Acoustic fish communities: sound diversity of rocky habitats reflects fish species diversity

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ABSTRACT: Assessing fish biodiversity patterns is a major concern in aquatic science and conservation. To be effectively used, fish diversity assessments benefit from the use of integrated complementary approaches. Passive acoustics has received increasing attention as a non-invasive, long-term monitoring tool, as it uses biological sounds produced incidentally or intentionally as natural tags to identify and estimate animal diversity. In the marine environment, there is little evidence about the link between taxonomic diversity (different species) and acoustic diversity (different sound types). Here we used underwater visual census fish data collected over multiple years from 3 sites within a Mediterranean Marine Protected Area as comprehensive information on local fish assemblages to be compared with acoustic recordings obtained in September 2015. Richness, diversity and community similarity indices as well as abundance analyses revealed a strong relationship between taxonomic diversity and acoustic diversity. Overall, acoustic communities showed pronounced differences between the study sites that were not observed in the respective taxonomic assemblages. Despite the lower number of sound type categories (12) compared to taxa (53) and the short recording period, passive acoustics showed a high discriminating potential, which supports its suitability as a complementary approach to visual-based surveys. The fish sound repertoire established here was organized into a dichotomous tree based on acoustic characteristics that are valuable for the development of automatic acoustic biodiversity appraisal tools for resource monitoring and management.

KEY WORDS: Biodiversity · Fish sounds · Species richness · Biophony · Underwater visual census · Passive acoustic monitoring · Soundscape · Community ecology

1. INTRODUCTION

Marine biodiversity plays a vital role in sustaining human livelihoods and well-being as well as water quality (Pauly et al. 2005), but it is facing substantial losses due to multiple cumulative human impacts on ecosystems, including overfishing, pollution and climate change (Sala & Knowlton 2006, Costello et al. 2010, Micheli et al. 2013). Fish are of particular concern because they represent one of the major sources of animal protein (FAO 2016) and provide a large number of essential ecosystem services to humans, including regulation of nutrient cycles and control of trophic networks (Holmlund & Hammer 1999). Because fishes exhibit a multi-faceted biological diversity that is shaped by environmental conditions (Nel-

son et al. 2016) and human impacts (Worm et al. 2006), they are also considered effective ecological indicators (Moyle & Leidy 1992).

Monitoring spatial and temporal fish biodiversity dynamics is a global priority (e.g. the Joint Communication on International Ocean Governance, https://ec.europa.eu/maritimeaffairs/policy/ocean-governance_en) and a difficult challenge encountered by ecologists and conservation biologists (Hutchings & Baum 2005). Underwater visual census (UVC) is the most commonly used non-destructive method for studying fish assemblages and assessing their diversity, especially in coastal habitats (Caldwell et al. 2016). In particular, UVC methods involving direct observation by SCUBA divers are effective in obtaining fish diversity data (Lincoln Smith 1988). The main advantages of UVC techniques are that (1) diverse and abundant assemblages can be rapidly censused (through the detection and identification of a high number of taxa), (2) costs and the necessary equipment to obtain the data are minimal, (3) the data are immediately available, and (4) complementary data on fish behaviour, and habitat complexity and patchiness can be easily gathered (Edgar et al. 2004, Guidetti et al. 2014). However, SCUBA sampling using UVC is (1) sensitive to the 'observer effect' (i.e. the experience of the observer that can result in the misidentification of species; Thompson & Mapstone 1997) and errors in seeing and counting organisms (Thresher & Gunn 1986, Williams et al. 2006) or in estimating their sizes (Edgar et al. 2004), (2) inadequate for detecting cryptic, elusive and nocturnal species (Willis 2001, Edgar et al. 2004, Feary et al. 2011) and (3) subject to some logistical constraints (i.e. visibility and time dive-limits related to depth). Therefore, fish diversity assessment would profit from the combination of *in situ* observations with complementary approaches that would help to overcome some of these limitations. Due to the importance of sound to the ecology of marine fauna and their life stages, soundscape measurements are considered promising for fish monitoring (Staaterman et al. 2013, Lindseth & Lobel 2018).

Biological sounds have been suggested as a means to quantify species diversity (Gasc et al. 2013, Sueur et al. 2014). In the last decades, passive acoustic monitoring (PAM) has been proposed as a potential non-intrusive and non-destructive approach to study changes in richness and diversity of natural communities of species in the terrestrial and aquatic realms (Krause & Farina 2016). Its complementarity with other methods lies in the fact that data can be recorded continuously, over long time periods (hours to years) and irrespective of abiotic conditions such as depth, light

or visibility. Furthermore, PAM has the potential to detect the presence of cryptic, elusive or uncommon species that produce sounds, which are rarely captured during UVC campaigns (e.g. Lambert & Mcdonald 2014, Picciulin et al. 2018). The major drawbacks of PAM, compared to UVC, are that (1) the ability to detect underwater sounds varies with background sound and ambient noise levels, (2) diversity results are not immediately available as acoustic data must be post-processed for the identification of sound types, (3) processing can be time-consuming if performed manually, when not using automatic detectors or indices, and (4) not all species vocalize and the identity of the emitter often remains unknown.

Fishes produce a wide range of sounds through diverse sound-producing mechanisms (Ladich & Fine 2006), mainly for communication (e.g. Amorim 2006, Fine & Parmentier 2015). Their vocalizations can serve as natural acoustic tags (Luczkovich et al. 2008, Parmentier et al. 2017) providing valuable information on the occurrence, onset, duration and periodicity of species behaviours (e.g. social interactions, reproductive activities, spawning) as well as on turnovers in local fish populations (Lobel 2002, Luczkovich et al. 2008). Recently, with the emerging field of 'soundscape ecology' (Krause 2008, Pijanowski et al. 2011) or 'eco-acoustics' (Sueur & Farina 2015), i.e. the study and understanding of the components of an acoustic environment and how they relate to the ecology of a habitat, there is an increasing interest in assessing whether passive acoustics can capture local biodiversity and, therefore, be applied as a complementary monitoring method. Most research tackling this critical ecological issue has focussed on terrestrial biodiversity (e.g. Sueur et al. 2014, Towsey et al. 2014). In marine environments, it is still unclear whether acoustic diversity reflects fish diversity (Kaplan et al. 2015, Nedelec et al. 2015, Bertucci et al. 2016, Harris et al. 2016). Most studies addressing the issue applied acoustic indices (specifically developed for terrestrial soundscapes), which represent estimates of the 'acoustic complexity' of a soundscape (e.g. Sueur et al. 2008, 2014, Pieretti et al. 2011). A recent study by Bolgan et al. (2018) clearly showed that acoustic indices, such as the acoustic complexity index (Pieretti et al. 2011), which is increasingly used to study biodiversity in aquatic environments, cannot discern between sound diversity and abundance. The comparison between the index and taxonomic diversity is therefore problematic. The detection and documentation of fish sounds are key to describing the biodiversity of any habitat through acoustics (Lindseth & Lobel 2018). A more detailed analysis of sound type occurrence and

