

Sound production in two carapids (*Carapus acus* and *C. mourlani*) and through the sea cucumber tegument

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Abstract

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Carapus acus and *Carapus mourlani* are able to live inside sea cucumbers and sea stars respectively. Unlike other carapids whose sounds have been recorded (*C. boraborensis*, *C. homei* and *Encheliophis gracilis*), these two species have a central constriction in their swimbladder and are unlikely to encounter heterospecific carapids within their hosts. We evoked sound production in *Carapus acus* and *Carapus mourlani* by adding several individuals to a tank with a single host and found that their sounds differ substantially from the sounds emitted by other carapids in pulse length, peak frequency and sharpness of tuning (Q_3 dB). Unlike the other carapids, *C. mourlani* and *C. acus* produce shorter and less repetitive sounds and do not produce sounds when they enter their host. Since sounds produced within a sea cucumber have the potential to be heard by distant carapids and are typically recorded outside the sea cucumber, we examined the effect of the sea cucumber tegument on acoustic transmission. Attenuation by the tegument was negligible at the frequencies within carapid sounds. Therefore, carapids have the potential to call from the relative safety of a sea cucumber without sacrificing the distance over which their transmissions are heard.

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Introduction

Some pearlfish (Carapidae) enter and reside in invertebrate hosts such as sea stars, sea cucumbers or bivalves (e.g. Trott 1981; Parmentier and Vandewalle 2005). The host reduces visual, chemical or tactile perception of both predators and congeners. The ability to communicate acoustically would be an advantage during host colonization and reproduction, and three species have been shown to produce species-specific sounds (Parmentier *et al.* 2003a). Sounds have only been recorded when an individual has entered a sea cucumber that was already occupied.

In areas of the Pacific Ocean where they live in sympatry (Markle and Olney 1990), *Carapus boraborensis*, *C. homei* and *Encheliophis gracilis* can inhabit the same host species but heterospecifics are rarely found together in the same host

(Smith 1964; Trott 1970; Trott and Trott 1972; Vanden Spiegel and Jangoux 1989). Of 257 *Bohadschia argus* collected in Opunohu Bay (Moorea, French Polynesia), 83% contained different species of carapids but less than 1% included heterospecific infestations (Parmentier and Vandewalle 2005). Laboratory experiments and field studies revealed that the fish do not appear to determine whether a potential host is already occupied; the fish penetrates the first host it contacts. However, when *C. boraborensis* and *C. homei* are inside the same holothurian, the interspecific confrontation is accompanied by short sound signals. Intraspecific confrontations are associated with longer and prolonged sounds. Interestingly, the first acoustic signals are emitted as the inter- or intraspecific types without passing through an intermediate enquiry-type stage (Lagardère *et al.* 2005).

The apparent silence of fish approaching a host is not understood. Since these species are capable of eating each other, it could be advantageous to be discrete. However, the meeting of two species does not automatically end in predation because one of the fish may leave the host (Parmentier and Vandewalle 2005). Therefore, the entering fish appears to be willing to risk an encounter to allow it to assess the size of any other fish that might be present.

The carapid sonic mechanism includes specialized anterior vertebrae, the swimbladder and associated muscles (Courtenay and McKittrick 1970; Markle and Olney 1990; Parmentier *et al.* 2000; Parmentier & Vandewalle 2003). The anteriormost lateral surface of the swimbladder possesses a horseshoe-shaped thinner zone, the swimbladder fenestra. The fenestra is covered dorsolaterally by the swimbladder plate, an extension of the third epineural rib. The sonic muscles originate on the orbital roof of the skull and insert into the anterior wall of the swimbladder (Parmentier *et al.* 2003b). The action of the sonic muscles in sound generation could stimulate movement of the fenestra (Parmentier *et al.* 2003a, 2003b), which presses against the swimbladder plate. The swimbladder plate is broader, thinner and more regularly shaped in the Carapini tribe (*Encheliophis* and *Carapus*) than in free-living carapids. Parmentier *et al.* (2002) suggested that the large swimbladder plate of the Carapini could be related to their way of life because the teguments of the host could disturb or attenuate sound propagation.

On the other hand, the genus *Carapus* can be divided into two subgroups: subgroup 1 (*C. acus*, *C. bermudensis* and *C. mourlani*) possesses a central constriction of the swimbladder (Fig. 1), which is not present in subgroup 2 (*C. homei*, *C. boraborensis* and *C. dubius*). Moreover, fishes of subgroup 1 can only have conspecific encounters in their host whereas they can be heterospecifics for *C. homei* and *C. boraborensis* (Markle and Olney 1990; Parmentier *et al.* 2000).

