# 2.09 Acoustic Ecology, Communication and Peripheral Signal Processing in Fishes

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## 2.09.1 Abstract

Fishes inhabit nearly all marine and freshwater environments. The high-density aquatic medium has shaped the evolution of their unique mechanisms of sound production and hearing, as well the basal characters used by terrestrial species for acoustic communication in a low-density gas environment. Sources of underwater sound produced by a vibrating swim bladder can be modeled as a monopole source, whereas sounds produced by a swimming or moving fish modeled as a dipole source. Particle motions, and in some cases sound pressure, are the two primary acoustic stimuli that are detected and perceived by fishes. Sounds produced by fishes are generally short pulses or pulse trains (peak frequencies from infrasound (1–20 Hz) to several kHz) and used during reproductive behaviors, defense of resources and aggression across species within large communities. The inner ear of fishes is of the basic vertebrate plan. However, many taxa have developed accessory hearing adaptations associated with the gas-filled swim bladder or other gas-filled structures, which can transduce sound pressure waves into local particle motions at the level of the ear. The ear of all fish is sensitive to particle motions associated with bulk hydrodynamic flow close to the source, and potentially nanometer particle motions associated with the spreading sound pressure wave at large distances. Auditory evoked potential studies show that many fish have a hearing frequency range of < 1000 Hz, with a higher sensitivity and extended range up to several kHz for those with modifications to detect sound pressure. Single cell neurophysiology experiments confirm that the fish saccule encodes

frequency, intensity and directional information from particle motion vectors, and is complemented by particle motion sensitivity of the utricle and lagena. Recent behavioral studies confirm that some females can locate vocalizing males by following the particle motion vectors from their advertisement calls.

### 2.09.2     What Is a Fish?

In the broad sense fishes are aquatic vertebrates that have gills throughout life, and fins for limbs when present (Nelson et al., 2016). They occur in nearly all freshwater and marine habitats, which share common physical constraints that have shaped their proximate mechanisms used for acoustic communication. Fishes represent the largest group of living vertebrates with more than 34,000 recognized species (fishbase.org). They appeared in the fossil record more than 500 million years ago (Long, 2011) and have since formed many distant lineages such as the jawless lampreys and hagfish, lungfishes, sharks and rays, lobed fin, and rayed-fin fishes (the latter of which includes the bichirs, sturgeons, gars, bowfins and the very speciose modern teleost fishes). Thus the living fishes have long and often separate evolutionary histories compared to the more recently derived mammals, dapsids (birds and "reptiles"), and amphibians.

   Studies on fish sound production and hearing have focused primarily on species that are amenable for observation and experiments in the laboratory. Some of the best developed models exist for those with specializations for enhanced hearing sensitivity that extend into the kilohertz range (e.g. the otophysic goldfish and relatives) and the relatively few species that produce loud calls with specialized swim bladder muscles. Work is expanding to interpret the mechanisms and functions of acoustic communication for additional species paying increasing attention to the particular physical properties of underwater sound sources in their native environments.

### 2.09.3     Underwater Sound

Particle motion, and in some cases also sound pressure, are the two acoustic stimuli that are detected and perceived by fishes. The relatively high density and velocity of sound in water (approximately 1500 m/s) have constrained and shaped the mechanisms of fish hearing when compared to terrestrial vertebrates that live in a low-density gas environment. There are several excellent comprehensive reviews on the physics of underwater sound in relation to fish evolution and hearing and the reader is referred to them for more details (Urick, 1983, Kalmijn, 1988, Rogers and Cox, 1988, Schellart and Popper, 1992, Fritzsch, 1999, Bass and Clark, 2003; Nedelec et al., 2016, Popper and Hawkins, 2018; Hawkins and Popper, 2018).

#### 2.09.3.1     Sound Pressure

Sound is a mechanical wave of disturbance, such as created by body movements of a vocalizing, moving or swimming fish. Collisions of the body with adjacent water particles are set in motion and produce a pressure wave that propagates away from the source in different directions. The spreading pressure wave produces small compressions, rarefactions, and directional particle motions (the vectors of displacement, velocity and acceleration) as the mechanical energy is transferred to adjacent water particles along the wave path. Sound pressure is most commonly measured with a hydrophone and allows rapid estimation of the scalar quantity of pressure, usually in reference to the Pascal (Pa) = 1 N/m$^2$.

