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Sexual dimorphism in the sonic system and otolith morphology of *Neobythites gilli* (Ophidiiformes)

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Abstract

Although males and females of many sound-producing fish species may show differences at the level of the sonic apparatus, otoliths are usually species specific having intraspecific variation only if exposed to different environmental condition or in relation with the fish size. This study reports sexual dimorphism at the level of both otolith shape and sonic apparatus in the ophidiid *Neobythites gilli*. As it is the case in other *Neobythites* species, sound-producing apparatus is better developed in males. Due to their way of life in darker or deep waters, differences at the level of the sound-producing apparatus support more constraints related to acoustic communication for sex recognition or mate localization. Otolith modifications concern only *Neobythites* male specimens, whereas otolith of females are virtually unchanged when compared to sister species without sexual dimorphism, meaning this feature would not be related to sexually induced differences in calling. Differences between the otoliths of males and females could therefore be related to their way of life.

Introduction

Interspecific morphological differences include both size and shape of the fish otoliths (Lombarte & Cruz, 2007). Some studies suggest that there is a relationship between otolith features and hearing ability but others support it is related to habitat (Parmentier, Vandewalle & Lagardère, 2001). Within species, otolith can show differences related to the fish size but not between conspecifics having the same size if exposed to the same environmental factors, meaning they can be reliable tools to study fish diversity (Tuset *et al.*, 2016).

Ophidiiform fishes possess at least three noteworthy characteristics. Firstly, most of the species live at a depth below the shelf break in benthopelagic zones (Nielsen *et al.*, 1999), that is, in a dark environment. However, certain groups are specialized to murky habitats in shallow water. Although the biology is poorly known for all species, it seems that species that live in shallow water favour a life in the dark, since they are mostly active at night. This is the case, for example, for certain ophidiid species that hide in the sand during the day (Mann, Bowers-Altman & Rountree, 1997; Parmentier *et al.*, 2010; Kéver *et al.*, 2016), for carapid fishes that mostly live inside different invertebrate hosts during the day (Parmentier & Vandewalle, 2003, 2005), or for dinematichthyid species that are cave dwelling, often in reef environments (Wourms & Bayne, 1973; Møller & Schwarzhans, 2008). The second important characteristic is related to way of life. Ophidiifom are known for their ability to produce sounds, a feature that is useful to identify or find conspecifics in dark environments. Because many species live in deep water, sound recordings are difficult to make and apply to only a few species from the carapid (Parmentier, Vandewalle & Lagardère, 2003; Kéver *et al.*, 2014d) and ophidiid genera (Rountree & Bowers-Altman, 2002; Kéver *et al.*, 2014a). These studies have also underlined the required morphological adaptations related to this way of communication: Ophidiiforms have a high diversity of sound-producing mechanisms (Howes, 1992; Parmentier *et al.*, 2006a; Nguyen *et al.*, 2008; Fine *et al.*, 2018).

The third intriguing characteristic concerns the sagittae otoliths, which are usually thick and large (Schwarzhans & Aguilera, 2016). In many species, they are so important that the whole brain is concentrated at the front of the braincase, and only a thin myelencephalon extends through the otic cavity (Fine, Horn & Cox, 1987; Parmentier *et al.*, 2001; Parmentier, Lagardère & Vandewalle, 2002b).

Within the genus *Neobythites* (Ophidiidae), some species are quite exceptional, since they exhibit sexual dimorphism in the morphology of the sagittae. In comparison with females, male otoliths are usually thicker, and the inner face is much more convex and smoother. Sulcus and colliculi are also more pronounced in females (Schwarzhans, 1994). Sexual dimorphism was recently shown in sonic muscles of *Neobythites longipes* (Smith and Radcliffe, 1913) and *N. unimaculatus* (Kamohara, 1938) (Ali, Mok & Fine, 2016). There is no apparent difference at the level of the otoliths in *Neobythites longipes* (Schwarzhans, 1994), whereas there is a clear difference in *N. unimaculatus.*

Neobythites gilli (Goode and Bean 1885) has been reported in the West Atlantic, between 60 and 230 m (Nielsen, 1999, 2002), and is also known for sexual dimorphism in otolith morphology (Schwarzhans, 1994). These fishes possess two distinct ocelli in the dorsal fin (Nielsen, Uiblein & Mincarone, 2009), meaning that they are probably not progressing into greater depth zones, because at that water depth ocelli can serve in social communication or as an anti-predator signal (Uiblein, 1995; Uiblein, Ott & Stachowitsch, 1996). It is not possible to distinguish sex externally in this species (Nielsen, 1999).

This study aims to describe and compare the otoliths and sound-producing apparatus between males and females of *Neobythites gilli* to examine whether both features can be related and provide explanation related to the species way of life.

Materials and methods

The material examined belongs to the Florida Museum of Natural History (Gainseville, USA). Six *Neobythites gilli* specimens (UF 118741) from the Gulf of Mexico have been examined. They were collected by the RV Oregon II at a depth of 114 m in June 1985. The total lengths were between 121 and 142 mm. Two additional specimens (UF 71392) from the Gulf of Mexico, collected by the RV Tursiops at a depth of 186 m in September 1970 and having a total length of 98 mm and 77 mm were also examined.

