaretto, Picciulin, Olsen, & Hawkins, 2014; Locascio & Mann, 2011; Mann, Bowers-Altman, & Rountree, 1997; Tellechea, Norbis, Olsson, & Fine, 2011), to study spatial and temporal patterns of fish reproduction (Luzckovich et al., 2008), to track fish vertical migrations (D'Spain & Batchelor, 2006), or to census cryptic fish species (Picciulin, Kéver, Parmentier, & Bolgan, 2018). More recently, acoustic diversity evaluated by PAM has been revealed to mirror the taxonomic diversity (Desiderà et al., 2019), and fish sounds have been used as an environmental proxy for habitat monitoring (Di Iorio et al., 2018).

Passive acoustic monitoring (PAM) can also be useful in the context of behavioural ecology (Rountree et al., 2006). Fish sounds are known to be associated with feeding and territorial or reproductive behaviour, and changes in the rate of sound production and acoustic repertoire according to behavioural states have been reported in several species (Amorim, 2006). The use of recording sounds as a method for the investigation of specific behaviours at sea has been explored in several locations worldwide, such as coastal areas of the USA, tropical areas of Australia, and along the South American Atlantic coast, as well as the Mediterranean Sea (Lobel et al., 2010; Luzckovich et al., 2008; Parmentier et al., 2018; Parsons, Salgado-Kent, Marley, Gavrilo, & McCauley, 2016; Picciulin et al., 2013; Scharer, Rowell, Nemeth, & Appeldoorn, 2012; Tellechea, 2019).

Some vocal fishes are amongst the most abundant and important commercial species, including some of the world’s most valuable fish: the Atlantic cod (Gadus morhua) (Rowe & Hutchings, 2006), the haddock (Melanogrammus aeglefinus) (Hawkins & Amorim, 2000), and the drum fishes (i.e. sciaenids, Ramcharitar, Gannon, & Popper, 2006; Tellechea, Fine, & Norbis, 2017). The Sciaenidae include 78 genera and about 298 species of coastal marine, estuarine, and freshwater fishes located in the temperate, tropical, and subtropical regions of the Atlantic, Pacific, and Indian Oceans (Nelson, 2006). These fishes live in small groups, but they may form large aggregations during the spawning season (Nelson, 2006; Ramcharitar et al., 2006), being multiple-batch spawners with group-synchronous oocytes (Barbaro et al., 2002; Chao, 1978). The spawning behaviour reported for some species (e.g. the red drum, Sciaenops ocellatus, Lowerre-Barbieri et al., 2008; the white seabass, Atractoscion nobilis, Aalbers and Drawbridge, 2008; the weakfish, Cynoscion regalis, Connaughton and Taylor, 1996; the shi drum, Umbra cirrosa, Francescon and Barbara, 1999; and the brown meagre, Sciaena umbra, Picciulin et al., 2012) suggests a general pattern of multiple courting males closely pursuing and spiralling around a female, and repeatedly nudging her urogenital region. Sound production while courting has been widely reported in this family (Ramcharitar et al., 2006). Although a common feature underlying the calls is the low intraspecific variability in the dominant frequency and the silent periods between pulses (Parmentier, Tock, Falguière, & Beauchaud, 2014), sciaenids demonstrate unique acoustic variety (reviewed by Ramcharitar et al., 2006) and have at least two different types of recognized calls, i.e. reproductive and disturbance calls, although there is a third type of call, the double knocks, that has been registered only in a few species of scienids (Lin, Mok, & Huang, 2007; Mok & Gilmore, 1983; Tellechea, 2019).

