Fish bioacoustics
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Bony fishes have evolved a diversity of sound generating mechanisms and produce a variety of sounds. By contrast to sound generating mechanisms, which are lacking in several taxa, all fish species possess inner ears for sound detection. Fishes may also have various accessory structures such as auditory ossicles to improve hearing. The distribution of sound generating mechanisms and accessory hearing structures among fishes indicates that acoustic communication was not the driving force in their evolution. It is proposed here that different constraints influenced hearing and sound production during fish evolution, namely certain life history traits (territoriality, mate attraction) in the case of sound generating mechanisms, and adaptation to different soundscapes (ambient noise conditions) in accessory hearing structures (Ecoacoustical constraints hypothesis).

Introduction
Fish bioacoustics comprises sound production, sound detection and the functional significance of both, namely acoustic communication and orientation. Although all will agree that the evolution of sound generating mechanisms (often termed sonic or vocal organs) serves acoustic communication (be it with conspecifics or heterospecifics), we know little about what fishes listen to besides conspecific vocalizations. Although the capacity for sound reception, based on hair cells, is a shared derived trait of all vertebrates, hearing enhancing structures and sound producing mechanisms appear to have evolved independently many times among the roughly 30,000 species of living fish [1,2,3].

Central goals of fish bioacoustic research therefore are to investigate the diversity in sound generating and detecting structures and to determine which selective forces acted during the evolution of these structures. How did life history traits and ecoacoustical conditions interact with each other? Here, I review the diversity in vocal organs, sounds generated, hearing organs, hearing sensitivities and how and if the evolution of sound generating and detecting structures are linked to each other.

Sound generating mechanisms
The first observation when studying sound production in fishes is the incredible diversity in sound generating mechanisms [4–7]. This diversity is unique among vertebrates and it is no exaggeration to call fishes the ‘insects’ among vertebrates (this also holds for the hearing organs). Terrestrial vertebrates have a main vocal organ — the larynx in anurans, reptiles and mammals and the syrinx in birds [8] — but no main vocal organ exists in fishes. How widespread is sound production in fishes from a systematic point of view? Our knowledge of their sound production stems entirely from modern ray-finned bony fishes (class Actinopterygii). Little is known from the more primitive jawless fishes (e.g. lampreys), cartilaginous fishes (e.g. sharks) or lobe-finned bony fishes (e.g. lungfishes) even though the latter are the closest relatives to tetrapods [7,9]. Thus, sound production in fishes and tetrapods is apparently the outcome of convergent evolutionary processes despite some similarity in neuronal vocal pathways (see [10], and Bass, this volume).

The occurrence of vocal organs in different species of fish does not follow any systematic pattern. Moreover, we do not know how many species in families known to be vocal (e.g. polypterids, gobiids, damsselfish) generate sounds. Due to the enormous structural diversity it is difficult to categorize vocal organs in fishes.

The most important mechanism comprises structures solely devoted to sound production such as sonic (drumming) muscles for swim bladder vibration. The drumming muscles can be directly attached to the bladder wall (intrinsic type, e.g. toadfishes; Figure 1a), or they originate on a structure outside the swim bladder and inserting on its wall (extrinsic direct type, e.g. pimelodid catfish). Finally, they can vibrate the bladder indirectly via broad tendons or bony plates without any attachment to its wall (e.g. doradid catfishes and piranhas) (extrinsic indirect type; Figure 1b) [37,7,11].

A second group of mechanisms uses pectoral fins and girdles for sound production. Structures (muscles) involved in these mechanisms have additional functions besides sound production, namely swimming. Representatives of
several catfish families have an enhanced first pectoral fin ray (pectoral spine) that can generate stridulatory sounds when rubbed against a groove of the shoulder girdle. The pectoral spine can furthermore be used as a predator defense mechanism when locked in a right angle to the body axis [7,11] (Figure 1c). In croaking gouramis (genus Trichopsis) two enhanced pectoral fin tendons are stretched and plucked similar to guitar strings during rapid fin beating (Figure 1d). In sculpins the entire pectoral girdle is vibrated by a sonic muscle [12] (Figure 1e). Note that there