The axial skeletons of four specimens from the lot UF 118741 were investigated with computed tomography (μCT) imaging systems. Structural images of otoliths and sound-producing apparatus were obtained using the X-ray Computed Tomography scanner *eXplore 120 microCT* (TriFoil Imaging, USA). The physical characteristics of this scanner have been described previously (Bahri *et al.*, 2010; Bretin *et al.*, 2013). This system acquires a set of images of samples with a high resolution (100 μm) that can be reconstructed to a three-dimensional volume. We used a customized protocol 'Fast-scan 360' (70 kV, 0.512 mAs, 360 views over 360°, continuous rotation). All CT data were reconstructed using Feldkamp's filtered back-projection algorithm with a cut-off at the Nyquist frequency and an isotropic voxel size of 100 μm. Three-dimensional processing and rendering followed the protocols of Boistel *et al.* (Boistel *et al.*, 2011) and Zanette *et al.* (Zanette *et al.*, 2013) after semiautomatic segmentation of different skeletal units (cranial, 12 first vertebrae and otolith) using 'Convert Image Type', converted into 8-bit voxels to obtain a mask and subsequently having used ImageJ (Abramoff, Magalhaes & Ram, 2014) for masking the anatomical structures we were not interested in, for each skeletal unit. Direct volume rendering was used for visualizing the subset of selected voxels of cranial, otolith and post cranial elements as well as gut content, in 8.0.1 (FEI, VSG, SAS, Merignac, France).

All the eight specimens were then dissected and the morphology of the sonic apparatus was examined with a Wild M10 (Leica) binocular microscope equipped with a camera lucida.

The terminology used for the description of the anatomy of the sound-producing apparatus follows the study on *Ophidion rochei* and *Ophidion barbatum* (Parmentier *et al.*, 2006a, 2010).

Results

Skeleton

The six anterior vertebrae possess epineurals that articulate with the vertebral bodies (Fig. 1). Subsequent vertebrae possess lateral parapophyses that become progressively longer and wider. Vertebral bodies IV to VII are ventrally enlarged, most probably to consolidate the attachment of the swimbladder. Epineurals from vertebrae IV to VI are rod-like, whereas epineurals from vertebrae I to III possess different shapes. The first epineural, called the 'wing-like process', is plate-like. It is oriented horizontally, but its axis tends to rotate distally in the vertical plane. The distal tip is connected to the anterior part of the swimbladder by connective tissue. The second epineural is oriented in the vertical plane and possesses a rounded horizontal plate at the level of the distal tip. This plate is intimately connected to the swimbladder. The third epineural is proximally wider and, distally, forms a rod.

We did not find many differences between males and females at the level of the skeleton of the sound-producing apparatus, except that males show rounded tips at the level of the second epineurals (Fig. 1).

Swimbladder

The swimbladder consists of a single elongated chamber that tapers posteriorly. It lies below the second through 12th vertebrae. It is fused to the ventral surfaces of vertebrae III through XI and also attaches firmly to the ribs, dorsally. The bladder is divided into three regions. The anterior region is short, and is the attachment site for the sonic muscles and the distal tips of the second epineurals. The second region, termed the 'swimbladder fenestra', is thin and transparent because it is deprived of the tunica externa. The fenestra covers the swimbladder dorsally and tapers laterally around the bladder sides. The fenestra is more flexible than other bladder tissue, which permits sonic muscle to displace the anterior wall of the anterior region. Dorsally, the region just caudal to the posterior edge of the fenestra attaches to epineurals rib three and correspond to the third region. This last region is the biggest, and is tightly coupled and firmly connected to the vertebral column.

Muscles

Four pairs of sonic muscles are involved in the sound-producing system (Fig. 2). They correspond, in fact, to two major groups, ventral and intermediate, that are each divided into two bundles, lateral and medial. Both ventral sonic muscles