Reproductive calls have been recorded largely in the wild (Borie, Mok, Chao, & Fine, 2014; Locascio & Mann, 2011; Luzckovich et al., 2008; Monczak, Berry, Kehrer, & Montie, 2017; Parmentier et al., 2018; Picciulin et al., 2013; Tellechea et al., 2011), showing clear seasonal patterns and often peaking during crepuscular (dawn and dusk) or nocturnal hours, probably in order to limit the predation on eggs by many juvenile and adult fishes (Holt, Holt, & Arnold, 1985). Sciaenids’ reproductive calls are generally made of trains of pulses with little frequency modulation (Ramcharitar et al., 2006) and, as far as we know, low intraspecific acoustic variability, linked to the physiological constraints of the sound-producing mechanism (Parmentier et al., 2018). As a consequence, information (e.g. species identity or behavioural state) is mainly encoded in the sound temporal domain (Winn, 1964).

As with other Sciaenids, the brown meagre emits drumming sounds during the reproductive period (Codarin, Wysocki, Ladich, & Picciulin, 2009; Picciulin et al., 2012). Sounds are produced by males, as the sonic apparatus is absent in females (Parmentier et al., 2018). Three vocal patterns have been recognized at sea: (i) an irregular pattern, where a variable number of sounds, composed of a variable number of pulses and lacking any fixed repetition rate, are produced; (ii) a regular rhythm, where a few vocalizing individuals emit stereotyped sounds that are highly regular in sound interval; and (iii) the chorus, where the production of sound is almost continuous, with the vocalizations of many individuals overlapping with one another (Picciulin et al., 2012). The regular rhythm occurs more frequently at dusk, ultimately leading to the formation of a chorus with a marked nocturnal peak from 20:00 to 24:00 h (Picciulin et al., 2012). The existence of different patterns of sound at sea is expected to reflect a different level of individual motivation and/or to have a different function for the whole fish aggregation. The regular rhythm is the most common sound pattern recorded over a vast spatial scale in the Mediterranean Sea (Di Iorio, pers. comm.) during the reproductive season of the brown meagre, suggesting that regularity is crucial for reproduction. This is not
surprising, as highly stereotyped, regular, and redundant signals make communication systems more resilient to transmission errors and masking (Hauser &Konishi, 1999).

Given the spatio-temporal consistency of its acoustic features (Parmentier et al., 2018), the presence of the brown meagre has been identified acoustically along the coastal areas of the Mediterranean Sea, with particular reference to the Northern Adriatic Sea (Bonacito, Costantini, Picciulin, Ferrero, & Hawkins, 2002; Colla, Pranovi, Fiorin, Malavasi, & Picciulin, 2018; Picciulin et al., 2013) and to the Western Mediterranean Sea, mainly along the French coast (Parmentier et al., 2018). The detection of sounds at sea indicates that vocal individuals are engaged in the reproductive process (Picciulin et al., 2012). The localization of the spawning habitats and the identification of their features are of particular interest for the conservation of this species: although an overall slow recovery has been reported recently (Garcia-Rubies, Hereu, & Zabalà, 2013; Harmelin, 2013), the brown meagre is actually listed in Annex III (Protected Fauna Species) of the Barcelona Conventions and is classified as a Vulnerable fish species by the International Union for Conservation of Nature (IUCN) (BiszéI et al., 2011; IUCN, 2019). This is because of its population decline in the Mediterranean Sea at the end of the 20th century, as a result of coastal commercial and recreational fisheries (Chao, 1986). Monitoring the distribution of brown meagre could also help in evaluating coastal environmental conditions, with this species recognized as indicative of favourable environmental quality (Garcia-Rubies et al., 2013) and defined as an umbrella species (i.e. a species selected for making conservation-related decisions) for the ecological community of rocky habitats (Picciulin et al., 2013).

