

How Fishes Use Sound: Quiet to Loud and Simple to Complex Signaling[☆]

IM Kaatz, AN Rice, and PS Lobel, Cornell Laboratory of Ornithology, Ithaca, NY, United States and Boston University, Boston, MA, United States

© 2017 Elsevier Inc. All rights reserved.

Glossary

Agonistic Aggressive behavioral conflicts or threat displays that can include competitive interactions or fighting between individuals, territory defense, attacks or chases.

Bioacoustic parameter Descriptions of a sound in terms of amplitude (loudness), temporal (duration) or frequency (sound pulse cycle per time) characteristics.

Call Acoustic display that may be associated with a particular posture or context, for example, courtship call produced when a male displays to a potential female mate.

Communication Patterns of energy produced by a sender, perceived by the sensory apparatus and decoded by the nervous system of a receiver, information from a sender may be cooperative or manipulative.

Communication modality Signals of a particular type classified according to the sensory receptor types that detect them such as electric, chemical, tactile, visual or acoustic.

Display Stereotypical behavior pattern that can consist of one or more different postural movements including one or more different signal modalities for communicating in either intra- or inter-specific contexts.

Disturbance sound Behavioral context in which physical restraint by a predator or other forms of aggressive contact may cause an acoustic response in an individual.

Interception Communication signal detected by an individual receiver for whom it was not intended and whose behavior changes in response to it.

Signal Energy pattern (sound, etc.) evaluated by a receiver that can convey false or honest information about physiological condition, social status, behavioral intent or motivational state of a sender.

Sound production Volitional sound production, sound signal communication, is proposed by researchers when they use the terms acoustic, sonic, soniferous or vocal; neurophysiologists restrict the use of vocal to fish whose mechanism is dedicated to sound mechanisms homologous with higher vertebrates; incidental sounds are typically or should be specifically stated as such and often occur as byproducts of feeding or swimming mechanical movements.

Introduction: Determining Acoustic Fish Diversity Detected With a Hydrophone

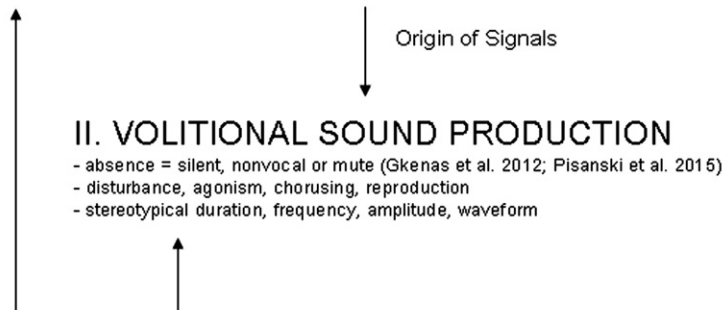
The acoustic underwater world of fishes encompasses three major domains: incidental, volitional and intercepted sounds (Fig. 1). Fish bioacoustics is still in an age of discovering acoustic lineages, describing their sounds and testing functional hypotheses. Major works in the literature on acoustic fishes (n=988) can be conceptually classified as: hydrophone studies of behavior or mechanisms (65%), descriptive morphology (17%) and physiology (excluding hearing) (18%). Hydrophone detection of sounds in disturbance, agonism or reproduction contexts or by means of passive acoustics (excluding known feeding or swimming incidental sounds and families with undetermined acoustic ability: freshwater eel, anchovy, salmon, halfbeak and sablefish) encompasses 82 families in 21 orders. A total of 384 species, in 69 families and 18 orders had sound patterns defined and were numerically described (Table 1). A total of 34 additional species in 19 families have evidence supportive of volitional sound production based on the presence of sound patterns (pulse or sound series, harmonic or tonal components) that were minimally analyzed but require further studies. Four of these families are in addition to those with more significant numerical data. A number of other taxa (60 species in 25 families; 9 of these families and the orders Myliobatiformes, Elopiformes, Albuliformes are not in the above counts) have had sounds recorded and minimally analyzed but evidence is limited to simple sounds (single or few pulses) that are not supported as signals and require further study. Species (n=177) in 42 families and 15 orders (Polypteriformes, Acipenseriformes, Osteoglossiformes, Cypriniformes, Characiformes, Siluriformes, Gadiformes, Ophidiiformes, Batrachoidiformes, Cyprinodontiformes, Beryciformes, Syngnathiformes, Scorpaeniformes, Perciformes and Tetraodontiformes) produce statistically supported sound signals in social contexts. Clupeiformes species produce biosignals and individuals produce sounds en masse. One Osmeriformes species has only had sounds described from within a school. One Zeiformes species has only had disturbance sounds recorded. More hypotheses have been proposed for fish call function in intra- and inter-specific communication than have been behaviorally experimentally evaluated (Table 1).

[☆]*Change History:* October 2015. I.M. Kaatz updated Table 1 and all sections of the body of the text to reflect discoveries and correct previous errors due to the acquisition of a larger literature cited supported database; added Tables 2–4 and Figs. 1 and 4. The literature cited had older reviews and papers replaced with more current examples. Key iconic reviews are retained.

FISH BIOACOUSTIC DOMAINS

I. INCIDENTAL SOUND PRODUCTION:

- byproducts of swimming or feeding (Fish & Mowbray 1970)
- escape “biosignals” (Fish & Mowbray 1970) with simple single pulses are interpreted as incidental
- adventitious byproducts of fish biology during behavioral displays (Lobel & Kerr 1999) that are not volitional, not communicative and not known to be produced by a derived sound producing mechanism



III. SOUND INTERCEPTION (Myrberg 1981):

a. Prey - Predator:

- fish prey calling modified by interception of predator calls (Remage-Healey et al. 2006)
- fish predator calling modifies invertebrate prey behavior (Hughes et al. 2014)

b. Predator - Prey:

- cetaceans eavesdrop on drum prey calls (Gannon et al. 2005)
- water snakes are attracted to minnow prey calls (Holt & Johnston 2009)

c. Conspecifics:

- males intercept and respond to calls of displaying males (Kenyon 1994)
- feeding noises act as cues to group feeding minnow conspecifics (Scholz & Ladich 2006)

d. Reef Soundscape

- coral reef soundscape includes fish sounds (Staatermann et al. 2014; Kaplan et al. 2015)

Fig. 1 Fish sound terminology definitions and key roles sounds play in aquatic ecosystems.

“Loud” and “Quiet” Sound Producers: Propagation Distances, Repertoires and Call Functions

Most fishes have only been recorded near the caller. Of 252 species examined representing 64 families, 78% have been recorded at less than 1 m. Fish whose sounds are detectable at or are estimated to propagate over 1 m (Fig. 2) could be considered “loud” sound signaler fishes, propagating sounds multiple body lengths from the signaler and precluding private close channel “whispering” communication. We do not know the maximum propagation distance for most signalers. A number of signalers with sounds that propagate ≥ 1 m have impressive acoustic communication abilities that are obvious to human observers and have been the focus of active research programs. The oyster toadfish (*Opsanus tau*) (Fig. 5) generates sound using the fastest known contracting vertebrate muscle, which is attached to its swimbladder and propagates several meters (Table 4). The domino damselfish (*Dascyllus albisella*) male produces sounds that propagate up to 12 m in coral reef habitats (Table 4). Plainfin midshipman (*Porichthys notatus*) acoustic displays can penetrate boat hulls and have alarmed new boaters in California! In general, fish repertoires range from 1–6 (2 ± 1 SD, $n = 384$ species). The largest repertoires are represented by species within the ≥ 1 m propagation distance group (2 ± 1 SD, 1–6, $n = 55$): six calls for the oyster toadfish (*O. tau*) and a sweeper (*Pempheris adspersa*); five calls for the Lusitanian toadfish (*Halobatrachus didactylus*), bicolor damselfish (*Stegastes partitus*) and an elephant fish (*Pollimyrus isidori*). Loud signaling is a trait which may identify male advertisement as a primary call function depending on how far individuals are dispersed in a population and how far the signal can travel and be audible to the listener.