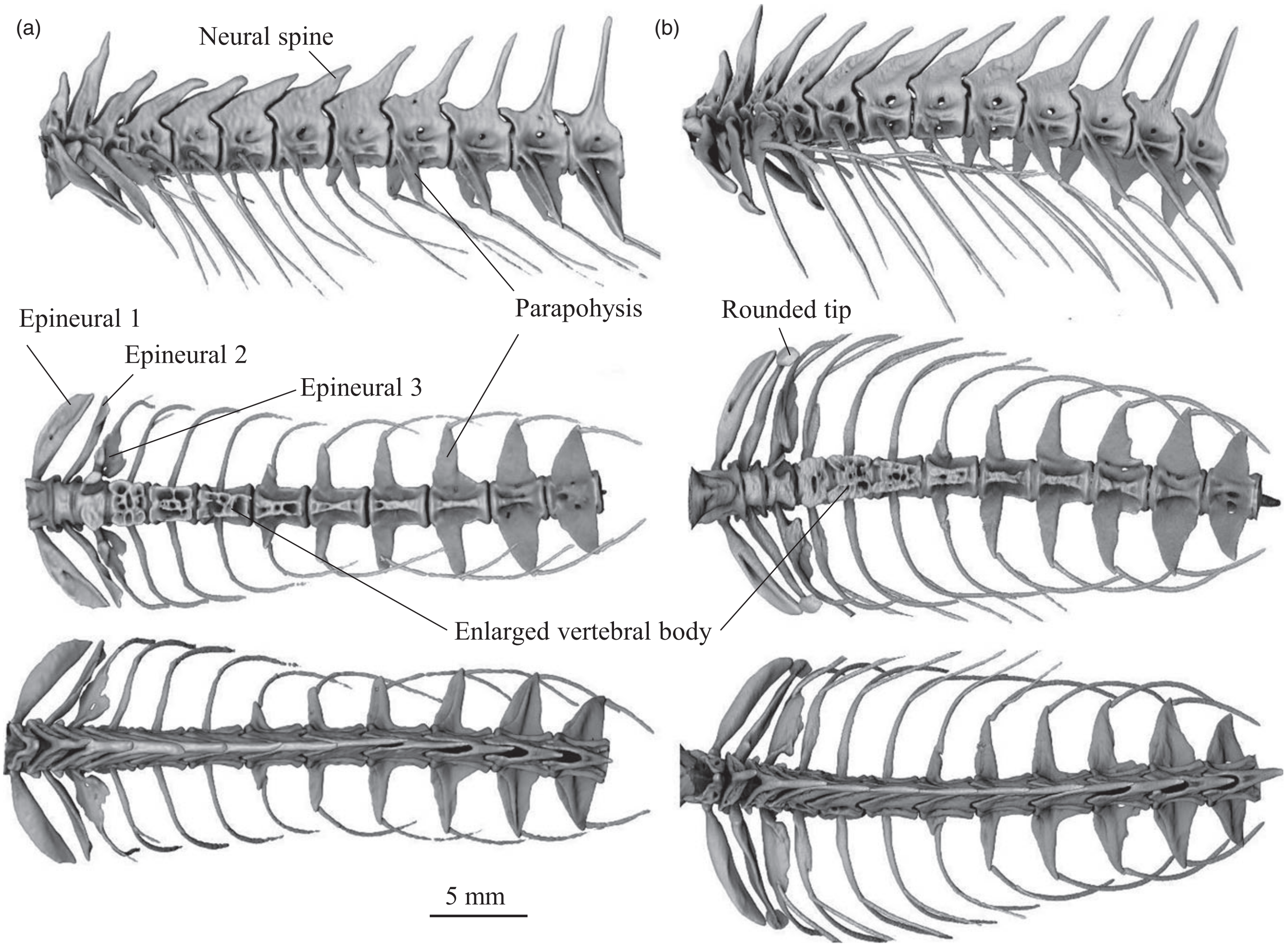

Figure 1 Left lateral, ventral and dorsal view of the anterior part of the vertebral column in female (a) and (b) male of *Neobythites gilli.*

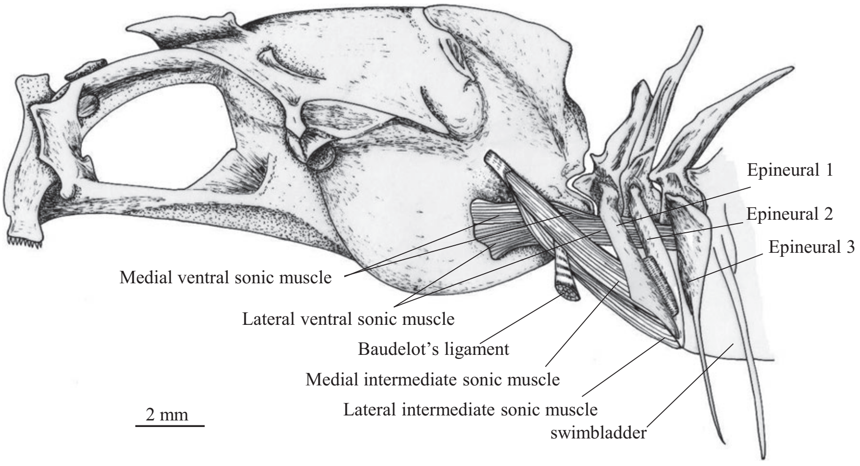

Figure 2 Left lateral view of the skull and sound-producing muscles in male of *Neobythites gilli.*