The goal of this study was dual. (1) The sounds of *C. acus* and *C. mourlani* were recorded for the first time and compared

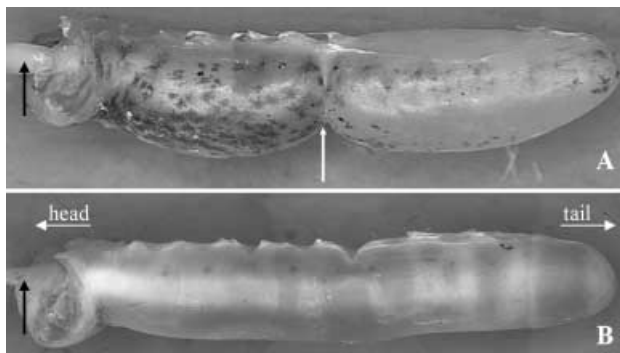


Fig. 1—Left lateral view of the swimbladder. —**A.** In *Carapus mourlani* —**B.** In *C. boraborensis*. White arrow: central constriction of the swimbladder. Black arrow: localization of the sound-producing muscle.

with previously recorded species (*C. boraborensis*, *C. homei* and *E. gracilis*) to know (i) how the central constriction of the swimbladder can influence the sound and (ii) if the differences in the ecology of both groups can be inferred from the sounds produced. (2) In the second experiment, the goal was to know if the tegument of the sea cucumber host could (or could not) disturb the propagation of sounds.

Carapus mourlani is commonly found in the Indo-Pacific as a commensal of sea stars such as *Culcita* sp. and *Acanthaster planci* (Meyer-Rochow 1977, 1979; Trott 1981; Eeckhaut *et al.* 2004). *Carapus mourlani* has been observed to swim along the ambulacral groove of the sea star *Culcita* before entering the stomach, tail first, through the oral cavity and finally reaching the general cavity (E. Parmentier, personal observation). *Carapus acus* lives in the Mediterranean Sea and on the east coast of North Africa. It is usually found in the sea cucumbers *Stichopus regalis*, *Holothuria tubulosa* and *Holothuria stellati*, which it enters tail first or head first (Kloss and Pfeiffer 2000; Eeckhaut *et al.* 2004).

Materials and methods

Carapus mourlani

Thirty-two *C. mourlani* (total length 6–10 cm) were collected by scuba diving in the lagoon in front of Tulear (Mozambic canal, west coast of Madagascar) in June 2004. They were found in the general body cavity of the sea star *Choriaster granulatus* ($n = 40$). Host and fish were stored in a community tank ($3.50 \times 0.7 \times 0.2$ m) with running sea water. Recordings were made at 26 °C in a smaller tank ($1 \times 0.5 \times 0.6$ m). A specimen of the host was placed in the centre of the tank, and several individuals were introduced successively into the aquarium. Sounds were recorded with an Orca hydrophone (sensitivity: -186 dB re 1 V/ μ Pa) 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 and 23.8 kHz. The hydrophone was placed above the sea star.

Carapus acus

Thirty-two *C. acus* (total length of 8–12 cm) were collected from dissection of 87 *Holothuria tubulosa* and 129 *Holothuria stellati* obtained in front of the STA.RE.SO station (Calvi Bay, Corsica) in April 2004. Fish were stored in a community tank ($0.6 \times 0.6 \times 0.4$ m) with running sea water. Recordings were made at 19 °C in a smaller tank ($0.4 \times 0.4 \times 0.31$ m). A specimen of the host (*H. stellati*) was first placed in the centre of the tank, and several individuals were introduced successively into the aquarium. Sounds were recorded with an HTI 16 400 hydrophone coupled with a preamplifier and connected to a Sony TCD-D8 digital audio tape-recorder (recording band width: 20 – $22\,000$ Hz ± 1.0 dB).