Captive studies reported that sciaenid spawning events are associated with high calling rates and high pulse repetition rates. Lowerre-Barbieri et al. (2008) demonstrated that reared red drum produce calls containing eight or more pulses prior to spawning, whereas sounds containing four or fewer pulses occur out-with the spawning period. This was confirmed by Montie et al. (2016), who showed that red drum calls have more pulses and pulses that are longer in duration when fish are getting close to spawning. Recently, Bolgan et al. (2020) showed that longer sounds, with a higher number of faster repeated pulses, are related to spawning not only in red drum but also in two other Sciaenidae species of high commercial value (Argyrosomus regius and Umbrina cirrosa) maintained in rearing facilities. All together, these findings indicate that the temporal features of sound (as defined by the number of pulses in a sound and the inter-pulse distance) can predict spawning in Sciaenidae, as these are related to physiological changes in the sonic muscle that occur during reproduction (Connaughton, Fine, & Taylor, 2002; Connaughton & Taylor, 1994). As a consequence, this study aims to: (i) characterize the variation in the temporal features of the sounds produced by the brown meagre; and (ii) evaluate whether this variation is consistently associated with the vocal rhythms (i.e. irregular pattern, regular rhythms, or chorus) recorded at sea, in order to establish a spawning proxy for wild brown meagre populations.

2 | MATERIALS AND METHODS

2.1 | The study species

The brown meagre is a slow-growing and long-lived species that can live for up to approximately 30 years and exceed 50 cm in total length (Fiorentino et al., 2001). It is sedentary with a limited capability for adult dispersal (La Mesa, Coltella, Riangetti, & Arnesi, 2008), and its mobility and activity decrease sharply outside of the reproductive season, showing high site fidelity (Alos & Cabanellas-Reboredo, 2012). It is a nocturnal species (La Mesa et al., 2008) that uses a smaller area during the day than during the night. Little is known about its movements during the reproductive season (May–August), when it forms breeding aggregations (Fiorentino et al., 2001; Grau, Linde, & Grau, 2009). It is often present at high densities in marine protected areas (Guidetti et al., 2014; Harmelin-Vivien et al., 2015; Picciulin et al., 2012), but is one of the species most frequently caught by spearfishers in the Mediterranean (Lloret et al., 2008).

2.2 | Study area

During summer 2019, three acoustic surveys were conducted at 40 listening points distributed along the three inlets connecting the Venice lagoon with the sea (Figure 1). All three inlets – Lido, Malamocco, and Chioggia – are made by long jetties (long rocky piers) that extend far offshore. Since 2003, the inlets have been part of the construction of the Modulo Sperimentale Elettromecanico (MOSE), i.e. Experimental Electromechanical Module, a system of mobile barriers positioned within each of the three inlets built to limit flooding of the historical city of Venice. This has contributed to the substantial modification of the inlet morphology and sedimentary regime (Toso et al., 2019).

The inlets present artificial hard substrates in an otherwise soft and mobile sea floor, increasing habitat heterogeneity and potentially enhancing biodiversity. It is well known (Bonacito et al., 2002; Colla et al., 2018) that artificial structures act as a site of attraction for brown meagre, resembling its typical reproductive habitat, i.e. rocky reefs with holes and shelters close to soft substrates, which are their preferred feeding grounds (Fabi, Panfili, & Spagnolo, 1998). A preliminary acoustic survey was undertaken in two of the three inlets by Picciulin et al. (2013), showing variable vocalization rates along the listening points. In its turn, this suggested the presence of a variable number of individuals heterogeneously distributed along the piers and the artificial rocky substrates built in recent years to protect the coasts from erosion (Cecconi et al., 2008).

2.3 | Sampling design

The recording points were localized along the Lido–San Nicolò inlet (Venice lagoon, north-eastern inlet; 13 recording stations), the Malamocco–Alberoni inlet (Venice lagoon, central inlet; 15 recording stations), and the Chioggia inlet (Venice lagoon, south-western inlet;
12 recording stations). These points were distributed facing both the internal side of the inlet (i.e. ‘internal stations’) and the sea side of the inlets (i.e. ‘external stations’), with each located about 300 m apart; this distance is based on the mean propagation range of brown meagre calls calculated from the sound source levels and assuming cylindrical spreading loss (for details, see Codarin et al., 2009).

