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ORIGINAL PAPER

Sound production and associated behaviours of benthic invertebrates from a coastal habitat in the north-east Atlantic

Laura Coquereau[1] · **Jacques Grall**[2] · **Laurent Chauvaud**[1,2] · **Cédric Gervaise**[3,4] · **Jacques Clavier**[1] · **Aurélie Jolivet**[1,5] · **Lucia Di Iorio**[3]

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Abstract Maerl beds are among the most endangered habitats in coastal temperate waters and a priority for conservation. Passive acoustics is a potential non-intrusive approach for surveying this fragile ecosystem with minor disturbances. Invertebrate sounds can be major contributors to natural coastal soundscapes but are not well studied. We conducted controlled tank-based experiments to identify sound-producing invertebrates inhabiting north-east Atlantic maerl beds and to characterise their sounds in terms of frequency features and source levels. We also determined which sound types are able to be detected above natural maerl ambient noise and suitable for in situ monitoring. Tank recording sessions of 20 abundant and potentially soniferous invertebrates from maerl beds revealed eight soniferous species and 15 different sound types. Two new sound-producing families were identified, Calyptraeidae and Majidae. Six sound types had properties consistent with detectability and identification for in situ acoustic studies: the feeding sound of sea urchins *Echinus esculentus*, *Paracentrotus lividus* and *Psammechinus miliaris*, snapping sound of the snapping shrimp *Athanas nitescens,* and feeding and other sounds of the spider crab *Maja brachydactyla*. Estimated detection distances ranged from a few metres for sea urchin feeding sounds up to about 40 m for *A. nitescens* snaps and spider crab feeding sounds. These invertebrates, particularly *A. nitescens,* probably make a substantial contribution to the maerl ambient noise. This invertebrate sound library sets a basis for in situ acoustic studies.

Introduction

Marine organisms may reveal their presence and behaviour through acoustic signals, which can be detected, recorded and analysed. Biological sources of underwater sound have been identified for a variety of marine organisms, including invertebrates (e.g. Everest et al. 1948; Iversen et al. 1963; Popper et al. 2001), fish (e.g. Myrberg 1981; Luczkovich et al. 2008; Picciulin et al. 2013; Tricas and Boyle 2014) and marine mammals (e.g. Moore et al. 2006; Mellinger et al. 2007). These sounds may be incidental, generated as a mechanical artefact during moving or feeding (Radford et al. 2008a; Di Iorio et al. 2012), or generated intentionally, such as for communication (McCauley and Cato 2000; Tyack and Clark 2000), reproduction (Lobel 2002; Lucrezi

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✉ Laura Coquereau
laura.coquereau@univ-brest.fr

[1] Laboratoire des Sciences de l'Environnement Marin, UMR 6539, Institut Universitaire Européen de la Mer, Université de Bretagne Occidentale, Rue Dumont D'Urville, 29280 Plouzané, France

[2] Observatoire Marin, UMS 3113, Institut Universitaire Européen de la Mer, Rue Dumont D'Urville, 29280 Plouzané, France

[3] Chaire CHORUS, Fondation Grenoble INP, 46 Avenue Felix Viallet, 38031 Grenoble, France

[4] GIPSA-LAB, 11 Rue des Mathématiques, Grenoble Campus, 38402 Saint Martin d'Hères, France

[5] TBM Environnement/Somme, 115 Rue Claude Chappe, Technopole Brest Iroise, 29280 Plouzané, France

and Schlacher 2014) or defence (Verslius et al. 2000; Patek 2001; Buscaino et al. 2011). A variety of organisms utilise biotic sounds for spatial orientation and habitat selection (Tolimieri et al. 2000; Simpson et al. 2005; Stanley et al. 2012; Lillis et al. 2013, 2014). Characterising this biological sound production is relevant to understanding ecological processes, such as biological rhythms (D'Spain and Batchelor 2006; Lammers et al. 2008; Staaterman et al. 2014), biotic interactions (Popper et al. 2001) and responses to threats (Au et al. 2012). A growing number of research activities are devoted to the temporal and spatial variability of soundscapes across benthic habitats and locations (e.g. Kennedy et al. 2010; Piercy et al. 2014; Staaterman et al. 2014; Nedelec et al. 2015). Indeed, the application of an acoustics-based monitoring can be a powerful complementary approach for long-term monitoring, measuring spatial heterogeneity, or assessing changes in marine habitats (invasion, losing, abundances changes), which can conjointly reflect the ecological status. However, much work is needed to adequately characterise soniferous species and behavioural factors that contribute to the soundscapes of specific marine environments.

Some marine invertebrates, especially those with hard body parts, generate sounds. A number of invertebrate acoustic studies have been conducted on unique species because of their ecological and/or economic interest or their conspicuous contribution to underwater ambient noise. Snapping shrimps (Johnson et al. 1947; Knowlton and Moulton 1963; Chitre et al. 2012), sea urchins (Radford et al. 2008a), lobsters (Meyer-Rochow and Penrose 1976; Patek 2001; Buscaino et al. 2011) and semi-terrestrial crabs (Salmon 1967, 1983) have been described as contributing to sound energy in many temperate, subtropical and tropical coastal habitats. However, these species are only a few of the potentially soniferous invertebrates in coastal benthic communities and are not representative of all types of habitats. To the best of our knowledge, no previous study has considered and detailed the complete soniferous invertebrate community in a marine habitat.

