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Sound-producing mechanisms and recordings in *Carapini* species (Teleostei, Pisces)

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Abstract *Carapus boraboreensis*, *C. homei* and *Encheliophis gracilis* are three species of Carapidae that display the ability to penetrate and reside in the holothurian *Bohadschia argus*. This study describes both the particular morphology of the sound-producing structures and, for the first time, the sounds produced by each species. The study of the structures composing the sound-producing system seems to indicate that the action made by the primary sonic muscles (i.e. the pulling and releasing of the front of the swim bladder) might be responsible for the sound emissions of these three species by provoking a vibration of a thinner zone in front of the swim bladder (swimbladder fenestra). The sounds were only emitted and recorded when several individuals of the same species were inside the same sea cucumber. They were composed of serially repeated knocks and were heard as drum beats or drum rolls. Their specific differences were mainly defined as variations in the timing or grouping of the knocking sounds. The recordings of these sound productions demonstrate a vocal ability for the three species, linked with the presence of particular organs associated with sound production. Moreover, the ecological significance of the sounds and of the sound apparatus system is discussed.

Keywords Adaptation · Carapidae · Sonic communication · Swim bladder

Abbreviations *I, II, III, IV* vertebra I, II, III, IV · *Bau lig* ligament of Baudelot · *BOC* basioccipital · *EPX* epaxial musculature · *ER I* epipleural rib 1 · *ER II* epipleural rib 2 · *ER III* epipleural rib 3 · *ER IV* epipleural rib 4 · *ER I lig* ligament of epipleural rib 1 · *ER II lig* ligament of epipleural rib 2 · *EXO* exoccipital · *FR* frontal · *i.* *PSP* insertion of PSP · *K. loc* kidney location · *lig* ligament · *MM* muscularis mucosa · *MU* mucosa · *NA* neural arch · *NO* notochord · *NS* neural spine · *PAR* parapophyse · *PSP* primary sound producing muscle · *SB* swim bladder · *SBF* swim bladder fenestra · *SBP* swim bladder plate · *SER* serosa · *S. lig.* ligament of the scapula · *SOC* supraoccipital · *SSP α* secondary sound producing muscle α · *SSP β* secondary sound producing muscle β · *SU* submucosa · *SW* swim bladder · *VP* vertebral body print

Introduction

Pearlfish are fish of the Carapidae family that are able to enter and reside in invertebrate hosts such as seastars, sea cucumbers or bivalves (e.g. Trott 1981; Parmentier et al. 2000). The three species of this study—*Carapus boraboreensis* (Kaup 1856), *Carapus homei* (Richardson 1844) and *Encheliophis gracilis* (Bleeker 1856)—live in the same holothuroid host species and in the same coral reef (Parmentier et al. 2002). If *E. gracilis* is parasitic, both other species are commensal (Parmentier et al. 2000). Inside the sea cucumber visual, chemical or tactile perception of predators or congeners are reduced or masked by the host. In this situation sound communication can be an advantage during host colonisation and reproduction phases as an intra- or interspecific method of communication.

In teleosts, the ability to emit sounds developed independently in distant phylogenetic taxa (Schneider 1967; Carlson and Bass 2000). Currently, members of more than 50 families include species with this capacity (Hawkins 1993). However, some sounds are not

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necessarily produced intentionally by a call or signal, for example while consuming food or swimming. Nevertheless, many fish do produce calls as part of a particular behavioural repertoire. These sonic emissions may be listed in two classes, stridulatory sounds and swim bladder vibration (Fine et al. 1977; Hawkins and Myrberg 1983). The first one is a stridulation mechanism where sounds are emitted by rubbing parts of the body against each other (pharyngeal teeth, pectoral fins). Stridulatory sounds are non-harmonic rasps and creaks, containing a wide range of frequencies from about 50 to 8000 Hz (Tavolga 1971; Hawkins and Myrberg 1983). In the second class, the sound production results from the vibrating of the swim bladder by the deformation of its bladder wall. However, the teleost groups that have this ability have developed different strategies (Alexander 1966; Tavolga 1967; Popper and Coombs 1980; Hawkins 1993; Ladich 2000). The swimbladder deformation may result from the action of intrinsic muscles completely attached to the swimbladder wall (Schneider 1967; Demski et al. 1973). Extrinsic muscles are inserted on the swim bladder and on neighbouring structures such as the cranium or ribs (Tavolga 1971; Ladich and Bass 1998). These muscles may also insert on other structures in order to strike the swim bladder (Carlson and Bass 2000).

Drumming muscles produce highly characteristic sounds that are usually recognizable by their harmonic structure. These are low-frequency sounds with a fundamental frequency of 50–500 Hz, depending upon the species. For several species (*Opsanus tau*, *Porichthys notatus*), it is known that the muscle contraction rate determines the fundamental frequency of the sounds (Skoglund 1961; Connaughton et al. 2000). In the majority of species, the sounds consist of single pulse with a duration of about 20–100 ms each (Tavolga 1971). Some forms produce trains of repeated pulses with each pulse decaying before the next pulse begins (Sprague 2000). On the other hand, different toadfish produce a continuous tone resulting from a long call (up to 0.5 s in duration) with a fundamental frequency of 200–300 Hz (Tavolga 1967; Dos Santos et al. 2000; Fine et al. 2001).