All of the stations in an inlet were acoustically monitored on a single-day survey, which was replicated in June, July, and August (on 28 June, 5 August, and 29 August 2019 in Lido inlet; on 1 July, 29 July, and 28 August 2019 in Malamocco inlet; and on 5 July, 1 August, and 27 August 2019 in Chioggia inlet). The surveys were run in the summer season from 19:00 to 24:00 h, corresponding to the yearly and daily periods of maximal acoustic activity of this species (Parmentier et al., 2018; Picciulin et al., 2012).

### 2.4 Acoustic recordings

Recordings were obtained using a pre-amplified GP1280 hydrophone (sensitivity, −170 dB re. 1 V/Pa; frequency range, 5 Hz–90 kHz; Colmar SRL, La Spezia, Italy) connected to a Tascam Handy Recorder (sampling rate, 44.1 kHz, 16 bit; Tascam, Montebello, CA) generating WAV files. Prior to each survey the signal was calibrated using a generator of sine waves of known voltage. The hydrophone was lowered from an open boat to an average depth of 4 m (range 2–6 m depth). Each recording lasted 5 minutes.

Sampling was only carried out in a sea state of less than two on the Douglas scale, and with a wind speed of less than 10 km h$^{-1}$. The water temperature was measured prior to each recording using a digital thermometer (HANNA Checktemp® 1 HI98509, ± 0.1 °C; Hanna Instruments, Woonsocket, RI), giving an average of 27.4 °C (range
26.6–28.5 °C) for the acoustic samples containing brown meagre sounds. The average water temperature did vary over the recording period (Kruskall–Wallis P < 0.001), although higher average values were recorded in July with decreasing values in August. This parameter differed on average among the different inlets (27.6 ± 0.4 °C at the Lido inlet, 26.8 ± 0.5 °C at the Malamocco inlet, and 27.6 ± 0.5 °C at the Chioggia inlet; Kruskall–Wallis, P < 0.001), whereas it did not significantly differ between the external stations (27.7 ± 0.7 °C) and the internal stations (27.3 ± 0.5 °C; Mann–Whitney U-test, P = 0.94).

2.5 | Data analysis

A total of 120 recordings were collected and analysed minute by minute using AUDITION (Adobe, San Jose, CA). Audial and visual assessment of the spectrograms (sampling rate 44.1 kHz, 16 bit) allowed each 1-min sample to be classified as a ‘no sound’ sample or into one of the three vocal patterns reported by Picciulin et al. (2012): irregular (I), regular rhythm (R), and chorus (C), with the chorus generated by large numbers of sounds produced at the same time.

Sounds were also analysed quantitatively by scoring the number of pulses per minute, defined here as pulse rate (PR), and the pulse rate was further scaled on an arbitrary quantitative scale (pulse code, PC), ranging from 0 (no sound) to 5 (maximum pulse rate), in accordance with Picciulin et al. (2013): 0, no sound production; 1, very few sounds (fewer than 30 pulses min⁻¹); 2, some sounds (30–50 pulses min⁻¹); 3, semi-continuous sound production (>50 pulses min⁻¹); and 4, continuous sound production (>100 pulses min⁻¹); and 5, chorus.’

For each acoustic sample where brown meagre sounds were identified and counted, an analysis was further conducted on a sample of between five and 15 sounds (i.e. a recognizable sequence of pulses produced by a single source) with an optimal signal-to-noise ratio, obtaining a total of 394 sounds (with an average of 6.6 sounds analysed for each 5-min recording containing brown meagre vocalizations). The following sound parameters were measured: (i) the number of pulses per sound units; (ii) the pulse period (i.e. the peak-to-peak time interval between consecutive pulses in a sound, measured in ms); (iii) the sound duration (i.e. the time measured from the first peak of the first pulse to the first peak of the last pulse of the same sound, in ms); and (iv) the pulse peak frequency (i.e. the frequency with the highest energy). The temporal features were measured from the waveform, whereas the frequency analyses were obtained from the power spectra using AVISOFT SASLAB PRO (fast Fourier transform (FFT) 1024 points, 50% overlap, Hamming window; Avisoft Bioacoustics, Glenicke/Nordbahn, Germany).