Among the most challenging endangered habitats to monitor in coastal temperate waters, maerl (rhodoliths) beds are a priority for conservation efforts (BIOMAERL Team 2003). This biotic habitat is characterised by the accumulation of loose-lying, non-geniculate calcareous red algae (Corallinales, Rhodophyta) and high biodiversity (up to 200 species m^{-2}) (BIOMAERL Team 2003; Peña et al. 2014). Worldwide, but especially in the north-east Atlantic, maerl beds suffer heavily from anthropogenic activities, such as extraction, fishing (dredging), eutrophication, mariculture and the spread of invasive species (Hall-Spencer 1998; Hall-Spencer and Moore 2000; Grall and Hall-Spencer 2003). The need to preserve maerl beds has been increasingly recognised over the last few decades (Hall-Spencer et al. 2006), not only due to their fragility and high biodiversity, but also for the benefits they offer fisheries, acting as nursery areas for a large number of commercial species (Kamenos et al. 2004a, b, c). Because most current methods that can be used to monitor this habitat (e.g. dredging and trawling) are punctual, intrusive and destructive (Hall-Spencer and Moore 2000), eco-aware techniques capable of capturing changes in an ecosystem are needed. The non-intrusive high-resolution and long-term nature of passive acoustics makes it a promising approach for surveying the fragile maerl ecosystem for its assessment of biological α- and β-diversities, contributing to establish a health indicator, or to better understand biological rhythms of this habitat.

It is unknown to what extent biological sound production can be used for ecological studies of maerl beds. A prerequisite for such work is the identification and characterisation of sounds generated by animals. The aim of the present study was to conduct controlled tank-based experiments to identify soniferous invertebrate species in maerl bed communities and characterise their sound production and potential contribution to natural soundscapes. To achieve these aims, we (1) recorded a large number of potentially sound-producing invertebrates inhabiting north-east Atlantic maerl beds, (2) characterised the emitted sounds in terms of frequency features and source level estimations and (3) examined the sound types for acoustic properties suitable for in situ detection and monitoring.

Materials and methods

Collection and housing of animals

The study was performed in a laboratory (chorus@lab, Fondation Grenoble INP) at the public aquarium Océanopolis in Brest, France, from February to May 2014. The laboratory is equipped with six identical tanks measuring 60 cm × 50 cm with a depth of 40 cm (Fig. 1a) for long-term housing and controlled experiments. Benthic invertebrates were collected at a depth of 4–8 m from a maerl bed in the south-western part of the Bay of Brest between November 2013 and April 2014 using naturalist dredges (width: 1 m, height: 0.2 m, net: 1.5 m long). The selection of potentially soniferous invertebrates was based on species presence and abundance in these maerl beds (Grall 2002; data obtained from the Observatory of the Institut Universitaire Européen de la Mer) and previous work on marine passive acoustics (Urick 1984; Schmitz 2002; Watanabe et al. 2002; Au and Hastings 2008; Radford et al. 2008a; Di Iorio et al. 2012). We sampled at least three individuals of each species depending on specimens' availability. After collection, animals were transferred to five of the six tanks

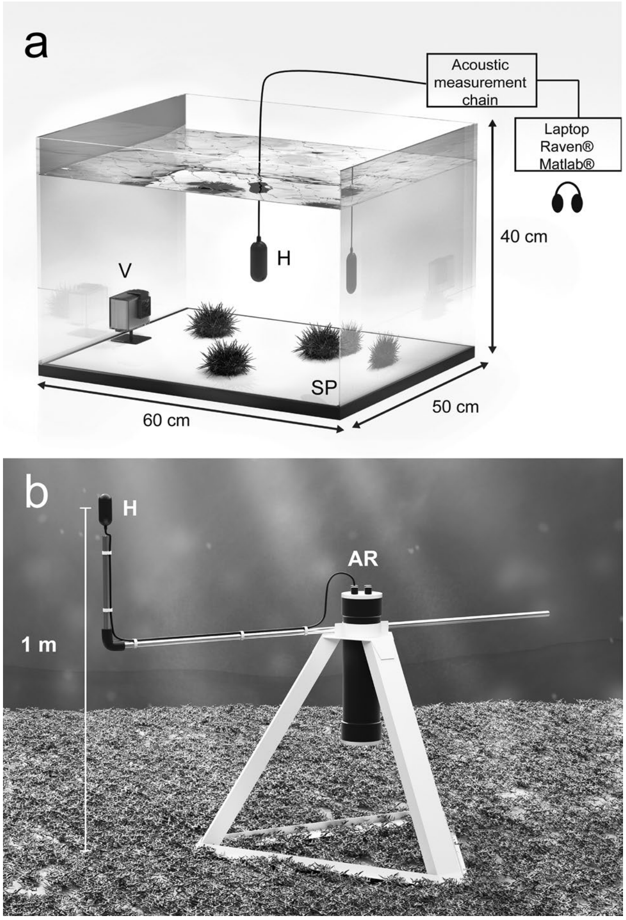

Fig. 1 **a** Experimental setup for recording sounds emitted by benthic invertebrates living in north-east Atlantic maerl beds. A silicone plate (SP; 0.5 cm thick) on the *bottom* of the tank prevented sound emissions due to friction between hard body parts and the glass when animals moved. Invertebrates were recorded using synchronised GoPro® HERO 2 video cameras (V). The hydrophone (H) was suspended above the tank and linked to the acoustic measurement chain. **b** A passive acoustic recorder (AR) was supported by a weighted aluminium tripod and used to record underwater sounds in a maerl bed habitat in the Bay of Brest, France

and continuously supplied with fresh seawater from the Bay of Brest in order to follow the natural temperature and salinity values during the experimental period (11.0–13.5, 32.9–33.7 °C). All water parameters and the well-being of the animals were controlled on a daily basis. Animals were maintained under a 12-h light/12-h dark photoperiod. Animals were acclimated to laboratory conditions for at least 4 weeks before recordings began.

