

Aspects of Sound Communication in the Pearlfish *Carapus boraborensis* and *Carapus homei* (Carapidae)

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ABSTRACT Several species of Carapidae are known to have symbiotic relationships with marine invertebrates. The two most common species in Moorea (French Polynesia), *Carapus boraborensis* and *Carapus homei*, undergo conspecific and heterospecific encounters in the same holothurian host during which they produce sounds. Another characteristic of these fish lies in their abilities to produce sounds. The objective of this study was dual: (1) to seek if there was a sexual difference in the sounds produced by *C. boraborensis*; (2) to seek if there was a difference in the sound emissions between heterospecific and conspecific encounters. In each trial, sounds were only recorded when one individual entered the sea cucumber that was already occupied. In encounters, sounds were structured in regular pulse emissions whose pulse lengths and periods allowed to significantly distinguish each species, as well as both sexes in *C. boraborensis*. In the latter species, results show for the first time that temporal features of the emitted sounds can have a functional importance in sex identification. In heterospecific encounters, sounds were reduced 68% of the time to a single pulse emission and there was a modification in the pulse length of each species: it shortens in *C. homei* and it lengthens in *C. boraborensis*. It highlights that both carapids are able to adapt their sounds to the facing species. Because a modification of the sound appears to be done at the first emission, it is supposed that recognition precedes the sound emission. *J. Exp. Zool.* 303A:1066–1074, 2005. © 2005 Wiley-Liss, Inc.

Certain pearlfish (Carapidae) are able to enter and reside in invertebrate hosts (e.g., Trott, '81; Parmentier et al., 2000). Species of *Carapus* and *Encheliophis* are mainly found in the respiratory trees or inside the body cavity of different holothurian species (Arnold, '56; Smith, '64; Shen and Yeh, '87). Species of *Carapus* genus are commensals and use their host as a shelter, while *Encheliophis* species are parasitic and eat the host's gonads (Parmentier and Vandewalle, 2003; Parmentier and Das, 2004). These fish have thus resting and active periods whose duration depended on energetic supply provided by ingested prey. In *C. bermudensis*, Smith et al. ('81) showed a feeding periodicity ranging from 15 to 24 days on average, but able to last up to 60 days.

In areas of the Pacific Ocean where they live in sympatry (Markle and Olney, '90), *Carapus boraborensis* (Kaup, 1856), *Carapus homei* (Richardson, 1844) and *E. gracilis* (Bleeker, 1856)

can inhabit the same host species. However, an infestation is usually monospecific (Smith, '64; Branch, '69; Trott, '81; VandenSpiegel and Jangoux, '89). Of the 257 *Bohadschia argus* specimens collected in Opunohu Bay (same study site as these Carapidae in this study), 84% contained pearlfish: *C. homei* in 39.3% of the cases and *C. boraborensis* in 59.2%. *C. boraborensis* and *C. homei* are likely to be in competition for colonisation of the same holothurian host. Only two holothurians (>1%) were infested by a paired *C. homei/C. boraborensis*, while a

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monospecific multi-infestation was observed in 6% of the holothurians (Parmentier and Vandewalle, 2005). On the other hand, field and laboratory experiments realised in the latter study showed that the fish penetrates the first host with which a contact is established. Field and laboratory experiments reveal a paradox: fish do not appear to be able to determine if a potential host is already occupied but the heterospecific multi-infestation is very weak. It means that the identification of the fish should appear only once the fish is in the host although the basis for this recognition is unknown.

Recently, Parmentier et al. (2003b) described for the first time the sounds produced by three species of Carapidae: *C. boraborensis*, *C. homei* and *E. gracilis*. The sound-producing system suggests 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 by provoking vibration in the thinner zone of the front of the swim bladder (Parmentier et al., 2003a,b). The sounds made by these fish are a series of repeated knocks that sound like drum beats or drum rolls to the human ear. In these preliminary investigations, the sound emissions were recorded whenever several individuals of the same species were inside the same sea cucumber host. No sound was recorded while the fish were approaching the potential host or while penetrating an unoccupied holothurian. Under these conditions, the sound emission inside the holothurian was interpreted as having a communicative function between conspecifics.

Generally, it has been widely assumed that temporal parameters are the main features for species recognition (Winn, '64; Myrberg et al., '78) or for intraspecific communication (Hawkins and Myrberg, '83; Hawkins, '93; Mann and Lobel, '98). On the other hand, spectral frequencies and, perhaps sound intensity, might also have a biological importance for interspecific as well as intraspecific recognition in fish (Ladich et al., '92).

The goal of this study was dual. (1) Because there is a difference in the body size and in the morphology of the swim bladder between males and females (Parmentier and Vandewalle, 2005), the first aim was to know if sounds are sexually dimorphic. (2) In the second group of experiments, the goal was to know if there was a difference in the sound emission between heterospecific and conspecific encounters in the same holothurian host. These experiments concern encounters between *C. homei* and *C. boraborensis*.