Statistical analyses were performed with non-parametric tests (Kruskal–Wallis test or Mann–Whitney U-test; Sokal & Rohlf, 1995), with an alpha level of 0.05. A Spearman rank correlation test was used to correlate the sound parameters, with significant correlations being considered for P < 0.05. Furthermore, a one-way analysis of covariance (ANCOVA) was run on the log numbers of the pulse period data with temperature as the covariate, pulse period as the dependent variable, and pulse code as the grouping variable, in order to evaluate the influence of water temperature on fish sound parameters, such as the pulse period, as highlighted by previous studies (Connaughton et al., 2002).

3 | RESULTS

Brown meagre sounds were found in about half of the acoustic samples (61 out of 120): R-calls occurred in 20% (Figure 2a), C-calls occurred in 18%, and I-calls occurred in 13% of the recorded samples. Nevertheless, although all the three main vocal patterns were recorded in the Lido and Malamocco inlets, only irregular sounds were recorded in the Chioggia inlet (for details, see Figure 1). Furthermore, any acoustic activity of the target species was detected in half of the sites within Malamocco and Chioggia inlets, whereas only three out of 13 sites in the Lido inlet showed an absence of brown meagre vocalizations.

Samples with sounds showed a slight decline throughout the summer (57% from the end of June to the beginning of July, 52% from the end of July, and 42% from the end of August), associated with a decline in the presence of the chorus and the R-calls and an increase in the I-calls (Table 1). The average brown meagre pulse rate (i.e. the number of pulses per minute, PR) did not change over the three survey periods (Kruskal–Wallis test, P = 0.173), suggesting an overall temporal homogeneity in the acoustic activity throughout the recording period.

3.1 | Sound analysis

The sounds (n = 394) were composed of an average of 5.8 ± 2.0 pulses (min. = 2, max. = 19), with an average pulse period equal to 92 ± 2 ms and an average peak frequency of 314 ± 99 Hz. Sounds lasted on average 442 ± 219 ms.

The number of pulses per sound significantly varied in relation to the PR calculated for the corresponding acoustic sample (Kruskall–Wallis P < 0.05), with the average PR being 79 ± 130 pulses per minute (max. 350 pulses per minute). It also increased according to the PC (calculated from the base of the classes of pulse rate; Figure 3) and the vocal patterns (Figure 4); this means that during the chorus a single sound was, on average, composed of a higher number of pulses compared with sounds produced in both the I-calls and the R-calls (see also Figure 2a, b).

A significant positive correlation was found between the number of pulses per sound and the duration of the sound (Spearman correlation coefficient 0.6, P < 0.001), as well as a significant negative correlation between the number of pulses per sound and the pulse period (Spearman correlation coefficient 0.55, P < 0.001). Not surprisingly, the sound duration and the pulse period also vary according to the PC of the corresponding acoustic sample (Kruskall–Wallis P < 0.05), increasing (Figure 5a) and decreasing (Figure 5b) according to the PC, respectively. Significant variation of the pulse period in relation to the PC has been confirmed by ANCOVA ($F_{3,2,118} = 32.7$, $P \leq 0.001$).
FIGURE 2  Sound spectrograms (above) and waveforms (below) of (a) three brown meagre, *Sciaena umbra*, sounds with a regularly repeated rhythm (R-call), (b) four multi-pulsed sounds in a mixed R-call and chorus sample, where another sound made by three pulses is clearly visible and additional sounds are present in the background (sampling frequency = 6 kHz; fast Fourier transform length = 512 points; bandwidth = 15 Hz; frame size = 100%; Hamming window, overlap = 96%)
irrespective of water temperature, used as a covariate, indicating that this abiotic factor did not affect the results.