Experimental procedure and acoustic laboratory recordings

Experiments were conducted in tanks in order to carefully control the acoustic context of the studied animals. Recordings were performed in one of the six tanks (referred to as the experimental tank). A silicone plate (0.5 cm thick) was placed at the bottom of the experimental tank to hinder sound emissions caused by friction between hard body parts and the glass. Recordings were performed separately for each species. Individuals of a given species were randomly collected from the five other tanks and released into the centre of the experimental tank. Densities were based on abundance data obtained over two decades from maerl beds in the Bay of Brest (Table 1) (Grall 2002; data obtained from the Observatory of the Institut Universitaire Européen de la Mer). Acoustic recordings were acquired using one of the two acoustical data loggers depending on their availability: a Brüel and Kjaer® 8106 pre-amplified calibrated hydrophone with a sensitivity of −174 dB re 1 V/μPa and a flat frequency response from 0.1 Hz to 80 kHz with the hydrophone connected to a conditioning amplifier (NEXUS, Brüel and Kjaer®, with a 50-, 60-, or 70-dB gain depending of the species recorded) and a Tascam® DR-680 digital recorder; or a HTI-92-WB pre-amplified hydrophone (High Tech Inc.) with a sensitivity of −155 dB re 1 V/μPa and flat frequency response from 2 Hz to 50 kHz connected to an EA-SDA14 compact autonomous recorder set at 14.7 dB gain (RTSys®). Both measurement chains had similar high-quality metrological characteristics. Acoustic recordings were acquired at a sampling rate (SR) of 192 kHz for the first recording system and 156 kHz for the second system, both with 24-bit resolution. During the recording sessions, the hydrophone was suspended at the centre of the tank 12–16 cm above the silicone plate depending on the size of the species present (Fig. 1a). Recordings started after a period of 20 min following the introduction of the animals into the experimental tank.

Sounds emitted by the specimens during active moving and feeding behaviours were selected for analysis because they are the most frequently encountered behaviours in the natural environment and occur year-round. No stimulation was used to encourage moving behaviour. To record feeding behaviours, we provided food corresponding to the natural diet of each species: macroalgae of the genus *Ulva* for sea urchins, and mussels and shrimps for sea stars, brittle stars and decapods. In addition, all other behaviours were recorded and analysed. To associate acoustic signal production with a particular behavioural event, video recordings (GoPro® HERO2) were synchronised with the acoustic recordings. Each recording session lasted 30 min to several hours.

Maerl bed ambient noise recordings

Field recordings were carried out to compare the invertebrate acoustic spectra to the ambient natural soundscape in

Table 1 List of the recorded invertebrates living in north-east Atlantic maerl beds and sound-producing species

Species recorded	Moving sound	Feeding sound	Other acoustic behaviour
Echinodermata			
Asterina gibbosa (Pennant 1777)			
Echinus esculentus (Linnaeus 1758)	x	x	
Marthasterias glacialis (Linnaeus 1758)			
Ophiocomina nigra (Abildgaard 1789)			
Ophiotrix fragilis (Abildgaard 1789)			
Paracentrotus lividus (Lamarck 1816)	x	x	
Psammechinus miliaris (Müller 1771)	x	x	
Mollusca			
Crepidula fornicata (Linnaeus 1758)	x		
Mimachlamys varia (Linnaeus 1758)	x		
Modiolus adriaticus (Lamarck 1819)			
Pecten maximus (Linnaeus 1758)	x		x
Venus verrucosa (Linnaeus 1758)			
Crustacea			
Athanas nitescens (Leach 1813)			x
Eurynome spinosa (Hailstone 1835)			
Inachus dorsettensis (Pennant 1777)			
Liocarcinus pusillus (Stimpson 1871)			
Macropodia rostrata (Linnaeus 1761)			
Maja brachydactyla (Balss 1922)		x	x
Pagurus spp (Fabricius 1775)			
Pisidia longicornis (Linnaeus 1767)			

maerl beds in an attempt to highlight the species that can be detected in field recordings because they produced a louder sound than the ambient noise. The recordings were performed in the same maerl bed from which the animals were sampled for laboratory experiments using the HTI-92 system with the EA-SDA14 10 recorder described above and calibrated as in the tank recording sessions. The recording device was placed on the seafloor supported by a weighted (15 kg) aluminium tripod at a water depth of 5–7 m depending on the tide and sites. The distance between the hydrophone and the seafloor was 1 m (Fig. 1b). Four recordings from five sites (approximately 100–200 m apart) were made during spring (April–June) 2015 during the daytime (from 10:00 to 15:00) and at dusk/beginning of the night to capture potential diurnal variability in sound production (Radford et al. 2008b; Staaterman et al. 2014). Acoustic data were acquired for a minimum of 10 min. Sea-state conditions ranged from 1 to 3 m s^{-1}.

Acoustic analyses

Acoustic signal features of maerl bed invertebrates

The sound data (.wav files) from the tank recordings were bandpass-filtered between 2 kHz and SR/214 kHz and analysed using Raven 1.5® and specific signal processing routines developed in Matlab®. To characterise acoustic signatures, signals for each sound type were selected manually. Due to reflection in small tanks, the acoustic parameters are submitted to distortion (Parvulescu 1964, 1967; Akamatsu et al. 2002). Theses authors explain that the duration is distorted because of the generally small size of tanks, which are rarely over 2 m length. Therefore, sound could result in reverberation, traduced by a persistence of sound in an enclosed space and a result of multiple reflections (tank walls, bottom and surface). In addition, they indicate that the recorded frequency could be the resonant frequency of the standing wave. To limit errors resulting from reverberation of the tank walls, acoustic measurements were performed on the initial portion of the transient signal which is poorly affected by tank artefacts (Fig. 2). Simulations of transient signal emissions with durations of 32–256 samples and the same experimental settings as the tank recordings were performed to evaluate the effect of reverberation on signal features (i.e. peak frequency, Online Resource 1 shows the estimation of peak frequency errors induced by tank reverberation).