“Quiet” sound signalers (Figs. 2 and 3) continue to be discovered. They are less obvious to human observers as sound communicators because they do not produce calls directly audible to casual human observers. These species' sounds require a hydrophone at close range, a few body lengths from the caller for detection and include species like the rock-pool blenny (*Parablennius parvicornis*), padanian goby (*Padagogobius bonelli*) and zebra mbuna (*Maylandia zebra*). Known “quiet” acoustic species use sounds in the same behavioral contexts as “loud” sound signalers but have a small repertoire (range 1–3, 1 ± 1 SD 0.5, $n = 110$, only quiet calls). Quiet signaling described as the whispers of female croaking gourami (*Trichopsis vittata*) suggest a private communication channel and selection pressures to avoid detection. Benthic quiet signalers could be producing seismic signals. Very low amplitude sounds could be stimulating the lateral line.

Table 1 Hypotheses for behavioral contexts for fish sounds detected with a hydrophone (n=640 publications; n=384 species)

<i>Behavioral context or behavioral phenomenon</i>	<i># Families (# species, %) # orders</i>	<i>Sound function hypotheses (“?”=proposed, requiring further observations and experimental testing)</i>
Chorusing (calling from field population or aggregation, volitional sounds produced by established acoustic mechanisms):	15 (50, 13%) 9 Orders	Mate attraction? Mate assessment? (lek behavior is evidenced) Acoustic tagging (individuals alternating calling, one species supportive evidence) Contact calls for group or school cohesion? Predator confusion? Predator alert alarm wave calling? Agonistic calls among colony neighbors Contact calls increase group cohesion in one species
Schools (individuals producing sounds from within a coordinated group, no specific context discerned for species):	6 (7, 2%) 3 Orders	
Reproduction: male and female courtship, female sound in courtship, male display or spawning:	29 (131, 34%) 13 Orders	Individual and species recognition Male advertisement call (could include solitary or patrolling male sounds) Male fitness Female attraction to male and mate preference Advertise spawning readiness? Synchronize courtship or gamete release?
Agonistic (chasing, fighting, territorial defense):	38 (156, 41%) 13 Orders	Acoustic signaling wins fights Fighting opponent assessment Nest and territory defense Social dominance? Competitive agonistic signal or incidental?
Feeding competition: Disturbance (restrained, held by human hand, prodded contact):	Triglidae (2, 0.5%) 37 (131, 34%) 11 Orders	Alarm conspecific about predator attack? (tethered fish during predator attacks produce sounds in field aggregations) Secondary predator attraction to disrupt attack? Startle, threaten or warn predator of defensive capabilities? Vigilance, alert conspecific? or threat?
Disturbance (human approach or subjected to predator model): Swimming away (escape or startle): produced by a known or proposed derived mechanism	8 (26, 7%) 5 Orders 6 (8, 2, 3%) 6 Orders	Conspecific alarm or alert?

Both quiet and loud sound producers may be active at times or in places difficult for humans to observe such as at night, in deep sea caves, seagrass beds, turbid waters, buried in the substrate or from covered nesting sites. Some fish even call inside other animals such as the pearlfishes (Fig. 5) who are symbionts of sea cucumbers and other invertebrates. Quiet and loud sound signalers exhibit diel and seasonal calling patterns.

Discovery and Evolution of Acoustic Fish Behavior

Acoustic fishes have been known since the time of Aristotle. Significant monographs of acoustic fish behavior were produced in the 1800s, especially by Leon Dufosse and William Sorenson. Few new fish families have been monitored extensively with hydrophones since the classic marine fish acoustic behavior surveys by Marie Poland Fish, especially her book with William Mowbray, and the classic review by Arthur Myrberg. The best studied taxa include minnows, catfishes, cod, pearlfishes, toadfishes, sea robins, cichlids, croakers, damselfishes, butterfly fishes, gourami, and gobies (Fig. 5). The earliest fishes evolved hearing to listen to the acoustic scene. Studies of the development of neurological control of sound production in fishes that allows them to discern temporally patterned sounds, suggests an equally early evolutionary origin for sound communication. Modern teleost fishes have independently evolved acoustic mechanisms from numerous different morphologies. Lack of acoustic ability in a fish can be the result of absence of acoustic ability in an entire taxonomic lineage or secondary mechanism atrophy or loss within an acoustic lineage. Among catfishes acoustic morphology is strongly correlated with and modified from well developed defensive spines for one mechanism type and most acoustic families are benthopelagic. Some deep-sea fish families have acoustic mechanism morphology but there is limited evidence yet from field studies of sound production. Sharks and rays are considered non-acoustic fishes although disturbance sounds were recorded from a stingray. Cartilaginous fishes lack structures commonly modified into acoustic mechanisms: bone and gas filled resonance chambers.

Although no particular ecosystem (freshwater and marine), ecotype (benthic to pelagic), activity period (nocturnal or diurnal), life history strategy (egg laying on substrate versus broadcast spawning into the water column) or social organization (solitary versus schooling) is exclusively associated with acoustic behavior in fishes (Fig. 2) some basic trends are emerging. Calling activity

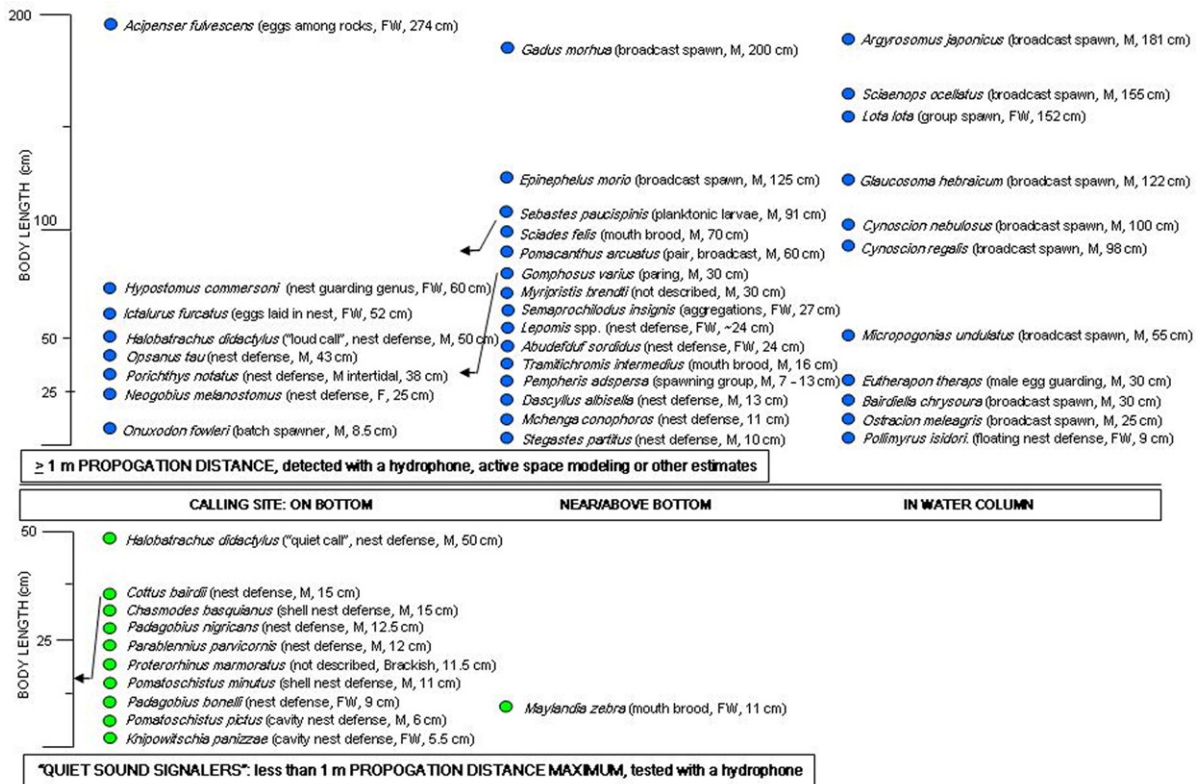


Fig. 2 Acoustic fish species ranging from freshwater ("FW"), through brackish to marine ("M") habitats, small to large body size, short to long range propagation distance vary in reproductive strategies. Body length is for maximum standard or total length as reported on FishBase (<http://www.fishbase.org/search.php>) or from the original publication. Fish calls for loud species represent family diversity, not all species are shown (n=55 species in 30 families). Quiet sound signaling has been proposed for 10 species in four families (the eleventh species and fifth family, *H. didactylus*, also produces loud signals).

is predominantly nocturnal (52%) and crepuscular (22%) as opposed to diurnal (22%) for 56 species in 22 families and 12 orders (3% no diel differences). Species whose social interactions are well developed include sound producers. Male display in polygynous species is correlated with abundant and complex calling. A cichlid with a cooperative, complex social system and biparental care is silent. Many acoustic species are found in benthic communities where individuals defend territories and in pelagic chorusing aggregations where individuals may form social dominance hierarchies and likely display to potential mates. Common themes among acoustic fishes include agonistic interactions and male display associated with a defended nest and extended parental care.