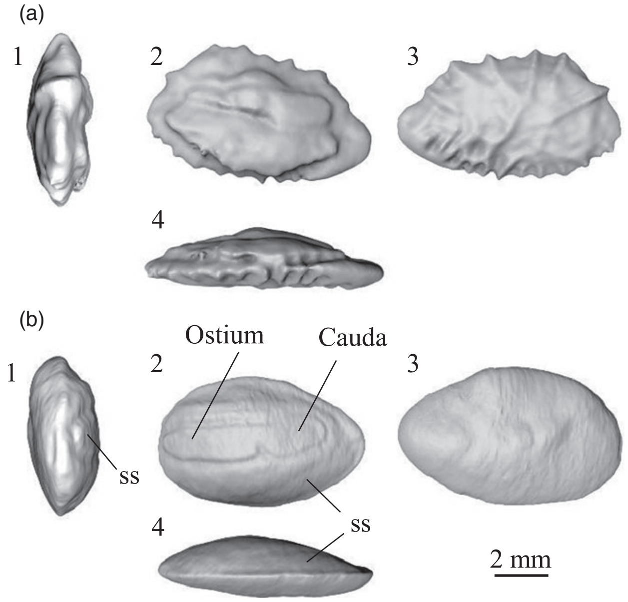

Figure 3 Frontal (1), medial (2), lateral (3) and dorsal (4) view of the left sagitta in female (a) and male (b) of *Neobythithes gilli*.

(VSMs) originate on the back of the otic region (basioccipital, the intercalarium and the exoccipital) and insert on the anterior region of the bladder in front of the swimbladder fenestra, the medial bundle inserting above the lateral bundle. Both bundles are separated by the Baudelot's ligament. Both intermediate muscles originate on the posterior part of the skull, above the VSMs, on the exoccipital. The medial intermediate muscle goes over the Baudelot's ligament and inserts on the distal tip of the first epineurals. The lateral intermediate muscle goes under the Baudelot's ligament and inserts on both the distal tips of both first and second epineurals.

The VSMs are much more developed in males than in females. In the female, both VSMs are so thin that their efficacy is doubtful. We were unable to identify sexual dimorphism at the level of the intermediate muscles.

Otoliths

The otoliths of *N. gilli* have a rather typical ophidiid-type morphology (Schwarzhans, 1994). In lateral view, otoliths are oval to elongate, about 1.6 to 1.8 times longer than they are high. The ventral rim is gently curving and usually quite shallow, but the dorsal rim exhibits more or less marked angles (smoother in the otoliths of males). It is characterized by a shallow, straight sulcus, with the ostium being about two times as long as the cauda, but having the same height.

Male otoliths are all larger and thicker than otoliths of females in fishes of comparable size (Fig. 3). More precisely, the male otolith volume is twice the female otolith volume. In males, the otolith inner (medial) face is much more convex and smoother than in females, which show ornamentations of different sizes.

Discussion

Sexual dimorphism in the sound-production apparatus of teleosts can occur in different ways. The sonic mechanism can be present only in the males (Hill, Fine & Musick, 1987; Tellechea & Norbis, 2012), some components of the sound-producing apparatus can have different sizes (Fine, Burns & Harris, 1990), or the sound-producing apparatus can show structural differences between males and females (Casadevall *et al.*, 1996; Kéver *et al.*, 2012, 2014b). Although in many Ophidiiforms it is not possible to externally distinguish males from females, there is growing evidence that sexual dimorphism in the sound-producing apparatus is important in this taxa. This has been shown in some Carapinae (Parmentier & Vandewalle, 2005; Kéver *et al.*, 2014d), Ophidiidae (Courtenay, 1971; Casadevall *et al.*, 1996; Nguyen *et al.*, 2008; Kéver *et al.*, 2012) and Neobythitinae (Carter & Musick, 1985; Ali *et al.*, 2016; Fine *et al.*, 2018). Due to their way of life in darker or deep waters, the environmental pressures on external features is probably more limited, which may help to explain the lack of differences between male and female phenotypes. Having important differences at the level of the sound-producing apparatus supports more constraints related to acoustic communication for sex recognition and mate localization.

In *N. gilli*, the obvious characteristic related to sound production concerns the size of the ventral bundles, which are much thinner in females than in males. The same kind of difference in muscle size between males and females was also recently reported in the sonic ventral muscles of sister taxa *N. unimaculatus* and *N. longipes* (Ali *et al.*, 2016). Moreover, this sonic dimorphism in muscle size (weight) was already shown in different Ophidiiform species (Fine *et al.*, 2007, 2018; Parmentier *et al.*, 2010; Kéver *et al.*, 2012). This difference is well marked in the ventral muscle, most probably because this muscle provides the power required for sound production, whereas the intermediate muscle appears to be confined to a preparation or support function (Parmentier *et al.*, 2006b, 2010; Kéver *et al.*, 2014b). In *N. gilli* females, however, sonic ventral muscles are so thin that their functional role is questionable. As in many other Ophidiiformes, knowledge concerning sound-producing apparatus and sexual dimorphism suggests that sound production is mainly developed in males, which use their calls to attract females (Casadevall *et al.*, 1996; Kéver *et al.*, 2014b; Ali *et al.*, 2016).

Beside the sonic system dimorphism, different *Neobythites* species, including *N. gilli*, also possess a sexual dimorphism in otolith morphology (Schwarzhans, 1994). The first idea would be to relate the hearing system with the sonic system, because the sagittal otolith is involved in the auditory process, since motion of the otolith relative to the sensory hair cells produces a shearing of the ciliary bundles and a corresponding physiological response from the sensory hair cells (Popper *et al.*, 1988).