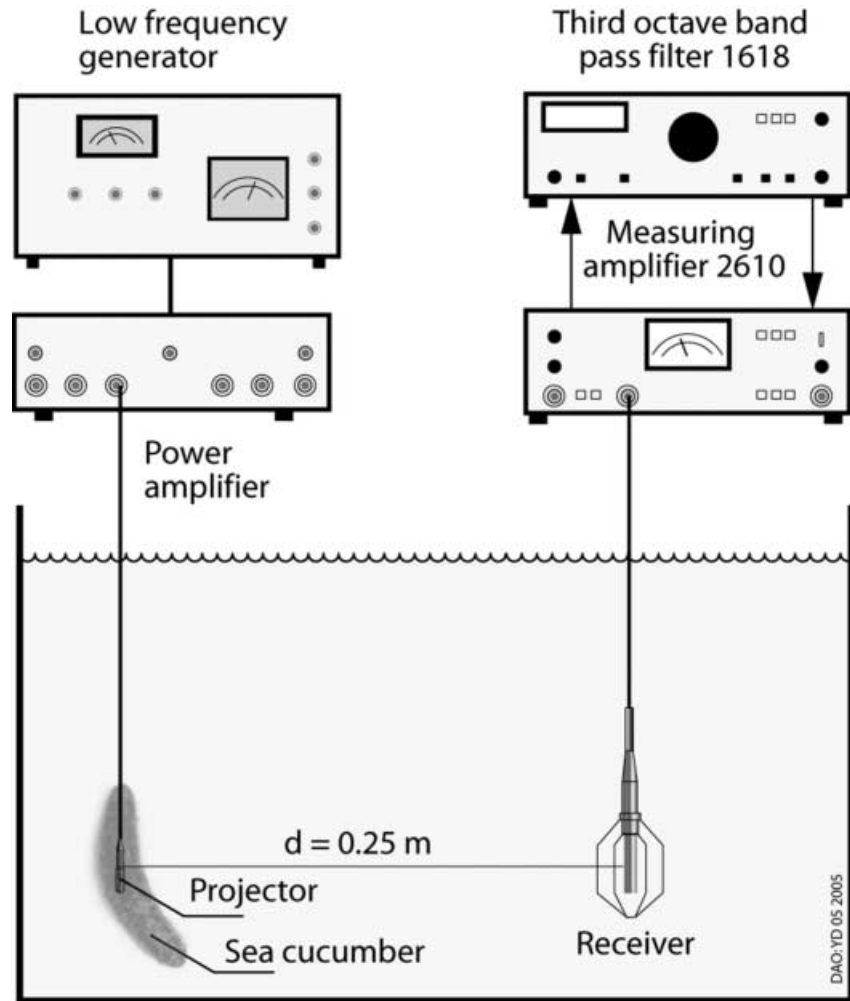


Fig. 2—Scheme of the experimental process used to study the transmission of sounds through the sea cucumber tegument.

Sound analysis

Sounds were digitized at 44.1 kHz (16-bit resolution) and analysed with AVISOFT-SAS LAB PRO 4.33 software (1024-point Hanning windowed FFT). The resonant frequencies of the tanks were calculated as 2.56 and 3.58 kHz respectively using an equation from Akamatsu *et al.* (2002), and low-pass filters of 2.56 kHz and 3.58 kHz were applied to the sounds of Madagascar and Calvi respectively. Temporal features were measured from the oscillograms, and frequency parameters were obtained from power spectra (filter band width 300 Hz, FFT size 256 points, time overlap 96.87% overlap, and a Hamming window). The following sound parameters were measured: sound duration; number of peaks per pulse; dominant frequency and $Q_{3\text{ dB}}$, i.e. the quotient of the dominant frequency divided by the band width 3 dB down from the peak frequency.

Attenuation of sounds by the sea cucumber tegument?

To determine the effect of the sea cucumber tegument on acoustic transmission, a set of experiments was conducted in

a large glass aquarium ($2.48 \times 0.7 \times 0.7$ m) (Fig. 2). A 8103 Brüel & Kjaer is used as a constant sound pressure transmitter, and a B & K, type 8101 hydrophone was the receiver. Tones from a frequency generator were fed into the transmitting hydrophone via a low distortion power amplifier. The signal from the receiver hydrophone was conditioned and amplified in a measuring amplifier (B & K, type 2610). With a meter scale (B & K, SA 0251) calibrated to the 8101 hydrophone sensitivity, the measuring amplifier coupled with a third octave band pass filter (B & K, type 1618) was used as a sound level meter to measure the ambient noise in the aquarium.