   The spatial features of a spreading pressure wave are dependent upon the polarity of the sound source. Sounds produced by an expanding and contracting swim bladder can be modeled as a pulsating sphere (Harris, 1964; Sand and Hawkins, 1973), or monopole source (Fig. 1A). In an unbounded monopole acoustic field, the pressure wave expands radially in all directions from the source. Field measures of sound pressure created by vocalizations from the toadfish swim bladder show that the peak pressure field is primarily monopolar (including some quadrupole motions of the swim bladder as described by Fine et al., 2001), distributed radially across the bottom, and is more intense behind than in front of the fish (Barimo and Fine, 1998) as initially reported for the marine catfish, *Arias felis* (Tavolga, 1977). In contrast, an acoustic field produced by body movements of a swimming or vibrating fish can be modeled as a rigid vibrating sphere, or dipole (or multipole) source (Fig. 1B). In a dipole field, sound pressure does not propagate symmetrically in a radial pattern, is greatest along the dipole axis of vibration, and is null in the transverse plane to the axis of vibration (Kalmijn, 1988; Rogers and Cox, 1988). Thus sound pressure associated with an underwater acoustic field is highly dependent on the spatial motions and mechanical intensity of the source, as well as the direction and distance of the receiver from the source.

   The intensity and spectral characteristics of sound pressure are the primary features detected by the ear of terrestrial vertebrates. Many terrestrial species use interaural time and intensity differences in sound pressure to estimate the direction and distance of a sound source (Heffner and Heffner, 2018; Schnupp and Carr, 2009). However, pressure sensitive fishes lack analogous structures (e.g. pinnae, outer ear canals) developed in mammals to enhance detection of interaural pressure differences. Pressure sensitivity is limited to those species which possess a swim bladder or other gas-filled structure on or near the ear, or have mechanical linkages between a gas-filled bladder and the ear (Braun and Grande, 2008). In these cases a gas-filled bladder acts as a pressure-to-displacement transducer, in which displacement of the chamber wall sets in motion an indirect and local mechanical stimulation of the ear.
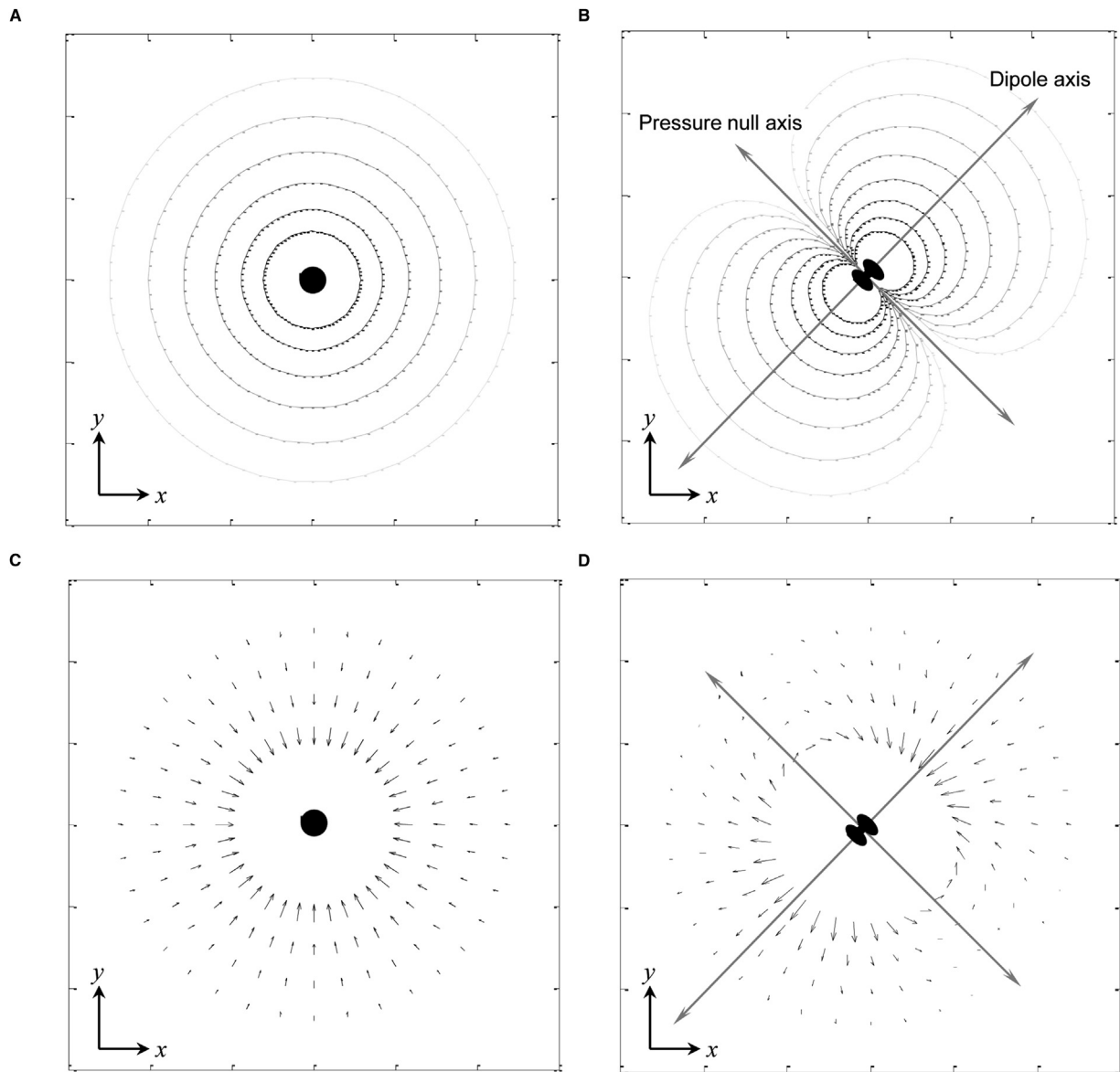
**Figure 1** **Two-dimensional contour plots of ideal monopole and dipole acoustic fields** (A) Pressure field for a monopole sound source is radially symmetric with higher pressures indicated by darkness of the contour band (B) Pressure field for a dipole sound source is bi-lobed with areas of high pressure along the dipole axis, and a pressure null orthogonal to the diploe axis (C) Particle motion vectors for a monopole source have radially symmetric particle motions with all vectors pointing toward (or away from) the source (D) Particle motion vectors for a dipole source along the dipole axis point toward (or away from) the source, whereas particle motion vectors along the pressure-null axis are parallel to the dipole axis. In addition, moving from the pressure-null to the dipole axis, the particle motion direction gradually changes from parallel to the dipole axis to pointing toward or away from the source. From Zeddies et al. (2012).