MATERIALS AND METHODS

Study location and animals

Sixty specimens of *B. argus* were collected by scuba diving in front of Opunohu Bay, Moorea (French Polynesia) between July and August 2002. The sea cucumbers were transferred by boat in 50-l containers for approximately 20 min to laboratory 15 m³ holding tanks (water temperature: 29°C; natural photoperiod: 13:11 hr light:dark).

Fifty holothurians were cut longitudinally and fish were found inside: 15 specimens of *C. boraborensis* (SL: 16–30 cm) and 12 *C. homei* (SL: 9–16 cm). These fish were stored in two different 4 m³ aquariums for a period of 12–48 hr prior to each experiment. Fish were not fed during this period but are able, in relation to their particular behaviour, to have long periods (more than 1 month) of starvation (Smith et al., '81; Parmentier et al., 2002). For *C. boraborensis*, the sex of specimens was determined using the non-invasive criteria given in Parmentier and Vandewalle (2005), based on the size of the specimen and the shape of the head. Males are smaller than females, with a mean total length (TL) 17.3 cm and none exceeded 20 cm; females have a mean TL of 21.7 cm and can exceed 30 cm. Females are also characterised by a larger head. The sex of *C. homei* was impossible to determine using external characteristics.

Recordings and signal acquisition

The sounds were recorded under the same conditions as those used by Parmentier et al. (2003b). Sounds were recorded in a small glass aquarium (0.9 × 0.5 × 0.4 m) containing the sea cucumber. In each experiment, the hydrophone was placed less than 20 cm away from the holothurian. For each experiment, 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. The experiments were completed in two steps.

Experiment A

The aim of this experiment was to know if there was a sexual difference between the sound produced by males and females of *C. boraborensis*. In a first set of trials, only males of *C. boraborensis* were introduced into the aquarium. In a second set of trials, males and females of *C. boraborensis* were introduced into the aquarium. In each case,

sounds were recorded when the second fish enters inside the sea cucumber host. Signals were collected in this manner of exchanges between several individuals of *C. boraborensis* (two males and four females).

Experiment B

The aim of this experiment was to know if there was a difference in the sound produced by the fish when the encounters were conspecifics or heterospecifics. A specimen of one fish species was placed in the aquarium and entered into the holothurian after which a specimen of the second fish species was introduced into the aquarium. The sound emissions were recorded when this second specimen entered into the holothurian. Twelve encounters were recorded between *C. boraborensis* and *C. homei*.

The sounds recorded during the first experiment, as well as those published in Parmentier et al. (2003b) in *C. boraborensis* and *C. homei*, were used as a control for sounds recorded during the second stage of the experiments.

Each recording session lasts between 2 and 5 min. The emissions were recorded with an Orca hydrophone with preamplifier (sensitivity: -186 dB ref 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 Hz and 23.8 kHz. Sounds were analysed using a Tektronix 2622 analyser and its IP analysis software (1,024-point hanning windowed FFT) providing oscillograms and averaged frequency spectra. The frequency spectrum was analysed using a sliding window of four pulses that was successively shifted over the entire sound recording. Sonographic analyses of the signals (previously digitised through a 16-bit acquisition card equipped with an antialiasing filter (low-pass filter, $f_c = 6.4$ kHz, -120 dB/octave)) at a sampling rate of 16 kHz were done with the SYNTANA analytical software (Aubin, '94; Lengagne et al., 2000). The following temporal characteristics of the sound waves were measured (Ladich, '97): (1) pulse and sound duration (msec): time interval between the onset of one pulse or sound and their end. (2) Pulse period (msec): time interval between the main peaks of two successive pulses.

Statistical analysis

A *t*-test was used to compare data between males and females of *C. boraborensis*, and inter- and

intraspecific sounds. A one-way ANOVA followed by a Tukey test was used to compare parameters between both sexes of *C. boraborensis* and *C. homei*.

RESULTS

For each species, sounds were emitted when an individual had just penetrated the host holothurian in which there was already one other fish.

Characteristics of the intraspecific sounds

1—*Carapus boraborensis*

In males, the sounds ranged from 3 to 5 sec. They were composed of series of 10–28 pulses (Fig. 1a), each pulse lasting an average of 83 msec ($n = 63$, $SD = 30$) with a period of 180.5 msec ($n = 55$, $SD = 88$). In females (Fig. 1b), the calls were longer: 3–14.5 sec. They were made up of a series of 16–83 pulses having an average duration of 136 msec ($n = 46$, $SD = 28$) and a period of 212 msec ($n = 32$, $SD = 59$).

Pulses of males and females of *C. boraborensis* were identifiable based on the significant differences between their sound pulse duration (Fig. 2a): pulse lengths of males are shorter than in females ($t = 9.44$, $df = 107$, $P < 0.0001$). On the other hand, the pulse period allows to discriminate both sexes ($t = 2.27$, $df = 85$, $P < 0.05$) (Fig. 2b).