This means that otoliths of different sizes (and masses) could respond to different frequencies relative to the sensory epithelium (Popper, Ramcharitar & Campana, 2005). If otoliths of females were larger, this might indicate that hearing ability is better, which could correspond to the fact that males have better developed sound-producing apparatus. In Ophidiiforms, the first experimental results showed that the hearing capacities of a fish species could not be predicted based only on sagitta size (Kéver *et al.*, 2014c). Shape differences were found in otoliths between cave and surface populations of the mollies *Poecilia Mexicana*, but this did not affect auditory sensitivity or acoustic behaviour (Schulz-Mirbach *et al.*, 2010).

Otoliths have been described from many different species and they are usually regarded as species specific, but without differences between males and females – meaning that the morphological dimorphism of sagittal otoliths in *Neobythtites* is exceptional. In other teleosts, studies have reported better hearing abilities during spawning season, but this was related to sensitive cells and concentrations in hormones (Maruska, Ung & Fernald, 2012; Zeyl, Love & Higgs, 2013), not to otolith shape or size. Many species whose sexes have different calling abilities do not show differences in the otolith. Male and female of different sciaenid species, for example, seem to have the same kind of otolith (Schwarzhans, 1993; Aguilera, Schwarzhans & Bearez, 2016) although in many cases only the males are able to make sounds (Ramcharitar, Gannon & Popper, 2006). In the Gadidae *Gadus morhua*, drumming muscles of males are larger than those of females (Rowe & Hutchings, 2004), supporting differences in sound production between sexes. While both male and female *G. morhua* are capable of producing sound (Brawn, 1961; Hawkins & Rasmussen, 1978; Rowe & Hutchings, 2006), only males produce grunts during the spawning season. However, sagitta shapes were found to be mainly identical between males and females. More precisely, differences in otolith shape, where they occur, appear to be related to growth rate differences (Campana & Casselman, 1993; Cardinale *et al.*, 2004; Bose, Adragna & Balshine, 2017), not to the sex.

Of course, it could be argued that both males and females must be able to detect sounds, even if females cannot produce sounds. In *Neobythtites*, all species studied so far (*N. gilli*, *N. unimaculatus* and *N. longipes*) show sexual dimorphism of the sound-producing apparatus, but sexual dimorphism in otolith morphology is only found in some species (Schwarzhans, 1994), that is, two of the three species above. Therefore, we suggest that the observed sexual dimorphism of otolith morphology in certain *Neobythites* species is unlikely related to sexually induced differences in hearing and calling.

Otoliths also perform vestibular functions that could also affect otolith shape and size. In carapids (Ophidiiformes), the thickest and heaviest sagittae are found in demersal or symbiotic species, whereas thin otoliths are found in free pelagic species (Parmentier *et al.*, 2001; Parmentier, Chardon & Vandewalle, 2002a). In Nototheniidae, the benthic feeders had the largest sagittae in relation to body size, and pelagic species had smaller and rounder shaped sagittae than benthic species (Lombarte *et al.*, 2010). In different *Neobythites* species that show a sexual dimorphism at the level of the otoliths (*N. analis*, *N. fasciatus*, *N. macrops*, *N. marginatus*, *N. multistriatus*), the dimorphism appears to affect otolith in a similar way (Schwarzhans, 1994; Schwarzhans & Aguilera, 2016). Modifications of the sagittae only concern male specimens, whereas otolith of females are virtually unchanged since their shape corresponds to sagittae from male and female of species without sexual dimorphism (e.g. *N. longipes*, *N. malayanus*, *N. nigromaculatus* or *N. trifilis*) (Schwarzhans, 1994; Schwarzhans & Aguilera, 2016). Differences between the otoliths of males and females could therefore be related to their way of life, metabolism (Grønkjær, 2016) or a difference in growth rate (Cardinale *et al.*, 2004; Hüssy, 2008).

Conclusion

Sexual dimorphism is found in both otolith shape and sonic apparatus in *Neobythites gilli* but not at the level of the external phenotype. Sound-producing apparatus is better developed in males, suggesting that they are more active callers than females for spawning activities. Comparison with sister species, that do also have dimorphism of the sonic apparatus but not at the level of the otoliths, support otolith modifications concerning only *Neobythites* male specimens. Differences between the otoliths of males and females could be related to the way of life and not to hearing abilities.

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References

Abramoff, M.D., Magalhaes, P.J. & Ram, S.J. (2014). Image processing with ImageJ. *Biophoton Int* **11**, 36–42.

Aguilera, O., Schwarzhans, W. & Bearez, P. (2016). Otoliths of the Sciaenidae from the Neogene of tropical America. *Palaeo Ichthyol.* **14**, 7–90.

Ali, H.A., Mok, H.-K. & Fine, M.L. (2016). Development and sexual dimorphism of the sonic system in deep sea neobythitine fishes: the upper continental slope. *Deep Sea Res Part I Oceanogr. Res. Pap.* **115**, 293–308.

