The SOUND Table in FishBase

Contrary to most people's perception, the underwater environment is by no means a quiet haven. In addition to the relatively high level of abiotic background noise (e.g. cavitation, wave movements etc.) invertebrates, fish and marine mammals produce a variety of acoustic signals, ranging widely in frequency and loudness (Schellart and Popper, 1992). Allusions to the sound production of fish in the literature date as far back as early Greek and Roman times (Moulton, 1963; Fish and Mowbray, 1970) and, thanks to the technological advances in underwater acoustics during the 1940's, the investigation of fish sounds has become an active field of study over the past decades (e.g. Moulton, 1963; Tavolga *et al.*, 1981). Although the majority of known fish species still remains to be tested, sonic activity could be demonstrated and recorded in more than 80 families of fish during the 20th century (Fish, 1948; Fish and Mowbray, 1970). Judged by the available evidence, it has been proposed that hundreds of species of marine and freshwater fishes are probably capable of generating acoustic signals (Moulton, 1963). Active vocalisations of most species are unique and distinctly species-specific (Fish and Mowbray, 1970) and have indeed been used to distinguish closely related species in some cases (Crawford *et al.*, 1997).

Many fish species have fairly advanced hearing abilities, mainly in the lower frequency ranges (Hawkins, 1981). There is a moderate but significant concurrence of vocalization bandwidth and hearing bandwidth for species for which data are available on both, hearing abilities and sound production, indicating that the improvement of hearing and refinement of vocalizations may have co-evolved in the context of intraspecific communication (Schellart and Popper, 1992). Recent findings have shown, however, that the auditory sensitivity of some species may reach into ultrasonic frequency ranges, thus exceeding the bandwidth of their own vocalisations by far (e.g. *Alosa sapidissima* (Mann *et al.*, 1997) or *Gadus morhua* (Astrup and Møhl, 1993)). It has been proposed that the development of such extended auditory thresholds may represent an adaptive response to the use of high frequency echolocating signals of piscivorous mammalian predators, such as odontocetes (Mann *et al.*, 1997; Astrup, 1999).

Humans across different cultures have exploited sonic abilities of fish for centuries, often to this present day. Localizing fish by listening to species-specific acoustic signals is an art form that has been employed in conjunction with fisheries (e.g. Sciaenid and carangid fisheries in Malaya (Moulton, 1963)). Alternatively, man-made low frequency sounds or noises have been employed both, as a means to either lure or scare fish into being caught in a variety of gear types ranging from gill and seine nets to hook and line (Moulton, 1963; Brandt, 1984). In a non-fisheries context, spawning sounds of some species, such as e.g. *Cynoscion regalis* and *Sciaenops ocellatus* have also been used more recently to map of breeding distributions (Luczkovich *et al.*, 1998; Sprague *et al.*, 1998).

Sources:

The main source for the information compiled in the SOUND tables is a report about the comprehensive investigation of the acoustic behaviour of 220 species of North Western Atlantic fishes published in 1970 by Fish and Mowbray (1970). The majority of fish sound files in this table stem from the original recordings that accompanied this book.

Please note, that most of the sound samples available on the web page have been amplified and/or filtered to reduce noise to improve the audio quality. Such modifications and the compressed audio file format (.mp3) used to reduce file size will result in some alterations of the frequency distribution and amplitude characteristics of original signal which are not necessarily detectable by the human ear. To perform any quantitative acoustic analysis of the fish sounds it is therefore strongly recommended to refer back to the original data.

To supplement the information compiled in the table, we have attempted to include cross-references to other sound archives, such as the National Sound Archive of the British Library, based on the information provided to us about their collection. In most cases, however, the actual recordings are not directly accessible on-line and may be difficult to obtain.

The SOUND Production table

Fields:

Fish may generate acoustic signals either passively or actively. The former type of signals - also referred to as ‘mechanical’ sounds (Fish, 1954) – are generated as by-products of foraging, moving or other activities. In contrast, active – or ‘biological’ (Fish, 1954) - sound production involves the use of organs, which, though initially developed to perform other functions (Fish, 1954), are also especially adapted to generate acoustic signals (Moulton, 1963). It is important to recognize that both types of signals, active and passive, may possess a biological significance (e.g. *Spheroides maculatus* may be attracted to a feeding site by the – passively produced - chewing sounds of other members of its species (Moulton, 1963), while *Holocentrus ascensionis* and other species are known to actively generate sounds during competitive feeding interactions (Fish and Mowbray, 1970)).