### 2.09.3.2    Particle Motion

#### 2.09.3.2.1    Hydrodynamic Flow

Close to a vocalizing or moving fish, the incompressible nature of water produces hydrodynamic flow in the surrounding medium. In a monopole field the hydrodynamic flow oscillates radially and is directed either toward or away from the source depending on the phase of oscillation (Fig. 1C). This is distinct from a dipole field (as produced by movement of the body along a single axis) in which elevated pressure in front and reduced pressure in the rear produces in an incompressible flow of water around the source (Fig. 1D). Particle motions have a maximum along the dipole axis and only here point directly toward or away from the source depending on the phase of oscillation. At other angles, particle motions can be in any direction including parallel to the dipole axis of vibration in the plane orthogonal to the axis of vibration. These bulk flows can induce whole body motions of a receiver

fish that is close to the source. They directly stimulate the inner ear by coupled motions of the sensory macula, as in the analogy of a shaking can of soda (the body) with a coin (an otolith) that moves across the bottom (the sensory macula). This mode of hearing can impart frequency sensitivities up to several hundred Hz (see Hearing section below).

### 2.09.3.2.2   Propagated Pressure Wave Motions

Far from the source where there is little bulk flow, the spreading pressure wave continues to produce small directional motions of water particles. These nanometer motions can theoretically be detected by the ear in all fish if of sufficient amplitude (see Hearing section below), and the high velocity of underwater sound extends this particle motion to distances farther from the source than in air.

### 2.09.3.3   The Near and Far Fields

The relative magnitude of particle motions associated with the incompressible water flow and the sound pressure wave are often used to distinguish the near field and far field regions of a sound source (summarized by Kalmijn, 1988; Rogers and Cox, 1988). In a spherically spreading wave as produced by a vibrating monopole, both particle velocity and the associated pressure fall of as $1/r$, where r = distance from the source. In contrast, particle velocity due to the hydrodynamic flow falls off more rapidly at $1/r^2$. Close to the source, where particle motions from hydrodynamic flow dominates, is termed the near field. Farther from the source, where particle motion from the spreading pressure wave exceeds that of incompressible flow, is termed the far field. The relationship between these particle motions is more complex in dipole fields. The particle motion vectors associated with the incompressible bulk movement of water near to the source decrease as $1/r^3$, the intermediate flow field as $1/r^2$, and those associated with the spreading sound pressure wave as $1/r$ (see Kalmijn, 1988; Coombs et al., 1992) (Fig. 2). These regions may be used to indicate the dipole near field (where particle motions associated with incompressible and intermediate flows dominate), and the dipole far field (where particle motions with the pressure wave dominate). The flow and propagated particle motion boundaries are overlapping, frequency dependent, and in an unbounded environment will extend to a distance of about one wavelength/$\pi$ for a sinusoidal dipole. The near field and far field regions do not delineate critical distances for fish hearing or communication, but are useful when considering the relative importance of these particle motions. Because of the low frequency characteristics and long wavelengths of most fish sounds, and the extended boundaries in water, it is argued that most fish hearing occurs primarily in the near field rather than the far field (Kalmijn, 1988). Very close to the source in the near field, the incompressible flow can not only stimulate the ear but also present a pressure gradient across the surface of a receiver fish which can stimulate the mechanosensory lateral line (Coombs et al., 1992; Higgs and Radford, 2016) and assist with sound source localization (Braun and Coombs, 2000, 2010; Braun et al., 2002). Thus considerations of the relevant stimulus used in the acoustic detection of environmental cues and communication signals are dependent upon the nature of the mechanical sound source, the distance of the receiver from the source, and the organization of the receptor organ systems that differ among species.