The features measured on the initial part of the recorded signals were:

1. Received level (RL; in dB re 1 µPa peak to peak, pp), calculated in the time window equal to signal selection;

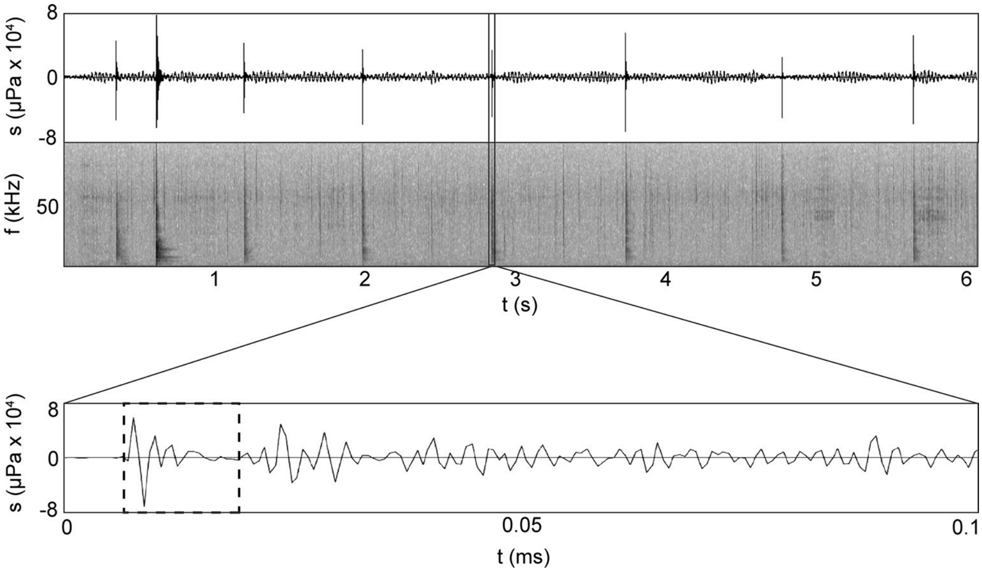

Fig. 2 Selection of a typical clip from which acoustic features were measured (*dotted box*). The *upper part* of the signal represents the waveform of the sound clip. The *lower part* is the spectrogram representation of the signal (*dark grey* higher values of sound intensity, *light grey* lower values of sound intensity). We selected the beginning of the transient sound in order to exclude most reverberation. The example here is the snapping sound produced by *Athanas nitescens*

2. Peak frequency (f_p; in Hz), defined as the frequency at which the power spectral density (dB re 1µPa2/Hz) is maximal within the selection. The power spectral density is estimated by the periodogram:

$$\gamma(f)(\mu\text{Pa2/Hz}) = \frac{1}{N \times \text{SR}} |\text{FFT}|^2 \tag{1}$$

with N the number of bin used to compute the Fast Fourier Transform;

3. Frequency bandwidth (B; in Hz), estimated as the measurement of the spread of the power spectral density (standard deviation) around the peak frequency:

$$B = \sqrt{\frac{\int \left(f - f_p\right)^2 \gamma(f) df}{\int \gamma(f) df}} \tag{2}$$

Mean, standard deviation (SD), minimum and maximum values were determined for each acoustic feature of each sound type. Signal duration was excluded because the selections did not always comprise the entire signal and reverberation applied on the entire signal positively biases the duration. The exception was the feeding spider crab signal, which was composed of a sequence of pulses, so the number of pulses per signal and the pulse-to-pulse time intervals were measured, as well as the entire signal duration, including all pulses (since in this case, duration is well higher than the duration of the reverberation). Source levels (SL; in dB re 1 µPa pp @ 1 m) were estimated from the measured RL (Erbe 2010) as follows: eSL = RL + $20\log_{10}(r)$, where r indicates the distance between the animals and the hydrophone (Table 2).

Acoustic spectra and estimated in situ detection ranges

Median acoustic spectra (dB re 1 µPa^2/Hz @ 1 m) between 2 and 50 kHz were determined for each invertebrate sound type (32-, 64-, 128- or 256-point fast Fourier transform, boxcar window, overlap 50 %). To study invertebrate behaviours in the natural environment using passive acoustics, the produced sounds must be detectable above ambient noise. Median ambient noise spectra were generated from the in situ maerl bed recordings using ambient background noise only, without individually identifiable sounds, such as benthic snaps. Acoustic recordings were cut into 10-s bins. The measurements were fast Fourier transformed (Hanning window, 1024-point FFT, 50 % overlap), and power spectrum levels were estimated within each bin. To estimate the spectrum of the background ambient noise only (γANL, ambient noise level; dB re 1 µPa^2/Hz) at a given frequency f0, the collection of power spectrum levels within each bin was sorted in ascending order. Background ambient noise spectrum levels are likely to correspond to the smaller values of the analysis bins. With Q being a low percentile (from 0.04 to 0.2) of the ranked power spectral density levels and γ_Q(f0) the value of this percentile at frequency f0, then the value of the ambient noise spectrum level was estimated with Eq. 3

$$\gamma\text{ANL}(f0) = \frac{\gamma_Q(f0)}{\log(1-Q)}. \tag{3}$$

This equation exploits the fact that the ambient noise is normally distributed. Consequently, its power spectral density level follows a centred Chi-squared distribution with two degrees of freedom (Kay 1998). This processing allows filtering out the loud biotic transient sounds. The algorithm

Table 2 Summary of the acoustic features of sounds emitted by benthic invertebrates living in north-east Atlantic maerl beds and their detection distances relative to Wenz's 1 and 5 kn wind regime and natural maerl bed ambient noise