The transmitting hydrophone was fed into the cloacal cavity of the sea cucumber (*H. stellati*) collected from the same area as *C. acus*, and the measuring hydrophone was placed at a distance of 25 cm. An equivalent set of measurements was made with the transmitting hydrophone in the identical position with the sea cucumber removed. Any difference between the two sets of measurements reflects attenuation by the tegument of the sea cucumber. Measurements were repeated five times with five different sea cucumbers, and values for

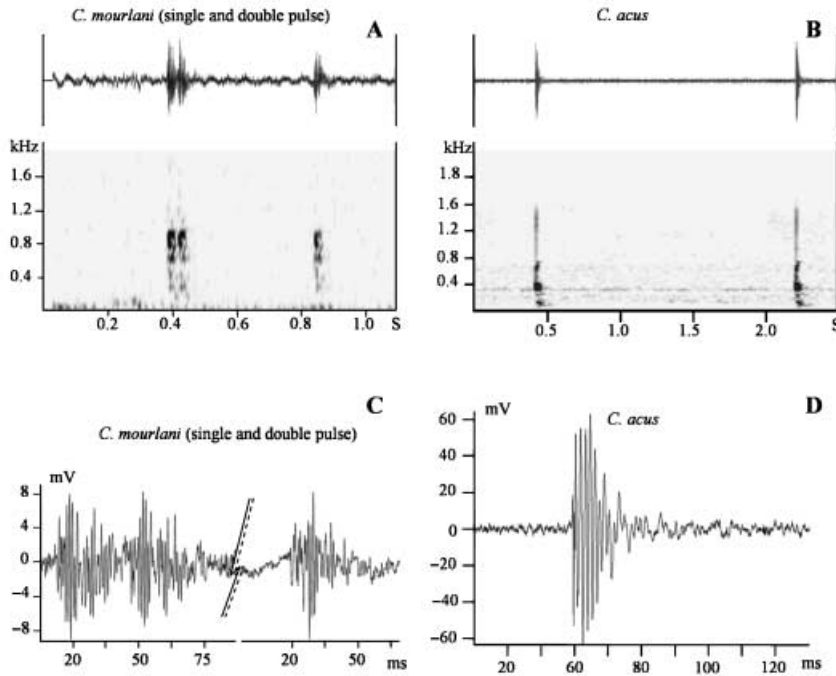


Fig. 3—**A, B.** Sonograms of pulses in *Carapus mourlani* and *Carapus acus*. —**C, D.** Oscillograms of pulses in *Carapus mourlani* and *Carapus acus*.

each frequency were averaged. Ambient noise was measured in each experiment and averaged.

Results

Description of sounds

Carapus mourlani produced single- and double-pulsed calls when competing for access to the oral aperture of the sea star. However, no sound was recorded once different fishes were in the host.

Single pulses (Fig. 3) had an average duration of 15.5 ± 5 ms (mean \pm SD) and contained 11–20 peaks (mean \pm SD, 16 ± 5). Peak frequency was 638 ± 167 Hz (Fig. 3A), and most sound energy ranged from about 570 to 1000 Hz. $Q_{3\text{ dB}}$ averaged 4 ± 3 .

Each unit of the double pulse (Fig. 3C) appeared to consist of an initial and a later energy peak: the sound amplitude built up, decayed and then increased to a second although smaller set of peaks within a pulse. Double pulses had an average duration of 54.4 ± 2.1 ms, and an interpulse interval of 9.26 ± 2.2 ms. Each pulse ranged from 16.2 to 29.3 ms (mean \pm SD, 22 ± 4.2) and contained 10–20 peaks (mean \pm SD, 16 ± 5). Peak frequency was 765 ± 124 Hz, and most sound energy ranged from about 210 to 1070 Hz. $Q_{3\text{ dB}}$ averaged 4 ± 1.38 . However, the pulses of both calls differed significantly only in their pulse length ($P < 0.005$). Therefore double pulses appeared to be a repetition of the single pulse (Fig. 3C).

Carapus acus produced sounds when the fish swam in the aquarium without any discernable interactions between

fishes. Sounds were not produced during or after penetration of the host. Sounds were composed of a single pulse of 12–13 peaks (Fig. 3D) with an average duration of 34.8 ms. Peak frequency was 341 ± 4.05 Hz, and most sound energy ranged from about 250 to 1600 Hz (Fig. 3B). $Q_{3\text{ dB}}$ averaged 8 ± 1.32 .

Sea cucumber attenuation

Background noise in the tank decreased by about 8 dB from a mean of 66.8 dB, re 1 (micro-pascal) μPa at 200 Hz to 58.4 dB at 1000 Hz (Fig. 4). The decrease in background noise over the range of recorded frequencies was the result of sound absorption by sea water; the higher the frequency, the greater the attenuation (Wenz 1962).