Fig. 1. Tavolara - Punta Coda Cavallo marine protected area (MPA) zonation. The 3 study sites are indicated. UVC: under-water visual census
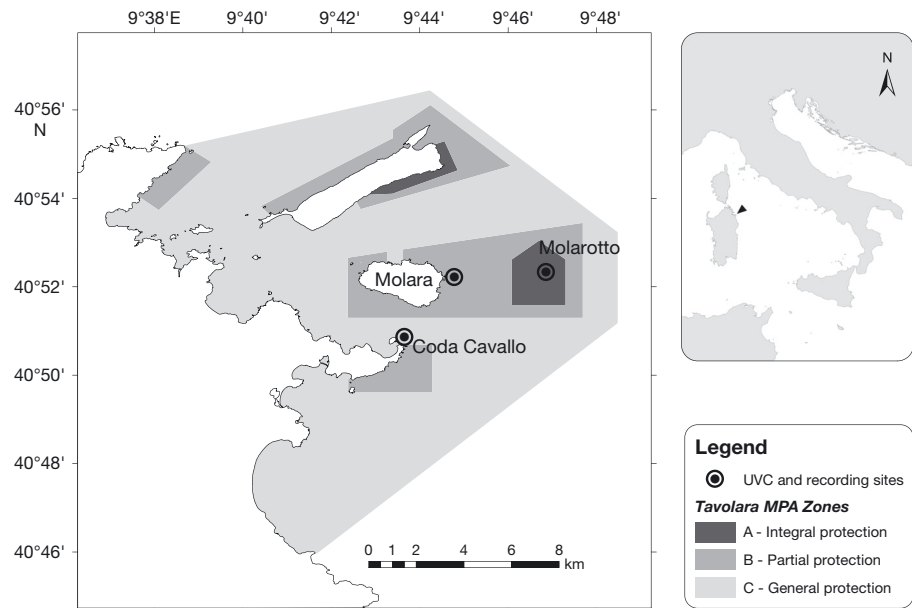
relative abundance is therefore imperative to better elucidate the relationships between acoustic diversity and taxonomic diversity. To our knowledge, no study has reported on the link between acoustic diversity based on individually identifiable sounds and diversity of fish taxa in temperate marine coastal habitats.

In this study, we investigated the link between Mediterranean rocky reef fish assemblages and sound production, and whether sound-type diversity reflects taxonomic diversity assessed using UVC. Because to date little is known about soniferous fish species in the Mediterranean Sea and only a few tens of fish species are known to vocalize (cf. Di Iorio et al. 2018), acoustic diversity was assessed based on fish sound types, categorised according to their acoustic characteristics. Data acquisition was conducted in a Mediterranean marine protected area (MPA) in which the spatial diversity of the coastal fish fauna has been established by extensive systematic UVC campaigns over multiple years (Guidetti et al. 2004, 2008, Di Franco et al. 2009). This provided strong baseline information on the spatial diversity of fish assemblages that was compared to the acoustic diversity.

2. MATERIALS AND METHODS

2.1. Study area

Fieldwork was carried out in the Tavolara - Punta Coda Cavallo MPA (TPCC MPA), located in the north-east of Sardinia, western Mediterranean Sea, Italy (40° 53′ N, 09° 43′ E). The MPA was established in 1997 but became effectively managed around 2003–2004. It comprises 76 km of coastline and a surface area of 153.57 km². Three types of zones with different levels of protection have been established: (1) A zones, corresponding to fully protected areas, where access is prohibited; (2) B zones, representing partially protected areas, where only authorized local artisanal fishing and diving are allowed; (3) C zones, corresponding to generally protected areas, where authorized artisanal and recreational fishing are allowed, except for spearfishing (Fig. 1). UVC standardized surveys have been carried out within and outside the TPCC MPA since 2005 by the same trained research team to avoid 'observer effects'. These surveys provide comprehensive baseline data on rocky reef fish assemblages within the study area (Di Franco et al. 2009, Guidetti et al. 2014). Three sampling sites with long-term UVC data within the MPA were selected for the present study. The 3 sites are comparable in terms of rocky habitat cover, slope, depth, complexity and mineralogical characteristics (i.e. granite rocks) (Guidetti et al. 2004, Di Franco et al. 2009) and are characterized by different protection levels. The study sites (Fig. 1) are named after their closest geographical locations and referred to as 'Molarotto' (A Zone), 'Molara' (B Zone) and 'Coda Cavallo' (C Zone).

2.2. Sampling design adopted for UVC surveys

We extracted data from the 8 most recent UVC campaigns carried out between 2012 and 2016 at

each of the 3 sampling sites. Data were collected during 2 sampling campaigns within the same year but in different seasons to allow a more representative description of the taxonomic diversity. Mean values of the within-year sampling campaign data were used to approximate average conditions in time, following Hedges et al. (1999), and for comparisons with the acoustic data.

Fish assemblages were assessed during daytime hours (between 10:00 and 14:00 h) by UVC along 25 m long × 5 m wide (125 m^2 surface area) strip transects (Harmelin-Vivien et al. 1985). Along each transect, fish taxa encountered and their relative abundance were recorded. Individuals belonging to the family Mugilidae were not recorded at the species level. Sampling campaigns within each of the 3 sites consisted of UVC replicated at 2 stations (separated by hundreds of metres) and at 2 depth intervals (5–10 m and 12–18 m). Four transects were surveyed randomly for each combination of stations and depths, yielding 8 transects per sampling site (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m608p183_supp.pdf). The 8 selected sampling campaigns resulted in a total of 192 replicated UVCs. Visual censuses were performed only on rocky reefs where other substrate types, such as sand or seagrasses, accounted for less than 5% in cover across the surveyed area.