The **Sound production** field contains two types of information: a.) if a fish has already been tested for sound production and b.) if it has been found to – actively or passively – produce one or several types of acoustic signals. If a species has been tested, detailed information about the experimental set-up etc is provided in the **SOUND Experiments** table

To differentiate between different acoustic signals, early categorization efforts used descriptive **sound types** to classify the recorded fish sounds. Unfortunately, however, although most people agree that a ‘thump’, a ‘bump’ and a ‘knock’ are different sounds, what some may call a ‘bump’ may be considered to be a ‘thump’ by others. Despite attempts to standardize such descriptive sound type definitions (e.g**.** Fish and Mowbray, 1970), a large degree of subjectivity remains associated with the qualitative classification approach. Consequently, analytical methods such as oscillograms (two dimensional representation of a sound plotting the change in amplitude of a waveform over time) and spectrograms (three dimensional representation of a sound plotting the change in frequency and amplitude/loudness over time) are generally employed today to quantitatively describe and compare acoustic signals. A real-time **oscillogram** of the acoustic signal can be viewed when playing the sound file using the settings recommended on the web page. In the future this will supplemented by a pre-generated **spectrogram** of the signal.

Despite the limited objectivity of qualitative descriptions, the **sound types** produced by a certain species - if mentioned in the original reference – is also included in the record as it may allow a coarse categorization and comparison of species based on their sounds.

The swim bladder is the most commonly used **sound production organ** in fish for active vocalizations. This membranous air-filled sac fulfills several other functions, most importantly regulating the animals’ buoyancy in the water, in addition to playing a role in the auditory system of fishes (Tavolga *et al.*, 1981; Schellart and Popper, 1992). In the context of sound production, the swim bladder can either function as the actual sound generator itself or as an amplifier for sounds generated by other body parts including e.g. the pectoral girdle, fin rays, various other bones or the incisors (Schellart and Popper, 1992). Most commonly, however, sounds amplified in such a way are generated by pharyngeal teeth (patches of mosaic-like denticles located far back in the pharynx) which most fish species possess (Tavolga, 1964).

When sounds are generated ‘passively’, as a by-product of other activities, the involved body parts, such as teeth (feeding sounds) or the entire body or the tail (swimming or hydrodynamic sounds) could essentially be regarded as the ‘sound production organ’ (Fish, 1954).

The **sonic mechanism** is the actual underlying physical mechanism that generates the sound. Fish actively produce sounds using a variety of different mechanism, one of the predominant ones being the vibration of the air-filled swim bladder through sudden contraction of the skeletal musculature, as associated with e.g. rapid acceleration, evasive movement or a startle reaction. The resulting ‘escape sounds’ are a type of acoustic signals which the majority of fish with swim bladders seem to be able to produce (Fish and Mowbray, 1970).

Alternatively, swim bladder vibrations may be initiated by means of specialized muscles sometimes working in conjunction with modified bones. These muscles may be embedded directly in the wall of the swim bladder (‘intrinsic musculature’ e.g. Triglidae) or may exist in the form of ‘drumming’ muscles extrinsically associated with the swim bladder (e.g. Sciaenidae) (Moulton, 1963; Fish and Mowbray, 1970). Furthermore, externally induced vibration of the swim bladder in some species may be achieved by means of rhythmic beating of finrays against the body surface (e.g. *Balistes carolinensis*) (Fish, 1954). The type of sound actually generated by the vibrating swim bladder is mainly determined by the size and the shape of the swim bladder

(Fish, 1954). Generally, however, these sounds are low-pitched, guttural and drum-like (i.e. ‘grunts’, ‘groans’, ‘thumps’, ‘knocks’, ‘clucks’, ‘booms’ or ‘barks’) with fundamental frequencies ranging between 25 – 250 Hz and an upper frequency of 800 Hz (Fish and Mowbray, 1970; Tavolga, 1971) and are quite loud (Fish, 1954). In contrast, sounds associated with the release of gas bubbles from the swim bladder, such as sometimes produced by Physostomi fish species, which have maintained a pneumatic duct, are generally relatively faint (Fish, 1954).

Relatively loud, higher pitched ‘rasping’ or ‘scratching’ sounds are produced by the grinding of incisors or – more commonly **-** the stridulation of pharyngeal teeth (Fish, 1954). In some species (e.g. Pomadasyidae) these stridulatory sounds may be amplified considerably by a resonating swim bladder located in close proximity to the pharyngeal teeth (Moulton, 1963; Fish and Mowbray, 1970). Other types of sonic mechanisms include the stridulation of different body parts against each other (e.g. some Syngnathidae) or the spasmodic contraction of heavy skeletal muscles resulting in a low-pitched droning, like the hum of an electric motor (e.g. Cottidae) (Fish and Mowbray, 1970).

In the case of passive or “mechanical” sound production, the sonic mechanism is generally the friction between body parts during foraging activities (Moulton, 1963). Alternatively, the sudden movement of a fish or a whole school in water may result in recordable compression waves with frequencies up to 1 kHz (Fish and Mowbray, 1970; Schellart and Popper, 1992). One of the loudest known fish sounds, produced by *Pogonias cromis* and frequently heard from boat decks probably falls into the category of mechanical sounds as is believed to be produced by fish beating their tails against the bottom of vessels to rid themselves of parasites ((Gunther, 1880) in (Moulton, 1963)).