The 200-Hz tone was above background by slightly over 2 dB, but other frequencies had a margin of at least 7.5 dB. The tegument of the sea cucumbers ranged between 5 and 12 mm in thickness and did not affect results. Differences between sound pressure level with the transmitter inside the sea cucumber and free in the water averaged 0.3 dB (Fig. 4) indicating that the sea cucumber had a negligible effect on transmission of carapid acoustic signals.

Discussion

This study describes sound production in *C. mourlani* and *C. acus*, species with a constriction in the swimbladder, and indicates that differences exist between their sound and sounds previously described for *C. boraborensis*, *C. homei* and

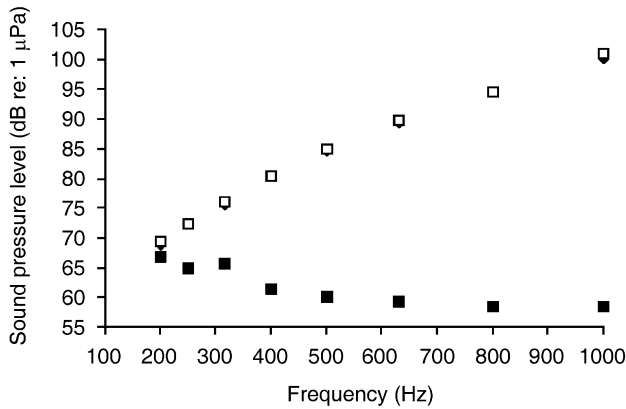


Fig. 4—Sound pressure level recorded 25 cm from a transmitting hydrophone emitting tone burst outside (◆) or inside (□) the sea cucumber (*Holothuria stellati*). Ambient noise (■) was measured with third-octave filters. Numbers represent the mean of five trials with five different sea cucumbers. Sounds recorded inside (□) and outside (◆) the sea cucumber are essentially overlapping.

E. gracilis (Parmentier *et al.* 2003a; Lagardère *et al.* 2005) (Table 1). *Carapus boraborensis* produces long sequences (25–30 s sound duration) of regular drum beats. These sounds are composed of trains of 11–30 pulses, with each pulse lasting between 80 and 140 ms. *Carapus homei* produces mainly brief sequences (3–5 s) of a slow regular beat on a ‘metal’ drum skin although in some cases double pulses are produced. The average length of these pulses is 220 ms. *Encheliophis gracilis* produces either single beats or drum rolls of less than 1 s duration. The pulse duration of single beats borders 362 ms.

Differences between carapids in this study and *C. boraborensis*, *C. homei* and *E. gracilis* lie in the pulse length, dominant peak frequency and the $Q_{3\text{ dB}}$; the pulse length, on average, is between 16 and 35 ms whereas it is between 83 and 362 ms in *C. boraborensis*, *C. homei* and *E. gracilis* (Parmentier *et al.* 2003a; Lagardère *et al.* 2005) and, values of $Q_{3\text{ dB}}$ are, respectively, between 4 and 8 in the first group, around 12 in *C. homei* and 15 in *C. boraborensis* (Parmentier, unpublished data). Peak frequency is between 300 and 800 Hz in *C. acus* and *C. mourlani*, whereas maximum sound energy was

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* (Parmentier *et al.* 2003a).

Carapus acus and *C. mourlani* of this study were smaller than the three other carapids, which ranged from 80 to 300 mm in total length (TL) (Parmentier *et al.* 2003a). The smaller size may relate to their shorter pulse length and the higher dominant peak frequency. Relationships between size and pulse length and peak frequency have been found in catfish (Fine and Ladich 2003), weakfish (Connaughton *et al.* 2000), damselfish (Myrberg *et al.* 1993; Lobel and Mann 1995) and gouramis (Ladich *et al.* 1992): the pulse duration increases and dominant frequency decreases in larger fish. Although frequency can vary over several hundred hertz in differently sized fish of the same species, it is unlikely that fish size alone could explain the difference in pulse length among carapids. How the central constriction (Fig. 1) in the swimbladder in *C. acus* and *C. mourlani* affects sound emission is unknown but it could conceivably increase the natural frequency of the anterior part of the swimbladder. Tuning is also less sharp (i.e. $Q_{3\text{ dB}}$ values are smaller) in these species, but it is not immediately apparent how the central constriction would affect this parameter. $Q_{3\text{ dB}}$ in croaker *Micropogonius chromis* is about 3 (Fine *et al.* 2004), which is considerably less than in any of the carapids. The croaker has a sonic muscle–swimbladder mechanism without the skeletal specializations that are present in carapids and is likely to represent a more typical tuning for a sonic teleost bladder. Parmentier and Vandewalle (2003) suggested that the swimbladder plate could function as a resonator. If the plate is set into motion by the sonic muscles and then functions to drive swimbladder vibrations, the tuning of the plate could explain the high Q tuning of carapid sounds.