Fish Call Characteristics: Simple Versus Complex

Fish call components may include elements of seven different categories of temporal and frequency patterns (Fig. 4). Fish sounds range from simple to complex (Table 2) although most are not as complex as those of some higher vertebrates. We define a sound as more complex based on the presence of more bioacoustic components in a sound relative to other species in the family. There are two common types that may serve functionally different roles. Multipulsed calls have interpulse intervals or "off-times" within the basic sound unit (silence between regularly timed pulses) and may be narrow or broad in their frequency bandwidth. Continuous pulse series often with tonal components (pure tones or narrower frequency range) lack interpulse intervals. Pulse number and repetition rate varies among sympatric conspecifics, supporting a hypothesis of species recognition, although for some congeners these differences are in amplitude, frequency or waveform. Playback studies have demonstrated damselfish neighbor versus nonresident recognition and female preference for their own species calls is based on pulse number and interpulse interval. The croaking gourami (*T. vittata*) produces pulsed sound series in all contexts. The most complex fish sounds are male courtship sounds that combine multipulsed sounds with highly regular interpulse intervals and continuous waveforms with tonal components. The quiet calling padanian goby (*P. bonelli*), all vocalizing toadfishes and several grouper are examples of species that produce complex male advertisement calls. Some goby males produce tonal sounds only as an advertisement call while a female is outside the nest and multipulsed sounds during courtship with a female inside the nest. The nonlinear calls of the three-spined frogfish (*Batrachomoeus trispinosus*) are comparable to complex vertebrate calls.

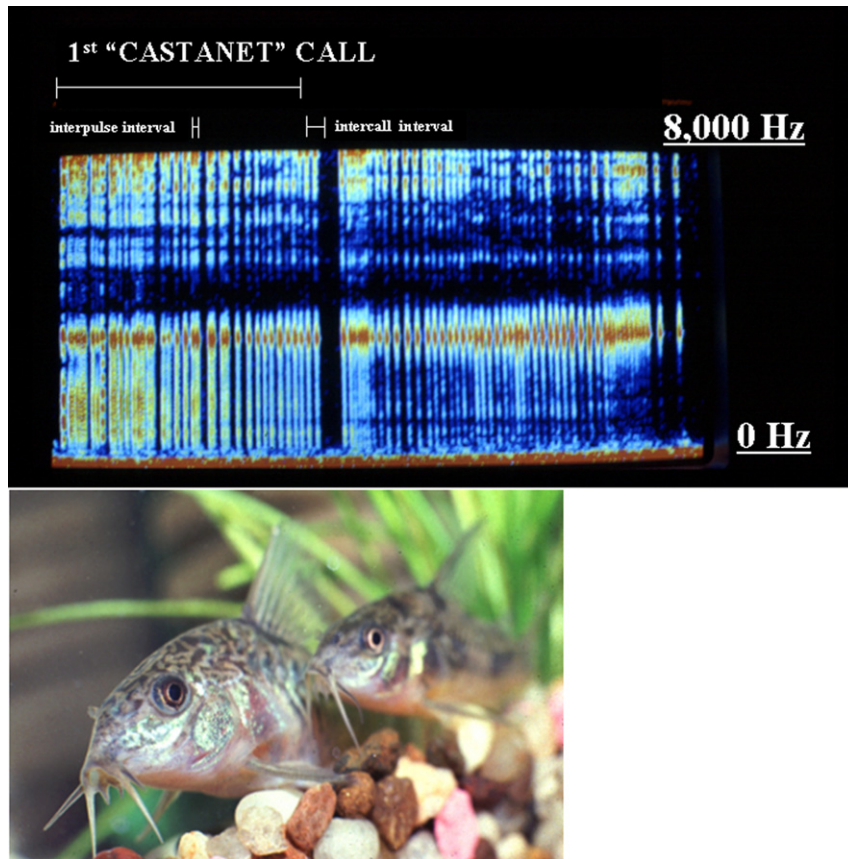


Fig. 3 A spectrogram (frequency vs. time graph) of two interpuised calls passively acoustically detected from an aquarium population of the diurnal miniature catfish *Corydoras paleatus*. The smaller male, see photo, produces a courtship associated sound while courting a silent female immediately prior to egg fertilization. These “castanet” calls consist of a series of pulses with interpulses (total time axis ~500 ms in duration) and cover a broad frequency range (~800–8000 Hz). The sounds are difficult to detect in large aquaria and are likely short range quiet sounds (I.M. Kaatz pers com 2015).

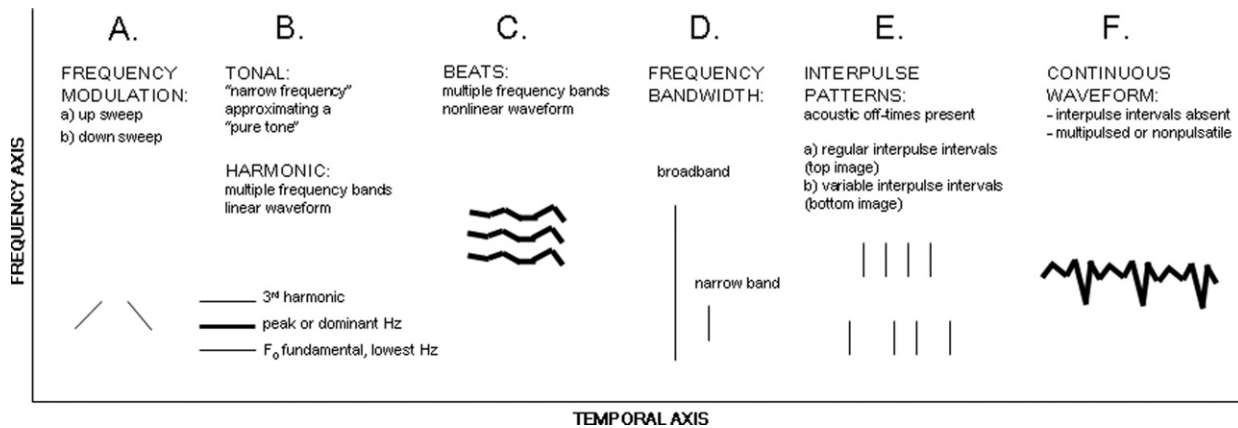


Fig. 4 Bioacoustic traits of fish sound signals for temporal and frequency components.