2.3. Acoustic data and sampling design

Recordings were performed from 14–17 September 2015 at the 3 selected sites within the TPCC MPA (Fig. 1). Alternate simultaneous acoustic recordings of 2 of the 3 sites were conducted (Table S2), such that 1 site was recorded over 2 d (i.e. Molara), and 2 sites over 1 d. Recorders were all moored at around 20 m depth (Table S2) using sand bags, and the hydrophones were all at 1.5 m from the bottom. Acoustic detection ranges can vary substantially depending on the underlying geology of the seabed. As the 3 sites shared the same water depths and seabed topography, we considered transmission loss, and as a consequence acoustic detection ranges, to be similar. The recording equipment consisted of 2 autonomous underwater acoustic recorders, Song-Meter SM2M and SM3M (Wildlife Acoustics). The SM2M recorder was equipped with a wideband omnidirectional hydrophone (HTI-96-MIN, High Tech, receiver sensitivity: –163.4 dB re. 1 μPa/V, flat frequency response: 2 Hz–30 kHz). The SM3M used an omnidirectional HTI-92-WB hydrophone with a receiver sensitivity of –164.5 dB re. 1 μPa/V and a flat frequency response between 2 Hz and 50 kHz. The recorders were programmed to record continuously with a 96 kHz sampling frequency and 16-bit resolution.

2.4. Acoustic data processing

Since most fish vocalize and hear in the low (below 2 kHz) frequency range (Amorim 2006), audio recordings were down-sampled to 4 kHz. Calls were selected from 17:00 to 08:00 h in order to investigate biological activity and acoustic diversity patterns during twilight hours and overnight, as acoustic activity of fishes is greater at dusk and night-time compared to daytime (Picciulin et al. 2013a, Kéver et al. 2016, Parsons et al. 2016). Furthermore, during night-time hours, sound production is less masked by anthropogenic noise (i.e. nautical activities) than during the day.

The 4 recorded nights were visually and aurally assessed by the same trained listener using the software Raven PRO 1.5 (The Cornell Lab of Ornithology). Visual inspection of spectrograms and associated sound waveforms was used to identify and manually select individual vocalizations. All individually identifiable calls were tagged to allow abundance estimation. In order to prevent bias in the selection process, audio files were analysed through a blind approach, in which the operator was not aware of the recording location. Because manual sound selection over 15 h (from 17:00 to 08:00 h) is extremely time consuming, a subsampling scheme was established. Based on the preliminary assessment of an entire night (15 h), a subsampling scheme consisting of 10 min of manual selections every 15 min was designed. The acoustic trends resulting from such subsamples well reflected the ones of the continuous recording assessment, suggesting a reliable subsampling method. At all 3 sites, sound selection was not impaired by anthropogenic noise, which was very low, as illustrated in Figs. S1 & S2.

Sound type categories were defined based on acoustic characteristics, with the aim of obtaining an objective and rather conservative acoustic sound diversity. However, whenever possible, calls were assigned to specific fish species in accordance with reported vocalizations of well-studied Mediterranean sound-producing species. Sound types were divided into 2 main categories in accordance with formal descriptions of vocalizations emitted by fishes (Amorim 2006): (1) frequency-modulated signals, (2) series of

Table 1. Descriptions of sound categories used for acoustic diversity/community analyses

Sound type	Abbreviation	Definition
Ultra-fast pulse series	UFPS /kwa /	Pulsed sound around 800 Hz with ultra short pulse periods that appear as 'pseudo-harmonics' in the spectrographic representation
Long tonal call	LT	Long tonal call with poor or no frequency modulation
Downsweep	DS	Frequency-modulated sound with start frequency > end frequency
Low-frequency downsweep	LDS	Frequency-modulated sound with start frequency > end frequency and a peak frequency around or ≤200 likely emitted by *Epinephelus marginatus* (Bertucci et al. 2015)
Downsweep series	DSS	Sequence of consecutive downsweeps
Low-frequency down-sweep pulse series	LDSPS	Sequence of consecutive downsweeps and pulses with peak frequencies ≤200 Hz
Pulse series	PS	Sequence of similar pulses (at least 3) with irregular pulse periods and a peak frequency ≥200 Hz
Low-frequency pulse sequence	LPS	Sequence of similar pulses (at least 3) with irregular pulse periods, a peak frequency around or ≤200 Hz and a bandwidth between 20 and 200 Hz (some emitted by *Epinephelus marginatus*; Bertucci et al. 2015)
Fast pulse train	FPT	Pulse sequence with very small, aurally almost undetectable pulse periods with a peak frequency ≥200 Hz
Low-frequency fast pulse train	LFPT	Pulse train with very small, aurally almost undetectable pulse periods with a peak frequency ≤200 Hz (sounding like a grunt)
Pulse series with alternating pulse period	APPPS *O. rochei*	Stereotyped accelerating pulse series with alternating pulse period as repeatedly emitted by *Ophidion richei* (Kéver et al. 2012)
Regular pulse series	RPS *S. umbra*	Stereotyped pulse series as repeatedly emitted by *Sciaena umbra* (Picciulin et al. 2012)

at least 3 short broadband transient pulses that can be either stereotyped or irregular. The sound types identified in this study are described in Table 1 and displayed in Fig. 2. A more in-depth description of the dichotomous branching is provided in Fig. S3. An interactive version of Fig. 2 and the sound files composing it can be accessed at https://chorusacoustics. com/dichotomy-of-fish-sounds/. Single pulses were excluded from the repertoire because they cannot always be unambiguously attributed to a living organism. The classification method we applied is also in agreement with that of Tricas & Boyle (2014) and avoids an ambiguous sound nomenclature (Lobel et al. 2010). Except for the low-frequency downsweeps and low-frequency pulse series that are likely emitted by groupers (Bertucci et al. 2015) as well as the stereotyped *Sciaena umbra* (Picciulin et al. 2013a) and *Ophidion rochei* calls (Kéver et al. 2012), the species responsible for the identified sound types and the context in which they are emitted are still unknown. The sound type /kwa/ is overall very common and forms mass phenomena, referred to as choruses (Cato 1978, Di Iorio et al. 2018). Because of their high abundance (i.e. 30 sounds min^{-1} on average), not every single /kwa/ was selected; thus, the total number of /kwa/ sounds is an underestimate of the actually emitted number. Consequently, this type of sound was only included in the analyses using presence-absence data, but was excluded from all those evaluating abundance data.