The frequencies of these sounds ranged between 55 and 800 Hz. The maximum sound energy was around 200 Hz: it varied between 204 ± 3.5 Hz ($n = 11$) for males and 203.5 ± 3 Hz ($n = 14$) for females.

2—*Carapus homei*

Sounds produced by *C. homei* occurred in short sequences lasting from 3 to 5 sec. Each sound was composed of a succession of about 10 isolated pulses or grouped in pairs. The average length of these pulses was 218 msec ($n = 26$, $SD = 86$) with a period of 334 msec ($n = 31$, $SD = 168$). These two temporal characteristics were significantly different (ANOVA, Tukey test, $P < 0.001$) from those measured in both male and female *C. boraborensis* specimens (Fig. 2a and b).

The range of sound frequencies emitted by this species was very broad (90–4,450 Hz), with a maximum acoustic energy between 90 and 912 Hz.

Characteristics of the interspecific sounds

Sound emissions made during encounters of fish of different species in the same host lasted from

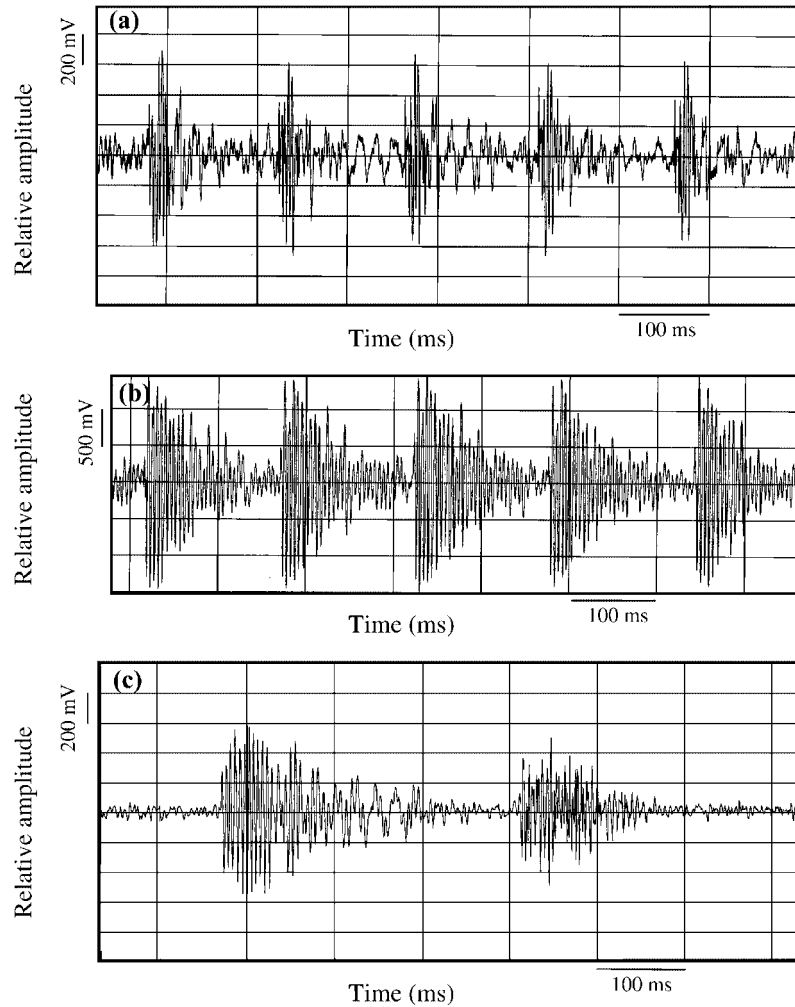


Fig. 1. Temporal characteristics of the sound (time scale: 100msec) produced by individuals of *C. boraborensis* during conspecific (a and b) or heterospecific encounters with *C. homei* (c). (a) Sound produced by a male of *C. boraborensis* during a male-male interaction in the same holothurian. (b) Sound produced by a female of *C. boraborensis* during exchanges between several individuals. (c) Interspecific sounds produced during encounters between *C. homei* and *C. boraborensis* individuals.