Fish Call Characteristics: Duration, Amplitude, Propagation Distance, and Frequency

The bioacoustic parameters of fish sounds are important for understanding their functions. Descriptions of fish sound ranges for 51 families and 181 species are 236 ms ± 275 SD for the minimum and 1892 ± 1241 SD for the maximum duration. The maximum

Table 2 Examples of fish sound variation across taxa within families. Call types are described according to onomatopoeia provided by authors in source publications

"Simple" relative to other species in family	"Complexity" greater compared to other species in family	Family
<i>Repertoire size</i>		
2 "Single click, click series" <i>Chromis viridis</i>	5 "Pop, chirp, long chirp, grunt, burr" <i>Stegastes partitus</i>	Pomacentridae
3 "Single knock, knock series, grunt" <i>Gadus morhua</i>	5 "Pulse series," continuous waveform "humming" <i>Melanogrammus aeglefinus</i>	Gadidae
1 "Grunt" <i>Bathygobius soporator</i>	2 "Grunt, stutter" <i>B. curacao</i>	Gobiidae
2 "Grunt, staccato" <i>Zosterisessor ophiocephalus</i>	4 "Harmonic, noisy, pulsed, complex" <i>Gobius cruentatus</i>	Gobiidae
2 "Hoot, growl" <i>Marcusenius altisambesi</i>	5 "Grunt, moan, growl, hoot, click train" <i>Pollimyrus isidori</i>	Mormyridae
3 "Short pop, long pop1 and 2" <i>Amphiprion akallopisos</i> from Indonesia	4 "Chirp, short and long pop, long pop 1 and 2" <i>A. akallopisos</i> from Madagascar	Pomacentridae
2 "Pop, pulsed" <i>Abudefduf sordidus</i>	6 "Pulsed" <i>Dascyllus flavicaudus</i>	Pomacentridae
1 "Monophasic pulse" <i>Cyprinella lepida</i>	3 "Burst, chirp, rattle" in other <i>Cyprinella gibbsi</i>	Cyprinidae
<i>Spectrographic pattern variation: single versus multiple call components during agonism and courtship</i>		
1 "Burst" irregular pulses <i>Codoma ornata</i>	3 "Knock, short knock, burst" <i>Cyprinella galactura</i>	Cyprinidae
1 "Tonal" <i>Padagogobius nigricans</i> , courtship only	2 "Pulsed and tonal" complex combination <i>Padagogobius bonelli</i> , courtship only	Gobiidae
<i>Call pulse number</i>		
1–2 Pulses <i>Cyprinodon bifasciatus</i>	1–14 Pulses <i>Cyprinodon variegatus</i>	Cyprinodontidae
1–2 Pulses for heterospecifics <i>Dascyllus albisella</i>	> 2 Pulses for conspecifics <i>D. albisella</i>	Pomacentridae
1–6 Pulses "knock" non-reproductive <i>Micropogonias undulatus</i>	> 6 Pulses disturbance and reproduction <i>M. undulatus</i>	Sciaenidae
<i>Call duration</i>		
Agonistic "grunt" 50–200 ms, <i>Porichthys notatus</i>	Male advertisement "hum" min to > 1 h, <i>P. notatus</i>	Batrachoididae
Agonistic intruder attack call 17 ms (max), <i>Chaetodon multicinctus</i>	Mated pair alert call 5700 ms (max), <i>C. multicinctus</i>	Chaetodontidae
Conspecific chase, shorter duration <i>D. flavicaudus</i>	Mating call, longer duration <i>D. flavicaudus</i>	Pomacentridae
Shorter calls interspecific competition <i>Carapus homei</i> and <i>C. boraborensis</i>	Longer calls intraspecific competition <i>C. homei</i> and <i>C. boraborensis</i>	Carapidae

call duration includes 60,000 ms for a toadfish grunt train. Amazing outliers include the plainfin midshipman (*P. notatus*) whose tonal "hum" can continue un-interrupted for 7.5 min, approximately 14 min and > 1 h. Another song or extended vocal display call is described as nearly continuous lasting 20 min for the haddock (Table 3). Among the simplest sounds are single pulsed escape "knocks" and "thumps" produced when a fish moves away from a threatening source, single knocks are produced by acoustic fishes, but these could be incidental to movement. Their duration ranges from < 20 to ~ 500 ms. Territorial or fighting sounds are highly variable but often of moderate duration, typically lasting from ~ 10 to 3000 ms.

Duration of individual agonistic calls is not a fitness correlate in a toadfish study but extended reproductive acoustic display could be a fitness correlate or indicator. A physiological estimate for continuous calling based on energy reserves is 15 min for the oyster toadfish (*O. tau*), but its muscles fatigued for individuals at 5 min. The longest duration and most temporally stereotyped calls are produced during pre-reproductive, courtship or spawning activity. Prolonged courtship displays or songs (Table 3), consisting of non-continuous sounds, can be repeated single sound types or may incorporate multiple basic sound units of different call types that last for 55 s for the "spawning chant" of temperate white weakfish (*Atractoscion nobilis*) (> 2000 "purrs" and 77 "knocks"). The longest calling bouts monitored have been > 2 h for a big-snout croaker male (*Johnius macrorhynchus*) and > 3 h for individual males of the plainfin midshipman (*P. notatus*).

Fish call amplitudes (n=58 species, 25 families) range from the lowest reported at close range, 63 dB_{rms} re 1 μPa at 5–10 cm, for the grass goby (*Zosterisessor ophiocephalus*) to the highest calculated source level (at 1 m), averaged 165 dB_{rms} re 1 μPa for the black drum (*Pogonias cromis*). Fish call amplitude values are described using different technical methods and are difficult to directly compare. Larger body size correlates with larger call amplitude for many species investigated. In the croaking gourami (*T. vittata*) agonistic calls are twice as loud as pre-spawning calls indicating a more private channel for mate communication. Amplitude is intertwined with call range for species and therefore, the distance over which sound can be used to communicate. Call distance can be divided into two broad categories, those whose sounds propagate well over 1 m, and those whose sounds propagate over much shorter distances (Fig. 2). Propagation distances range from cm to m in propagation distance for individuals. Choruses of breeding aggregations can be detected up to several km. However based on calling initiation and response to playback fish are known to react at ranges of centimeter or up to 4.5 m (Table 4). Propagation distance varies according to call frequency and can be influenced by recording conditions: ambient noise level, water depth, substrate type.

Table 3 Extended acoustic displays or songs of individual fishes. Species examples are reproduction associated or from aquarium or field populations during reproductive season unless otherwise noted. The plainfin midshipman produces very long duration continuous calls and multiple call extended vocal displays. All other sound bursts, bouts, trains, series, or sequences include intersound intervals that extend beyond the typically described basic sound type. Extended acoustic displays could reflect motivation, physiological condition, or fitness variables

Taxonomy: family species	Duration	Sound descriptions, "onomatopoeia" (context or source)
Sciaenid <i>Aplodinotus grunniens</i>	3–5 s	Multiple sound series in call (field and aquarium populations)
Mormyrid <i>Pollimyrus isidori</i>	3–10 s	"Moan, growl and grunt" (male complex song episode, reproductive condition)
Osphronemid <i>Trichogaster leerii</i>	3.5 s	Pharyngeal sound sequence (aquarium populations)
Gobiid <i>Pomatoschistus marmoratus</i>	4.8 s	Variable interval multiple pulse trains (male call, reproductive condition)
Pempherid <i>Pempheris schwenkii</i>	15 s	(Distress sounds)
Triglid <i>Prionotus carolinus</i>	10–15 s	"Clucking series" (spontaneous sounds from aquarium populations)
Mormyrid <i>Pollimyrus marianne</i>	17 s	"Moan-grunt" bout (male song to visiting female)
Gobiid <i>Gobiosoma bosc</i>	~18 s	Irregular pulse series (male reproductive display)
Characid <i>Mimagoniates inaequalis</i>	25 s	"Croaking" pulsed series and bursts (male courtship display)
Carapid <i>Carapus boraborensis</i>	25–30 s	Variable "drumbeat" sequence (unknown context)
Batrachoidid <i>Batrachomoeus trispinosus</i>	36 s	"Hoot" call train (passive acoustic, aquarium)
Gadid <i>Gadus morhua</i>	37 s	"Single knocks, knock series and grunts" long call (territorial behavior)
Sciaenid <i>Atractoscion nobilis</i>	7–55 s	"Thud" and "drum roll" with variable sound intervals (spawning chant)
Cyprinid <i>Pseudobarbus burchelli</i>	~1 min	Burst of rapid "chirps" (male, reproductive season)
Sciaenid <i>Micropogonius furnieri</i>	1–3 min	Pulsed series male advertisement call repeated in bouts (reproductive condition aquarium population)
Gadid <i>Melanogrammus aeglefinus</i>	~20 min	"Nearly continuous humming" (male reproductive call)
Batrachoidid <i>Porichthys notatus</i>	7.5, ~14 min, >1 h	Continuous "humming" calls (male call at nest)
Sciaenid <i>Cynoscion regalis</i>	65–85 min	"Drumming" activity (solitary males in aquaria)
Sciaenid <i>Johnius macrorhynchus</i>	143 min	Variable multiple call series (solitary male in aquarium)
Batrachoidid <i>Porichthys notatus</i>	218 min	Multiple non-continuous "hums" (passive acoustics)