The muscles present in the Carapidae (Ophidiiformes) are extrinsic. These muscles are directly (Parmentier et al. 2000) or indirectly (through the medium of the ribs) in relation with the physoclistous swim bladder (Courtenay and McKittrick 1970). However, in order to obtain deeper insight into the mechanisms involved in sound production we need a complete description of the swim bladder, the muscles and associated osseous structures. This anatomical study is mainly focused on the pearlfish *C. boraborensis* (Kaup 1856) and is completed with particularities or observed differences in two other species: *C. homei* (Richardson 1844) and *E. gracilis* (Bleeker 1856). In relation to these sonic structures, the first recordings of the sound productions of these three species were obtained and analysed to show their vocal ability.

Material and methods

Twenty specimens of *C. boraborensis* (TL: 13–30 cm), 16 *C. homei* (TL: 8–17 cm), and 4 *E. gracilis* (TL: 16–24 cm) were collected by scuba diving in front of the Opanohu bay, Moorea, French Polynesia. They were found inside specimens of sea cucumber *Boludschia argus*. They were stocked in tanks (15 m³) filled with running seawater. Several specimens of each Carapidae species were coloured with Alizarin according to the Taylor and Van Dyke's method (1985) in order to visualise osseous structures. The latter and intact fishes, were dissected and examined with a Wild M10 (Leica Camera) binocular microscope equipped with a camera lucida. After formalin fixation, *C. boraborensis* examples were dehydrated in butanol, embedded in paraffin and serial cut with a Reichert microtome (10 µm thick). Three types of coloration were used (Gobe 1968): Romer's cartilage and bone distinctive coloration, Gallego's ferric fushin coloration in order to see elastic fibres and Masson's trichromatic to reveal the presence of collagen fibres. Histological sections were observed with a polarizing Olympus BX50 binocular microscope coupled with an Olympus OM-4 Ti camera.

Sounds were recorded in a small glass aquarium (0.9 m×0.5 m×0.4 m) with sea cucumbers. For each Carapidae species, several individuals were introduced one after another into the aquarium in order to allow enough time for each one to enter the sea cucumber host. During this operation, the hydrophone was placed less than 20 cm away from the holothurian. The sonic emissions were produced when several individuals were inside the same holothurian host. The emissions were satisfactorily recorded during several minutes for *C. boraborensis* and twenty seconds for the two other species with an Orca hydrophone with preamplifier (sensitivity: -186 dB ref 1 V/µPa) connected via an Orca-made amplifier (ORCA Instrumentation, France) to a mini-disc recorder (JVC, XM-228BK). This system has a flat frequency response range (± 3 dB) between 10 Hz and 23.8 kHz. Sounds were analysed using a Tektronix 2622 analyser and its IP analysis software (1024-point hanning windowed FFT) providing oscillograms and averaged frequency spectra. Sonographic analysis of the signals, previously digitized through a 16-bit acquisition card equipped with an anti-aliasing filter (lowpass filter, fc = 6.4 kHz, -120 dB/octave) at a sampling rate of 16 kHz, were conducted with the SYNTANA analytic package (Aubin 1994; Lengagne et al. 2000).

Results

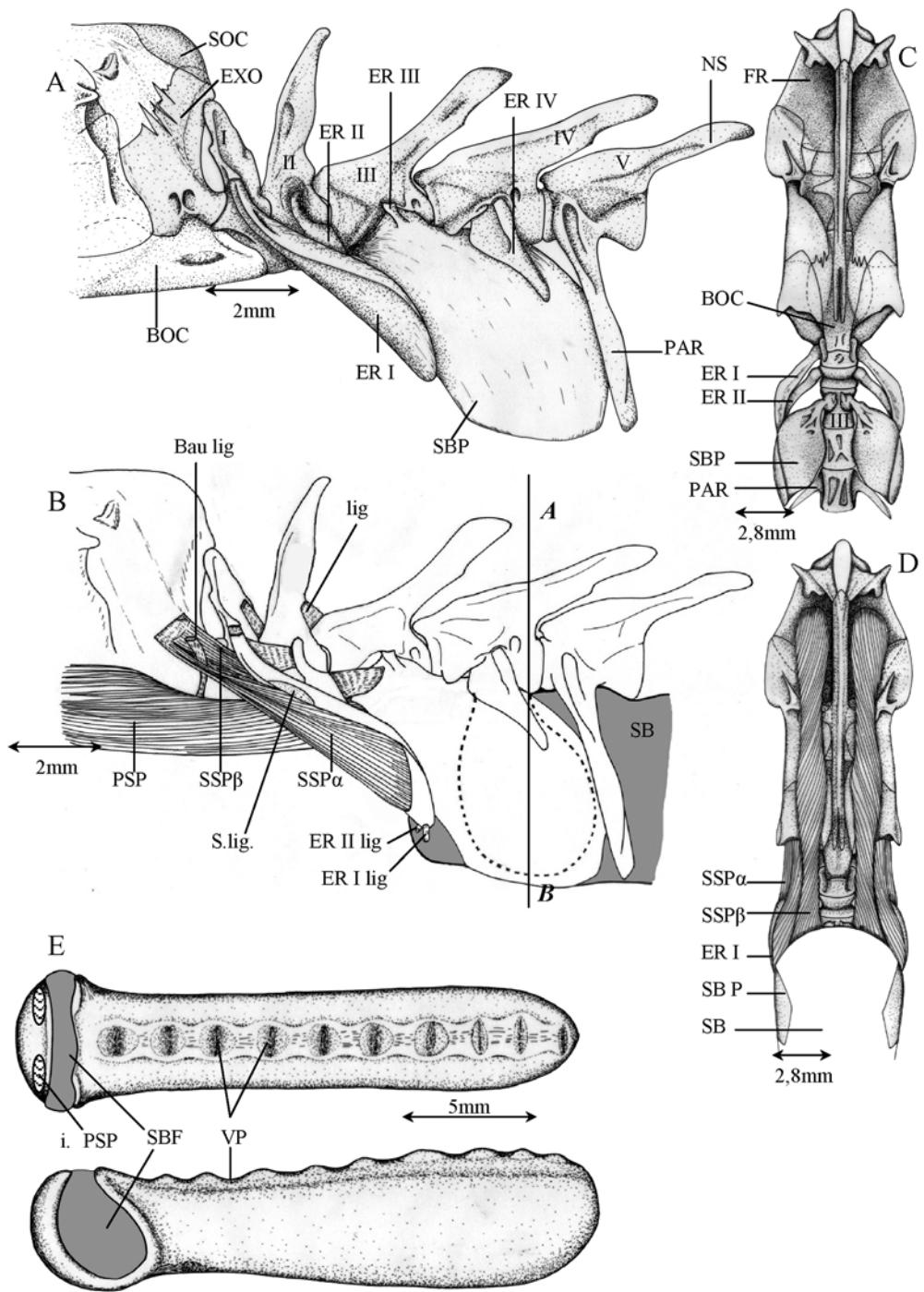
Sound producer organ functional morphology