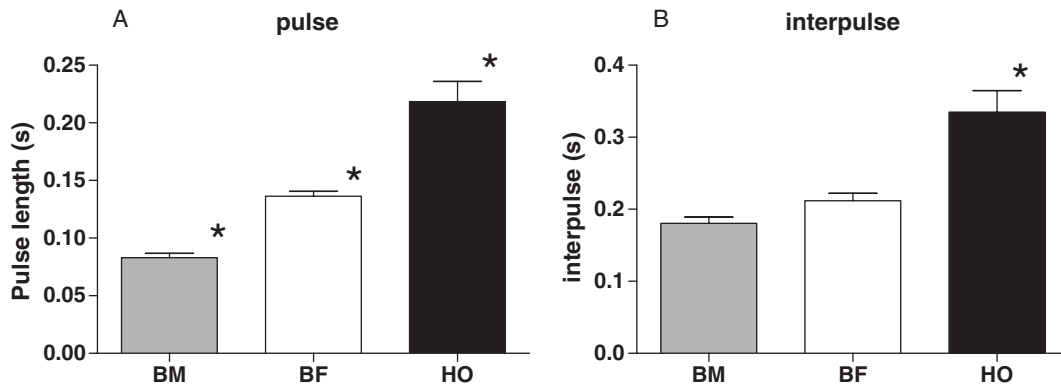


Fig. 2. Comparisons of pulse lengths (a) and interpulse lengths (b) between males of *Carapus boraborensis* (BM), females of *C. boraborensis* (BF) and *Carapus homei* (HO). (*) indicates that the data are significantly different (ANOVA, Tukey test, $P < 0.001$).

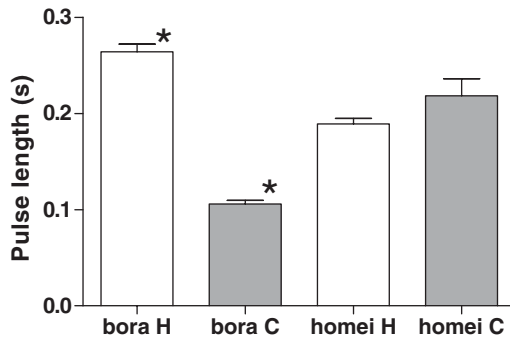


Fig. 3. Comparisons between the mean pulse durations during heterospecific and conspecific encounters in both Carapini species. Bora: *Carapus boraborensis*; homei: *Carapus homei*; H: heterospecific; C: conspecific. The pulse length varies significantly (*) in the case of *C. boraborensis* (*t*-test, $P < 0.001$).

10 to 15 sec. In most of the cases (68%), the sounds were composed of the alternation of isolated pulses coming from each species (Fig. 1c). In other cases, it was a combination of alternate series of two or three pulses (Fig. 4). The average length of the pulses (Fig. 3) from *C. boraborensis* (264 msec, $n = 99$, $SD = 81$) increased compared to intraspecific conditions ($t = 18.12$, $df = 205$, $P < 0.001$). In contrast, the pulse duration decreased in *C. homei* (189 msec, $n = 26$, $SD = 30$) but this decrease is not significant ($t = 1.63$, $df = 48$, $P = 0.1$).

DISCUSSION

The sounds emitted by the two species are made up of a series of low-frequency pulses which are typical of sounds produced by the “drum muscles” (Moulton, '63; Tavalga, '64; Hawkins and Myrberg, '83; Ladich and Fine, '94; Crawford and Huang, '99) and are characteristic of the two species (Parmentier et al., 2003b). The main differences between both species are based on the number of pulses, their durations, periodicity and sound spectrum (Parmentier et al., 2003b). The number of pulses and the pulse period is unaffected by the recording tank (Mann et al., '97), but the pulse length could be increased by multiple reflections from the tank walls and the water surface (Parvulescu, '64; Hawkins and Chapman, '66; Hawkins and Rasmussen, '78; Akamatsu et al., 2002). Nevertheless, as the sound was recorded at a distance of less than 20 cm, this probability was very low (Akamatsu et al., 2002). Under our experimental conditions, the spectrum shape could be measured without artefacts up to 2,600 Hz, minimum resonant frequency of our

tank (Okumura et al., 2002). However, in *C. homei*, it is possible that some emission peaks between 3,500 and 4,500 Hz could be attributed to resonance particular to the aquarium. Nonetheless, these frequencies contribute to the identification of the temporal signal of the species in addition to giving the metallic tone to the emitted sound which made identification easier (Fig. 1c).

The behaviour of the Carapidae seems paradoxical. Despite the capacity of each species to prey on the other (Parmentier and Das, 2004), laboratory and field experiments indicate these fish enter the first holothurian encountered (Parmentier and Vandewalle, 2005). Moreover, a recognition of another “inhabitant” is not done using sound emissions before entering into the holothurian (Parmentier et al., 2003b, this study). In contrast, it appears obvious that the entering fish and the fish already in residence are capable of identifying each other once inside the sea cucumber. When two fish are inside the same holothurian and sound production begins, it was observed that an intraspecific confrontation generates complex and prolonged sound signals while an interspecific confrontation is associated with shortened and condensed sounds. It is also interesting to note that the type of emitted signal corresponds from the start to the type of signals identified as being from inter- or intraspecific encounters without passing through any intermediate inquiry-type stage.