3.2 | Spatial patterns

Acoustic files containing brown meagre sounds were not equally distributed along the three inlets, showing a clear north–south gradient: brown meagre vocalizations were present in 64% of the 39 samples recorded at the Lido inlet, 53% of the 45 samples recorded at the Malamocco inlet, and 33% of the 36 samples recorded at the Chioggia inlet. The chorus was recorded only at the Lido and Malamocco inlets, whereas I-calls were the most common brown meagre vocalizations at the Chioggia inlet. The average PR significantly differed among the three inlets (Kruskal–Wallis test, $P < 0.05$; Figure 6a). A similar trend has been found when considering the average number of pulses per sound recorded at the three inlets, which differed significantly (Kruskal–Wallis test, $P < 0.001$; Figure 6b).

Despite the spatial heterogeneity of the brown meagre vocalizations along the three inlets, in all three inlets the sounds were recorded mainly at the internal stations, i.e. the stations facing the internal side of the inlet (70% of the 60 recorded samples), compared with the external stations, i.e. the stations facing the sea side of the inlets (32% of the 60 recorded samples). The average PR was significantly higher in the internal stations compared with the external stations (Mann–Whitney U-test, $P < 0.001$; Figure 7), as well as the average number of pulses per sound (7.1 ± 2.0 versus 5.4 ± 2.0 pulses per sound; Mann–Whitney U-test, $P < 0.001$), with consequent shorter pulse periods (90 ± 20 versus 100 ± 20 ms; Mann–Whitney U-test, $P < 0.001$).

Considering the 40 different sampling stations, in 34% of them brown meagre sounds have always been recorded whereas in 33% of them brown meagre sounds have never been recorded; sounds have been recorded twice out of the three monthly monitoring sessions at seven listening points (18%) and only once at six listening points (15%). At four stations located in the internal side of both the Lido and the Malamocco inlets the chorus was always recorded in each of the three monitoring sessions.

4 | DISCUSSION

4.1 | Relationship between the temporal features and the vocal rhythms of brown meagre sounds

The presence of brown meagre has been identified in the Venice lagoon inlets through the species-specific typical features of the recorded sounds (Parmentier et al., 2018), in accordance with previous studies in the Mediterranean Sea (Bonacito et al., 2002; Colla

<p>| TABLE 1 | Percentages of occurrence for: (i) the irregular pattern, where a variable number of sounds lacking any fixed repetition rate are produced (I-calls); (ii) the regular rhythm, where a few vocalizing individuals emit stereotyped sounds that are highly regular in sound interval (R-calls); and (iii) the chorus, where the production of sounds is almost continuous as a result of the vocalizations of many individuals overlapping one with another along the three acoustic surveys; the highest percentage values are highlighted |</p>
<table>
<thead>
<tr>
<th>Chorus</th>
<th>R-calls</th>
<th>I-calls</th>
</tr>
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<tbody>
<tr>
<td>End of June</td>
<td>22%</td>
<td>25%</td>
</tr>
<tr>
<td>End of July</td>
<td>20%</td>
<td>17%</td>
</tr>
<tr>
<td>End of August</td>
<td>10%</td>
<td>15%</td>
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**FIGURE 3** Mean (± standard error) number of pulses per brown meagre, *Sciaena umbra*, sound according to the pulse code (PC), a quantitative scale defined following Picciulin et al. (2013): 1, very few sounds (<30 pulses min$^{-1}$); 2, some sounds (30–50 pulses min$^{-1}$); 3, semi-continuous sound production (>50 pulses min$^{-1}$); 4, continuous sound production (>100 pulses min$^{-1}$); 5, chorus
et al., 2018; Parmentier et al., 2018; Picciulin et al., 2013). All of the different vocal patterns described by Picciulin et al. (2012) were recorded here: the irregular as well as the regular rhythms and the chorus. Nevertheless, considering the structures of the single sounds, a higher number of faster repeated pulses were found during the chorus compared with the regular and irregular patterns of calls. This is the first case in which a relationship between sound temporal features and vocal rhythms has been highlighted by an in situ study. In captivity, longer sounds with a higher number of faster repeated pulses are associated with sciaenid spawning events (Lowerre-Barbieri et al., 2008; Montie et al., 2016). Recently Bolgan et al. (2020) showed that the shi drum, *Umbrina cirrosa*, a species phylogenetically closely related to the brown meagre (Sazaki, 1989), increases its call rate when approaching spawning, producing longer sounds characterized by a higher number of pulses and a shorter pulse period, as with the other vocal Mediterranean sciaenid *Argyrosomus regius*. It is possible to conclude that the chorus has a clearly identifiable behavioural value in the context of the brown meagre reproductive system: in particular, that the chorus acts as proxy for spawning events. This is supported by the case of other sciaenids, where the association between vocalizations and reproduction has been investigated by the simultaneous recording of sound and sciaenid-type eggs (Locascio & Mann, 2008; Luczkovich et al., 1999; Mok & Gilmore, 1983; Montie et al., 2016) or by the physiological evaluation of fish reproductive readiness: in the weakfish, *Cynoscion regalis*, for example, the gonadosomatic indices, sperm motility, and plasma androgen levels peaked within the period of maximal seasonal drumming (Connaughton & Taylor, 1995).