Active sound production in fish may vary considerably with time and space. For example many fishes become most loquacious in the breeding season and at night time, following a seasonal and/or diurnal cycle (Fish, 1954; Fish and Mowbray, 1970). Although the vocabulary of most fish species is very limited (Fish and Mowbray, 1970) and the acoustical signals are mostly lacking in fine graded complexity, it seems certain that sounds do serve a purpose in communicating gross information about environmental and internal physiological states (Winn, 1964). This basic information is most likely encoded in the repetition rate or duration of the signal or the intervals between signals or its the harmonic frequency distribution (Winn, 1964)

The specific **behavioural context** in which a given sound was produced is documented in the corresponding field in the table. As already indicated by the examples above, fish may actively vocalise for a variety of different purposes. The behavioural contexts during which sounds are produced may be roughly divided into three major categories: i. startle and escape reactions (e.g. *Arius felis* or *Bagre marinus* (Tavolga, 1960; Fish and Mowbray, 1970)) ii. agonistic inter- or intraspecific interactions, such as competitive feeding (e.g. *Haemulun melanurum* (Fish and Mowbray, 1970) or *Hippocampus erectus* (Colson *et al.*, 1998)) or territorial defense (e.g. *Pomacentrus partitus* (Myrberg, 1997) *Gaidropsarus mediterraneus* (Almada *et al.*, 1996)

Opsanus tau (Gray and Winn, 1961) and iii. sounds produced in a reproductive context, such as basic species identification and discrimination (e.g. some closely related Momyridae species (Crawford *et al.*, 1997)), courtship (e.g. *Hippocampus erectus* (Fish, 1954; Fish and Mowbray, 1970)) or spawning (e.g. many Sciaenidae (Fish, 1954) or more specifically *Hypoplectrus unicolor* or *Scarus iserti* (Lobel, 1992)). In addition, there is some evidence that acoustic signals may also be produced for non-communicative purposes, such as the orientation in a new environment, i.e. a simple form of echo-location (Vincent, 1963). A classic example of this are the clicks produced by *Hippocampus erectus* specimen when introduced into a new environment (Fish, 1954; Fish and Mowbray, 1970). Spontaneous sound production, i.e. without an apparent external stimulus, is fairly rare in fish, the so-called ‘boatwhistle’ of *Opsanus tau* being one of the few exceptions (Winn, 1964).

Recording sounds in the field is quite difficult, partly because of the background noise level in these circumstances, but mainly due to the problems of matching the recorded signals to specific individuals, if a number of animals and/or species are present. Therefore the sonic abilities of a certain species have often been tested under controlled experimental conditions or while a specimen is caught in fishing gear rather than in situ. Furthermore, since spontaneous vocalizations in these circumstances are rare, sound production was sometimes initiated by using artificial stimuli such as manual or electrical stimulation (Fish and Mowbray, 1970). Although these experiments may not establish the natural occurrence of sound for a specific species, they may appraise the sonic ability of a species. Moreover, experiments have shown such artificially stimulated sounds to be very similar to naturally occurring alarm calls (Fish and Mowbray, 1970). The use of artificial stimuli was nonetheless documented in the behavioural context field.

If provided in the original source, information about the circumstances under which the recording was made is given in the **remarks** field. This includes details about the specific external experimental set-up, such as the recording environment (i.e. field pen or enclosure, wooden tank, aquarium etc.) as these have an impact on the quality of the recording (e.g. acoustic recordings made in closed space will include reverberations of the walls, which may interfere with the targeted signal etc.). Furthermore, the number of specimen vocalising and/or present at the time of recording is given if such information was available. Sometimes it is specifically noted in the source, whether or not sounds were ever produced spontaneously or if sound production associated exclusively with artificial stimulation. If mentioned this information was included in the remarks field as it may provide some indication of the likelihood of encountering the recorded sounds in the wild.

All acoustic recordings are affected to some extent by distortion introduced through the particular sensitivities of all parts of the recording system, which need to be taken into account when trying to analyse or interpret a recorded sound. For the technical specifications of hydrophones and preamplifiers please refer back to the original sources, as these could not be included in appropriate detail in this table.

In many cases sounds are recorded using filters, often employed to reduce the noise level in the recordings. Depending on the specific attributes of a filter, certain frequency ranges in the recording will be blocked out completely or at least dampened considerably. Filters can either cut out all frequencies above ("lowpass") or below ("highpass" filters) a certain specified threshold. Alternatively, so-called "bandpass" filters allow the selective recording of pre-defined frequency ranges with an upper and lower set boundary. As all of these filters will obviously have a significant impact on the resulting frequency distribution of the recorded signal, the use of filters is reported in the remarks field, if mentioned in the source.

During the digitization and extraction process necessary to make sounds available on FishBase, the recordings were sometimes amplified and/or an additional noise reduction filter was employed, to improve the overall audio quality. Again, this will have had an effect on the acoustic properties of the final signal and is therefore documented in the table.

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