Carapus mourlani and *C. acus*, unlike *C. homei*, *C. boraborensis* and *E. gracilis*, do not produce sounds when they enter their host. *Carapus acus* is the only symbiotic carapid found in Corsica, and *C. mourlani* is a commensal in sea cucumbers that do not host other carapids (Markle and Olney 1990; Parmentier *et al.* 2006). However, *C. mourlani* is found in sea stars (Eeckhaut *et al.* 2004) in locations that are sympatric with other symbiotic carapid species (*C. boraborensis*, *C. homei* and *E. gracilis*) but appears to avoid contact with other carapid species. In contrast *C. boraborensis*, *C. homei* and *E. gracilis* are usually found in the same species of sea cucumber

Table 1 Description of sounds made by different carapids

	Sound duration (s)	No. pulses/train	Pulse period (ms)	Pulse duration (ms)	Dominant peak frequency (Hz)	$Q_{3\text{ dB}}$
<i>Encheliophis gracilis</i>	< 1	1–2	–	362	60	–
<i>Carapus homei</i>	3–5	2–10	334	220	90–280	12
<i>Carapus boraborensis</i>	3–30	11–30	180–212	80–140	80–200	15
<i>Carapus acus</i>	0.035	1	–	35	341	8
<i>Carapus mourlani</i>	0.015–0.055	1–2	8–12	16–30	638–765	4

(Parmentier *et al.* 2000; Eeckhaut *et al.* 2004; Parmentier and Vandewalle 2005), and interspecific contact is likely. Since an individual entering a sea cucumber that is already inhabited by the same or a different species can lead to eviction or death (Parmentier and Vandewalle 2005; Lagardère *et al.* 2005), it would be adaptive to produce repetitive calls. This constraint is apparently removed in *C. acus* and *C. mourlani* because they have no chance of encountering another fish species in the host.

The brief sequences emitted by these two species may be associated with the spawning period. In many teleost species, sound production is linked to the spawning season because sounds may have a role in female choice and timing of gamete release (Hawkins 1993; Zelick *et al.* 1999; Hawkins and Amorim 2000). The spawning period appears to occur from July to September in *C. acus* but is unknown for *C. mourlani* (Trott and Olney 1986). Fish were recorded in June, and the short pulses were produced close to the assumed reproductive period. Moreover, at the end of October, 24 specimens of *C. acus* did not produce sounds under the same experimental conditions. Furthermore, electron micrographs of the sonic muscles from this period indicate atrophied fibres (Parmentier, unpublished data). A seasonal cycle of hypertrophy–atrophy in the sonic muscle has been demonstrated in haddock (Templeman and Hodder 1958), *Cynoscion regalis* (Connaughton *et al.* 1997), a Portuguese toadfish (Modesto and Canario 2003) and codfish (Rowe and Hutchings 2004).

Damping

Parmentier and Vandewalle (2003) suggested that the sonic structures might be adapted to compensate for the loss of energy of sonic vibrations as they travel through the thick host tegument, which contains calcareous plates. This hypothesis was tested in a laboratory tank. Because of resonance and reflections, small tanks are quite complex acoustically (Akamatsu *et al.* 2002) and have the potential to distort sound waveforms. However, because the transmitting and receiving hydrophones were maintained in position, any artefacts from the tank would have equal effects on sound transmitted inside and outside the sea cucumber and should not compromise the current study, which clearly demonstrates that the sea cucumber teguments do not attenuate or modify the frequency spectrum of carapid sounds. Although the signal was weakest at 200 Hz, the long wavelengths associated with low frequency sounds are least likely to be affected by the tegument.

Transparency of the tegument to sound is similar to findings from fish tissue, which has a similar acoustic impedance to water (Von Frish 1936; Dijkgraaf 1960; Tavolga 1971; Popper and Coombs 1980). Although previous sounds from five carapid species were all recorded from within the host (Parmentier *et al.* 2003a; Lagardère *et al.* 2005), the current result suggests the intriguing possibility that males could

communicate to females outside from the safety of the sea cucumber cavity.