## 2.09.4   Sound Production by Fishes

Fishes show the greatest morphological diversity of sound production mechanisms among vertebrates. There are numerous and excellent detailed reviews on these mechanisms (e.g. Kasumyan, 2008; Ladich, 2019; Ladich and Fine, 2006; Lobel et al., 2010;
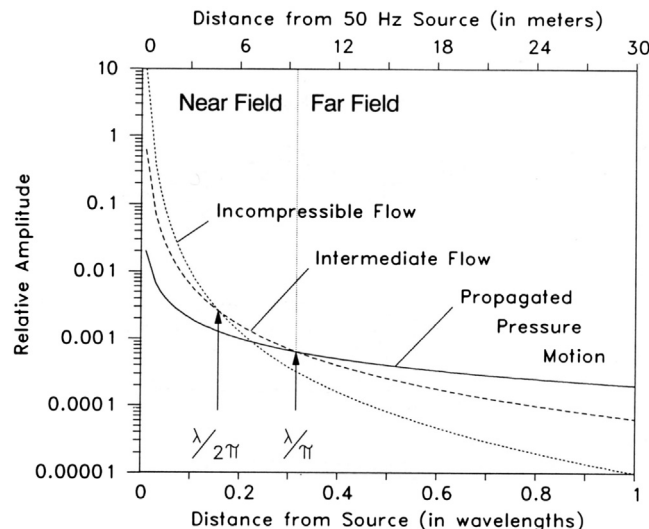


**Figure 2**   Flow attenuation with distance from a dipolar source for incompressible flow, intermediate flow, and propagated pressure flow. Distances at which intermediate and propagated pressure flows begin to predominate are marked with arrows. From Coombs et al. (1992).

Parmentier and Diogo, 2006; Tavolga, 1964, 1971) and will be briefly summarized here. The mechanisms of sound production include many cases of convergent evolution among distant taxa and do not follow clear evolutionary patterns (Fine and Parmentier, 2015). In addition, it is not possible to categorize the great diversity of sound producing mechanisms into useful categories (Ladich and Fine, 2006). This is largely due to the lack of a comprehensive fish phylogeny, especially for the extant and very speciose spiny-finned 'percomorphs' which show great diversity of sound production mechanisms. Recent applications of molecular and morphological techniques are beginning to resolve these systematic relationships in the fish tree of life (e. g. Betancur et al., 2013) and will undoubtedly provide the basis for future inferences on parallel, convergent and divergent processes in the evolution of fish sound production mechanisms.

### 2.09.4.1    Mechanisms

Sound production mechanisms can be classified according to the morphological features of muscles that are associated with the swim bladder or other structures and are diverse in fishes. The presence of intrinsic swim bladder muscles, which attach at both ends to the bladder without a typical origin and insertion, is uncommon but present in the best studied systems. These include the batrachoidid midshipman and toadfish (Fig. 3A), some gadid cods, scorpaeniform sea robins, and the sciaenid black drum. Many other species possess extrinsic swim bladder muscles, which link other body parts such as the cranium, pectoral girdle, vertebrae, or ribs either directly to the swim bladder, or via intervening hard or soft tissues that are attached to the swim bladder. There are great variations on this latter theme found in many taxa including some siluriform catfishes, piranhas and other characiforms (Fig. 3B), beryciform squirrelfishes, some ophidiiform pearlfishes and cusk eels, many sciaenid drum and other groups. The direct or indirect vibration of the swim bladder in the above groups usually produces tonal harmonic sounds with a fundamental frequency of up to near 300 Hz that is set by the contraction rate of the muscle (see below). The sounds can be short pulses, pulse trains, or longer sustained hums of several minutes as in the midshipman.

