

Boombbox(fish)

EVOLUTIONARY TRANSITIONS IN
BOXFISH ACOUSTIC COMMUNICATION



by Eric Parmentier

Among the 37,000 recognised species of fish, boxfishes (families Ostraciidae and Aracnidae), which live in coral reefs, are instantly recognisable thanks to their rigid, box-shaped bodies. Formed by the fusion of hexagonal bony plates, it is a striking anatomical detail. But other unusual morphological innovations have recently been revealed regarding the species' ability to communicate. Eric Parmentier gives a glimpse into novel research recently published in the *Biological Journal of the Linnean Society*.

OPPOSITE: Boxfish are well named, with their bodies shaped by hexagonal bony plates. This limits mobility but has resulted in other adaptations.

Boxfishes from the Ostraciidae family are divided into two distinct lineages: the Lactophryinae, which includes seven species, are found exclusively in the Atlantic, and the Ostraciinae, which comprises 18 species, all inhabiting Indo-Pacific reefs. In both groups, this natural armour provides effective protection against predators but also drastically limits their bodily flexibility. Unable to undulate their bodies like most fish, boxfishes had to develop an unusual mode of locomotion, relying wholly on their pectoral, dorsal and anal fins. This gives them a hovering, almost drone-like appearance.

Buzzing

Being protected by armour also proves useful during reproduction. Typically during spawning, the male and female slowly rise through the water column, between 2–15 m, which exposes them to predators. At the top of this ascent a buzzing sound is emitted, serving as a signal for the simultaneous release of gametes outside the body. As early as 1804, naturalist George Shaw was noted as describing a sort of 'growl' emitted from a trunkfish (*Lactophrys trigonus*), though believed the sound to be generated by air being pushed through the animal's branchial structures (Sorensen 1884). (An interesting idea, but as we now know, incorrect.)

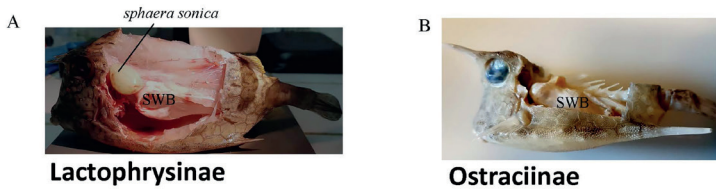
This behaviour also results in fertilised eggs being released near the surface, which increases their chances of being dispersed by favourable currents. In addition to buzzing sounds linked to reproduction, 'booms' can be produced during male–male confrontations, and a short buzz may occur when a male tries to interrupt a mating.

The study

In our case, we recorded a total of eight species during various field missions carried out in the Pacific and the Atlantic. These fish have the advantage of producing sounds when held in hand. Although this technique is sometimes debated, it does allow all fish to be recorded under the same behavioural conditions, with the individual placed at the same distance from the same recording equipment. The sounds recorded in species from the Ostraciinae group exhibit remarkable features: they can produce two types of sounds simultaneously. The fish emits long sounds lasting several seconds, composed of hundreds of pulses which, when produced at regular intervals, create a typical hum strongly resembling those recorded during spawning behaviour on the reef. In addition, during the humming, irregular low-frequency pulses occur that are 10 to 40 times more intense. These short 'bumps' are immediately reminiscent of fight sounds. Usefully, this also allowed us to record the humming and the bumping sounds separately—the two are not systematically produced together, though in the Atlantic species, we were not able to record this dual message. However, when held in hand, individuals from some species were able to emit isolated or repeated bumps, also giving the impression of a hum, but much shorter (less than a second).