2.5. Data analyses

2.5.1. Diversity analyses

For the UVC data, statistical tests were performed on the number of individuals per taxon per transect, combining data from all 8 sampling campaigns (N = 64 transects per site) to estimate average condition across time. For the acoustic data, tests were carried out on the number of sounds per sound type (selected based on the duty cycle) per clock hour (N = 15 nighttime clock hours of recordings per site). Since recordings in Molara occurred over 2 consecutive nights and the within-site variability was lower than the between-site variability (Figs. S4 & S5, Table S3), mean values of the number of sounds per sound type per clock hour were considered.

The same analyses were performed on both UVC and acoustic data separately. Richness, diversity indices and the Gower community similarity index were assessed for both taxa and sound types across sites. Pairwise comparisons of taxonomic and sound type richness between sites were performed using randomization tests with 999 iterations on presence/

Fig. 2. Dichotomy of fish sounds composed of spectrograms of the main sound type categories found during the visual inspection of the audio files, ordered using the acoustic properties of the signals. Detailed descriptions and definitions are provided in Table 1. An interactive version with lager spectrograms and sound files is available at https://chorusacoustics.com/dichotomy-of-fish-sounds/

absence data. Confidence intervals were set to 95%. Accumulation curves (using presence/absence data) were also built, allowing for meaningful comparison of community-wide changes (Gotelli & Colwell 2001, Gotelli & Chao 2013). Shannon and Simpson's Index of Diversity were calculated based on bootstraps with 99 iterations for both taxa censused and sound types using abundance information. To prevent the effects of numerical dominance by gregarious species (Guidetti & Sala 2007, and references therein), we excluded *Boops boops*, *Chromis chromis*, *Oblada melanura*, *Sarpa salpa*, *Spicara maena*, *Spicara smaris* and the omnipresent */kwa/* from the diversity indices analysis. The Shannon index assumes all species are represented in a sample and that they are randomly sampled. The Simpson's index of diversity gives more weight to common or dominant species. Statistical significance of diversity index differences between the sites was evaluated by performing bootstrap ANOVAs with 99 iterations followed by Tukey's HSD tests for multiple comparisons.

Furthermore, to assess acoustic community similarity and taxonomic community similarity across sites, we estimated the Gower index excluding gregarious species and the */kwa/*. The Gower index is based on dissimilarity matrices that are built using abundance data (i.e. the relative density of taxa or sound types at each site). It takes into account negative matches (i.e. instances where a taxon is not observed in either of the 2 samples being compared) and is recommended for detecting underlying ecological gradients (Johnston 1976, Gardener 2014).

2.5.2. Abundance analyses

Total abundances were assessed for taxa, using the data from all years, and for sound types. Differences between sites in calls and taxa were tested

using a negative binomial generalized linear model (GLM) for count data with a Poisson distribution using a logarithmic link function (Zuur et al. 2009) on densities, i.e. number of individuals per UVC transect and number of sounds (selected based on the duty cycle) per hour of recording, excluding gregarious species and the /*kwa*/. The call or taxon density was the response variable, site and sound type or taxon the explanatory variables. Because relative abundance/density may be influenced by the presence of particular sound types or taxa, an interaction term was included representing the multiplicative relationship between sites and sound types or taxa. The model was graphically validated by means of diagnostics plots. We also calculated a deviance statistic (i.e. residual deviance/degrees of freedom) to assess the goodness of fit of the model. If the model and the designated distribution are correct, this value should be approximately 1.0.

All statistical analyses were carried out using the R software (version 3.3.0, R Core Team 2016) including the packages 'rich' (Rossi 2011), 'vegan' (Oksanen et al. 2017), 'BiodiversityR' (Kindt 2016) and 'boot' (Canty & Ripley 2016) for richness, diversity and community similarity analyses, and 'MASS' ('glm.nb' function, Ripley et al. 2016).

2.5.3. Sound type diversity patterns

Because acoustic diversity patterns in terms of frequency or temporal segregation of the acoustic space are known to be linked to community stability and habitat quality (Sueur et al. 2008), we graphically examined acoustic diversity patterns in terms of hourly proportions of sound types (excluding the /*kwa*/).

3. RESULTS

Overall, 53 fish taxa were recorded using UVC across the 3 selected sites: 45 taxa were censused in Molarotto, and 42 in Molara and Coda Cavallo (Table S4). A total of 34 fish taxa were common to the 3 sites, while 5 fish taxa were exclusively censused in Molarotto, 4 in Molara and 2 in Coda Cavallo (Table S4).

Across the study sites, a total of 12 sound type categories were identified, with 5 sound types common to all sites (Table 1, Fig. 2, Table S4). The classification used in this study represents a rather conservative estimate of sound diversity, because some categories (e.g. pulse sequences, fast pulse trains,

downsweeps) include calls with similar acoustic characteristics for which a more detailed classification may be possible. This, however, was not done here because of an overall high within-class variability (Fig. 2). An in-depth acoustic analysis of each call as well as the collection of additional sounds of these broad categories in the future may allow a more detailed within-group classification. Among the 3 sites, Molarotto included 12 acoustic categories, Molara 9, and Coda Cavallo included 5 sound types (Table S5). *Sciaena umbra* vocalizations were only present at Molarotto.

3.1. Diversity

UVC taxonomic richness was the highest at Molarotto, whereas Molara and Coda Cavallo did not differ in terms of both cumulative and mean richness (Fig. 3, Table 2). Mean and cumulative sound type richness differed significantly between all sites, with Molarotto showing the highest acoustic richness followed by Molara and Coda Cavallo (Fig. 3, Table 2). Therefore, the sites showed more pronounced differences in sound richness compared to taxonomic richness.