The four first abdominal vertebrae bear articulated epipleural ribs of different sizes. The other abdominal vertebrae are devoid of epipleural ribs but possess unarticulated parapophysis oriented perpendicularly to the vertebral body.

The two first epipleural ribs are elongated rods oriented caudally (Fig. 1A, C). The presence of a single articulation head allows these ribs to perform movements in different spatial directions. Each of these ribs presents at its posterior extremity a short ligament that joins to the lateral anterior part of swim bladder (Fig. 1B).

The third pair of epipleural ribs is really particular. It is composed of a widespread bony plate that dorso-laterally covers the anterior part of the swim bladder (i.e. the swimbladder plate), moreover its ventral and posterior margins creep within the tissues of the swim bladder (Fig. 2). The elongated articulation of the swim bladder plate (Fig. 1A, C) on the third vertebral body

Fig. 1A–E *Carapus boraborensis*. **A** Lateral view of the anterior part of the vertebral column. **B** Idem with the anterior end of the swim bladder and its associated musculature. **C** Ventral view of the skull and the anterior part of the vertebral column. **D** Ventral view of the musculature associated to the swim bladder. **E** Dorsal and lateral view of the swim bladder. Dark dotted line: place of the swim bladder thinner zone; smaller dotted line: posterior end of the PSP; line AB: see Fig. 2

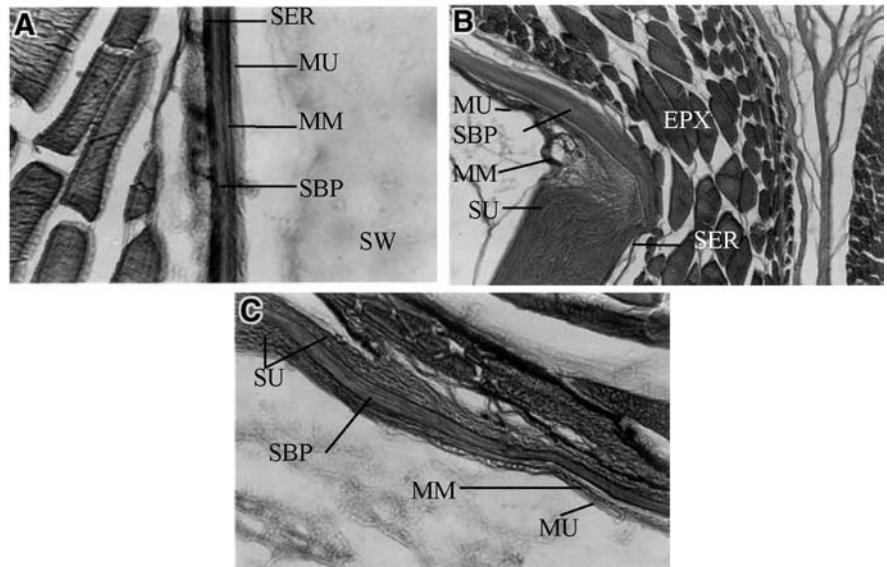
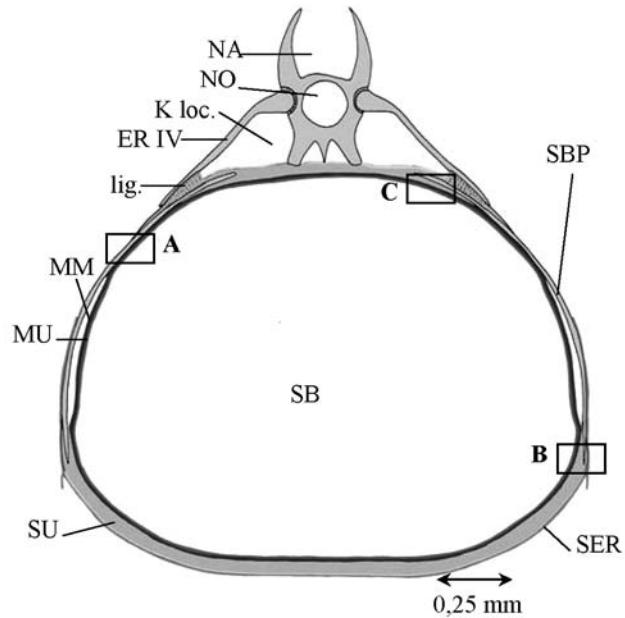