Species	Behaviour	No. of signals	No. of individuals tested	Distance to hydrophone (cm)	Acoustic features																		
					RL (dB re 1 μPa (pp))				eSL (dB re 1 μPa (pp) @ 1 m)				Peak frequency (kHz)				Bandwidth (kHz)				Estimated in situ detection ranges (m)		
					Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Mean	SD	Min	Max	Wenz 1 knot	Wenz 5 knots	ANL
Echinodermata																							
Echinus esculentus	Moving	221	3	13	105	6	93	130	87	6	75	113	38	15	9	63	16	5	6	36	1.3	0.6	0.48
	Feeding	64			125	10	103	142	107	9	85	124	46	8	23	62	15	4	8	28	12.1	6.1	4.5
Paracentrotus lividus	Moving	111	3	13	100	8	87	126	83	8	69	109	39	14	9	60	17	6	6	37	0.8	0.4	0.28
	Feeding	45			107	14	86	130	90	14	69	112	45	9	26	59	15	7	6	30	1.7	0.8	0.62
Psammechinus miliaris	Moving	104	6	13	100	6	90	117	78	8	68	132	47	11	11	72	14	5	5	30	0.7	0.4	0.26
	Feeding	23			117	5	110	125	100	5	92	108	49	4	42	57	14	5	8	28	5.4	2.7	2.02
Mollusca																							
Crepidula fornicata	Moving	245	10 chains	14	102	4	91	121	85	4	74	104	45	13	8	63	17	5	7	31	1.0	0.5	0.36
Mimachlamys varia	Jumping	96	10	12	103		8	125	85	8	70	106	37	14	4	62	17	5	9	29	0.9	0.5	0.35
	Swimming	25			100	7	92	114	82	7	74	96	35	14	8	62	15	5	7	25	0.7	0.3	0.26
Pecten maximus	Swimming	71	6	12	116	11	93	134	97	11	74	115	35	16	12	57	12	7	3	37	4.1	2.1	1.52
Crustacea																							
Athanas nitescens	Snapping (lower frequency)	192	15	12	145	6	102	152	127	6	84	133	9	2	5	11	18	6	7	41	124.7	62.5	46.3
	Snapping (higher frequency)												33	17	12	60							
Maja brachydactyla	Type 1 (lower frequency)	18	5	10	136	7	127	145	117	7	107	129	7	2	5	11	20	9	15	35	42.7	21.4	15.9
	Type 1 (higher frequency)												38	11	22	45							
	Type 2	72			106	4	95	116	86	4	75	96	4	2	3	8	16	7	4	37	1.1	0.6	0.42
	Type 3 (feeding)	223			145	3	132	150	125	3	112	129	5	0	3	5	3	1	1	6	101.4	50.8	37.7

RL = received level measured in the tank; eSL = estimated source level @ 1 m. Estimated in situ detection ranges calculated from the formula described by Di Iorio et al. (2012): $R_{\max} = R0 * 10((RL - (NL + 8))/20)$ where R0 distance between the hydrophone and organism in metres, NL = Wenz noise level with wind speed of 1 kn (NL = 77) or 5 kn (NL = 83) (dB re 1 μPa), ANL = background ambient noise level from in situ maerl recordings to compute γANL is fully detailed in Kinda et al. (2013) for Arctic soundscapes and applied in Mathias et al. (2016) for coastal temperate ecosystems.

In addition to the field measurements, a set of standard empirical noise levels were computed using the Wenz formula (Wenz 1962) for different wind conditions (wind speeds from 0 to 20 m s^{-1}). *In situ* detection distances (R_{max}) were also evaluated for each sound type assuming spherical transmission loss. R_{max} is given by

$$R_{max} = R_0 10^{\frac{RL-(NL+8)}{20}} \tag{4}$$

with R_0 being the mean distance (m) between the sound source and the hydrophone, RL the mean received level of a species' sound type (dB re 1 μPa), NL (dB re 1 μPa) either the Wenz noise level with wind speed at 1 kn (NL = 77) and at 5 kn (NL = 83) or the mean in situ ANL (NL = 85.6 dB). 8 dB corresponds to the minimum signal-to-noise ratio needed to detect the signal above noise.

Results

Features of the acoustic signals of maerl bed invertebrates

Among the 20 species of invertebrates investigated in the laboratory settings (Table 1), a total of 15 different sounds were recorded from eight species (Table 2). All sounds, except those of *Maja brachydactyla*, were short, single, transient broadband signals or presented with an initial transient broadband. Twelve species did not produce any recordable sound during recording sessions: the echinoderms *Asterina gibbosa*, *Marthasterias glacialis*, *Ophiocomina nigra* and *Ophiotrix fragilis*; the molluscs *Modiolus adriaticus* and *Venus verrucosa*; and the crustaceans *Eurynome spinosa*, *Inachus dorsettensis*, *Liocarcinus pusillus*, *Macropodia rostrata*, *Pagurus* spp and *Pisidia longicornis* (Table 1).

Table 2 summarises all acoustic features measured in the initial transient portion of the sounds recorded in the experimental tank. Overall, three sound level classes emerged: those below ($n = 3$ invertebrate sounds), around ($n = 4$ invertebrate sounds) or above ($n = 6$ invertebrate sounds) natural background ANLs (i.e. 85.6 dB re μPa (root mean square, rms). Peak frequencies formed two classes: one of audible mid-frequency sounds (mean $f_p = 4$–9 kHz) and one of ultrasonic sounds (mean $f_p = 33$–49 kHz). Except for the type 3 sound of *M. brachydactyla*, all recorded invertebrate sounds were broadband, with mean bandwidths of 14–18 kHz but generally high standard deviations.

The three sea urchin species *Echinus esculentus*, *Paracentrotus lividus*, and *Psammechinus miliaris* produced sounds during moving and feeding. For both behaviours, the signals were composed of two parts approximately 30 % of the time: an initial transient broadband signal used for the acoustic measurements, followed by a longer single-frequency tone visible on the spectrogram (Fig. 3a). The first part was characterised by high frequencies ($f_p = 37$–49 kHz) and the second part by lower frequencies ($f_p = 3000$–6000 Hz). This longer portion of the signal occurred 10–20 % of the time during moving behaviour and 20–75 % of the time during feeding behaviour depending on the species. Generally, the initial transient parts of the feeding sounds were less variable in terms of f_p except for *P. lividus* and approximately 7–20 dB higher than the moving sounds (Table 2).

Video observations of *Crepidula fornicata* (family Calyptraeidae) showed that individuals made regular slight lifting movements that created friction between the shells (~5 to 10 movements per minute for one individual). The acoustic signals recorded during moving were characterised by low RLs and high f_p variability.