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**Figure 1**

Diversity of sound generating mechanisms in fishes and sonagrams of sounds produced by these mechanisms. (a) Intrinsic sonic muscles (SMi) attached to both swim bladder lobes (SL) in the Lusitanian toadfish Halobatrachus didactylus, (b) extrinsic sonic muscles (SMe) originating at the second rib (2R) and inserting on a broad tendon (BT) ventrally of the swim bladder in the black piranha Serrasalmus rhombeus, (c) in the stridulatory mechanism in catfish a ridged dorsal process (DP) of the pectoral spine (PS) rubs in a groove of the shoulder girdle (SG), (d) enhanced pectoral fin tendons (ETs) are plucked similar to guitar strings in the croaking gourami Trichopsis vittata, (e) Pharyngeal teeth (PT) stridulation in damselfish, sunfish, among others, and pectoral girdle vibration in sculpins by a sonic muscle (SM) originating at the skull and inserting at the dorsal part of the pectoral girdle. 2R: second rib, BT: broad tendon, DP: dorsal process of pectoral spine, ET: enhanced tendons, PG: pectoral girdle, PM: pectoral adductor muscle, PT: pharyngeal teeth, PS: pectoral spine, SL: swim bladder lobes, SM: sonic muscle, VC: vertebral column. All sonagrams show sounds produced in agonistic contexts. Note different x-axes and y-axes ranges. Modified partly after [7,11]. With permission from Elsevier.
is no clear separation between swim bladder and pectoral girdle mechanisms because intermediate forms exist [13]. Finally, there are mechanisms completely different from the organs mentioned above and not known well enough to be categorized clearly. Pharyngeal structures including teeth may be moved against each other to produce sounds. Such mechanisms were suggested for sunfishes and cichlids (Figure 1e) and described in more detail in clownfish [14]. A simple organ homologous to the larynx is present in lungfish [15]. The distribution of the mechanisms across taxa is quite diverse. The tendon-plucking mechanism occurs in only three species of the genus *Trichopsis* (Anabantoidei), whereas intrinsic swim bladder muscles are found in all genera within the toadfish family (Batrachoididae) and in a few more species of other families. The pectoral spine stridulatory mechanism is found in hundreds of species of several catfish families. Sonic organs are lacking in numerous fishes, whereas some species may even possess two different mechanisms (doradid or pimelodid catfishes) [11].

Fish vocalizations generally consist of pulse series whose main energies depend on the mechanisms involved [16,17]. Swim bladder drumming sounds have mostly a harmonic structure and main energies below 500 Hz. Unlike periodic vocalizations in most tetrapods, the fundamental frequency is determined directly by the contraction rate of swim bladder drumming muscles and ranges from 50 to 200 Hz (Figure 1a,b). Drumming sounds can last from a few milliseconds up to several minutes in the Californian midshipman *Porichthys notatus*. Pectoral stridulatory sounds, in contrast, consist of pulses whose energies are concentrated at higher frequencies than those of swim bladder sounds. Energies extend up to several kilohertz with main energies at a few hundred hertz or even above 1 kilohertz, such as in the croaking gourami (Figure 1c,d). Low-frequency pulsed sounds are also observed in species emitting pharyngeal or pectoral girdle vibration sounds [12,14]. Fishes often emit different sounds types in different behavioural contexts by modifying the duration, temporal pulse patterns or amplitudes [18–20].

### Sound detecting mechanisms

Sound detecting organs are present in all vertebrates including all fish species, in contrast to sound generating organs [21]. The hearing organs can be divided morphologically into those consisting solely of the inner ears and those utilizing additional peripheral structures to improve hearing. Inner ears consist of three semicircular canals and three otolithic end organs (utricle, saccule, lagena), each one consisting of a calcareous otolith overlaying a sensory field of hair cells. Because fish have the same density as the surrounding medium (in contrast to terrestrial animals) they move back and forth with the sound wave excluding any net movement between the animal and the water. Only the heavier otoliths lag behind these movements and create a deflection of hair cell ciliary bundles. This process enables fish to detect particle motion at low frequency (up to a few hundred hertz) [22*,23]. Close to a sound source (nearfield) the ear’s ability to detect sound may overlap with the ability of the lateral line to detect fluid flow near a sound source [24]. The lateral line is a mechanosensory system consisting of sensory cells termed neuromasts which are found in subdermal lateral line canals was well as directly on the skin [25]. Its main task is the detection of water movement generated by conspecifics, heterospecifics such as prey or inanimate sources (ocean currents, river flows, among others).