and its overlapping in the swim bladder limit its movement possibilities. In *C. boraborensis* and *C. homei*, the swimbladder plate spreads until it is underneath the fourth vertebrae; in *E. gracilis*, it spreads until it is underneath the fifth vertebrae parapophysis.

The fourth epipleural rib pair is short and overhangs the swimbladder plate but remains distinct (Fig. 1A). Despite a unique articulation on the fourth vertebral body, its mobility is reduced because its ventral face is tightly joined to the swim bladder plate through short conjunctive fibres.

The swim bladder (Fig. 1E) has the shape of a closed oblong tube situated dorsally in the abdominal cavity and firmly applied against the vertebral bodies by the means of conjunctive fibres. The swim bladder is characterised by a thinner zone of its forward wall, just below the swimbladder plate. This thinner zone has a horseshoe-like shape: it is made of two lateral parts dorsally connected by a narrower band (Fig. 1E). Transverse cross-sections of the thicker part of the swim bladder show the presence of several layers of tissue (Fig. 2B). The swim bladder is composed from

Fig. 2 Cross-section through line AB of Fig. 1. Panels A, B and C are enlargements of frames A, B and C shown on the cross-section

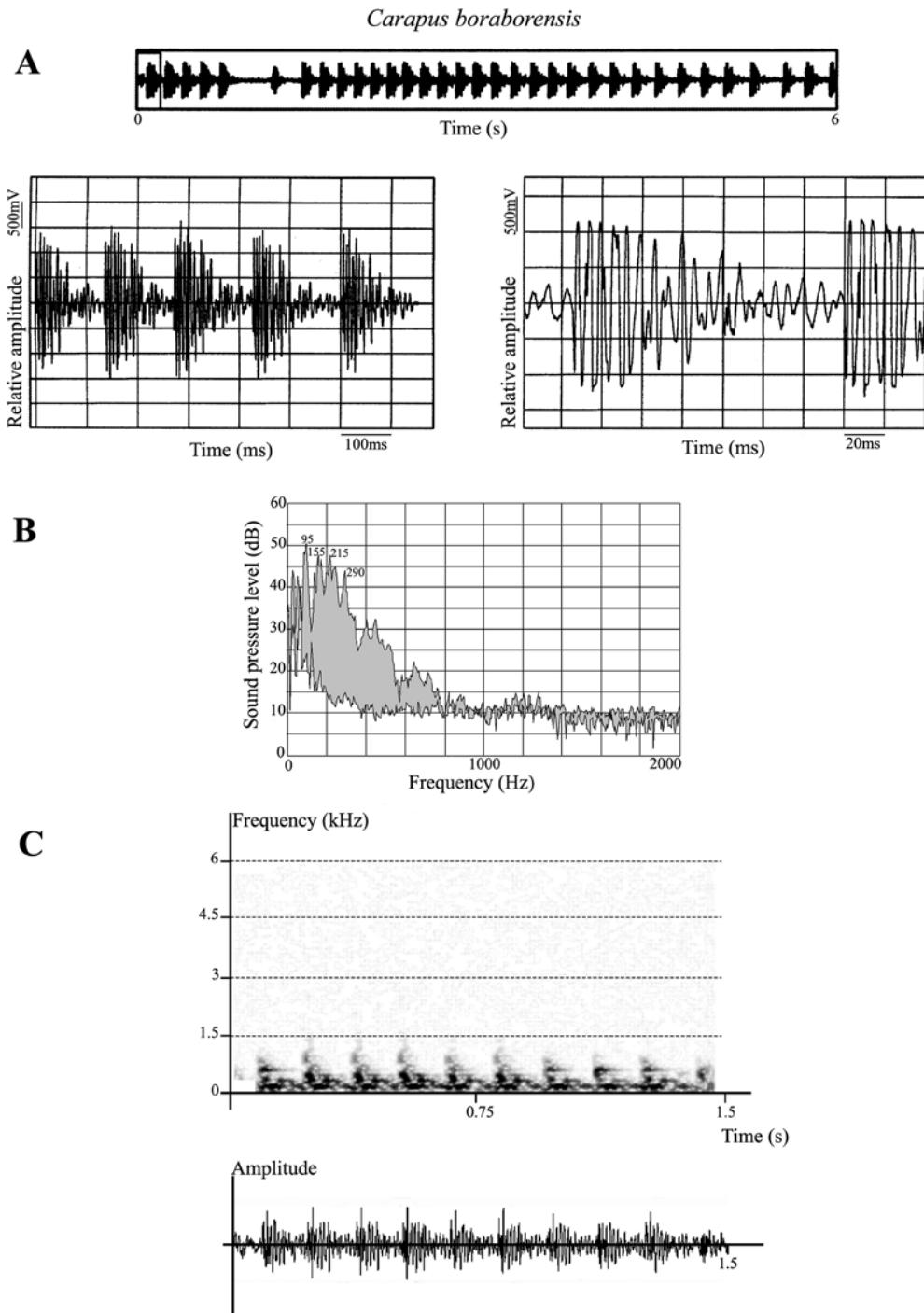


the inner to the outer part of (1) an epidermic tissue (mucosa), (2) a thin fibrous layer made of collagen fibres (muscularis mucosa), (3) a thick layer of elastic fibres (submucosa), and an endodermic tissue (serosa). At dissection, the submucosa appears to be composed of two layers of fibres which confer a net shape on the whole structure : the external fibres have a vertical disposition while the inner fibre layer is disposed obliquely from an antero-ventral to postero-dorsal direction. The horseshoe-like fenestra displayed by the swimbladder structure (Fig. 2A) is composed, from the inner to the outer side of (1) an epidermic tissue (mucosa), (2) a thicker muscularis mucosa, (3) the serosa attached to the bone. The serosa is surrounded by epaxial musculature bundles.