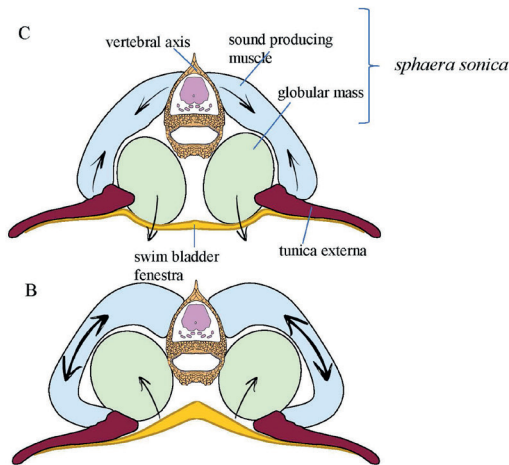
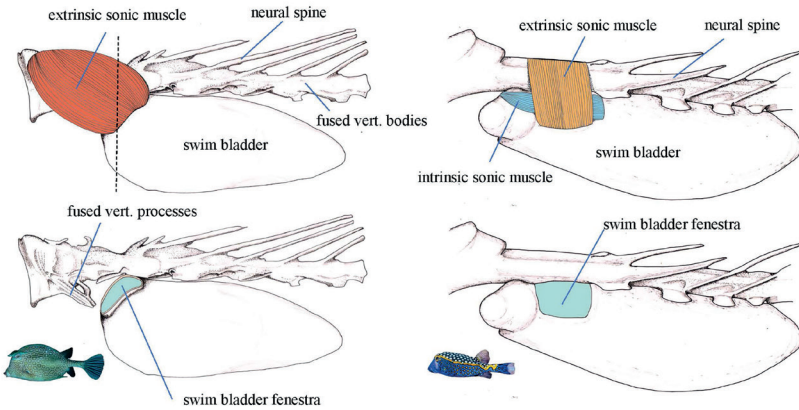
Morphology and discovery

As morphologists, we needed to see how sound-producing mechanisms are organised in these boxfishes and so...we had to look inside. Both groups are capable of producing sounds, but the mechanisms they use differ. Atlantic species have two small balls (sphaera sonica) on the dorsal



Lactophryinae

Ostraciinae



ABOVE:

Schematic view of the sound producing mechanisms in different Ostraciidae: *Lactorphrys triqueter* (A), and *Ostracion meleagris* (B). Schematic transversal view (C) showing the movements of the globular masses (generating the sound in Lactophryinae) inside the swim bladder during muscle contraction (single arrows) and relaxation (double arrows). The dotted line shows where the transverse section is made.

Image: Eric Parmentier et al.

anterior part of the swim bladder; surrounding muscles push them into the bladder, and this back-and-forth motion generates sound. Indo-Pacific species have lost these balls, but the surrounding muscles have evolved into two distinct muscles that, when contracting, cause the swim bladder itself to vibrate, with the very cool ability to produce two different sounds simultaneously.

But the story does not stop there: we wanted to understand how such a mechanism could have evolved. Most fish swim by undulating their bodies, but when you're trapped inside a rigid bony box, bending is not an option. Boxfishes have therefore adopted a swimming style that relies entirely on their fins, and as a result, the large trunk muscles (the ones you find in a fish steak) had to be reconfigured. Some muscles disappeared, others became specialised for fin control, and some may have been repurposed as sonic muscles.

Comparison with the sister family, the Aracanidae, helped us explore these hypotheses. A comparative anatomical analysis revealed the absence of a sonic mechanism in Aracanidae, whose external armour is less solid, as their bony plates are not fused. The comparison between the two families highlights that some muscles involved in undulatory swimming in Aracanidae may be homologous to the sonic muscles of Ostraciidae.

In the latter, being enclosed in a more rigid bony box likely led to the loss of the original locomotor function of these muscles. At that point, two evolutionary paths were possible: either their complete disappearance, or the development of a new function. It is this second path that took shape over the course of evolution in Ostraciidae, with the emergence of acoustic

communication. This transformation illustrates a marked evolutionary transition, from silent fish to vocal species, accompanied by the progressive specialisation of sound-producing structures. Earlier studies showed that Atlantic boxfishes are closer to an ancestral form, less specialised and once spread all over the globe. The typical Indo-Pacific shape likely evolved later, somewhere in that vast ocean, but never made it into the Atlantic. So today, the Lactophryinae species can be seen as living relics of an earlier stage in boxfish evolution.

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