On the whole, changes in the temporal features of brown meagre sounds should be related to the physiology of the sound-producing mechanism. In sciaenid species, the swim bladder is surrounded by bilaterally symmetrical, highly vascularized muscles, called drumming muscles, characterized by their rapid contractile properties (reviewed by Ramcharitar et al., 2006): the contraction of the sonic muscles causes multiple swim-bladder oscillations that radiate sound into the surrounding water (Parmentier & Fine, 2016). During the reproductive period, androgens stimulate sonic muscle hypertrophy, enabling the muscles to contract more often and faster (Connaughton, Fine, & Taylor, 1997): the number of pulses corresponds to the number of muscle twitches and the pulse repetition rate corresponds to the muscle contraction rate, whereas the sound duration relates to the time in which the sonic muscles undergo cycles of contraction and relaxation (Connaughton et al., 1997; Lagardère & Mariani, 2006; Parmentier & Fine, 2016). In the brown meagre, however, the high-speed sonic muscles acting on the swim bladder do not allow for wide variability in sound structure, as a result of physiological constraints (Parmentier et al., 2018), and the size effect on call frequency is minor (Parmentier & Fine, 2016). In turn this means that if the female’s choice of partner is influenced by sound production, as is the case for sciaenidae (Sargent, Rush, Wisenden, & Yan, 1998), this would be more likely related to the number of sounds produced per unit time or to the number of pulses per sound than to other characteristics, such as sound frequency. This further supports the role of the long multi-pulsed sounds in the brown meagre chorus as an indication for courtship and spawning.
4.2 Use of brown meagre multi-pulsed sounds as a proxy for locating spawnings events

The use of multi-pulsed sounds within the chorus is proposed as an acoustic indicator of spawning, similar to the work of Lowerre-Barbieri et al. (2008), who categorized red drum calls in the field as either spawning related or non-spawning sounds based on the number of pulses, in accordance with Luczkovich et al. (1999). On the basis of this metric, the three inlets that connect the Venice lagoon to the open sea have been classified as more or less suitable for reproduction, showing a clear preference following a north–south gradient and highlighting higher spawning activity on the internal sides of the inlets compared with the external sides.

On the whole, the results indicate that the chorus occurs consistently in localized areas throughout the breeding season. The brown meagre is an iteroparous batch spawner, i.e. eggs are released in batches over a relatively protracted period, but not all breeders show the same ovarian maturity stage at the same time, in order to expand the population’s overall number of spawns (Grau et al., 2009); consequently, it seems more likely that different fish move to these preferred areas to spawn, rather than the same few fish, characterized by
high site fidelity, being repeatedly acoustically sampled during their spawning. It is possible to conclude that spawning is not a spatially diffuse and dynamic event in brown meagre, but instead is concentrated in preferred locations.