Inside the host, the species identification could be based initially on olfactory signals. Is it possible that fish can identify each other using a sense of olfaction? This appears reasonable based on other observations of the use of olfactory clues to identify water masses (Westerberg, '84; Døving et al., '85), prey (Atema et al., '80; Kleerekoper, '82), predators (Chivers and Smith, '93) and for courtship motivation (for review see Kenyon, '94) or kin recognition (McKaye and Barlow, '76; Barnett, '77, '81; Brown and Brown, '93). Olfactory capacities appear to be present in the Carapidae. Different species of Carapini seem to be capable of recognising the odour of their usual host species (Trott, '70; Van Meter and Ache, '74). *C. boraborensis* and *C. homei* can, in experiments with Y tubes, recognise their own species and swim towards them (Parmentier and Vandewalle, 2005). On the other hand, recognition could be mediated by the lateral line. When the host is found, carapids turn around the sea cucumber by touching it with their nose in order to locate the cloaca, their way of entry. Most of the time, the

presence of the fish is detected and the sea cucumber closes its cloaca and begins an “apnea”. The sea cucumber must however finally stop its apnea and ends up exhaling (Parmentier and Vandewalle, 2005). The fish, mostly found in the respiratory tree of the host, should feel this

perturbation of the inhaling–exhaling rhythm, and know a second fish is entering.

Interspecific sound

Cohabitation of specimens from two species of Carapidae seems to be unusual under natural

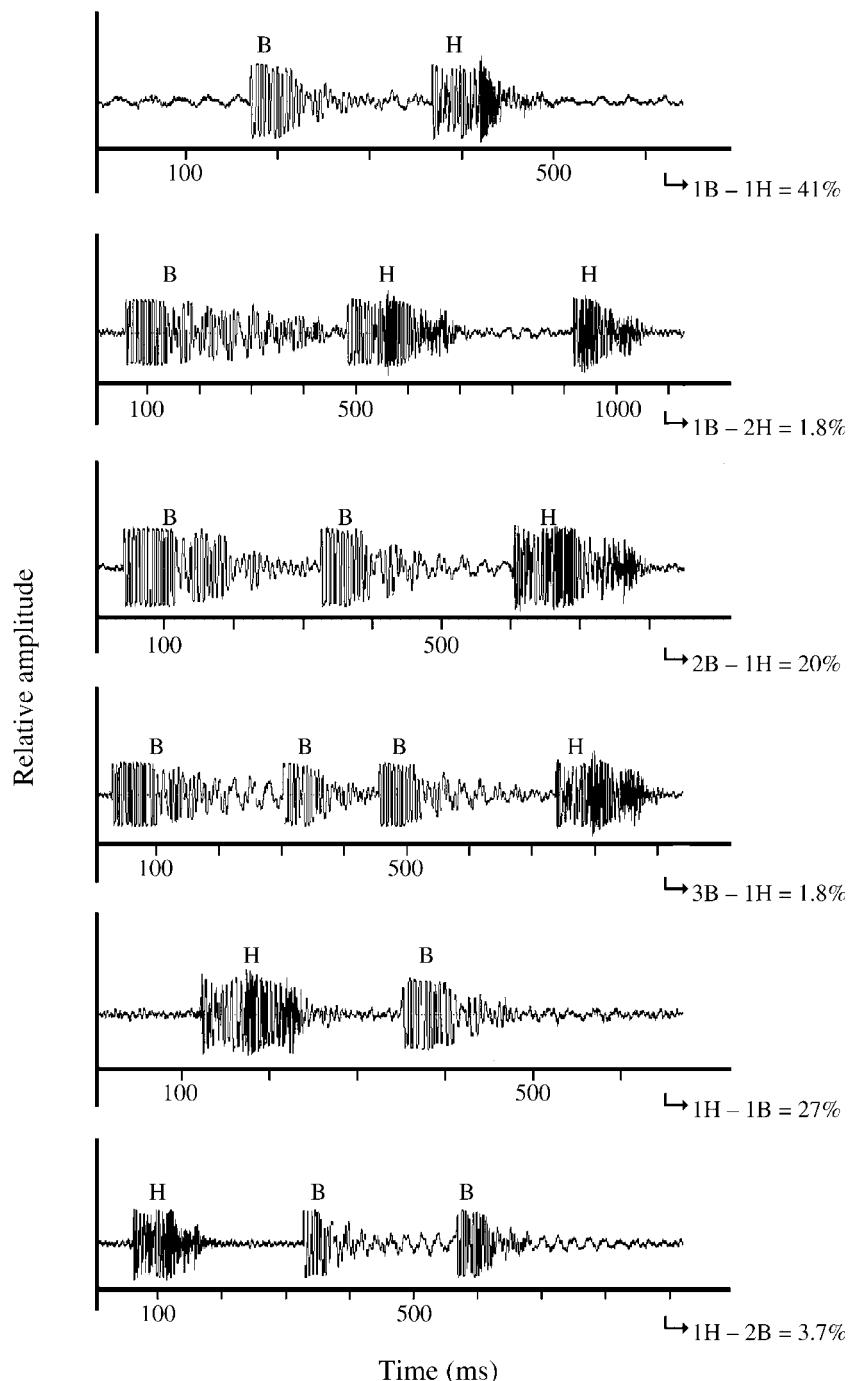


Fig. 4. Oscillograms of the sounds produced during several aggressive interactions between the two Carapini species: *C. boraborensis* (B) and *C. homei* (H) in the same holothurian. The syntax of the sound elements exchanged between individuals of the two species is given with an indication of their frequency percentages.