Fish sound frequencies are wider than fish hearing, ranging from infrasound below 10 Hz for butterfly fishes, up to 20 kHz for sturgeon pre-spawning sounds and pinfish agonistic jaw snapping and 22 kHz for herring sounds. Descriptions of fish call ranges for 165 species in 60 families are $322 \text{ Hz} \pm 609 \text{ SD}$ for the minimum and $2803 \text{ Hz} \pm 3778 \text{ SD}$ for the maximum frequency. These values overlap with a typical fish's hearing range. Sounds with frequency ranges above fish audibility could target non-fish listeners. Dominant frequency (Fig. 4) is behaviorally significant. It is correlated with body size for species in many tested families but has not been as widely described. Frequency call traits are assessed by females during mate choice and correlate with male fitness physiological indicators. The Lusitanian toadfish male calls are individually distinctive based on dominant frequency and frequency modulation. Female damselfishes prefer larger males that produce lower dominant frequency calls. Low fundamental frequency reflects high androgen levels possibly reflecting male fitness. Tonal (vs. broader band) frequency sounds are almost exclusively associated with male reproductive display.

Chorusing and Shoaling Behavior: Silent, Incidental and Volitional Sound Production

Several schooling fish families are silent, lack evidence for well established volitional sounds in monitoring studies (butterfishes, mullets, new and old world silversides, tuna, cardinalfishes). Salmon and anchovy "biosignals" detected from migratory aggregations and the feeding associated clicks of pipefish and seahorses are undetermined in nature. Herring contribute significantly to the marine soundscape producing pulsed sounds in a diel pattern but non-acoustic functions are also proposed. The plankton feeding "popping" sounds detected in the area of mesopelagic aggregations of hypothesized lanternfishes are distinctive incidental sounds. In the stone moroko (*Pseudorasbora parva*), that associates in feeding aggregations, individuals intercept and are attracted to feeding sound cues of conspecifics.

True chorusing is well documented for higher amplitude or "loud" signalers. Large schools of marine catfishes forage near the bottom in poor visibility coastal waters and produce nocturnal short pulse burst "percolator" as well as other distinctive sounds that could function as contact calls. A sweeper (*P. adspersa*) has been experimentally shown to produce calls that influence group cohesion. A burbot, drum, cod, toadfishes and groupers produce sounds in the breeding season in aggregations with evidence of lekking behavior in cod. Chorusing activity typically begins close to or after sunset. Diel peak patterns are most often crepuscular or nocturnal. Fewer species have diurnal calling peaks. Chorusing locations and sound levels vary seasonally and can also be influenced by depth, light, salinity, turbidity, lunar phase, tidal stage, strong wind or storm and temperature which directly constrain acoustic mechanism function. Choruses have the greatest propagation distances (Table 4).

Table 4 Fish call propagation distances (n=30 species in 15 families) and acoustic behavioral reaction or initiation distance (15 species in 12 families; one cue, all other sounds signals). Two chorus examples which include undetermined fish species and sounds are included for comparison as well as one hypothesized seismic signaler

<i>Communication categories: family genus species</i>	<i>Maximum propagation distance estimates^a</i>	<i>Notes</i>
<i>Sound propagation shorter-range (< 1 m)^b</i>		
Gobiid <i>Knipowitschia panizzae</i>	1–2 cm “rec. max”	Rapid amplitude decline, limited sound propagation proposed
Gobiid <i>Pomatoschistus pictus</i>	approximately 2 cm “rec. max”	Clear wave patterns of spectrograms near not far away from fish
Gobiid <i>Pomatoschistus minutus</i>	1–3 cm	Low amplitude, propagation proposed to be limited close to nest
Batrachoidid <i>Halobatrachus didactylus</i>	10 cm “rec. max”	One low amplitude call type, not detected far from caller
Cottid <i>Cottus bairdii</i>	~10 cm	Acoustic estimate for hydrophone detected sounds
Gobiid <i>Proterorhinus marmoratus</i>	10 cm	Waveforms unclear below this distance
Blenniid <i>Parablennius parvicornis</i>	25 cm	Less under noisier conditions
Blenniid <i>Chasmodes bosquianus</i>	20–30 cm	Distance maximally detectable with hydrophone
Cichlid <i>Maylandia zebra</i>	40 cm “rec. max”	Very low amplitude sound, waveform nearly undetectable at 40 cm
Gobiid <i>Padagobius nigricans</i> and <i>P. bonelli</i>	50–60 cm	Significant attenuation of sounds by this distance in quiet conditions
<i>Sound propagation longer-range (≥ 1 m)^c</i>		
Serranid <i>Hypoplectrus nigricans</i> “mating sound”	A few meters	Barely audible to human hearing, maximum distance tested with hydrophone
Mormyrid <i>Pollimyrus isidori</i>	0.5–2 m	Waveform coherent up to 0.5 m, longer range environmentally influenced
Pomacentrid <i>Abudefduf sordidus</i>	2 m	Field tested
Batrachoidid <i>Porichthys notatus</i>	2–3 m	Near field
Centrarchid species	3–4 m	Maximum in shallow water tested
Batrachoidid <i>Halobatrachus didactylus</i>	4 m	Boatwhistle call
Batrachoidid <i>Opsanus tau</i>	5 m	Maximum detectable
Sciaenid <i>Bairdiella chrysoura</i> individual in chorus ^c	1–7 m	Detection distance
Pomacentrid <i>Stegastes partitus</i>	6–8 m	Field study
Sciaenid <i>Micropogonias undulatus</i>	8 m	Estimate based on idealized propagation
Pomacentrid <i>Dascyllus albisella</i>	11–12 m	Field study
Batrachoidid <i>Halobatrachus didactylus</i>	up to 8 m vs. up to 30 m	“Boatwhistle” call shallow vs. deeper water
Pempherid <i>Pempheris adspersus</i>	0.6–31.6 m	Estimated active space varies seasonally with moon phase and noise levels
Sciaenid <i>Sciaenops ocellatus</i>	32 m	Estimate based on spreading model
Carapid <i>Onuxodon fowleri</i>	37 m	Estimate based on pulse reflection
Sciaenid <i>Cynoscion regalis</i>	32 m, 50 m	Estimate based on spreading model
Serranid <i>Epinephelus morio</i>	70 m	Estimate based on hearing and noise
Glaucosomatid <i>Glaucosoma hebraicum</i>	100 m	Hypothetical based on amplitude and spherical spreading
Sciaenid <i>Pogonias cromis</i>	33–108 m	Estimate based on hearing and background noise
Sciaenid <i>Cynoscion nebulosus</i>	128 m	Estimate based on idealized propagation
Sciaenid <i>Bairdiella chrysoura</i>	1–316 m	High to low background noise
Fish and invertebrate marine chorus	2 km	Field study
Terapontid <i>Terapon theraps</i> fish chorus	5–8 km	From center of school
Gadid <i>Gadus morhua</i> chorus	10 km	Hypothetical calculation
Planktivorous fish “pops” chorus (incidental sound)	> 15 m	Active source from reef; chorus effect on ambient noise > 15 km
<i>Behavioral response distance</i>		
Cobitid <i>Yasuhikotakia modesta</i>	A few millimeter to 15 cm	Initiation of agonistic sounds
Syngnathid <i>Hippocampus reidi</i>	Less than ~ 15 cm	Initiation of courtship sounds
Cichlid <i>Archocentrus centrarchus</i>	20 cm	Agonistic sound production most common
Callichthyid <i>Megalechis thoracata</i>	Less than ~ 26 cm	Initiation of agonistic sounds
Mormyrid <i>Marcusenius</i> spp. (three species)	Less than 30 cm	Initiation of social calls in dyadic encounters
Gobiid <i>Padagobius martensii</i>	40 cm	Playback response distance
Cyprinid <i>Pseudorasbora parva</i>	40 cm	Feeding sound cue initiates attraction in conspecifics
Pomacentrid <i>Dascyllus flavicauda</i>	50 cm–1 m (territory size)	Female entry into male territory initiates male calling
Holocentrid <i>Myripristis argyrosomus</i> and <i>M. brendti</i>	2–2.9 m	Response to conspecific sounds