Bahri, M.A., Warnock, G., Plenevaux, A., Choquet, P., Constantinesco, A., Salmon, E., Luxen, A. & Seret, A. (2010). Performance evaluation of the General Electric eXplore CT 120 micro-CT using the vmCT phantom. *Nucl. Instr. Meth Phys. Res.* **648**, 181–185.

Boistel, R., Herrel, A., Lebrun, R., Daghfous, G., Tafforeau, P., Losos, J.B. & Vanhooydonck, B. (2011). Shake rattle and roll: the bony Labyrinth and aerial descent in squamates. *Integr. Comp. Biol.* **51**, 957–968.

Bose, A.P.H., Adragna, J.B. & Balshine, S. (2017). Otolith morphology varies between populations, sexes and male alternative reproductive tactics in a vocal toadfish *Porichthys notatus*. *J. Fish Biol.* **90**, 311–325.

Brawn, V.M. (1961). Aggressive behaviour in the cod (*Gadus callarias* L.). *Behaviour* **18**, 108–147.

Bretin, F., Warnock, G., Luxen, A., Plenevaux, A., Seret, A. & Bahri, M.A. (2013). Performance evaluation and X-ray dose quantification for various scanning protocols of the GE eXplore 120 micro-CT. *IEEE Trans. Nucl. Sci.* **60**, 3235–3241.

Campana, S.E. & Casselman, J.M. (1993). Stock discrimination using otolith shape analysis. *Can. J. Fish Aquat. Sci.* **50**, 1062–1083.

Cardinale, M., Doering-Arjes, P., Kastowsky, M. & Mosegaard, H. (2004). Effects of sex, stock, and environment on the shape of known-age Atlantic cod (*Gadus morhua*) otoliths. *Can. J. Fish Aquat. Sci.* **61**, 157–167.

Carter, J.H. & Musick, J.A. (1985). Sexual dimorphism in the deep-sea fish *Barathrodemus manatinus* (Ophidiidae). *Copeia* **1**, 69–73.

Casadevall, M., Matallanas, J., Carrasson, M. & Munoz, M. (1996). Morphometric, meristic and anatomical differences between Ophidion barbatum L., 1758 and O. rochei Muller, 1845 (Pisces, Ophidiidae). *Publ. Espec. Inst. Esp. Oceanogr.* **21**, 45–61.

Courtenay, W.R.J. (1971). Sexual dimorphism of the sound producing mechanism of the striped cusk eel *Rissola marginata* (Pisces: Ophidiidae). *Copeia* **2**, 259–268.

Fine, M.L., Horn, M.H. & Cox, B. (1987). *Acanthonus armatus*, a deep-sea teleost fish with a minute brain and large ears. *Proc. R. Soc. Lond. B Biol. Sci.* **230**, 257–265.

Fine, M.L., Burns, N.M. & Harris, T.M. (1990). Ontogeny and sexual dimorphism of sonic muscle in the oyster toadfish. *Can. J. Zool.* **68**, 1374–1381.

Fine, M.L., Lin, H., Nguyen, B.B., Rountree, R.A., Cameron, T.M. & Parmentier, E. (2007). Functional morphology of the sonic apparatus in the fawn cusk-eel *Lepophidium profundorum* (Gill, 1863). *J. Morphol.* **268**, 953–966.

Fine, M.L., Ali, H.A., Nguyen, T.K., Mok, H.-K. & Parmentier, É. (2018). Development and sexual dimorphism of the sonic system in three deep-sea neobythitine fishes: mid and lower continental slope. *Deep Sea Res Part I Oceanogr. Res. Pap.* **131**, 41–53.

Grønkjær, P. (2016). Otoliths as individual indicators: a reappraisal of the link between fish physiology and otolith characteristics. *Mar. Freshw. Res.* **67**, 881–888.

Hawkins, A.D. & Rasmussen, K.J. (1978). The call of gadoid fish. *J. Mar. Biol. Assoc. U.K.* **58**, 891–911.

Hill, G.L., Fine, M.L. & Musick, J.A. (1987). Ontogeny of the sexually dimorphic sonic muscle in three sciaenid species. *Copeia* **3**, 708–713.

Howes, G.J. (1992). Notes on the anatomy and classification of Ophidiiform fishes with particular reference to the abyssal genus *Acanthonus Gunther*, 1878. *Bull Br. Mus. Nat. Hist.* **58**, 95–131.

Hüssy, K. (2008). Otolith shape in juvenile cod (*Gadus morhua*): ontogenetic and environmental effects. *J. Exp. Mar. Bio. Ecol.* **364**, 35–41.

Kéver, L., Boyle, K.S., Dragičević, B., Dulčić, J., Casadevall, M. & Parmentier, E. (2012). Sexual dimorphism of sonic apparatus and extreme intersexual variation of sounds in *Ophidion rochei* (Ophidiidae): first evidence of a tight relationship between morphology and sound characteristics in Ophidiidae. *Front. Zool.* **9**, 34.