conditions. Taking into account the rate of infestation (Parmentier and Vandewalle, 2005), these fish species could be in competition. Laboratory experiments over a period of about 10 days have shown that the cohabitation of *C. boraborensis*–*C. homei* pairs in the same holothurian resulted in the expulsion of one fish or in its death, killed inside the host (Parmentier and Vandewalle, 2005). The communication inside the host could be an aggressive behaviour to either provoke the expulsion of one of the two fish or a warning before a direct attack. The sounds produced by the Carapidae resemble strongly (with respect to sound type of a single pulse) the aggression sounds emitted by several species of Pomacentridae (Godwin, '95; Amorim, '96; Mann and Lobel, '98) in which an interspecific confrontation is also associated with shortened sounds. In *Dascyllus albisella*, one and two pulse sounds were often addressed to heterospecific fish, whereas multiple-pulsed sounds were more often made toward conspecifics (Mann and Lobel, '98). In *C. boraborensis* and *C. homei*, the interspecific sounds present a lower number of pulses. It reinforces the hypothesis that aggressive communication by sounds between species has a tendency toward simplification in fish. Fewer pulses towards heterospecifics could indicate that other species are perceived as a lower threat than conspecifics (Dr. M. Fine, pers. comm.).

Intraspecific sound

When an emitted sound is addressed to a congener, the number of pulses is more important and their period is also shorter. It results in a more varied signal that could be related to the motivation to give a clear identification.

In *C. boraborensis*, male and female sounds differ with short pulses for males and longer ones for females. In teleost fish, temporal features within a call, including pulse duration, rate and number, can all be important to a call's communicative value. This is generally used for species recognition rather than sexual identification. However, the number of pulses, as well as pulse intervals are likely to be important for recognition (review in Bass and McKibben, 2003). To the best of our knowledge, this is the first time where the pulse duration has been described as sexually dimorphic. With the potential to resolve pulses shorter than 1.5 msec (Wysocki and Ladich, 2002) or equal to 2 msec (Myrberg et al., '78), many teleost fish are capable of a precise measurement

of the pulse duration. The repetition of these pulses reinforces the quality of the measurement at the scale that the fish can detect (Fay and Coombs, '83; Mann and Lobel, '98).

Sound emissions may give an indication about the relative size of the fish producing the sound. In the weakfish (Connaughton et al., 2000), damselfish (Lobel and Mann, '95) and gouramis (Ladich et al., '92), the pulse duration increases and dominant frequency decreases in larger fish. In *C. boraborensis*, mature females are longer than males (Parmentier and Vandewalle, 2005) and have also the longest pulse duration. However, to prove this would require more experiments with fish of known size. On the other hand, there is also a sexual difference between the male and female swim bladder; the latter does not have a distinct bulb at their posterior end. The functional signification of this bulb is unknown but it should have an influence on the sound characteristics (Parmentier and Vandewalle, 2005).

In the coral reefs where Carapidae live, different species are capable of inhabiting the same host species and the presence of sexual pairs in sea cucumbers was observed in *C. homei*, *C. mourlani*, *C. bermudensis* (Aronson and Mosher, '51; Trott and Trott, '72; Meyer-Rochow, '77; Smith et al., '81) and *C. boraborensis* (Parmentier and Vandewalle, 2005). Thus, our observations suggest a variety of communication functions for which the calls could serve. In a confrontation between species, the emission of a short series of pulses seems sufficient for an aggressive communication between the individuals. In confrontations between conspecifics, a larger number of pulses allowed individuals to identify both status and sex. Sound communication in the Carapidae could occur after an initial olfactory identification or recognition since the fish use, from the start, the appropriate "signal".

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LITERATURE CITED

- Akamatsu T, Okumura T, Novarini N, Yan HY. 2002. Empirical refinements applicable to the recording of fish sounds in small tanks. *J Acoust Soc Am* 112:3073–3082.