Interestingly, numerous taxa among ray-finned bony fishes connect their inner ears to gas-filled chambers, which allow them to detect sound pressure [1]. Walls of these chambers vibrate in a sound field. These vibrating walls function as internal ear drums (tympana) which transmit these oscillations in various ways to the inner ears. This enables these species to detect sound at lower levels and higher frequencies (up to a few kilohertz) (for reviews see [26*,27*]). The diversity in inner ears and in accessory hearing structures is astonishing, as is the diversity in vocal organs [1,23,28*]. Sound pressure fluctuations of the swim bladder can be transmitted via an ossicular chain to the inner ear (‘Weberian ossicles’), very similar to mammals [29], or swim bladder extensions can contact the inner ear directly, or the inner ears may contact the air-breathing organs [28*]. Even in fish that lack a direct connection between inner ear and gas-filled chambers, a possible function of the swim bladder in sound pressure detection cannot be ruled out without complicated experiments [30,31].

One major shortcoming in analysing the functional significance of fish hearing abilities is the scarcity of knowledge — except for a few indications — about what fishes are listening to beyond conspecific vocalizations. The general assumption is that fishes ‘glean’ acoustic information from their environment (also termed auditory scene, soundscape, ‘acoustic daylight’) [32–34]. It is assumed that fishes gain advantages from listening to abiotic (e.g. coastal surf, coral reefs) and biotic sound/noise sources (conspecifics and heterospecifics, predators, prey), independent of vocalizations. Various soundscapes may help larvae and adults to find suitable habitats [33,35,36] or help to avoid danger. One example for the interception of predator sounds is the detection of toothed whales by some herrings and toadfish: the former exhibit an evasive response during playbacks of echolocation clicks, the latter suppress calling behaviour [37–40]. Important biotic sound or noise sources in the intraspecific context may include feeding, digging or swimming noise of conspecifics or heterospecifics (prey). This list of incomplete observations and assumptions points to a large gap in our knowledge on the importance of hearing in fish, calling for phonotaxis experiment using sounds other than (conspecific or heterospecific) vocalizations as stimuli.
The distribution of morphological specialization for hearing improvement across taxa does not reveal any clear pattern. Weberian ossicles are present in all otophysines (four orders, 8000+ species); other specializations may be present in one suborder such as the suprabranchial chamber in Anabantoidei, and some may not even be present in all representatives within a single family, such as in holocentrids, sciaenids or cichlids [22,41,42]. The perciform family Cichlidae illustrates this diversity and the effects on auditory sensitivity within a single family (Figure 2). In the Indian species Etroplus maculatus a huge swim bladder extends rostrally up to the inner ear, whereas in the African species Hemichromis guttatus and Steatocranus tinanti the swim bladder does not contact the inner ears at all; the latter two species, however, differ considerably in swim bladder size. These differences in size and distances to the inner ears are reflected in their hearing abilities, with E. maculatus having the highest and S. tinanti the lowest sensitivity (Figure 2) [43]; see also [44] for the effects of bladder size on hearing in catfishes. Rostral swim bladder extensions and auditory ossicles certainly serve only in hearing, but swim bladders are primarily organs for buoyancy and suprabranchial chambers serve in air-breathing.

**Evolutionary considerations**

Why did sound generating mechanisms evolve in certain taxa and not in other taxa, and why are they so diverse?

The answer to the first question may lie in the life histories of vocalizing species. In general, vocal species produce sounds when defending limited resources (mainly territories) against opponents, for example, territorial intruders, or when trying to attract mates (females) to nest sites and during mating [45,46]. These life history traits explain the absence of sonic organs in pelagic species such as sharks, but they do not provide an explanation for the large diversity in sonic mechanisms among vocal fishes.

Which selective forces resulted in the evolution of hearing specializations, their large diversity and the systematic distribution among fishes? One potential answer is that they are evolved to facilitate acoustic communication [8,47]. Nonetheless, a more detailed analysis of the presence of both vocal and hearing organs across taxa does not support this hypothesis [2]. Well-known vocalizing taxa such as toadfishes and gobies lack any specialization for hearing, whereas cypriniforms are hearing specialists but rarely signal acoustically (and no vocal organs are known). Rather than acoustic signaling, hearing in many species seems to be adapted to the ambient noise in a fish’s habitat. The ‘ecoacoustical constraints hypothesis’ postulates that species living in quiet waters should have high auditory sensitivities, whereas the opposite should be the case in species living in noisy environments where...
Diversity in sound generating and detecting structures in fishes, their functional significance and potential constraints during their evolution. Sound generating mechanisms are divided into mechanisms with sonic muscles exclusively devoted to sound production and into pectoral mechanisms/muscles that serve additional functions (swimming, predator defense). The third group comprises mechanisms not known well enough to be categorized definitively, such as pharyngeal or neck mechanisms (clownfish, seahorses). Sound detecting mechanisms are divided into those consisting merely of the inner ears (tiny or no swim bladders), those having well-developed peripheral structures for hearing (e.g. Weberian auditory ossicles) and those in which the mechanism for improved hearing (sound pressure detection) is unknown (e.g. damselfish). Sonic/vocal organs always serve acoustic communication, whereas hearing organs primarily serve interception of acoustic information emanating from various biotic sources (conspecifics and heterospecifics, predators, prey) and abiotic sources (coral reefs, coastal surf, among others). Thus, different constraints have apparently acted during the evolution of sound generating and detecting mechanisms. It is proposed here that vocal organs are linked to particular life history traits (territory defense and mate attraction), whereas the diversity in hearing organs is due to different ambient noise conditions (soundscapes; ecoacoustical constraints hypothesis).