Kéver, L., Boyle, K.S., Bolen, G., Dragičević, B., Dulčić, J. & Parmentier, E. (2014a). Modifications in call characteristics and sonic apparatus morphology during puberty in *Ophidion rochei* (Actinopterygii: Ophidiidae). *J. Morphol.* **275**, 650–660.

Kéver, L., Boyle, K.S., Dragičević, B., Dulčić, J. & Parmentier, E. (2014b). A superfast muscle in the complex sonic apparatus of *Ophidion rochei* (Ophidiiformes): histological and physiological approaches. *J. Exp. Biol.* **217**, 3432–3440.

Kéver, L., Colleye, O., Herrel, A., Romans, P. & Parmentier, E. (2014c). Hearing capacities and otolith size in two ophidiiform species (*Ophidion rochei* and *Carapus acus*). *J. Exp. Biol.* **217**, 2517–2525.

Kéver, L., Colleye, O., Lugli, M., Lecchini, D., Lerouvreur, F., Herrel, A. & Parmentier, E. (2014d). Sound production in *Onuxodon fowleri* (Carapidae) and its amplification by the host shell. *J. Exp. Biol.* **217**, 4283–4294.

Kéver, L., Lejeune, P., Michel, L.N. & Parmentier, E. (2016). Passive acoustic recording of *Ophidion rochei* calling activity in Calvi Bay (France). *Mar. Ecol.* **37**, 1315–1324.

Lombarte, A. & Cruz, A. (2007). Otolith size trends in marine fish communities from different depth strata. *J. Fish Biol.* **71**, 53–76.

Lombarte, A., Palmer, M., Matallanas, J., Gómez-Zurita, J. & Morales-Nin, B. (2010). Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nototheniidae. *Environ. Biol. Fishes* **89**, 607–618.

Mann, D.A., Bowers-Altman, J. & Rountree, R.A. (1997). Sounds produced by the striped cusk-eel *Ophidion marginatum* (Ophidiidae) during courtship and spawning. *Copeia* **3**, 610–612.

Maruska, K.P., Ung, U.S. & Fernald, R.D. (2012). The African cichlid fish *Astatotilapia burtoni* uses acoustic communication for reproduction: sound production, hearing, and behavioral significance. *PLoS ONE* **7**, 1–13.

Møller, P.R. & Schwarzhans, W. (2008). Review of the Dinematichthyini (Teleostei, Bythitidae) of the Indo-west Pacific, Part IV. *Dinematichthys* and two new genera with descriptions of nine new species. *The Beagle* **24**, 87–146.

Nguyen, T.K., Lin, H., Parmentier, E. & Fine, M.L. (2008). Seasonal variation in sonic muscles in the fawn cusk-eel *Lepophidium profundorum*. *Biol. Lett.* **4**, 707–710.

Nielsen, J.G. (1999). A review of the genus *Neobythites* (Teleostei, Ophidiidae) in the Atlantic, with three new species. *Bull. Mar. Sci.* **65**, 335–372.

Nielsen, J.G. (2002). Revision of the Indo-Pacific species of *Neobythites* (Teleostei, Ophidiidae), with 15 new species. *Galathea Rep.* **19**, 5–105.

Nielsen, J.G., Cohen, D.M., Markle, D.F. and Robins, C.R. (1999). *FAO species catalogue. Ophidiiform fishes of the* *world (Order Ophidiiformes): an annotated and illustrated catalogue of pearlfishes, cusk-eels, brotulas and other ophidiiform fishes known to date*: 178. Rome: FAO. Fish. Synopsis No. 125. 18.

Nielsen, J.G., Uiblein, F. & Mincarone, M.M. (2009). Ocellus bearing *Neobythites* species (Teleostei: Ophidiidae) from the West Atlantic with description of a new species. *Zootaxa* **2228**, 57–68.

Parmentier, E. & Vandewalle, P. (2003). Morphological adaptations of Pearlfish (Carapidae) to their various Habitats. In *Fish adaptations: 261–276*. Val, A.L. & Kapoor, B.G. (Eds). India: Oxford & IBH.

Parmentier, E. & Vandewalle, P. (2005). Further insight on carapid-holothuroid relationships. *Mar. Biol.* **146**, 455–465.

Parmentier, E., Vandewalle, P. & Lagardère, F. (2001). Morpho-anatomy of the otic region in carapid fishes: eco-morphological study of their otoliths. *J. Fish Biol.* **58**, 1046–1061.

Parmentier, E., Chardon, M. & Vandewalle, P. (2002a). Preliminary study on the ecomorphological signification of the sound-producing complex in Carapidae. In *Functional and Ecological Vertabrate Morphology: 139–151*. Aerts, P., D'Aoùt, K., Herrel, A. & Van Damme, R. (Eds). Maastricht: Shaker Publishing.

Parmentier, E., Lagardère, F. & Vandewalle, P. (2002b). 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., Vandewalle, P. & Lagardère, J.P. (2003). Sound-producing mechanisms and recordings in Carapini species (Teleostei, Pisces). *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **189**, 283–292.