(Continued)

Table 4 Continued

Communication categories: family genus species	Maximum propagation distance estimates ^a	Notes
Chaetodontid <i>Chaetodon multicinctus</i>	> 3 m	Initiation of pair approaching model bottle live intruder
Batrachoidid <i>Porichthys notatus</i>	4.5 m	Female attraction to male calls
Ariid <i>Sciaedes felis</i>	4.5 m	Lemon shark attracted to distress calls

^aEstimates reported on the basis of one or a combination of the following techniques: mathematical sound propagation models, audiograms, bioacoustic signal pattern degradation at increasing distances from a calling fish, behavioral reactions of listener fish to fish sounds at known distances; values are estimates for a given species under particular field or semi-natural laboratory conditions.

^b"Record. max." = maximum recording distance at which hydrophone was placed, absolute maximum propagation distance may be further; we only included values for species if authors proposed short range propagation.

^c"chorus" = multiple individuals calling in a designated area over a similar time period.



Fig. 5 Example of acoustic fishes (a) the oyster toadfish *Opsanus tau*; (b) the plainfin midshipman *Porichthys notatus*; (c) the graceful peafish *Encheliophus gracilis*; and (d) a driftwood catfish *Trachelyopterus galeatus*. Panel (b) shows a large type I singing male next to a smaller female fish. Photo credits Margaret Marchaterre ((a),(b)), Eric Parmentier (c) and Ingrid Kaatz (d).

Reproductive Sound Signaling: Male Display and Female Mate Choice

Sound production increases during the breeding season for many acoustic fishes and the characteristics of these calls potentially convey information about an individual's age, sex, reproductive condition, size, identity and health or fitness. Species comparisons within families have identified differences in courtship associated sounds in 10 families representing five orders. Gobies can use male advertisement calls for localizing conspecifics. Sound production during the breeding season is predominantly by males on territories, between males during conflicts over resources, by males displaying to females and less frequently between females or rarely by females during courtship. Male calling is multifunctional serving to attract mates and repel competitors. Agonistic sounds are louder than courtship sounds of both sexes in the croaking gourami (*T. vittata*). This suggests a cost to loud sounds (interception by predators or conspecifics) and a priority for a close and intimate channel of communication between sender and receiver. In the plainfin midshipman and blennies, males vocalize as two different phenotypes. Smaller sneaker males intercept sounds of larger displaying bourgeois males in order to locate females and steal egg fertilization. Sneaker male appearance and sounds are similar to those of females while larger males defend nests and produce complex sounds.

Female preference for male courtship associated calling traits is an important selection force that shapes a male's acoustic display. Male signals could be constrained by mechanism design (eg, body size, muscle mass). These would be inherently "honest" signaling features indicating health, vigor or energy reserves. Female choice and playback studies indicate females are likely evaluating males for fitness characters on the basis of frequency, amplitude or temporal call traits. Female gobies mate with males whose calls are longer in duration and have higher condition factors than other males. Female toadfish and plainfin midshipman (Fig. 5) are attracted to speakers broadcasting male calls. Choice experiments of plainfin midshipman females show preference for louder and longer duration male sounds and tonal over pulsed sounds. In mating partners of the hermaphroditic butter hamlet (*Hypoplectrus unicolor*) individuals alternate acoustic roles with one partner producing a spawning sound just before gamete release. The production of spawning sounds, which have been identified in other families and species, could play a role for breeding synchrony for external fertilizers.

Agonistic Sound Signaling Within Species

Acoustic social dominance hierarchies among conspecifics could determine access to resources in communities of social species. Unlike during reproduction, when patterned sounds are important for species recognition, agonistic contexts may require less

complexity and specificity, as has been shown for the simple and similar sounds of *Amphiprion* species. However in defending resources, communicating the age, size or strength of an individual is advantageous. Individual identity may play a role within damselfish species for neighbor versus intruder recognition. Contest winning is enhanced by the use of sound signals in size matched gourami and reduces aggression and fight escalation in a cichlid and a toadfish. Both females and males produce similar agonistic sounds in many species. Toadfish populations exhibit alternation of calling among neighboring males, antiphonal calling, where social dominance is the proposed function. Nest and territory defense calls correlate with frequency and temporal traits as well as acoustic muscle lipid content in a toadfish. "Keep out" signals are produced by damselfishes to repel intruders from resting crevice territories. Sound production is reported during feeding competition in many species and could function to repel or alert conspecific competitors but no tests have been conducted. Agonistic sounds, compared for species within families, differ significantly for a greater number of families than those that have conserved call traits.

Avoiding and Repelling Predators

Predators could place very strong selection pressures on whether or not fishes are acoustic as well as how, where and when sounds are produced. Predator and prey could acoustically interact with each other in several ways: (1) predator interception of prey calls; (2) prey interception of predator calls; (3) prey production of "distress," "alarm," "escape," "startle," "warning," or "threat" sounds when seeing or attempting to flee from a predator before attack; and (4) "disturbance," prey responding to a predator once physically restrained. Catfish families produce disturbance sounds when handheld or after a predator has physically attacked them in conjunction with weaponized defense mechanisms that can include chemical secretions, pinching, stabbing and envenomating devices that could be warning calls. Two studies of this hypothesis failed to evidence sounds as predation deterrents. Tigerperch increased disturbance calling rate is triggered by predator presence and attack. This experiment supports the proposed alarm function of these calls. Herring sound production during predator attacks accompanies bubble-release that could confuse predators. Playback of distress sounds of the hardhead sea catfish (*Sciades felis*) attracts sharks (Table 4). A comparison of disturbance sounds within families among piranha, squeaker catfishes and squirrel fishes showed no significant difference in bioacoustic traits. Swimbladder disturbance sounds compared among species within drum, bigeye, triggerfish, talking and driftwood catfish families are significantly different.

Predator interception of prey fish signals has been demonstrated. Dolphins can locate and are attracted to the acoustic signals of sciaenids. Eavesdropping by prey of predator calls has been demonstrated in a toadfish whose calling is reduced when dolphin calls are broadcast. In fact, toadfish show increased levels of stress hormones in response to dolphin sounds. Sharks are attracted to pulsed but not tonal sounds, indicating a risk element of many fish calls. A recent study identified that the calls of the black drum and sea catfish significantly reduce feeding activity of a marine crab, invertebrate prey.

Escape sounds produced by fishes include hydrodynamic broadband incidental sounds, simple knocks which could be volitional or incidental, or more complex volitional sounds. Squirrel fish alarm calls have been reported in the presence of potential predators but tests of this hypothesis have been negative.

Signal Modality Trade-Offs, Multimodal Complimentary and Modality Shifts

Trade-offs where acoustic signals play either a dominant or absent role are evidenced among fishes and within acoustic clades. Salmon produce infrasound spawning sounds, while their ear can detect such low frequencies the lateral line has been demonstrated as a key sensor. Catfish chemical alarm signals are inversely related to the development of sound production. Electro-signaling has been derived from swimbladder acoustic muscles in the blotched upside-down catfish (*Synodontis nigriventris*), with an acoustic species with long calls (*Synodontis grandioops*) lacking electric organ discharge. Electric signaling is similarly proposed to have arisen from vocal muscles in stargazers. Some gourami species (paradisefish *Macropodus opercularis*) produce few social sounds and are proposed to communicate visually while others are predominantly acoustic indicating tradeoffs between signal modalities. Cichlid male acoustic displays have been proposed to differ most among species where males are visually more similar, which would support the hypothesis of communication modality trade-off.