This diversity of sound production mechanisms that are observed in fishes was recently proposed to represent variations on two functional themes (Parmentier and Fine (2016). The *forced-response model* (Fine, 2012) states that the fundamental frequency of a fish sound results from the contraction rate of the swim bladder muscle. This mechanism requires the presence of superfast muscle contractions to move the swim bladder and generate a sound of relatively high fundamental frequency. The forced response model is applied to sound production by the toadfish, midshipman, and sea robin, and also the extrinsic swim bladder muscles and associated attachments as found in the piranhas and zeid dories (Onuki and Somiya, 2004). Superfast swim bladder muscle fibers are best described for the toadfish (*Opsanus tau*) and longspine squirrelfish (*Holocentrus rufus*), which can perform work under partial tetany at frequencies near 200 Hz, the highest known for vertebrate muscle fiber (Gainer et al., 1965; Rome et al., 1996). In the swim bladder prep, in which muscle contractions interact with rebound expansion from the swim bladder, muscles on the swim bladder are most effective at around 200 Hz, but can contract 1:1 at frequencies up to 400 Hz (Fine et al., 2001). In the field, toadfish boatwhistles occur at fundamental frequencies up to 280 Hz (Fine, 1978). In comparison, the *swim bladder rebound model* states that the vibration properties of structures, such as ribs or epineural projections that surround the swim bladder, determine the resonant spectrum of a sound, and not the contraction rate of the associated muscles (Parmentier et al., 2006, 2010). This complementary model is most notably applied to the remarkable sound production mechanisms of some cusk eels and pearlfish, which have slow twitch muscles but an elaborate drumming system of fast and slow muscles that stretch and release the anterior portion of the swim bladder and may have a peak frequency > 1 kHz. However, the rebound model may be relevant to other species that produce sound with extrinsic muscles and associated structures that surround the swim bladder, in which the fundamental frequency is not related to muscle contraction and is produced during the relaxation phase of the muscle. This model remains to be considered and tested for many fish species. Many other sound production mechanisms, not directly related to swim bladders, are associated with muscles and structures of the pectoral girdle, pectoral fins and fin tendons. Such mechanisms occur in the stridulation of pectoral spines in many catfishes (e.g. the slip stick mechanism of Mohajer et al., 2015 not previously described in vertebrates) (Fig. 3C), plucking of modified tendons of the pectoral fin rays of the osphronemid croaking gouramis (Fig. 3D), and vibration of the pectoral girdle by scorpaenid sculpins (which lack a swim bladder). There are also several other sound production mechanisms beyond these categories which involve stridulation of dorsal spines or the pharyngeal/jaw teeth (Fig. 3E). One recent discovery was the fast jaw slam that is apparently unique to the damselfishes (Parmentier et al., 2007). In this system the stretched ceratomandibular ligament forces the rapid closure of the mouth onto the ceratohyal bone without the use of fast adductor mandibulae muscles for closure.