Dissection and cross-section observations reveal that the submucosa displays short expansions that include and immobilize the swimbladder plate all along its posterior and ventral margin. As a consequence of this the swimbladder plate could be the result of an ossification of the serosa and/or the submucosa which would have merged with the third epipleural rib pair. Dissection also reveals that the horseshoe-like fenestra of the swim bladder is loosely attached to the swimbladder plate.

The anterior part of the swim bladder is connected to different extrinsic striated muscles whose terminology is given by Courtenay and McKittrick (1970). The primary sound-producing muscles are attached to the orbital roof, on the inner face of the frontal, and to the antero-dorsal portion of the swim bladder, ahead of the

Fig. 3A–C Characteristics of the sounds produced by *Carapus boraboreensis*. **A** The signal is provided on oscillograms of three different time scales (6 s, 100 ms and 20 ms) to show the whole signal and its finer structure. **B** Frequency spectrum. The lower line corresponds to the recorded ambient noise before or after sound emissions. **C** Sonogram (filter bandwidth: 25 Hz) and corresponding oscillogram of representative pulse trains of a sound emission



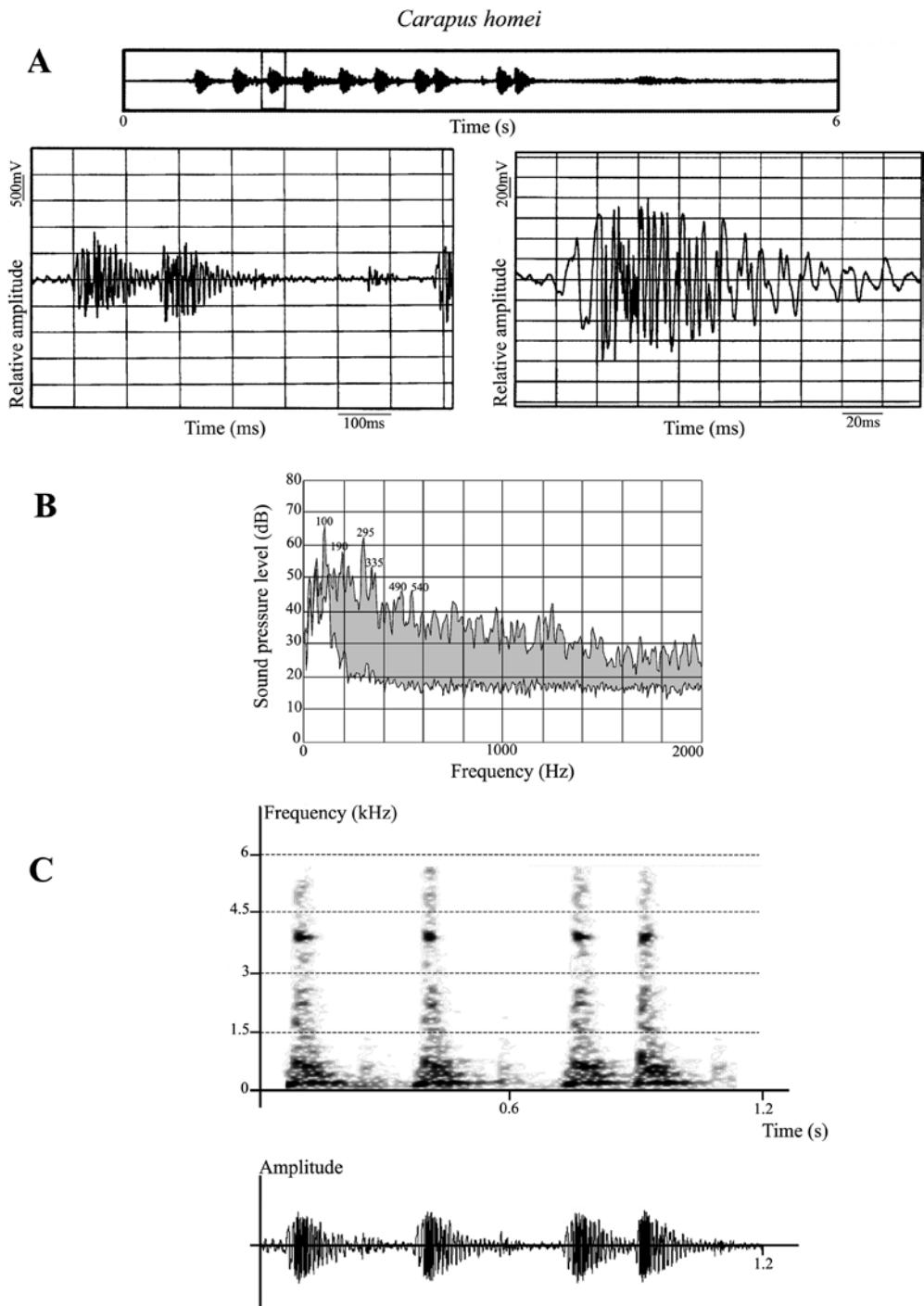
horseshoe-like fenestra (Fig. 1B, D). The three species also have two pairs of muscles that are connected to the anterior part of the swim bladder by the ligaments of the two first epipleural ribs. The secondary sonic muscle α is inserted on the epiotic and on the distal portion of the first epipleural rib. The dorsal secondary sonic muscle (β) has its anterior part attached to the epiotic and joins the ventral part of the second epipleural rib. These two muscles are separated anteriorly by the Baudelot's ligament.