The complementarity of different signal types is evidence in acoustic fishes. The electric catfish (*Malapterurus beninensis*) produces both electric and acoustic signals. Females of the painted goby (*Pomatoschistus pictus*) require visual stimuli to respond to the calls of a male in a playback study, indicating the importance of multimodal components in communication, other acoustic fishes exhibit similar mate choice behavior. In the elephantfish (*P. isidori*), males court females with complex calls while sex discrimination can occur with electric signals. A recent study of the lake sturgeon *Acipenser fluvescens* has revealed the presence of electric pulses and sounds during reproductive behaviors, their function requires further study. There is a significant overlap between the auditory and lateral line system in fish. Postural changes evaluated in butterfly fishes produce simple water current sounds, infrasound, that are likely sensed by the lateral line and inner ear at close proximity while derived mechanisms produce more complex sounds known as detectable by the inner ear. All of these examples indicate potential or demonstrated complimentary of different modalities.

Modality shifting may occur within acoustic fish lineages. The sculpin (*Cottus bairdii*) produces courtship sounds that transmit further in the substrate than in the water column, seismic signaling is proposed as more important than water-borne signaling. Two freshwater sculpins produce water-borne agonistic sounds which may only function as tactile or seismic signals as their audibility in high flow regimes is masked. Other sculpin sounds have been treated as waterborne signals by researchers. A gobiid mudskipper (*Periophthalmodon septemradiatus*) produces complex signals detected in the substrate when courting on terrestrial mudflats while most gobies are waterborne acoustic signalers. Continued study of the apparent modality shifting between electric, visual, tactile, possibly seismic and water-borne signals across and within fish families will offer special insight into the function of audible sounds as well as the process of signal evolution.

Conclusions

What Fish Sounds Can and Cannot Do

Like all other sound signaling animals, fishes use sounds to enhance their behavioral displays. Fish sounds include components that correlate with age, size, sex, social status, male fitness, species and individual identity, reproductive condition and spawning readiness. Individual identity of acoustic call parameters has been shown for male courtship calls within species of cichlids, cod, toadfishes and freshwater elephant fishes but how fish might use such information beyond neighbor recognition has not been determined. Communication functions that fish sounds are not known to serve include release calls, parent-offspring signaling, sibling recognition, acoustic aposematism and mimicry. Many fish taxa are known to produce volitional sounds with derived sound producing mechanisms in disturbance but remain unexamined in terms of their social behavior and call acoustics. Because we now know that short propagation distance and low amplitude sounds occur more commonly than was once thought we cannot be certain of the acoustic status of casually observed fish. High amplitude, interception-prone, complex calls function in species that can either avoid predation by calling from protected sites or avoid the risk of predation by other means to communicate over longer distances are being actively explored by fish bioacousticians with the tools of passive acoustic detection of wild populations.

New Research Areas

New studies continue to reveal how fishes use sounds: a larval planktonic snapper has been discovered as acoustic in aggregations or as solitary individuals; many species of larval fishes are attracted to soundscapes that include fish sounds on coral reefs however the role of the fish sound component has not been supported as primary; sounds are supported as innate in two examined species; juveniles of all newly investigated species continue to evidence acoustical capability in agonistic interactions; calls are amplitude modulated in noise varying habitats (Lombard effect); and geographic variation continues to support the presence of dialects for more examined species. New environmental influences on calling have been observed: sand piling on calling burrows of a male goby and invertebrate host bivalve shells of pearlfishes both increase the amplitude of calls. Supporting evidence for interference avoidance calling was demonstrated in a marine coastal canyon cave soundscape, proposed fish nocturnal sounds are acoustically divergent while diurnal sounds overlap. Finally there is a growing recognition that there are mute species in acoustic fish lineages (a sand goby), non-acoustic contexts in various acoustic species and non-acoustic geographic subpopulations as well as individuals within acoustic species (cichlids). Non-acoustic contexts are exemplified by all examined species in the genus *Amphiprion*, agonism is an acoustic context while sounds are absent during courtship. On a broader ecosystem scale a low frequency sound band widely demonstrated as produced by calling fishes, generated on coral reefs correlated with reef health. Each of these new studies opens areas of research in fish bioacoustics that have not been realized before and will provide opportunity for ongoing research. Fish acoustic ability is not only important for the success of particular species but is showing prevalence in the soundscape and in ecological interactions with other species in examined aquatic ecosystems.

Further Reading

- Amorim, M.C.P., Conti, C., Modesto, T., Goncalves, A., Fonseca, P.J., 2015. Agonistic sounds signal male quality in the Lusitanian toadfish. *Physiol. Behav.* 149, 192–198.
- Amorim, M.C.P., Pedroso, S.S., Bolgan, M., *et al.*, 2013. Painted gobies sing their quality out loud: Acoustic rather than visual signals advertise male quality and contribute to mating success. *Functional Ecology* 27, 289–298. doi:10.1111/1365-2435.12032.
- Bertucci, F., Attia, J., Beauchaud, M., Mathevon, N., 2012. Sounds produced by the cichlid fish *Metracrilma zebra* allow reliable estimation of size and provide information on individual identity. *J. Fish Biol.* 80, 752–766.
- Bocast, C., Bruch, R.M., Koenigs, R.P., 2014. Sound production of spawning lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Lake Winnebago watershed, Wisconsin, USA. *J. Applied Ichthyol* 30 (6), 1186–1194. doi:10.1111/jai.12556.
- Boyle, K., Colleye, O., Parmentier, E., 2014. Sound production to electric discharge: Sonic muscles evolution in progress in *Synodontis* spp. catfishes (Mochokidae). *Proc. R. Soc. B* 281, 20141197.
- Casaretto, L., Picciulin, M., Hawkins, A.D., 2015. Seasonal patterns and individual differences in the calls of male haddock *Melanogrammus aeglefinus*. *J. Fish Biol.* 87, 579–603.
- Colleye, O., Ovidio, M., Salmon, A., Parmentier, E., 2013. Contribution to the study of acoustic communication in two Belgian river bullheads (*Cottus rhenanus* and *C. peritretum*) with further insight into the sound-producing mechanism. *Front Zool.* 10, 71.
- Colleye, O., Parmentier, E., 2012. Overview on the diversity of sounds produced by clownfishes (Pomacentridae): Importance of acoustic signals in their peculiar way of life. *PLOS ONE* 7 (11), e49179.