In some sciaenid species such as Cynoscion squamipinnis and Sciaenops ocellatus, aggregation sites have been reported to be most easily characterized by relatively high salinity (approx. 30) and fast-moving water (Baltz & Campos, 1996), and fish activity has been linked to tidal variations (e.g. Dresser & Kneib, 2007), which affects the current speed of the water. The preferred areas reported here could possibly be characterized by abiotic factors such as the current speed in the inlets, which has been enhanced recently by changes in the inlet configuration (Ghezzo, Guerzoni, Cucco, & Umgasser, 2010) through the construction of the MOSE (the system of mobile barriers positioned within each of the three inlets designed to limit the flooding of the historical city of Venice), or alternatively the 3D artificial structures could create boulders, local crevices, or overhangs along the piers that represent the ideal habitat for spawning aggregations. Our understanding of the physical and structural factors influencing spawning habitat selection by the species is beyond the aims of the present study, however, and will be the specific focus of future investigations.

**FIGURE 6** Mean (± standard error) pulse rate (a) and average number of pulses in brown meagre, *Sciaena umbra*, sound (b) recorded at the Lido, Malamocco, and Chioggia inlets.
4.3 Applications of our results for brown meagre monitoring and conservation

The present paper shows that PAM is a non-invasive tool suitable not only to infer the spatial distribution of brown meagre aggregations but also to locate its preferential spawning areas on a very fine scale by evaluating the sound temporal parameters. The use of pulse numbers per sound appears to be more conservative than other sound characteristics used for in situ monitoring, as it has the twin advantages of being strictly related to fish behavioural contexts (Amorim, 2006) and is little affected by uncontrollable variables. The sound pulse period, for example, is not appropriate because it is dependent on the water temperature (Kéver, Boyle, & Parmentier, 2015), which at sea is rarely constant in time and space. Similarly, the intensity of sounds is not a reliable proxy for spawning, as was suggested to be the case by Montie et al. (2017) for brown meagre in captivity, as a result of the unknown distance between the emitting moving fish and the hydrophone, which influences the sound levels received.

Locating the relationship between sound temporal parameters and the vocal patterns of species, the present results validate the use of the chorus in field studies as a proxy for spawning. Compared with the study of single sound parameters, this simplified approach could be widely expanded in Mediterranean studies by using fixed automatic recorders that allow monitoring for extended periods of time (Mann, Locascio, & Wall, 2016; Sousa-Lima et al., 2013) and automatic detectors of fish sounds (Monczak et al., 2017; Monczak, Ji, Soueidan, & Montie, 2019; Vieira, Pereira, Pousão-Ferreira, Fonseca, & Amorim, 2019). PAM becomes a valid alternative to more time-consuming and costly methods, such as egg sampling, which is possibly biased by predator activity and water currents.

Locating brown meagre breeding sites is essential for planning permanent or temporal protection of sensitive areas during sensitive periods; this would include the reduction of fishing pressure as well as the mitigation or compensation for adverse impacts from non-fishing activities. Locating spawning aggregations also allows the evaluation of the connectivity between adjacent groups and provides valuable input for possible marine reserve design. In the end, investigating the characteristics of the spawning habitats— including the associated biological communities that make these areas suitable for brown meagre (e.g. prey availability) or the need for completing all life stages (e.g. egg dispersal and larval settlement) — provides clues to prevent continuing habitat loss or to minimize adverse effects on such habitats located along the Mediterranean coasts. All of these measures would enhance the conservation status of this vulnerable species.

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ORCID

Marta Picciulin  https://orcid.org/0000-0003-3689-1151

REFERENCES


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