Similar results were found for both the diversity indices and the Gower similarity index. UVC taxonomic diversity and sound type indices significantly differed between sites (Table S6). The highest taxon and sound type diversity indices were found in Molarotto (Fig. 4, Table 3). However, differences between sites were more pronounced in terms of acoustic diversity compared to UVC taxonomic diversity, as Molara and Coda Cavallo only significantly differed in terms of sound types but not taxa assessed by UVC (Fig. 4). This trend was also reflected in community similarities. For both acoustic and UVC communities, Molarotto and Coda Cavallo showed the greatest differences, while Molara and Coda Cavallo showed the smallest ones (Table 4).

3.2. Abundance analyses

Without taking into account gregarious species, we censused 5205, 3744 and 3006 individual fishes at Molarotto, Molara and Coda Cavallo, respectively, by UVC. Without considering the /*kwa*/, at Molarotto, Molara and Coda Cavallo, 2211, 274 and 53 total fish sound selections were identified, respectively. Both fish abundances assessed by UVC (ind. 125 m^{-2}) and call abundances (no. calls
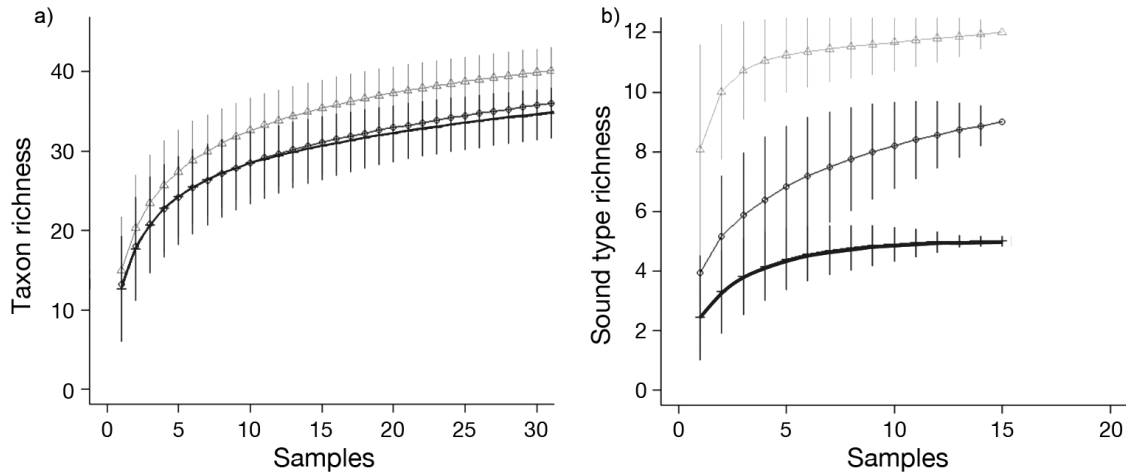
Fig. 3. Sample-based accumulation curves for (a) taxa and (b) sound types. The vertical lines on each accumulation curve represent the 95% confidence intervals, calculated from the unconditional variance. Light grey with triangles: Molarotto; dark grey with circles: Molara; solid black: Coda Cavallo

h^{-1}) showed a significant site effect (UVC fish densities: df = 2, deviance = 14831, Pr (> χ) < 0.0001; call densities: df = 2, deviance = 184.93, Pr (> χ) < 0.0001). Visually censused fish and sound densities followed a similar pattern among the 3 sites, with Molarotto showing the highest densities, followed by Molara and Coda Cavallo (Table 5). However, differences between Molara and Coda Cavallo were statistically more pronounced in UVC than in acoustic data (Table 5). Both taxa and sound type also strongly influenced fish and call densities (UVC taxa: df = 52, deviance = 2360.1, Pr (> χ) < 0.0001, sound type: df = 10, deviance = 235.6, Pr (> χ) < 0.0001), indicating that certain taxa or sound types were more abundant than others. The deviance statistic for the negative binomial model was 1.03 for call abundance and 0.9 for fish abundance, suggesting a good fit to the data.

3.3. Sound type diversity patterns

The relative percentage of occurrence of the sound type categories identified at the study sites (cf. Table 1, Fig. 2) varied during the recording sessions. *Sciaena umbra* vocalizations were highest at the beginning of the evening and generally decreased over the course of the night, while DS and DSPS (see Table 1 for definitions) generally showed the opposite trend (Fig. 5). LDS and LDSPS (likely associated with the dusky grouper, Bertucci et al. 2015) tended to be recorded more often between midnight and 08:00 h (Fig. 5). PS and FTP showed no particular overall temporal pattern, and *Ophidion rochei* sound occurrence was rather bimodal with 2 peaks, one around 20:00 h and one around 05:00 h (Fig. 5). However, the night-time patterns of the sound types varied between sites. The partition and complexity of the temporal acoustic space were highest at Molarotto compared to Molara and Coda Cavallo, which showed the lowest sound type occurrence and no clear nocturnal acoustic activity pattern (Fig. 5).