### 2.09.4.2    Spectral and Temporal Characteristics

The spectral features of fish sounds span multiple frequency decades and vary with the associated production mechanism. Collectively, communication sounds produced by most teleost fishes can be described as short duration (10–500 ms), single pulses or pulse trains, which have fundamental frequencies in the lower range of the 1000 Hz band (Fine et al., 1977; Myrberg, 1981; Ladich, 1997; Ladich and Fine, 2006; Tricas and Boyle, 2014). The fundamental frequency of a sound may be determined by the contraction rate of sonic muscles (50–250 Hz) that may also generate several harmonics as found in the toadfishes and some catfishes (Fine, 1978; Brantley and Bass, 1994; Ladich, 1997). Sounds produced by motions of the pectoral fins and pectoral spines can produce broadband pulses with peak frequencies > 1 kHz (Ladich et al., 1992, 1997). Many species produce multiple types of sounds that are context specific with spectral features near or above 100 Hz. These are best characterized for several species of the gadid cods and hake, toadfishes, sea robins, mormyrids, damselfishes, gouramis, cichlids and other species (Amorim, 2006).
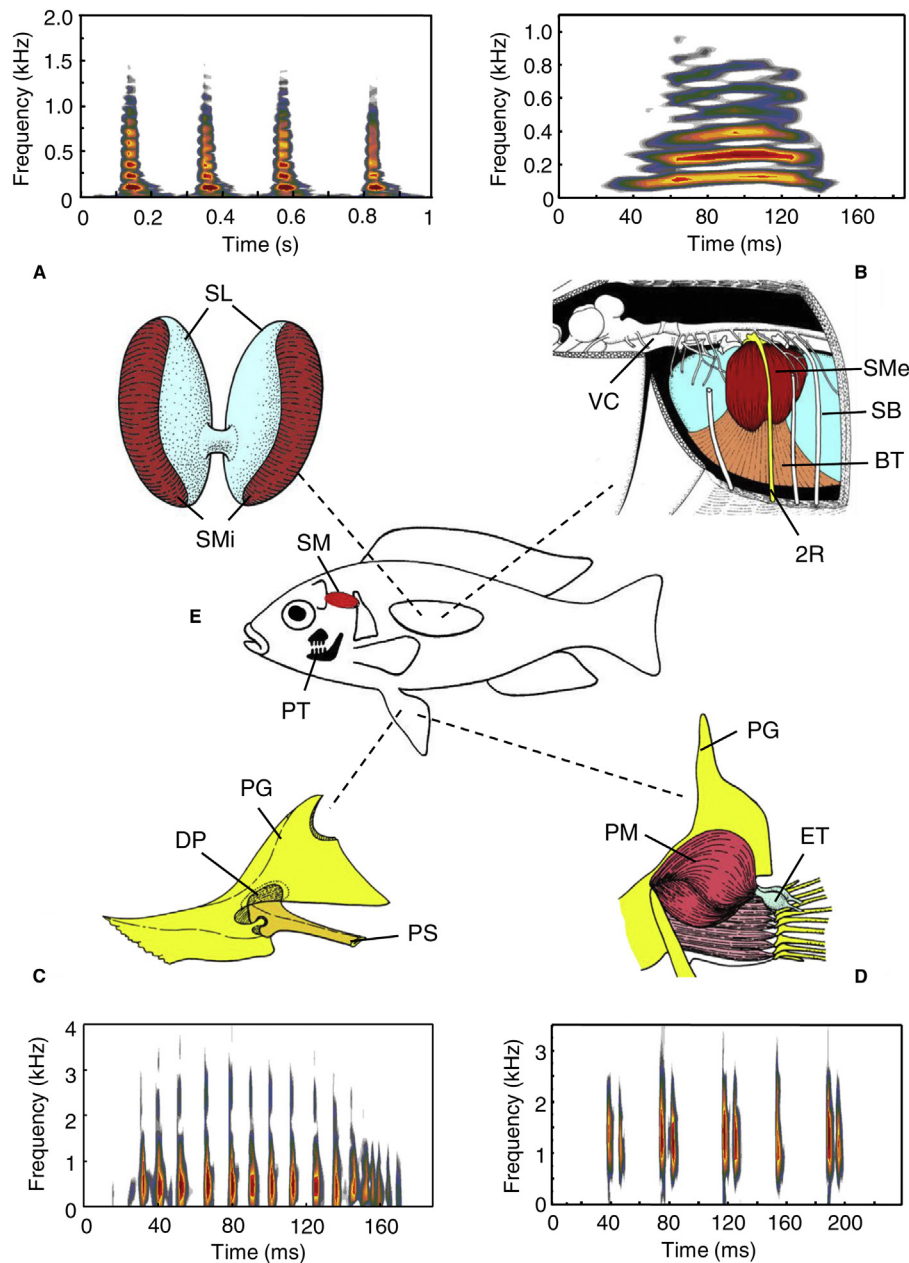
**Figure 3** **Diversity of sound generating mechanisms in fishes and sonagrams of sounds produced by these mechanisms.** (A) Intrinsic sonic muscles (SMi) attached to both swim bladder lobes (SL) in the Lusitanian toadfish *Halobatrachus didactylus*, (B) extrinsic sonic muscles (SMe) originating at 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 sonograms show sounds produced in agonistic contexts. Note different x-axes and y-axes ranges. From Ladich (2014).