- Amorim MCPD. 1996. Sound production in the blue-green damselfish, *Chromis viridis* (Cuvier, 1830) (Pomacentridae). *Bioacoustics* 6:265–272.
- Arnold DC. 1956. A systematic revision of the fishes of the teleost family Carapidae (Percomorphi, Blennioidea), with description of two new species. *Bull Br Mus Nat Hist Zool* 4:247–307.
- Aronson LH, Mosher C. 1951. Observations on the behaviour and ecology of the West Indian pearlfish. *Anat Rec* 111:489.
- Atema J, Holland K, Ikehara W. 1980. Olfactory responses of yellowfin tuna (*Thunnus albacares*) to prey odors: chemical search image. *J Chem Ecol* 6:457–465.
- Aubin T. 1994. Syntana: a software for the synthesis analysis of animal sounds. *Bioacoustics* 6:80–81.
- Barnett C. 1977. Chemical recognition of the mother by young of the cichlid fish *Cichlasoma citrinellum*. *J Chem Ecol* 3:461–466.
- Barnett C. 1981. The role of urine in parent-offspring communication in a cichlid fish. *Z Tierpsychol* 55:173–182.
- Bass AH, McKibben JR. 2003. Neural mechanisms and behaviors for acoustic communication in teleost fish. *Progr Neurobiol* 69:1–26.
- Branch JB. 1969. Observations on the ecology and behaviour of Guam pearlfishes (Carapidae). Master of science in biology, Graduate School of the University of Guam, p 1–251.
- Brown GE, Brown JA. 1993. Social dynamics in salmonid fishes: do kin make better neighbours? *Anim Behav* 45:863–871.
- Chivers DP, Smith RJF. 1993. The role of olfaction in chemosensory-based predator recognition in the fathead minnow, *Pimephales promelas*. *J Chem Ecol* 19:623–633.
- Connaughton MA, Taylor MH, Fine ML. 2000. Effects of fish size and temperature on weakfish disturbance calls: implications for the mechanism of sound generation. *J Exp Biol* 203:1503–1512.
- Crawford JD, Huang X. 1999. Communication signals and sound production mechanisms of mormyrid electric fish. *J Exp Biol* 202:1417–1426.
- Døving KB, Westerberg H, Johnson PB. 1985. Role of olfaction in the behavioral and neural responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Can J Fish Aquat Sci* 42:1658–1667.
- Fay RR, Coombs S. 1983. Neural mechanisms in sound detection and temporal summation. *Hearing Res* 10:69–92.
- Godwin J. 1995. Phylogenetic and habitat influences on mating system structure in the humbug damselfishes (Dascyllus, Pomacentridae). *Bull Mar Sci* 57:637–652.
- Hawkins AD. 1993. Underwater sound and fish behaviour. In: Pitcher TJ, editor. *Behaviour of teleost fishes*. London: Chapman & Hall. p 129–169.
- Hawkins AD, Chapman CJ. 1966. Underwater sounds of the haddock, *Melanogrammus aeglefinus*. *J Mar Biol Ass UK* 46:241–247.
- Hawkins AD, Myrberg AA. 1983. Hearing and sound communication underwater. In: Lewis B, editor. *Bioacoustics, a comparative approach*. London: Academic Press. p 347–405.
- Hawkins AD, Rasmussen KJ. 1978. The calls of gadoid fish. *J Mar Biol Ass UK* 58:891–911.
- Kenyon TN. 1994. The significance of sound interception to males of the bicolor damselfish, *Pomacentrus partitus*, during courtship. *Environ Biol Fishes* 40:391–405.
- Kleerekoper H. 1982. The role of olfaction in the orientation of fishes. In: Toshiaki JH, editor. *Chemoreception in fishes*, Amsterdam, Oxford, New York: Elsevier Scientific Publishing Company. Developments in Aquaculture and Fisheries Science 8:201–225.
- Ladich F. 1997. Comparative analysis of swimbladder (drumming) and pectoral (stridulation) sounds in three families of catfishes. *Bioacoustics* 8:185–208.
- Ladich F, Fine ML. 1994. Localization of swimbladder and pectoral motoneurons (sonic and hovering) in the croaking gourami *Trichopsis vittatus*. *Brain Behav Evol* 39:1–7.
- Ladich F, Bischof C, Schleinzner G, Fuchs A. 1992. Intra and interspecific differences in agonistic vocalization in croaking gouramis (Genus: *Trichopsis*, Anabantoidei, Teleostei). *Bioacoustics* 4:131–141.
- Lengagne T, Aubin T, Jouventin P, Lauga J. 2000. Perceptual salience of individually distinctive features in the calls of adult king penguins. *J Acoust Soc Am* 107:508–516.
- Lobel PS, Mann DA. 1995. Spawning sounds of the domino damselfish, *Dascyllus albisella* (Pomacentridae), and the relationship to male size. *Bioacoustics* 6:187–198.
- Mann DA, Lobel PS. 1998. Acoustic behavior of the damselfish *Dascyllus albisella*: behavioral and geographic variation. *Environ Biol Fishes* 51:421–428.
- Mann DA, Bowers-Altman J, Rountree RA. 1997. Sounds produced by the striped cusk-eel *Ophidion marginatum* (Ophidiidae) during courtship and spawning. *Copeia* 1997:610–612.
- Markle DF, Olney JE. 1990. Systematics of the Pearlfish (Pisces: Carapidae). *Bull Mar Sci* 47:269–410.
- McKaye KR, Barlow GW. 1976. Chemical recognition of young by the Midas cichlid, *Cichlasoma citrinellum*. *Copeia* 1976:276–282.
- Meyer-Rochow WB. 1977. Comparison between 15 *Carapus mourlani* in a single holothurian and 19 *Carapus mourlani* from starfish. *Copeia* 1977:582–585.
- Moulton JM. 1963. Acoustic behaviour of fishes. In: Busnel RG, editor. *Acoustic behaviour of animals*. Amsterdam: Elsevier Publishing Company. p 655–693.
- Myrberg AA, Spanier E, Ha SJ. 1978. Temporal patterning in acoustical communication. In: Reese E, Lighter F, editors. *Contrast in behavior*. New York: Wiley. p 139–172.
- Okumura T, Akamatsu T, Yan HY. 2002. Analyses of small tank acoustics: empirical and theoretical approaches. *Bioacoustics* 12:330–332.
- Parmentier E, Das K. 2004. Commensal vs parasitic relationship between Carapini fish and their host: some further insight through $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements. *J Exp Mar Biol Ecol* 310:47–58.
- Parmentier E, Vandewalle P. 2003. Morphological adaptations of pearlfish (Carapidae) to their various habitats. In: Val AL, Kapoor BG, editors. *Fish adaptations*. India: Oxford & IBH. p 261–276.
- Parmentier E, Vandewalle P. 2005. Further insight on carapid-holothuroid relationships. *Mar Biol* 146:455–465.
- Parmentier E, Castillo G, Chardon M, Vandewalle P. 2000. Phylogenetic analysis of the pearlfish tribe Carapini (Pisces: Carapidae). *Acta Zool* 81:293–306.
- Parmentier E, Lagardere F, Vandewalle P. 2002. Relationships between inner ear and sagitta growth during ontogenesis of three Carapini species and consequences of life-history events on the otolith microstructure. *Mar Biol* 141:491–501.
- Parmentier E, Gennotte V, Focant B, Goffinet G, Vandewalle P. 2003a. Characterisation of the primary sonic muscles in