- Conti, C., Fonseca, P.J., Picciulin, M., Amorim, M.C.P., 2015. How effective are acoustic signals in territorial defence in the Lusitanian toadfish? *J. Exp. Biol.* 218 (Pt 6), 893–898. doi:10.1242/jeb.116673.
- Estramil, N., Bouton, N., Verzijden, M.N., *et al.*, 2013. Cichlids respond to conspecific sounds but females exhibit no phonotaxis without the presence of live males. *Ecol. Freshw. Fish* 23, 305–312.
- Fine, M.L., Waybright, T.D., 2015. Grunt variation in the oyster toadfish *Opsanus tau*: Effect of size and sex. *Peer J.* 3, e1330. doi:10.7717/peerj.1330.
- Fish, M.P., Mowbray, W.H., 1970. *Sounds of the Western North Atlantic Fishes: A Reference File of Biological Underwater Sounds*. Baltimore, MD: The Johns Hopkins Press.
- Gannon, D.P., Barros, N.B., Nowoczek, D.P., *et al.*, 2005. Prey detection by bottlenose dolphins (*Tursiops truncatus*): An experimental test of the passive listening hypothesis. *Anim. Behav.* 69, 709–720.
- Gkenas, C., Malavasi, S., Georgalas, V., Leonardos, I.D., Torricelli, P., 2012. The reproductive behavior of *Economidichthys pygmaeus*: Secondary loss of sound production within the sand goby group? *Environ. Biol. Fish* 87, 299–307.
- Holt, D., Johnston, C., 2009. Signaling without the risk of illegitimate receivers: Do predators respond to the acoustic signals of *Cyprinella* (Cyprinidae)? *Environ. Biol. Fish* 84, 347–357.
- Holt, D.E., Johnston, C.E., 2014. Evidence of the Lombard effect in fishes. *Behav. Ecol.* 25 (4), 819–826. doi:10.1093/beheco/aru028.
- Hughes, A.R., Mann, D.A., Kimbro, D.L., 2014. Predatory fish sounds can alter crab foraging behaviour and influence bivalve abundance. *Proc. R. Soc. B* 281, 20140715.
- Kaplan, M.B., Mooney, T.A., Partan, J., Solow, A.R., 2015. Coral reef species assemblages are associated with ambient soundscapes. *Mar. Ecol. Prog. Ser.* 533, 93–107.
- Kenyon, T.N., 1994. The significance of sound interception to males of the bicolor damselfish, *Pomacentrus partitus*, during courtship. *Environ. Biol. Fish* 40, 391–405.
- Keiver, L., Boyle, K.S., Dragicevic, B., *et al.*, 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 of Ophidiidae. *Front Zool.* 9, 34.
- Kihlslinger, R.L., Klimley, A.P., 2002. Species identity and the temporal characteristics of fish acoustic signals. *J. Comp. Psychol.* 116 (2), 210–214.
- Knight, L., Ladich, F., 2014. Distress sounds of thorny catfishes emitted underwater and in air: Characteristics and potential significance. *J. Exp. Biol.* 217, 4068–4078. doi:10.1242/jeb.110957.
- Ladich, F., 2007. Females whisper briefly during sex: Context- and sex-specific differences in sounds made by croaking gouramis. *Anim. Behav.* 73, 379–387.
- Ladich, F. (Ed.), 2015. *Sound Communication in Fishes. Animal Signals and Communication*, vol. 4. Wien: Springer-Verlag.
- Ladich, F., Collin, S.P., Moller, P., Kapoor, B.G. (Eds.), 2006. *Communication in Fishes*, 2 vols. Enfield (NH): Science Publishers.
- Lobel, P.S., Kaatz, I.M., Rice, A.N., 2010. Acoustical behavior of coral reef fishes. In: Cole, K.S. (Ed.), *Reproduction and Sexuality In Marine Fishes*. Berkeley, CA: University of California Press, pp. 307–348.
- Longie, N., Fine, M.L., Parmentier, E., 2008. Innate sound production in the cichlid *Oreochromis niloticus*. *J. Zool.* 275, 413–417.
- Lugli, M., 2013. Sand pile above the nest amplifies the sound emitted by the male sand goby. *Environ. Biol. Fish* 96 (8), 1003–1012.
- Malavasi, S., Collatuzzo, S., Torricelli, P., 2008. Interspecific variation of acoustic signals in Mediterranean gobies (Perciformes, Gobiidae) comparative analysis and evolutionary outlook. *Biol. J. Lin. Soc.* 93, 763–778.
- McIver, E., Marchaterre, M.A., Rice, A.N., Bass, A.H., 2014. Novel underwater soundscape: Acoustic repertoire of plainfin midshipman fish. *J. Exp. Biol.* 217, 2377–2389.
- Mitchell, S., Poland, S.P., Fine, M.L., 2008. Does muscle fatigue limit advertisement calling in the oyster toadfish *Opsanus tau*? *Anim. Behav.* 76, 1011–1016.
- Montie, E.W., Vega, S., Powell, M., 2015. Seasonal and spatial patterns of fish sound production in the May River, South Carolina. *Trans. Am. Fish Soc.* 144, 705–716.
- Myrberg Jr., A.A., 1981. Sound communication and interception in fishes. In: Tavolga, W.N., Popper, A.N., Fay, R.R. (Eds.), *Hearing and Sound Communication in Fishes*. New York, NY: Springer-Verlag, pp. 395–426.
- Pedroso, S.S., Barber, I., Svensson, O., Fonseca, P.J., Amorim, M.C.P., 2013. Courtship sounds advertise species identity and male quality in sympatric *Pomatoschistus* spp. gobies. *PLOS ONE* 8 (6), e64620.
- Phillips, C.T., Johnston, C.E., 2008. Geographical divergence of acoustic signals in *Cyprinella galactura*, the whitetail shiner (Cyprinidae). *Anim. Behav.* 75, 617–626.
- Pisanski, K., Marsh-Rollo, S.E., Balshine, S., 2015. Courting and fighting quietly: A lack of acoustic signals in a cooperative Tanganyikan cichlid fish. *Hydrobiologia* 748, 87–97.
- Radford, C.A., Ghazali, S., Jeffs, A.G., Montgomery, J.C., 2015. Vocalisations of the bigeye *Pempheris adspersa*: Characteristics, source level and active space. *J. Exp. Biol.* 218, 940–948. doi:10.1242/jeb.115295.
- Ramage-Healey, L., Nowoczek, D.P., Bass, A.H., 2006. Dolphin foraging sounds suppress calling and elevate stress hormone levels in a prey species, the Gulf toadfish. *J. Exp. Biol.* 209, 4444–4451.
- Rice, A.N., Land, B.R., Bass, A.H., 2011. Nonlinear acoustic complexity in a fish “two-voice” system. *Proc. R. Soc. B* 278, 3762–3768.
- Rollo, A., Higgs, D., 2008. Differential acoustic response specificity and directionality in the round goby, *Neogobius melanostomus*. *Anim. Behav.* 75, 1903–1912.
- Rosenthal, G.G., Lobel, P.S., 2006. Communication. In: Sloman, K.A., Wilson, R.W., Balshine, S. (Eds.), *Behavior and Physiology of Fish*. Fish Physiology, vol. 24. Amsterdam: Elsevier, pp. 39–78.
- Ruppe, L., Clement, G., Herrel, A., *et al.*, 2015. Environmental constraints drive the partitioning of the soundscape in fishes. *Proc. Natl. Acad. Sci.* 112 (19), 6092–6097. doi:10.1073/pnas.1424667112.
- Scholz, K., Ladich, F., 2006. Sound production, hearing and possible interception under ambient conditions in the topmouth minnow *Pseudorasbora parva*. *J. Fish Biol.* 69 (3), 892–906.
- Staaterman, E., Paris, C.B., DeFerrari, H.A., *et al.*, 2014. Celestial patterns in marine soundscapes. *Mar. Ecol.-Prog. Ser.* 508, 17–32.
- Staaterman, E., Paris, C.B., Kough, A.S., 2014. First evidence of fish larvae producing sounds. *Biol. Lett.* 10, 20140643.
- Tricas, T.C., Boyle, K.S., 2014. Acoustic behaviors in Hawaiian coral reef fish communities. *Mar. Ecol.-Prog. Ser.* 511, 1–16.
- Tricas, T.C., Boyle, K.S., 2015. Diversity and evolution of sound production in the social behavior of the *Chaetodon* butterflyfishes. *J. Exp. Biol.* 218, 1572–1584. doi:10.1242/jeb.114256.
- Vasconcelos, R.O., Alderks, P.W., Ramos, A., *et al.*, 2015. Vocal differentiation parallels development of auditory saccular sensitivity in a highly soniferous fish. *J. Exp. Biol.* 218, 2864–2872.
- Verzijden, M.N., Heusden, J., Bouton, N., *et al.*, 2010. Sounds of male Lake Victoria cichlids vary within and between species and affect female mate preferences. *Behav. Ecol.* 21 (3), 548–555.
- Vicente, J.R., Fonseca, P.J., Amorim, M.C.P., 2015. Effects of temperature on sound production in the painted goby *Pomatoschistus pictus*. *J. Exp. Mar. Biol. Ecol.* 473, 1–6. doi:10.1016/j.jembe.2015.08.003.

Relevant Websites

- http://core.ecu.edu/BIOL/luczkovichj/fishsounds/fish_sounds.htm
East Carolina University.
- <http://www.fishecology.org/soniferous/soniferous.htm>
Studies on Soniferous Fishes.