Moreover, *E. gracilis* displays a muscle which links the third rib to the base of the scapular girdle.

Description of sounds

The sound emission displayed by these three Carapidae species was produced during penetration by one individual into a sea cucumber in which several individuals of the same species were already present. The sounds are

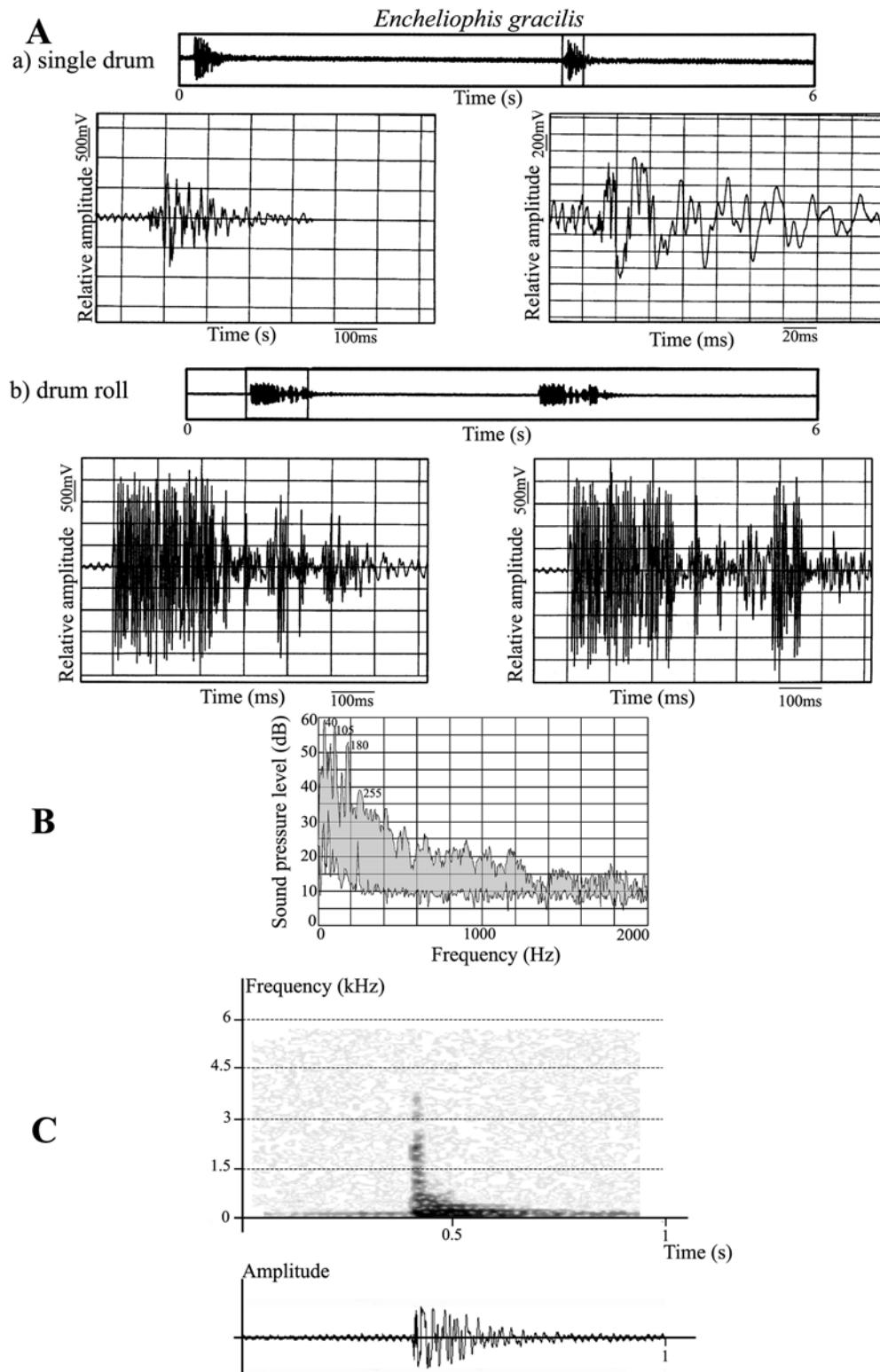
Fig. 4A–C Characteristics of the sounds produced by *Carapus homei*. A The signal is provided on oscillograms of three different time scales (6 s, 100 ms and 20 ms) to show the whole signal and its finer structure. B Frequency spectrum. The lower line corresponds to the recorded ambient noise before or after sound emissions. C Sonogram (filter bandwidth: 25 Hz) and corresponding oscillogram of a representative pulse trains of a sound emission