#### 2.09.4.2.1   Infrasound

Very few studies have investigated sound production during social interactions in the infrasound range (<20 Hz). Recent work on coral reef butterflyfishes demonstrates that sounds in the 100–1000 Hz range are most commonly produced during social interactions that involve movements of the head, pectoral girdle and ribs that are coupled to the anterior swim bladder (Boyle and Tricas, 2011; Tricas and Boyle, 2015a). In addition, several species also produce intense infrasound pulses (peak frequencies from 1–10 Hz) that are associated with lateral motions of the body and tail during close social interactions (**Fig. 4**). The tail slap behavior
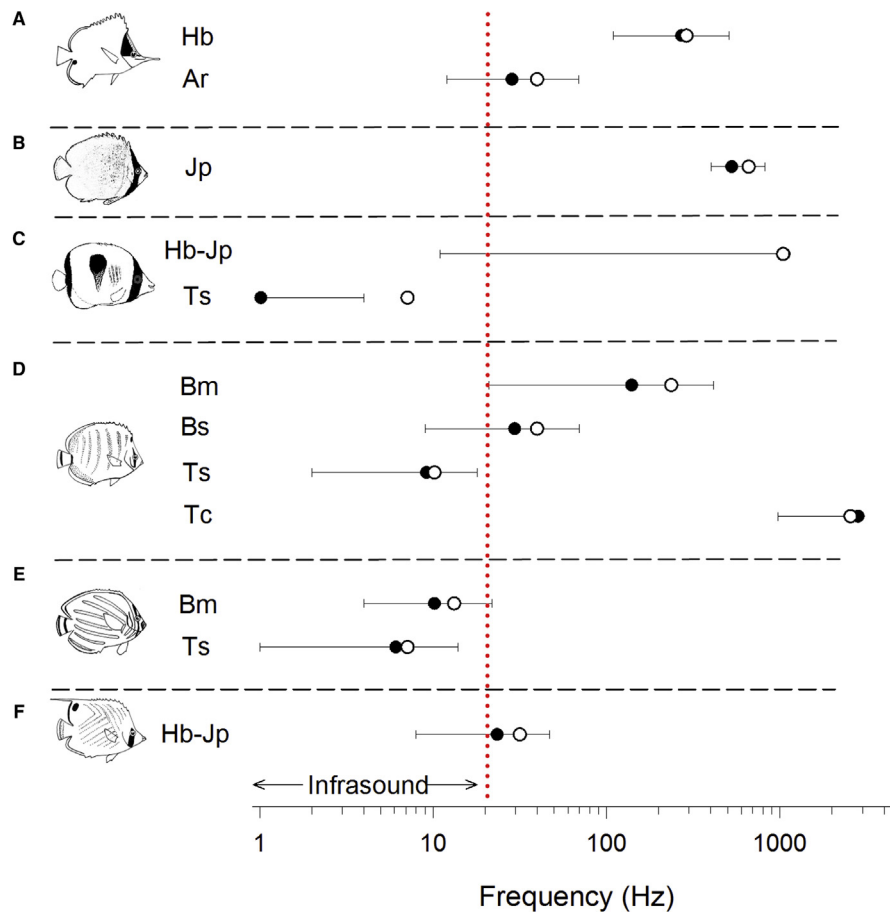
**Figure 4**    Diversity of infrasound and higher frequency sounds produced by *Foricipiger* and *Chaetodon* butterflyfishes during social interactions with conspecifics (A) *F. flavissimus* produced the head bob and anal fin retract sounds that collectively span the 10–1000 Hz band (B) *C. kleinii*, produced only the jaw protrusion sound which was limited to near 500–1000 Hz (C) *C. unimaculatus* produced an infrasonic tail slap and the head bob–jaw protrusion sound that extends to 1000 Hz (D) *C. multicinctus* produced the body motion, body shake, tail slap and tail click sounds that span the <1 to >1000 Hz band (E) *C. ornatissimus* produced the body motion and tail slap sounds which span the infrasound range (F) *C. auriga* produced a single low-frequency head bob–jaw protrusion sound type. Both peak (*black circles*) and median (*open circles*) frequencies and 6 dB frequency band are shown for each sound type. Vertical dotted line indicates upper limit of the < 20 Hz infrasound range. From Tricas and Boyle (2015a).

is used primarily during intense aggressive interactions at close distances, and when delivered at high intensities results in physical displacement of the receiver fish body (Tricas et al., 2006). Such hydrodynamic infrasound stimuli are produced by swimming fish (Moulton, 1963; Kalmijn, 1989), and may provide acoustic information associated with many agonistic and reproductive motor patterns in many species. The ear of many species is highly sensitive to linear accelerations in the infrasound spectrum (Sand and Karlsen, 1986; Karlsen, 1992) and may also provide acoustic cues about their aquatic environment (Sand and Karlsen, 2000). Much work remains to determine how fish use and process infrasound stimuli during social interactions and other behaviors.

## 2.09.5    For What Do Fish Use Sound?

There are many excellent and detailed reviews of the behavioral contexts in which fish use acoustic signals and cues in natural settings (see Fine et al., 1977; Amorim, 2006; Ladich and Myrberg, 2006; Myrberg and Lugli, 2006; Amorim et al., 2015). Many species live in groups and engage in social interactions that involve acoustic communication using context-specific sounds during social interactions with conspecific or heterospecific individuals.