improved hearing would be meaningless [42*]. Several investigations and analyses show that most species with improved hearing live in quiet stagnant freshwater (at least two thirds of freshwater fish possess specializations), whereas non-specialized species inhabit rather noisy marine habitats [48*,49,50]. Studies indicate that fish are adapted to the ambient noise in their habitats and that artificial (anthropogenic) noise hinders acoustic communication and prey detection [51–53,54*] (Figure 3). To test this ‘ecoacoustical constraints hypothesis’ many more ambient noise measurements and masking experiments need to be carried out in fish species differing in their hearing sensitivities [49,52,55–58]. Moreover, this hypothesis does not rule out that fish are well adapted to detect conspecific or even heterospecific sounds as long as the sound levels are high and communication distances short enough to be detectable — also during different stages of ontogenetic development ([59–61]; but see [57,62]).

Conclusions
Based on the phylogenetic distribution of sound generating mechanisms and vocalizations it is concluded that acoustic communication evolved multiple times in non-related fish taxa. Sound communication is primarily linked to the mode of reproduction namely territoriality and substrate breeding and seems to be unrelated to the evolution of hearing enhancements.

Conflict of interest statement
There exists no conflict of interests.

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as:
• of special interest
•• of outstanding interest

126 Communication and language

This review provides an overview of sound generating mechanisms and their neuronal control in fishes. The latter is best investigated in representatives of the toadfish family.


This book chapter gives a short introduction in fish bioacoustics including the physics of underwater sound, sound production, vocal behaviour and hearing mechanism.


This book summarizes all available data on hearing in fishes (and other vertebrates) up to 1988. All auditory data were redrawn in standard figures to make comparisons for readers easy. It has become a classic in fish bioacoustics. It does not include AEP-data because the AEP-technique became popular several years later (see [27]).

This review covers all 100+ papers on hearing in fish using the Auditory Evoked Potential (AEP) technique since 1998. Baseline hearing abilities were described and compared in 111 species from 51 families. In addition, studies on the functional significance of accessory hearing structures, on the ontogenetic development of hearing, and on the effects of masking by and exposure to various noise types (white, ambient, ship noise) were listed, along with the effects of various ecological, genetic, methodological and behavioural factors on hearing.

This book chapter reviews the literature on peripheral mechanisms for enhanced hearing in fishes. It illustrates the morphology of accessory hearing structures with a number of helpful drawings but does not give audiograms. The authors also mention that in numerous families we do not know whether specializations such as anterior swim bladder extensions improve hearing.


42. Ladich F: Diversity in hearing in fishes: ecocoustical, communicative, and developmental constraints. In Insights...

This book chapter reviews the literature on the diversity of hearing abilities in fishes and attempts to explain this diversity from an ecoacoustical, communicative and ontogenetic point of view. Based on our current knowledge the review concludes that ecoacoustical constraints, namely differences in noise levels and noise spectra, are the most likely explanation for the diversity in hearing sensitivities. This notion is summarized in the ‘ecoacoustical constraints hypothesis’.


This is the most comprehensive study showing the effect of swim bladder size and its distance to the inner ear on hearing sensitivity in closely related fishes belonging to the same family.


This is the first review summarizing all investigations on acoustic signalling during agonistic behaviour in fishes.


This is the first review summarizing all investigations on acoustic signalling during reproductive behaviour in fishes.


This book chapter lists basic anatomical, auditory and habitat data and feeding behaviour of representatives of 28 families out of 16 orders of fishes and formulates general principles (hypotheses) on fish hearing. It is highly interesting comparing these principles to the conclusions of the present review.


This book chapter summarizes our current knowledge on the effects of ambient noise as well as anthropogenic noise on hearing in general and on the detection of communication sounds in particular.