strongly species specific. *C. boraborensis* (Fig. 3) produces long sequences (25–30 s sound duration) of regular drum beats which progressively slow down toward the end of the sequence (pulse period: 124–165 ms). The sounds are composed of trains of 11–30 pulses ($b = 18.8$, $n = 7$, $SD = 8.5$), each pulse lasting 112 ms ($n = 40$, $SD = 22$). The frequency of these sounds ranges between 80 and 800 Hz with the maximum of sound energy between 80 and 440 Hz (Fig. 4). The average dominant frequency is about 80 Hz.

C. homei (Fig. 4) produces mainly brief sequences (3–5 s duration) of a slow regular beat on a “metal” drum skin although in some cases a double beat (pulse) can be observed (pulse period: 289–612 ms). The duration of each pulse is longer than for the previous species: 262 ms ($n = 10$, $SD = 33$). The frequency range of these sounds is wider as well: 90 Hz to more than 10,000 Hz. The maximum of sound energy is concentrated between 90 and 280 Hz (Fig. 5).

Fig. 5A–C Characteristics of the single drum and drum roll sounds produced by *Encheliophis gracilis*. **A** The signal is provided on oscillograms of three different time scales (6 s, 100 ms and 20 ms) to show the whole signal and its finer structure. **B** Frequency spectrum. The lower line corresponds to the recorded ambient noise before or after sound emissions. **C** Sonogram (filter bandwidth: 25 Hz) and corresponding oscillogram of a representative pulse trains of a sound emission



E. gracilis (Fig. 5) produces either single beats or drum rolls of less than 1 s duration. The pulse duration of single beats is 362 ms ($n=9$, SD = 35). The greater part of sound energy is carried by frequencies below 600 Hz. The average dominant frequency of the swim-bladder vibration is around 60 ± 20 Hz (Fig. 5).

Discussion

Comparison of the sound-producing organs

The sound production based on muscles which produce a vibration of the swim bladder has developed differently

and independently within several distantly related groups (e.g. Ladich and Bass 1998; Carlson and Bass 2000). Extrinsic drumming muscle contraction is a very common mechanism in order to produce sound (Jones and Marshall 1953; Tavolga 1962). In catfish of the Ariidae, Doradidae and Mochokidae, sonic swimbladder muscles originate at various cranial elements and insert onto an 'elastic spring' (distal part of the Müllerian ramus) that vibrates the swim bladder; while in Pimelodidae, the muscles insert ventrally on the swim bladder (Ladich and Bass 1996, 1998). As described for the Holocentridae *Holocentrus rufus* and for several Sebastidae like the genus *Sebastes* (Winn and Marshall 1963; Hallacher 1974), in other non-otophysian teleost families, the drumming muscle bundles are attached on one side to the neurocranium and on the other side to the first ribs tightly attached to the swim bladder. *Therapon jarbua* (Terapontidae) and *Sargocentron cornutum* (Holocentridae) are characterized by muscular fibres directly fixed on the outer layer of the swim bladder (Schneider 1967; Carlson and Bass 2000). Some ophidiiforms and the three Carapidae species studied possess both types of muscles: those attached to the ribs in connection with the swim bladder and those directly attached to the swim bladder (Rose 1961; Courtenay and McKittrick 1970; Tyler 1970; Courtenay 1971; Carter and Musick 1985; Howes 1992).

The striking feature of the three Carapidae studied is due to the conformation of the swim bladder rather than the presence of sonic muscles. In other teleosts; the swim bladder layers are uniform and the very rapid contractions of the drumming muscles result in the deformation of the whole structure leading to fast volume changes and production of sounds (Skoglund 1961; Winn and Marshall 1963; Demski et al. 1973). The sound-production mechanism of the three Carapidae species appears to be more complex with regard to two morphological particularities of the swim bladder: the presence of the horseshoe-like fenestra and its associated covering osseous swimbladder plate. The contraction of the primary sound-producing muscle pulls forward the dorso-anterior part of the swim bladder but not its posterior part, which is fixed to the vertebral bodies and to the swimbladder plate. This forward movement has the effect of abruptly stretching the thinner zone of the swim bladder which finally begins to vibrate.