4. DISCUSSION

Our study identified a clear link between fish and acoustic communities. Analyses of richness, diversity and similarity indices provided evidence of a strong positive relationship between acoustic and
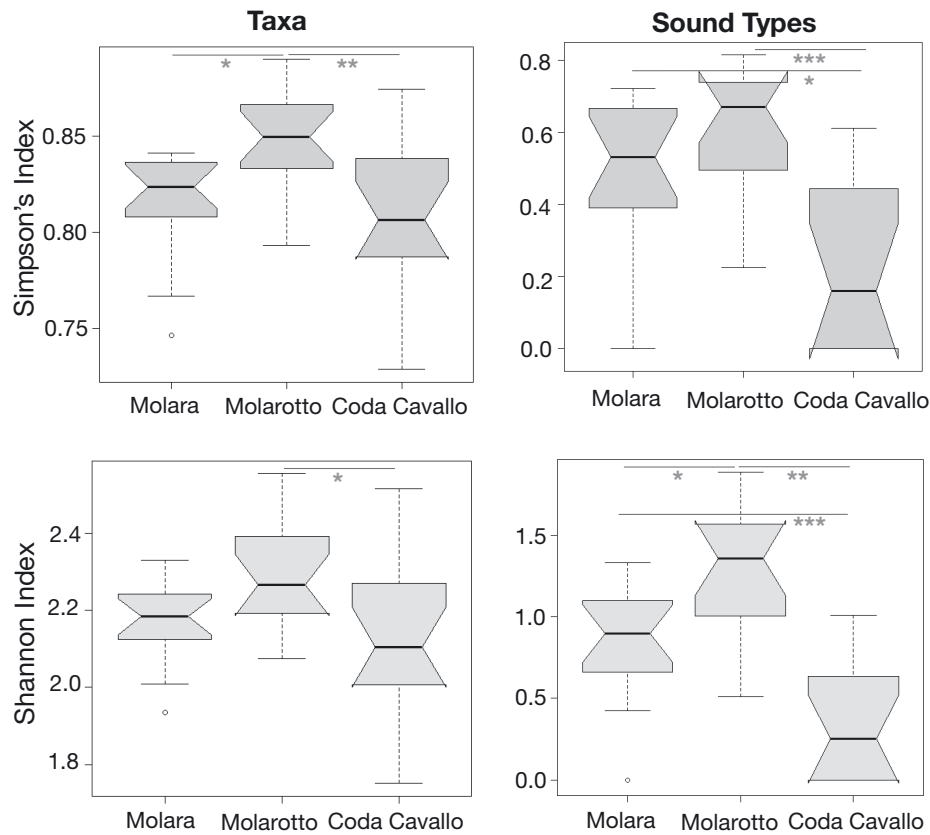
Table 2. Bootstrap taxonomic and sound type richness per site based on presence/absence data and pairwise richness comparisons between sites. *p < 0.05, **p < 0.005. UVC: underwater visual census

	UVC taxonomic richness			Sound type richness		
	Cumulative	Mean	SD	Cumulative	Mean	SD
Site						
Molarotto	45	14.97	3.4	12	8.07	1.83
Molara	42	13.25	2.94	9	3.93	1.03
Coda Cavallo	42	11.97	4.32	5	2.47	0.74
	Difference	Mean		Difference	Mean	
Comparison						
Molarotto–Molara	3	1.78**		3*	4.1**	
Molarotto–Coda Cavallo	3	3**		7*	5.6**	
Molara–Coda Cavallo	0	1.3		4*	1.5**	

Fig. 4. Taxonomic and sound type differences across sites. *p < 0.05; **p < 0.01; ***p < 0.001. Box plots indicate median values, first and third quartiles, as well as minimum and maximum values excluding outliers

visually assessed taxonomic diversity. Links between fish assemblages and acoustic diversity have been studied in coral reefs with inconsistent patterns. Some authors found positive relationships (Bertucci et al. 2016, Harris et al. 2016), while others did not (Kaplan et al. 2015, Nedelec et al. 2015, Harris et al. 2016). These studies did not assess acoustic diversity based on sound types but on eco-acoustic indices that are useful proxies of acoustic species assemblages, but are not able to discern between sound diversity and abundance or between individual rare sounds or mass phenomena (Bolgan et al. 2018). Although more time-consuming, our approach based on individual sound types allowed fine diversity gradients to be highlighted, revealing marked differ-

ences in all measured bioacoustic diversity variables between the study sites. Furthermore, a comparison between the diversity of the 2 consecutive nights at Molara revealed low intra-site variability (Figs. S4 & S5, Table S3). However, these outcomes have to be confirmed over time, because a few days of recordings are not representative of the overall fish acoustic diversity, and because the contribution of fish calls to marine soundscapes can substantially vary on a weekly, monthly and yearly basis (Parsons et al. 2016, McWilliam et al. 2017). Nevertheless, one of the possible explanations for the strong differences found in acoustic diversity across sites may be related to the fact that the individuals of a species may produce multiple sound types. For instance, it has been suggested that the dusky grouper *Epinephelus marginatus* could produce both simple transient sounds (i.e. low-frequency pulses, LPS) and frequency-modulated sounds (i.e. low-frequency downsweeps, LDS) (Bertucci et al. 2015), while the red-mouthed goby *Gobius cruentatus* is capable of emitting 4 different sound types (Sebastianutto et al. 2008). Call differences are also likely related to

Table 3. Summary of Simpson's and Shannon indices representing taxonomic and sound type diversity

Site	Taxon			Sound type		
	n	Simpson	Shannon	n	Simpson	Shannon
Molarotto	64	0.87	2.45	15	0.68	1.55
Molara	64	0.83	2.29	15	0.55	1.15
Coda Cavallo	64	0.82	2.27	15	0.5	0.93

Table 4. Results of the multivariate analysis emphasizing differences in taxa and sound types between sites. Values represent Gower indices of dissimilarity. Greater values indicate greater dissimilarities and thus greater differences between sites

Site	Taxon		Sound type	
	Molarotto	Molara	Molarotto	Molara
Molara	0.81		0.89	
Coda Cavallo	0.69	0.50	0.95	0.16

sex or age. Males and females have been reported to emit distinct sounds (Kéver et al. 2012) and juvenile fish sounds have different acoustic features than adult calls (Lechner et al. 2010, Ladich 2015).

Acoustic space partitioning at night was more pronounced and heterogeneous at Molarotto than at Molara and Coda Cavallo. Molarotto was the site with the maximum number of different sound types and species assessed using UVC. In an environment where acoustic communities share similar ambient noise, higher acoustic diversity may result in an increased need for soundscape partitioning, likely to avoid interference with signals of different species (Krause 1993, Farina 2014, Ruppé et al. 2015). Sueur et al. (2008) showed that the more species occupy the same habitat, the more heterogeneous the soundscape they generate is. Acoustic heterogeneity appears to be more significant in preserved communities compared to perturbed ones. The differences in partitioning and all acoustic diversity parameters found between the 3 sites may therefore also be related to the management protection levels across the 3 sub-zones of the MPA. Molarotto is the most remote site and falls within the no-take and no-access area (A Zone) of the TPCC MPA. As such, it can be considered the most intact environment hosting the most preserved community among the 3 study sites. In contrast, Coda Cavallo, with the lowest acoustic partition and acoustic and taxonomic diversity, falls within the least protected zone C of the

MPA, as human activities are allowed, including boat moorings and artisanal or recreational fishing. Specifically designed field campaigns with an increased number of sites and replicates are necessary to investigate the link between acoustic communities and different protection levels, and to compare the findings with the reserve-effect outcomes obtained using long-term UVC data (Di Franco et al. 2009, Sahyoun et al. 2013, Guidetti et al. 2014).