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References

- Akamatsu, T., Okumura, T., Novarini, N., Yan, H. Y. 2002. Empirical refinements applicable to the recording of fish sounds in small tanks. – *Journal of the Acoustical Society of America* 112: 3073–3082.
- Connaughton, M. A., Fine, M. L., Taylor, M. H. 1997. The effects of seasonal hypertrophy and atrophy on fiber morphology, metabolic substrate concentration and sound characteristics of the weakfish sonic muscle. – *Journal of Experimental Biology* 200: 2449–2457.
- Connaughton, M. A., Taylor, M. H., Fine, M. L. 2000. Effects of fish size and temperature on weakfish disturbance calls: implications for the mechanism of sound generation. – *Journal of Experimental Biology* 203: 1503–1512.
- Courtenay, W. R., McKittrick, F. A. 1970. Sound-producing mechanisms in carapid fishes, with notes on phylogenetic implications. – *Marine Biology* 7: 131–137.
- Dijkgraaf, S. 1960. Hearing in bony fishes. – *Proceedings of the Royal Society of London Serie B* 152: 51–54.
- Eeckhaut, I., Parmentier, E., Becker, P., Gomez da Silva, S., Jangoux, M. 2004. Parasites and biotic diseases in field and cultivated sea cucumbers. In: Lovatelli, C. Conand, Purcell, S. Uthicke, S., Hamel, J.-F. and Mercier, A. (Eds): *Advances in Sea Cucumber Aquaculture and Management*. – *FAO Fisheries Technical Paper* 463: 311–325.
- Fine, M. L., Ladich, F. 2003. Sound production, spine locking and related adaptations. In: Kapoor, B. G., Arratia, G., Chardon, M. and Diogo, R. (Eds): *Catfishes*, pp. 248–290. Science Publishers, Inc., Enfield, NH.
- Fine, M. L., Schrinel, J., Cameron, T. M. 2004. The effect of loading on disturbance sounds of the Atlantic croaker *Micropogonius undulatus*: air vs. water. – *Journal of the Acoustical Society of America* 116: 1271–1275.
- Hawkins, A. D. 1993. Underwater sound and fish behaviour. In: Pitcher, T. J. (Ed.): *Behaviour of Teleost Fishes*, pp. 129–169. Chapman & Hall, London.
- Hawkins, A. D., Amorim, M. C. P. 2000. Spawning sounds of the male haddock, *Melanogrammus aeglefinus*. – *Environmental Biology of Fishes* 59: 29–41.
- Kloss, K., Pfeiffer, W. 2000. Zur biologie des «eingeweidefisches» *C. acus* (Brunnich, 1768) (Carapidae, Teleostei), mit hinweisen auf eine nich-parasitische ernährung. – *Revue Suisse de Zoologie* 107: 335–349.