- Carapus acus* (Carapidae): a multidisciplinary approach. Proc R Soc Lond B 270:2301–2308.
- Parmentier E, Vandewalle P, Lagardère JP. 2003b. Sound-producing mechanisms and recording in *Carapini* species (Teleostei, Pisces). J Comp Physiol A 189:283–292.
- Parvulescu, A. 1964. Problems of propagation and processing. In: Tavalga WN, editor. Marine bio-acoustics. Oxford: Pergamon Press. p 87–100.
- Shen SC, Yeh HS. 1987. Study on Pearlfishes (Ophidiiformes: Carapidae) of Taiwan. Taiwan Mus 40:45–56.
- Smith CL. 1964. Some pearlfishes from Guam, with notes on their ecology. Pacific Sci 18:34–40.
- Smith CL, Tyler JC, Feinberg MN. 1981. Population ecology and biology of the pearlfish (*Carapus bermudensis*) in the lagoon at Bimini, Bahamas. Bull Mar Sci 3: 876–902.
- Tavalga WN. 1964. Sonic characteristics and mechanisms in marine fishes. In: Tavalga, WN, editor. Marine bio-acoustics. Oxford: Pergamon Press. p 195–211.
- Trott LB. 1970. Contribution of the biology of Carapid fishes (Paracanthopterygian: Gadiformes). Univ Calif Publ Zool 89:1–41.
- Trott LB. 1981. A general review of pearlfishes (Pisces, Carapidae). Bull Mar Biol 31:623–629.
- Trott LB, Trott EB. 1972. Pearlfishes (Carapidae: Gadiforme) collected from Puerto Galera, Minobra, Philippines. Copeia 1972:839–843.
- VandenSpiegel D, Jangoux M. 1989. La symbiose entre poissons Carapidae et holothuries autour de l'île de Laing (Mer de Bismarck, Papouasie Nouvelle Guinée). Indo-Malayan Zool 6:223–228.
- Van Meter VB, Ache BW. 1974. Host location by the pearlfish *Carapus bermudensis*. Mar Biol 26:379–383.
- Westerberg H. 1984. The orientation of fish and the vertical stratification at fine and micro-structure scales. In: McCleave JD, Arnold GP, Dodson JJ, Neill WH, editors. Mechanisms of migration in fishes. New York: Plenum Press. p 179–203.
- Winn HE. 1964. The biological significance of fish sounds. In: Tavalga WN, editor. Marine bio-acoustics. Oxford: Pergamon Press. p 213–231.
- Wysocki LE, Ladich F. 2002. Can fish resolve temporal characteristics of sounds? New insights using auditory brainstem responses. Hearing Res 169:36–46.