Acoustic richness, diversity and community similarity differences between sites were more pronounced compared to the respective fish taxonomic diversity patterns. In fact, significant differences between all 3 sites were only found in terms of sound types but not visually assessed taxa, which showed similar patterns between Molara and Coda Cavallo. Although the 2 consecutive recording nights at Molara showed low intra-site variability, these differences can be related to the distinct temporal scales over which the 2 surveys (i.e. visual and acoustic) were conducted. Additional repeated acoustic recordings at each site over large temporal scales are needed to confirm and elucidate these patterns. Furthermore, the different times of the year at which sound recordings were carried out compared to UVC (acoustics: early September, UVC: between May and November) also potentially contribute to the observed differences. Other potential factors influencing differences between taxonomic and acoustic diversity are the metrics themselves. UVC data were collected over relatively short dives along transects, but repeated in space and time (i.e. the unit is the transect), while acoustic data were collected continuously, over several hours (i.e. the unit is the clock hour) and within a volume, which is given by the detection range of the sounds. Another possible explanation is the time of day at which the data were obtained. Data on fish assemblages were collected by visual assessments during daytime, while acoustic data were obtained mainly from dusk till dawn, because the majority of the sound-producing behaviours of fishes occur during night-time hours. Diel fluctuations in the abundance and taxonomic composition of rocky-reef fish assemblages are known to occur between day and night (Azzurro et al. 2007, 2013). At night-time, the number of fish species encountered is generally smaller than during the day, and species contribute with different compositions and abundances to fish assemblages.

Table 5. Negative binomial generalized linear model for testing site effect on fish and call abundance. The site effects were coded in reference to Molara (the intercept). Model-based standard errors (SE) are also shown

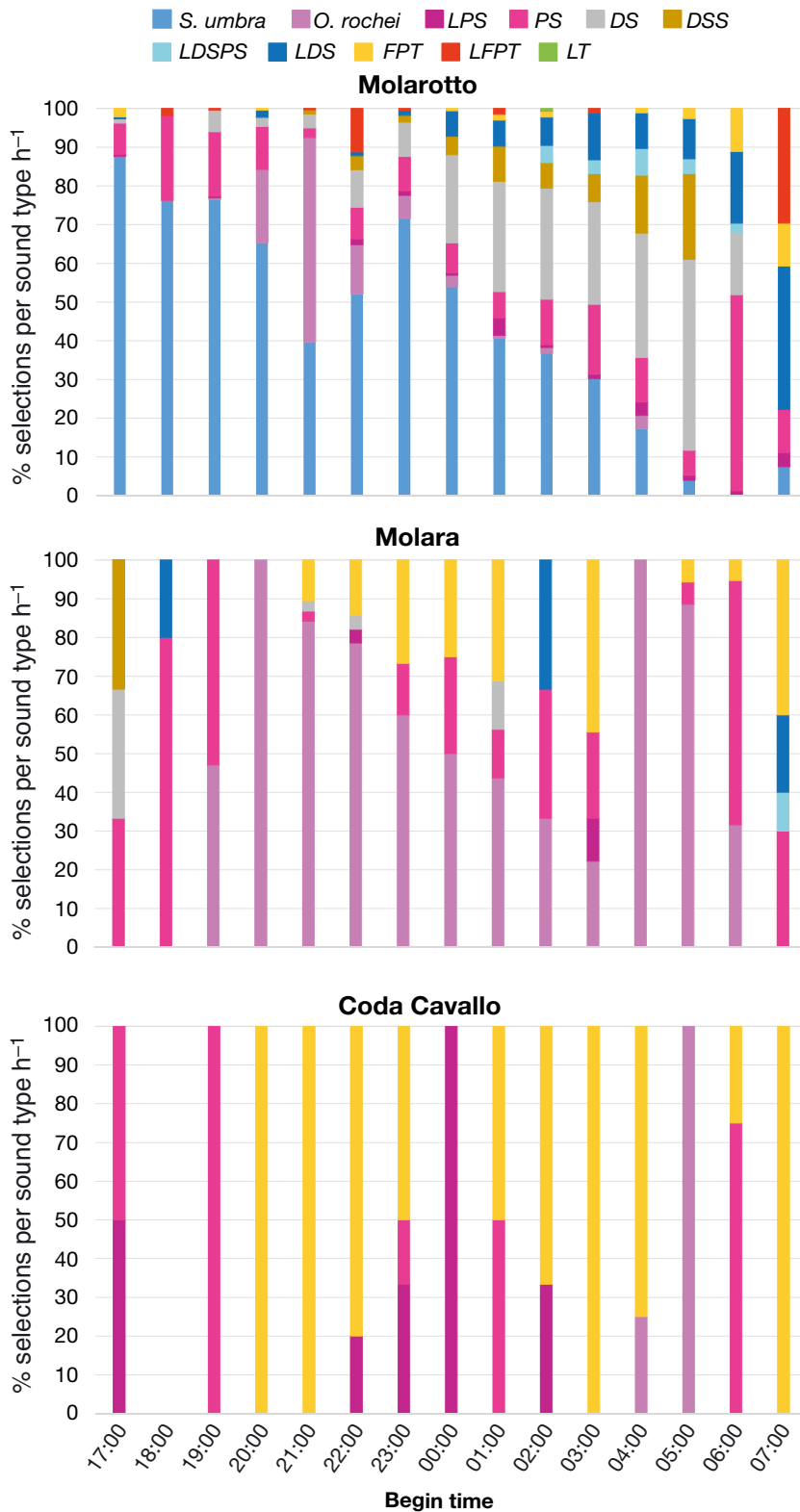|	Calls				Fish			
	Estimate	SE	χ	Pr(>|χ|)	Estimate	SE	χ	Pr(>|χ|)
Molara	2.3	0.4	5.75	0	1.54	0.15	10.38	0
Molarotto	2.12	0.35	6.07	0	0.37	0.04	9.58	0
Coda Cavallo	−0.15	0.55	−0.27	0.789	0.08	0.04	1.99	0.05

Fig. 5. Night-time acoustic temporal variation expressed as the percentage of different sound types assessed per clock hour based on the subsampling scheme. For Molara, the percentages refer to sound type abundances averaged over 2 consecutive nights. Abbreviations are defined in Table 1. */kwa/* sounds were excluded. In the 18:00 h interval at Coda Cavallo, the only sound type recorded was the */kwa/*

Furthermore, during the day, some species are inactive and hidden in dens (Dulčić et al. 2004, Azzurro et al. 2013). However, our study indicates that daytime fish diversity, richness and densities are positively correlated with night-time sound diversity, richness and densities and that both follow similar patterns across sites.