- Ladich, F., Bischof, C., Schleizer, G., Fuchs, A. 1992. Intra- and interspecific differences in agonistic vocalization in croaking gouramis (Genus: *Trichopsis*, Anabantoidei, Teleostei). – *Bioacoustics* 4: 131–141.
- Lagardère, J. P., Millot, S., Parmentier, E. 2005. Aspects of sound communication in the pearlfish, *Carapus boraborensis* and *Carapus homei* (Carapidae). – *Journal of Experimental Zoology A* 303: 1066–1074.
- Lobel, P. S., Mann, D. A. 1995. Spawning sounds of the damselfish, *Dascyllus albisella* (Pomacentridae), and relationship to male size. – *Bioacoustics* 6: 187–198.
- Markle, D. F., Olney, J. E. 1990. Systematics of the Pearlfish (Pisces: Carapidae). – *Bulletin of Marine Science* 47: 269–410.
- Meyer-Rochow, V. B. 1977. Comparison between 15 *Carapus mourlani* in a single Holoturian and 19 *Carapus mourlani* from starfish. – *Copeia* 1977: 582–585.
- Meyer-Rochow, V. B. 1979. Stomach and gut content of *Carapus mourlani* from starfish and a holothurian. – *Annals Zoologica Fennici* 16: 287–289.
- Modesto, T., Canario, A. 2003. Morphometric changes and sex steroid levels during the annual reproductive cycle of the Lusitanian toadfish, *Halobatrachus didactylus*. – *General and Comparative Endocrinology* 131: 220–231.
- Myrberg, A. A. Jr, Ha, S. J., Shablott, M. J. 1993. The sounds of bicolor damselfish (*Pomacentrus partitus*): predictors of body size and a spectral basis for individual recognition and assessment. – *Journal of the Acoustical Society of America* 94: 3067–3070.
- Parmentier, E., Vandewalle, P. 2003. Morphological adaptations of Pearlfish (Carapidae) to their various habitats. In: Val, A. L. and Kapoor, B. G. (Eds), *Fish adaptations*, pp. 261–276. Oxford & IBH, India.
- Parmentier, E., Vandewalle, P. 2005. Further insight on the Carapini – holothurian relationships. – *Marine Biology* 146: 455–465.
- Parmentier, E., Castillo, G., Chardon, M., Vandewalle, P. 2000. Phylogenetic analysis of the pearlfish tribe Carapini (Pisces: Carapidae). – *Acta Zoologica* 81: 293–306.
- Parmentier, E., Chardon, M., Vandewalle, P. 2002. Preliminary study on the ecomorphological signification of the sound-producing complex in Carapidae. In: Aerts, P., D'Août, K., Herrel, A. and Van Damme, R. (Eds): *Topics in Functional and Ecological Vertebrate Morphology*, pp. 139–151. Shaker Publishing, Maastricht.
- Parmentier, E., Vandewalle, P., Lagardère, J. P. 2003a. Sound producing mechanisms and recordings in three Carapidae species. – *Journal of Comparative Physiology A* 189: 283–292.
- Parmentier, E., Gennotte, V., Focant, B., Goffinet, G., Vandewalle, P. 2003b. Characterization of the primary sonic muscles in *Carapus acus* (Carapidae): a multidisciplinary approach. – *Proceedings of the Royal Society of London Serie B* 270: 2301–2308.
- Parmentier, E., Mercier, A., Hamel, J. F. 2006. New host and geographical distribution for the pearlfish *Carapus mourlani* (Carapidae) with a discussion on its biology. – *Copeia* 2006: 122–128.
- Popper, A. N., Coombs, S. 1980. Auditory mechanisms in teleost fishes. – *American Scientist* 68: 429–440.
- Rowe, S., Hutchings, J. A. 2004. The function of sound production by Atlantic cod as inferred from patterns of variation in drumming muscle mass. – *Canadian Journal of Zoology* 82: 1391–1398.
- Smith, C. L. 1964. Some Pearlfishes from Guam, with notes on their ecology. – *Pacific Sciences* 18: 34–40.
- Tavolga, W. N. 1971. Sound production and detection. In: Hoar, W. S. and Randall, D. J. (Eds): *Fish Physiology*, pp. 135–205. Academic Press, New York.
- Templeman, W., Hodder, V. M. 1958. Variation with fish length, sex, stage of sexual maturity and season in the appearance and volume of the drumming muscles of the swimbladder in the haddock, *Melanogrammus aeglefinus*. – *Journal of the Fisheries Research Board of Canada* 15: 355–390.
- Trott, L. B. 1970. Contribution of the biology of Carapid fishes (Paracanth-Ofterygini: Gadiformes). – *University of California Publications in Zoology* 89: 1–41.
- Trott, L. B., Trott, E. B. 1972. Pearlfishes (Carapidae: Gadiformes) Collected from Puerto Galera, Minobra, Philippines. – *Copeia* 1972: 839–843.
- Trott, L. B. 1981. A general review of the pearlfishes (Pisces, Carapidae). – *Bulletin of Marine Science* 31: 623–629.
- Trott, L. B., and, Olney, J. E. 1986. Carapidae. In: Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. and Tortonese, E. (Eds): *Fishes of the North-Eastern Atlantic and the Mediterranean*, pp. 1172–1176. UNESCO, Paris.
- Vanden Spiegel, D., Jangoux, M. 1989. La Symbiose entre poissons Carapidae et Holoturies autour de l'île de Laing (Mer de Bismark, Papouasie Nouvelle Guinée). – *Indo-Malayan Zoology* 6: 223–228.
- Von Frish, K. 1936. Über den Gehörsinn der fische. – *Biological Review* 11: 210–246.
- Wenz, G. M. 1962. Acoustic ambient noise in the ocean: spectra and sources. – *Journal of the Acoustical Society of America* 34: 1936–1956.
- Zelick, R., Mann, D. A., Popper, A. N. 1999. Acoustic communication in fishes and frogs. In: Fay, R. R. and Popper, A. N. (Eds): *Comparative Hearing: Fish and Amphibians*, pp. 363–411. Springer, New York.