The role of the secondary muscles is more difficult to explain. However, their relations with the swim bladder by the means of the epipleural ribs and their linked ligaments clearly imply the existence of a particular function. The contraction of these muscles necessarily involves the forward and outward displacement of the posterior tips of the epipleural ribs. The ligaments of the two epipleural ribs thus separate the right and left anterior parts of the swim bladder from the body axis. In this situation, the anterior part is transversally stretched and is capable of shorter-amplitude movements at the time of the contraction of the primary sound-producing muscles. On the other hand, a first tension being created,

the displacements of the anterior part of the swim bladder will facilitate the vibrating of its swimbladder fenestra. The secondary sonic muscles should complete the primary sound-producing muscles. From this viewpoint, the pitch of the produced sound could depend on the amplitude of the two first epipleural rib movements. A similar mechanism was described by Courtenay (1971) in *Rissola marginata* (Ophidiidae). He proposed that this system could function to maintain a single frequency range by offsetting pressure differentials at various depths. Nevertheless, this system could also allow the existence of a larger sonic repertoire.

The teleost swim bladder is a resonant structure acting as an underwater loudspeaker (Tavolga 1967, 1980). However, it is also a damped structure preventing prolonged resonant vibrations and is not completely efficient (Blaxter et al. 1981; Fine et al. 2001). Demski et al. (1973) demonstrated that resonance was better in isolated swim bladders removed from the fish. Damping seems to result more from the influence of the surrounding tissues than from the swim bladder wall itself. In the three Carapidae, the swimbladder plate may decrease the damping by covering the fenestra and so protecting it from the pressure and movements of the hypaxial musculature. The swimbladder plate is broad, thin and regularly shaped in the three *Carapini* species. This system could be an adaptation to increase the signal amplitude by improving resonance produced at the level of the fenestra. However, this kind of system also implies a loss of energy in a given direction, although it should improve the radiation. This amplification system could be related to two aspects of the way of life of these fish. The three species live inside sea cucumbers where the tegument ossicles and plates most likely disturb sound propagation. On the other hand, the host is also a territory to protect against individuals of the same species and of other species. The amplification system could be necessary in order to emit sounds through the host or to improve an aggressive behaviour.

Vocal ability in Carapidae

The three species studied show an ability to produce sound. This ability was known in a closely related family: Ophidiidae (Courtenay 1971; Mann et al. 1997; Sprague and Luczkovich 2001), but it is reported here for the first time in Carapidae. It also possible to clearly validate the relation between the sound produced and the anatomical structures implied.

Emitted sounds are composed of series of separate low-frequency pulses typically resulting from drumming muscles (Moulton 1963; Tavolga 1964; Hawkins and Myrberg 1983; Ladich and Fine 1994; Crawford and Huang 1999). Nevertheless, the sounds of each Carapidae species can be distinguished from those of the other species by differences in temporal structure. The main differences are based on the number of knocking pulses and pulse period unaffected by recording in tank (Mann

et al. 1997). The pulse duration, shorter in *C. boraborensis*, more prolonged in the two other species, can not be considered in absolute value because it can be increased by multiple reflections from the tank walls and the water surface (Parvulescu 1964; Hawkins and Chapman 1966; Hawkins and Rasmussen 1978). However, the three species were recorded in the same experimental conditions; the relative differences observed in the duration of their knocking pulses should correspond to specific characteristics that will be specified when recordings are made in open-water conditions. Differences are also observed in the spectral composition of the sounds emitted in each species: maximum of sound energy between 40 and 80 Hz for *E. gracilis*, between 80 and 160 Hz for *C. boraborensis* and between 90 and 280 Hz for *C. homei*. In our recording conditions (180-l tank and hydrophone placed within the range of the attenuation length from the fish, <23 cm), the spectrum shape can be measured without artefacts for a frequency range lower than the minimum resonant frequency of the tank (in our case close to 2.6 kHz) (Okumura et al. 2002). In the frequency domain, these differences could be useful to distinguish the three species, even if the fish itself refers to the temporal pattern and pulse duration for species recognition (Winn 1967; Fish and Mowbray 1970; Myrberg et al. 1978; Spanier 1979; Tavolga 1980).

Behavioural context of sound emission

It is clear that these preliminary investigations only take into account a single behavioural pattern associated with sound emission. However, due to their unique morpho-functional features, a greater variety of sound expression is strongly suspected. As indicated by Hawkins and Myrberg (1983), the context in which sound production occurs varies greatly from one species to another. The sound production can be related to courtship, agonistic interactions, competition, alarm or territorial sounds (Alexander 1966; Tavolga 1971; Fine et al. 1977; Myrberg et al. 1978; Myrberg 1981; Torricelli et al. 1990; Dos Santos et al. 2000, Hawkins and Amorim 2000). In the framework of the present study, sounds are not likely to be used by the fish to identify the presence of an eventual congener in the holothurian before penetration but are produced in the presence of the congener, inside the holothurian. Indeed, no sound has been recorded while the fish were approaching the potential host or while penetrating the unoccupied holothurian. The sound emission inside the holothurian could be a communication system in a place where visibility is strongly reduced (Popper and Coombs 1980; Hawkins 1993) and where chemical communication may be masked by the host.

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