Each of the two pectinid species emitted two types of acoustic signals, and both species produced sounds during swimming behaviour. *Mimachlamys varia* also produced a transient sound when jumping, a rapid valve closure used by the scallop to move or turn to a desired position, whereas *Pecten maximus* produced a transient sound when coughing, a rapid valve adduction associated with the expulsion of water, faeces and other substances from the mantle cavity. Comparisons between the acoustic features of swimming sounds revealed similarities between the two species; despite size differences, they had similar peak frequencies and variabilities, but during swimming, *P. maximus* produced a sound that exceeded that of *M. varia* by 16 dB.

Among all sound-producing species, *Athanas nitescens* produced the loudest sounds (eSL, 127 ± 6 dB re 1 μPa pp). The sounds had two potential peak frequencies: an audible frequency of approximately 9 kHz and an ultrasonic frequency of approximately 33 kHz (Fig. 3a).

Maja brachydactyla presented the greatest variety in sound types. All sounds produced by this species were characterised by relatively low f_p (4–7 kHz) and the lowest associated SD (Table 2). The first type of sound, referred to as type 1, was audible as a short acoustic pulse and presented with high RL (136 ± 7 dB re 1 μPa pp) and two distinct peak frequencies. The type 1 sound was generally bi-modal (90 % of the time) with a transient and more variable broadband beginning, followed 30 % of the time by a narrow-band, single-frequency tone of longer duration (Fig. 3a) occurring at regular intervals (1.7 ± 0.5 s between each sound emission). We were not able to establish a clear relationship between the type 1 sound and a behaviour because the individuals were immobile during the sound

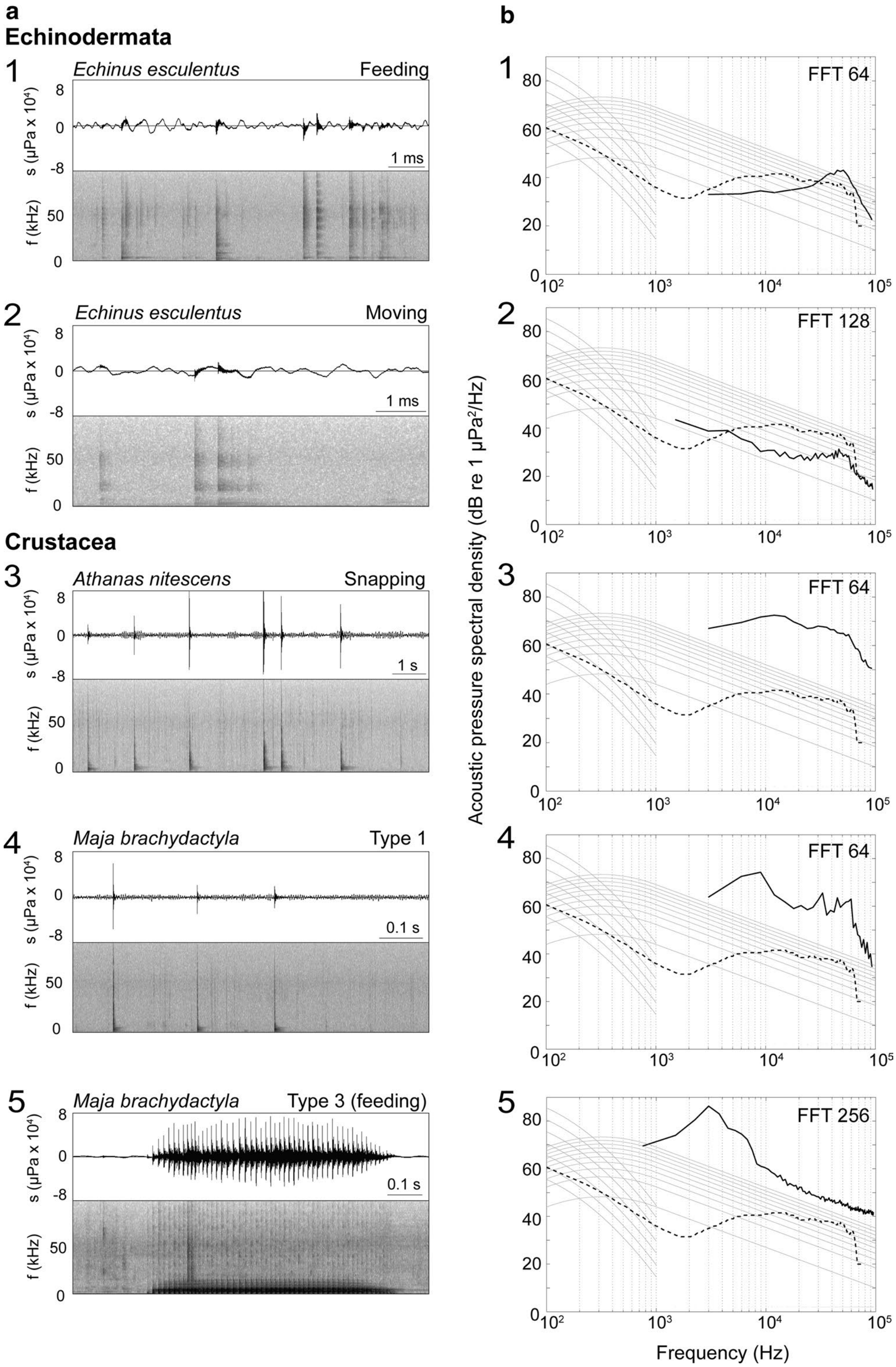

Fig. 3 **a** Selections of waveforms and spectrograms of sounds emitted by the candidate species (expected to be detectable in field recordings) from north-east Atlantic maerl beds recorded in tanks. Spectrograms were colour scaled identically. **b** Acoustic spectra (1 µPa^2/Hz @ 1 m) of the stack of all signal selections for each sound type emitted by the candidate species ($L = 64$, 128, or 256 depending on the frequency range of the sounds, rectangular window with 50 % overlap). *Dashed line* indicates maerl background ambient noise recorded in situ and *grey lines* indicate Wenz's wind and traffic noise curves

emissions, moving only their antennules. The second type of sound recorded from *M. brachydactyla* (type 2) occurred less frequently in our recordings than the other two sounds. The type 2 sound was composed of a series (~5 to 20) of acoustic signals with the lowest f_p measured in this study. As with the type 1 signal, *M. brachydactyla* did not exhibit any particular movements except their antennules when the type 2 signal was recorded. While feeding, *M. brachydactyla* emitted a well-structured sound (type 3; Fig. 3a) composed of regular pulse sequences (29 ± 11 pulses, inter-pulse interval: 0.011 ± 0.004 s) with stable and low f_p (5 ± 0.2 kHz). Compared to other invertebrate sounds, this acoustic signal had an elevated RL (145 ± 3 dB re 1 μPa pp). Visual observations confirmed that the sound coincided with the animal tearing its food. The same type of sound was recorded irrespective of the type of food ingested (fish, squid, shrimp or macroalgae).