Parmentier, E., Fontenelle, N., Fine, M.L., Vandewalle, P. & Henrist, C. (2006a). Functional morphology of the sonic apparatus in *Ophidion barbatum* (Teleostei, Ophidiidae). *J. Morphol.* **267**, 1461–1468.

Parmentier, E., Lagardère, J.-P., Braquegnier, J.-B., Vandewalle, P. & Fine, M.L. (2006b). Sound production mechanism in carapid fish: first example with a slow sonic muscle. *J. Exp. Biol.* **209**, 2952–2960.

Parmentier, E., Bouillac, G., Dragicevic, B., Dulcic, J. & Fine, M. (2010). Call properties and morphology of the sound-producing organ in *Ophidion rochei* (Ophidiidae). *J. Exp. Biol.* **213**, 3230–3236.

Popper, A.N., Rogers, P.H., Saidel, W.M. & Cox, M. (1988). The role of the fish ear in sound processing. In *Sensory Biology of Aquatic Animals: 687–710*. Atema, R.R., Fay, R.R., Popper, A.N. & Tavolga, W.N. (Eds). New York: Springer Verlag.

Popper, A.N., Ramcharitar, J.U. & Campana, S.E. (2005). Why otoliths? Insights from inner ear physiology and fisheries biology. *Mar. Freshw. Res.* **56**, 497–504.

Ramcharitar, J.U., Gannon, D.P. & Popper, A.N. (2006). Bioacoustics of fishes of the family Scianidae (croackers and drums). *Trans. Am. Fish. Soc.* **135**, 1409–1431.

Rountree, R.A. & Bowers-Altman, J. (2002). Soniferous behavior of the striped cusk-eel, *Ophidion marginatum*. *Bioacoustics* **12**, 242–244.

Rowe, S. & Hutchings, J.A. (2004). The function of sound production by Atlantic cod as inferred from patterns of variation in drumming muscle mass. *Can. J. Zool.* **82**, 1391–1398.

Rowe, S. & Hutchings, J.A. (2006). Sound production by Atlantic cod during spawning. *Trans. Am. Fish. Soc.* **135**, 529–538.

Schulz-Mirbach, T., Ladich, F., Riesch, R. & Plath, M. (2010). Otolith morphology and hearing abilities in cave- and surface-dwelling ecotypes of the Atlantic molly, *Poecilia mexicana* (Teleostei: Poeciliidae). *Hear. Res.* **267**, 137–148.

Schwarzhans, W. (1993). A Comparative morphological treatise of recent and fossil otoliths of the family Sciaenidae (Perciformes). In *Piscium Catalogus: Part Otolothi Piscium*, vol. 1: 1–245. Pfeil, F. (Ed). München: Verlag Dr. Friedrich Pfeil.

Schwarzhans, W. (1994). Sexual and ontogenetic dimorphism in otoliths of the family Ophidiidae. *Cybium* **18**, 71–89.

Schwarzhans, W. & Aguilera, O.A. (2016). Otoliths of the Ophidiiformes from the Neogene of tropical America. *Palaeo Ichthyol.* **14**, 91–124.

Tellechea, J.S. & Norbis, W. (2012). Sexual dimorphism in sound production and call characteristics in the striped weakfish *Cynoscion guatucupa*. *Zool. Stud.* **51**, 946–955.

Tuset, V.M., Farré, M., Otero-Ferrer, J.L., Vilar, A., Morales-Nin, B. & Lombarte, A. (2016). Testing otolith morphology for measuring marine fish biodiversity. *Mar. Freshw. Res.* **67**, 1037–1048.

Uiblein, F. (1995). Morphological variability between populations of *Neobythites stefanovi* (Pisces: Ophidiidae) from the deep Red Sea and the Gulf of Aden. *Mar. Ecol. Prog. Ser.* **124**, 23–29.

Uiblein, F., Ott, J.M. & Stachowitsch, M. (1996). Deep-sea and extreme shallow-water habitats: affinities and adaptations. *Biosyst. Ecol. Ser.* **11**, 165–182.

Wourms, J.P. & Bayne, O. (1973). Development of the viviparous brotulid fish, *Dinematichthys ilucoeteoides*. *Copeia* **1973**, 32–40.

Zanette, I., Daghfous, G., Weitkamp, T., Gillet, B., Adriaens, D., Langer, M., Cloetens, P., Helfen, L., Bravin, A., Peyrin, F., Baumbach, T., Dischler, J.-M., Loo, D.Van., Praet, T., Poirier-Quinot, M. & Boistel, R. (2013). Looking Inside Marine Organisms with Magnetic Resonance and X-ray Imaging. In *Imaging Marine Life: 122–184*. Reynaud, E.G. (Ed). Weinheim, German: Wiley-VCH Verlag GmbH & Co. KGaA.

Zeyl, J.N., Love, O.P. & Higgs, D.M. (2013). Condition-dependent auditory processing in the round goby (*Neogobius melanostomus*): links to sex, reproductive condition and female estrogen levels. *J. Exp. Biol.* **216**, 1075–1084.