In addition, the methods applied characterize the fish assemblages by acquiring information linked to different sensory modalities (i.e. visual and acoustic). In particular, UVC surveys allow us to determine the presence of taxa, while PAM surveys can be used to detect behaviours and activities of sound-producing species. In fact, as biological sounds are associated with key processes, including reproduction (Amorim et al. 2015), spawning (Lobel 1992), feeding (Versluis et al. 2000) and competition (Picciulin et al. 2006), nighttime non-intrusive acoustic surveys provide valuable complementary information on the nocturnal behaviour of sound-producing fishes that can play a vital role in the functioning of marine communities.

Differences between acoustic and taxonomic diversity across the study sites could also be due to the fact that sound type richness and diversity may not depend on taxonomic richness or diversity alone. In fact, 2 sites characterized by the same number of species can differ in terms of acoustic repertoires, because either (1) they differ in the proportion of soniferous species or (2) the sound-producing species differ in the number of emitted sounds (Staaterman et al. 2017, McWilliam et al. 2018). In the first case, abundant species dominating the acoustic space could reduce the local acoustic diversity because they lack competitors that use the same communication window (Sueur et al. 2008). In the second case, analogous to gregarious species contributing most to overall densities as a result of

their schooling behaviour (García-Charton & Pérez-Ruzafa 2001), some soniferous species produce more calls than others, as a result of their acoustic behaviour (i.e. choruses) (Cato 1978, Staaterman et al. 2017). This is confirmed by the significant interaction found between sound type and call abundance, implying that some sound types have greater relative abundances than others (i.e. mass phenomena) and therefore significantly influence overall abundances.

This work represents a first attempt at emphasizing the complementarity between UVC and PAM methods for fish biodiversity assessment. The number of sound type categories identified is considerably lower than the number of taxa recorded using UVC at the study sites, indicating that not all fish species produce sounds and that passive acoustics cannot provide an exhaustive picture of the entire fish community. However, sound type diversity analysis of longer recording periods over different seasons will likely increase the number of sound categories, as many fish species only vocalize at certain times of the year (McWilliam et al. 2017). Furthermore, it has also been shown that vocal species can be associated with a specific taxonomic composition and therefore serve as biological indicators of fish communities irrespective of the number of vocalizing species (Picciulin et al. 2013b). Passive acoustic fish surveys also provide information about nocturnal diversity and cryptic species, which is often lacking and arduous to obtain in traditional visual surveys (Picciulin et al. 2018). For instance, *Ophidion rochei* vocalizations were highly abundant, but the species was not censused during the visual surveys.

A better knowledge of the species emitting these sounds is necessary to help to establish robust correlations between acoustic and species assemblages, and elucidate which proportion of the community is vocally active. Out of the 53 fish taxa censused during the UVC campaigns used for this study, only 5 species are known to emit sounds (Table S4). In fact, our knowledge about soniferous Mediterranean species is still very limited. Of the 12 fish sound type categories described in this study (see Table 1 for definitions), only 4 sounds could be attributed to fish species (*S. umbra*, *O. rochei, E. marginatus*), with the remainder referring solely to their main acoustic properties. Some of the sounds of the FPT category share similarities with air movement sounds (Rountree et al. 2018) or with 'grunting sounds' emitted by several species recorded elsewhere (Fish & Mowbray 1970). Within the large PS category, there are likely irregular sounds produced by *S. umbra* (Picciulin et al. 2013a) or other Sciaenidae such as *Umbrina cirrosa*, although

this species has not been reported within the MPA. The red-mouthed goby also produces pulse series that may fall within the PS category (Picciulin et al. 2006, Sebastianutto et al. 2008). However, the other sounds emitted by this species were not recorded here, and as their propagation ranges are short (Amorim et al. 2018), it is likely that even if present, sounds from small Gobiidae could not be captured. The LT sound shares many similarities with the vocalization reported for the meagre *Argyrosomus regius* (Lagardère & Mariani 2006), but this species was not visually assessed within the MPA. Many fish species are known to produce LPS, a category with a relatively high signal variability. Potential sources of the recorded LPS may be other grouper species (i.e. *Epinephelus costae*, *Mycteroperca rubra*), and representatives of the Sparidae or the Phycidae families, such as *Diplodus argenteus* or *Urophycis* spp., respectively, of the Northwest Atlantic are also known to emit LPS (Fish & Mowbray 1970). Other potential sound-producing species include the European seabass *Dicentrarchus labrax* or species from the family Serranidae, as representatives of the respective families in the North Atlantic are soniferous (Fish & Mowbray 1970).

Despite the lack of knowledge on the source of the sound types, this study provides the first description of the acoustic repertoire of Mediterranean rocky reefs related to fish assemblages and suggests that bioacoustic analysis can provide new and complementary information (Hastings & Širović 2015). The dichotomy of fish sounds established here also provides a basis for developing sound detectors and eco-acoustic descriptors to appraise fish acoustic diversity particularly over long periods of time. Since high acoustic diversity appears to be determined by uncommon sounds, automated methods should not only be representative of the sound diversity and the fine patterns of variation as the ones reported here, but they should also be capable of identifying rare sounds. Temporal patterns of fish sounds, particularly their rhythm (i.e. pulse period and its variation, calling rate), are critical for species recognition (Parmentier et al. 2017). Detectors based on rhythms (Le Bot et al. 2015) may for instance be effective in depicting a large variety of fish sounds. Overall, the combined use of passive acoustics, including representative automatic signal processing tools, and UVC surveys provide a more comprehensive picture of fish diversity and can therefore have major implications for conservation, particularly considering the biodiversity changes and losses that many marine habitats are facing (Hughes et al. 2017, Schluter & Pennell 2017).

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