To evaluate whether these families of sounds are present in the field recordings, peak frequency was chosen as the most discriminant features for both aquarium and in situ transient signals. Peak frequency estimations were performed on benthic impulsions of the in situ recordings (Online Resource 2 shows the acoustic features of in situ transient benthic sounds). The in situ peak frequencies overlapped with the ones of the species identified as susceptible to be detected above background ambient noise (Online Resource 2).

Acoustic spectra and estimated in situ detection ranges

Mean background ambient noise level in the maerl bed within the biogenic frequency band was of the order of 85.6 dB re 1 μPa. Because of the absence of anthropogenic sounds (mainly engine noise) and low wind regimes, maerl bed ANLs were composed mainly of more or less distant biological benthic choruses that reduced the detection distances of invertebrate sounds compared to Wenz wind regimes.

The acoustic spectra for the three sea urchin feeding sounds were similar in shape (Fig. 3b). The detection distances were about seven times greater for the feeding sounds than the moving sounds (mean of 6.4 and 0.9 m for feeding and moving, respectively) (Table 2; Fig. 3b). The largest sea urchin species among the three studied, *E. esculentus,* had greater detection distances during moving and feeding than the other two species. *Crepidula fornicata* and *M. varia* moving sounds had low SLs with short estimated detection distances (≤1 m). In contrast, the detection distances for the swimming sound of *P. maximus* were 2–4 m. *Athanas nitescens* had the highest estimated detection distances (≥63 m depending on the wind regime), and its acoustic spectrum was substantially above both maerl ambient noise and Wenz's wind curves (Fig. 3b). *Maja brachydactyla* produced three different acoustic spectra with distinct peak frequencies (Fig. 3b). The acoustic signatures of sound type 1 and sound type 3 were greatly above the maerl ambient noise and Wenz's wind curves and had relatively large estimated detection distances (21–101 m).

Discussion

Although numerous studies have investigated the ecology of benthic ecosystems (e.g. Gray et al. 1988; Alongi 1990; Bremner et al. 2003; Harley 2006), to the best of our knowledge, this study is the first to test and describe the sound production of a majority of the abundant invertebrates living within a benthic habitat and to estimate in situ detection ranges.

Amongst the 20 tested species, eight produced sounds, implying that a majority of the marine invertebrates tested did not emit detectable sounds during the tank recording sessions. The recorded sounds were produced mainly by species with calcareous parts that the animals rub, tap or clack together (Online Resource 3 presents sound extracts produced by the species *A. nitescens*, *C. fornicata*, *E. esculentus* moving and feeding, *M. brachydactyla* sound types 1, 2 and 3, and *P. maximus* swimming). To detect the presence of species in field recordings and distinguish between species and/or behaviours, sounds have to be loud enough to be detected above ambient noise. Furthermore, to distinguish species, a signal must have acoustic features with different distributions and low variability, and the signal type emitted during behaviour has to be shared among individuals. Among the recorded sounds, sea urchin feeding, *A. nitescens* snapping, and sound types 1 and 3 of *M. brachydactyla* had properties consistent with simultaneous detectability and identification in field recordings.

The three species of sea urchins sampled (*E. esculentus*, *P. lividus* and *P. miliaris*) produced sounds during moving and feeding behaviours. Feeding sounds were, on average, 16 dB louder and had more stable f_p than moving sounds. This was also reflected in the estimated in situ detection ranges, with feeding sounds estimated to be detectable up to nine times further than moving sounds. Thus, feeding sounds are more likely to contribute to the maerl soundscape than moving sounds, which is in agreement with previous studies (Cato 1978; Radford et al. 2010). The feeding signal was composed of an initial transient broadband portion that has not been described previously and could potentially result from the closure of the Aristotle's lantern, and a second mono-frequency portion likely corresponds to the resonance inside the calcareous skeleton as described by Radford et al. (2008a). According to our visual observations and this previous study, the feeding mechanism appeared to be a mechanical sound due to the closure of the Aristotle's lantern. Sounds with f_p of the same order of magnitude as the second part of the signal were reported for *Evechinus chloroticus* in New Zealand waters (800–2800 Hz) (Radford et al. 2008a).

The powerful snap produced by *A. nitescens* was the loudest sound recorded in this study and was estimated to be detected from approximately 45 m in natural maerl bed environments, which is notable in terms of the animal's size. This type of sound production has already been documented for *Alpheidae* and *Synalpheidae* and has been reported to be dominant in soundscapes at different latitudes (e.g. Knowlton and Moulton 1963; Au and Banks

1998; Freeman et al. 2014). The frequency spectrum of snapping sounds recorded in the tanks and the spectrum of the in situ ANL showed strong similarities. This suggests that the distant chorus of *A. nitescens* dominates the natural background ambient noise of maerl beds. This may result from both the high abundance of *A. nitescens* compared to other soniferous species in maerl beds and the high intensity of the snaps compared to other biogenic sounds. This, however, does not imply that snapping shrimp sounds mask all the sounds from other species. The sounds of feeding sea urchins and *M. brachydactyla* show acoustic differences that allow simultaneous detection and identification, despite the prevailing presence of snapping shrimp snaps. The snapping sound described in this study had a relatively high f_p (9 and 33 kHz) compared to other snapping shrimp species described in acoustic studies (Au and Banks 1998; Koay et al. 2003). Thus, this sound may reflect a species-specific trait (Schmitz 2002). The small size of adult *A. nitescens* (1–2 cm in length) (Smaldon et al. 1993) implies the creation of smaller bubbles with higher f_p (Clay and Medwin 1977). The sound described in this work was also characterised by a relatively moderate sound level compared to the sound reported by Au and Banks (1998), which was approximately 60 dB higher. This difference could be explained by a low clamp closing power and a slower snapping velocity of the small shrimp species reported here compared to the one described by Au and Banks (1998) (Kim et al. 2010), as well as potentially less precise source level estimations in small tanks.

Sounds from *M. brachydactyla* have not been described previously, and this species produced generally loud sounds relative to our database (mean 109 dB re 1 µPa pp @ 1 m). Because sound types 1 and 2 were produced without evidence of body movement, no sound-producing mechanisms could be identified. Sound type 3, which was recorded during feeding behaviour as the animal tore its food into small pieces, had regular pulse sequences and stable low f_p (Online Resource 4 shows a video of a spider crab feeding during the recording session). A stridulatory mechanism can be hypothesised for this sound. Because of its acoustic characteristics (i.e. low stable frequencies), this part of the signal has the potential to be detected more easily in the wild than the transient broadband onset. The acoustic properties of the sounds of *M. brachydactyla,* particularly sound types 1 and 3, have the potential to be an important source of ecological information for conspecific (e.g. presence of food or mates) or heterospecific (e.g. deterring predators) relationships, analogous to what has been reported for other crab species (e.g. Budelmann 1992; Popper et al. 2001; Patek 2002; Staaterman et al. 2011). Whether the described sounds serve as a form of communication or a form of defence remains to be elucidated, but these behaviours have been observed in stomatopods, spiny lobster and paddle crab (e.g. Patek and Caldwell 2006; Buscaino et al. 2011, 2015).

In contrast to the sounds described above, the remaining acoustic signals recorded in this study were highly variable and/or presented low RLs with short estimated detection distances (≤1 m). The moving sounds produced by *C. fornicata*, *M. varia, P. maximus* and the two smaller sea urchin species *P. lividus* and *P. miliaris* did not seem to represent acoustic properties suitable for in situ monitoring (Online Resource 5 shows acoustic spectra of these soniferous species recorded and not represented as candidate species).

Overall, the number of soniferous species suitable for in situ monitoring was limited compared to the high biodiversity of maerl beds in north-east Atlantic waters. However, these species play key ecological or economic roles and are ubiquitous or inhabit other habitats. For example, the number of snaps produced by snapping shrimps has been shown to serve as an indicator of ecological state in oxygen-deficient water (Watanabe et al. 2002). In addition, sea urchins are known to affect the benthic community structure through their grazing activity (Lawrence 1975; Harrold and Pearse 1987; Kelly et al. 2011) and to be highly sensitive to pollution (Harmelin et al. 1981; Guillou et al. 2002). Spider crabs and others are exposed to significant fishing pressure (Le Foll 1993; Lawrence 2006; Andrew et al. 2003), which may drastically reduce their local abundance and reduce their sound production, which could be detected by passive acoustic monitoring and inform on overfishing. The sound production of these key species and their presence/abundance may help to inform on their biological rhythms and those of maerl habitat, as well as on the fishing impacts through the biotic sound production.

Care must be taken when extrapolating results from tank-based experiments to a natural context, as tank recordings are not equivalent to natural sound measures (Parvulescu 1964, 1967; Okumura et al. 2002). However, recording invertebrate sounds in tanks allows the identification of sound-producing species, precise behavioural observations and better control of extraneous noise. Furthermore, numeric simulations revealed that all peak frequency errors induced by tank reverberations were smaller than the frequency resolution of the Fourier transform (Online Resource 1 shows the estimation of peak frequency errors induced by tank reverberation). This implies that tank-induced errors do not significantly affect peak frequency estimations of short transient signals in experimental tanks. Therefore, the values presented here are representative and should not deviate greatly from those measured in the field. This conclusion is supported by the peak frequency estimations of transient sounds in maerl bed field recordings. *In situ* peak frequencies matched the ones of feeding sea urchins (in situ $f_p = 48.5 \pm 1.7$ kHz), type 1 sound of

M. brachydactyla (in situ $f_p = 37.4 \pm 1.6$ kHz) and type 1 sound of *M. brachydactyla* and *A. nitescens* snaps (in situ $f_p = 7 \pm 1.3$ kHz).

Finally, this study highlights two new sound-producing families (Calyptraeidae and Majidae) and eight new soniferous species among several taxa already known to emit sounds (*Alpheidae*, *Echinoidea* and *Pectinidae*). Most of the recorded sounds appeared to be unintentional. *Maja brachydactyla* seems to be an exception, as the characteristics of its sounds (i.e. type 3) suggest intentionality. Except for the snapping sound of *A. nitescens*, all sounds described here likely result from tapping, cracking or rubbing calcareous body parts. Feeding sounds were generally more stable, with a higher probability of being detected in the field than moving sounds. The invertebrate sounds described in this study indicate the presence of two main classes of sounds: (1) sounds with stable, often audible, peak frequencies and higher source levels, and (2) highly variable faint ultrasonic sounds. Class 1 sounds have a higher discriminatory potential than class 2 sounds (i.e. better detectability).

The invertebrate sound library obtained in this work sets a basis for interpreting and documenting the in situ use of passive acoustic monitoring in maerl beds. The results of this study offer the possibility to monitor the ecological status in maerl beds by passive acoustics since healthy and degraded beds display differences in species and abundance, especially for soniferous sea urchins, spider crabs and snapping shrimps (Grall 2002, data obtained from the Observatory of the Institut Universitaire Européen de la Mer). Future research building on this study will consist of determining which of these species and behaviours are detectable in field recordings.

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