### 2.09.5.1    Species Comparisons

#### 2.09.5.1.1    *Reproduction*

A wide range of sounds are produced by males to attract and court females at spawning sites such as the hum of the midshipman and boat whistle of the toadfish on shallow marine reefs (Ibara et al., 1983; Winn, 1964), drums, tones, pulse trains and grunts by gobies in

freshwater streams, lagoons, estuaries and grass flats (Lugli and Torricelli, 1999, Torricelli et al., 1990; Lugli et al., 1996, Stadler, 2002), chirps, growls, grunts and pulsed sounds by damselfishes on coral reefs (Myrberg, 1972; Myrberg et al., 1986; Lobel and Mann, 1995; Maruska et al., 2007) to cite only a few. Intense reproductive vocalizations are produced by male toadfishes and midshipman at nest sites in the intertidal and subtidal zones, respectively. These calls are of low fundamental frequency (100–300 Hz), often harmonic and of high intensity 120–140 dB re:1 µPa near the source (Barimo and Fine, 1998; McKibben and Bass, 1998). However, the transmission distances of these low frequency signals are on the order of only a few meters (Fine and Lenhardt, 1983; Bass and Clark, 2003) at least partially due to the propagation limits of sound in shallow waters caused by the repeated interactions of the low frequency acoustic waves with the shallow bottom and surface (Rogers and Cox, 1988). The formation of reproductive choruses and vocal interactions between individual toadfish males are complex, call rate dependent and male condition dependent (Remage-Healey and Bass, 2005; Amorim et al., 2010). In the midshipman, the sustained hums produced by neighboring males overlap and create an acoustic beat envelope that the females may use to distinguish among individual males (McKibben and Bass, 1998; 2001; Bass and McKibben, 2003). The short effective distance of these long and loud advertisement calls of the midshipman is quite different from that of the short and loud acoustic advertisement of male back drum in the estuarine environment. Here males produce boom calls of 600 ms duration with a peak frequency of about 94 Hz, several harmonics and an average source level of 165 dB RMS re:1 µPa (Locascio and Mann, 2011). The sound pressure level of this short sound is several orders of magnitude greater than that of the toadfish, and rivals the peak intensity of many great whales. The effective communication distance of this call in shallow estuarine waters is estimated to be about 100 m, and is considered to be limited by environmental background noise in the estuary rather than the hearing sensitivity of a receiver black drum.

### 2.09.5.1.2   Agonistic Interactions

Sounds are produced frequently by fishes during agonistic interactions among conspecific individuals, which are related to defense of a territory, potential mates or competition for food. Agonistic sounds are usually short pulses of low frequency in a variety of freshwater and marine species (see Ladich, 1997; Ladich and Myrberg, 2006). The use of sound for individual and species recognition during agonistic and reproductive interactions comes from work on the damselfishes. Members of this family are common inhabitants of tropical reefs, produce pulsed sounds, and are well known for their aggressive behavior and territorial defense. Male bicolor damselfish, *Stegastes partitus*, produce the chirp-sound to attract females for spawning. Females use the chirp sound to locate male nest sites and also distinguish different males based on the dominant frequency of the call (Myrberg et al., 1993). Males also produce the chirp as a territorial 'keep out' signal to other males (Myrberg, 1997). Male bicolor damselfish will acoustically respond to playbacks from conspecific individuals, and show greater responses to recorded sounds made by individuals from adjacent territories than unfamiliar individuals (Myrberg and Riggio, 1985). These experiments show that damselfish can recognize neighbors based on the acoustic features of their calls, and are likely mediated by frequency differences associated with body size. Male damsels also show a greater response to sounds from conspecifics than heterospecifics, and supports the ability to acoustically discriminate different species based on pulse rate and pulse train length (Spanier, 1979). Recent studies on vocalization behavior on two other sympatric *Stegastes* species in the West Indies, show differences between species in the temporal measures of chirps, pops and pulse trains between species, and more active vocal activity produced toward an egg predator wrasse than to congeners (Weimann et al., 2017). The question of whether the wrasse perceives and responds to a signal from the damselfish (heterospecific communication) remains to be demonstrated. The transfer of multiple forms of information with a single call type is also known for courting male sand gobies that potentially contains important information for both species recognition and also mate assessment (Pedroso et al., 2013). Much work remains to identify how the spectral and temporal features of different sound types may convey context specific information to a receiver fish.

### 2.09.5.2   Fish Soundscapes and Communication in Ecological Communities

Comparative studies on the features of fish sounds used for communication are based largely on meta-analyses of sound production mechanisms compared in broad taxa (e.g. Ladich and Bass, 2003; Ladich and Fine, 2006; Parmentier and Diogo, 2006) and the characteristics of sounds produced by different genera within fish families (Amorim, 2006). A few studies on sympatric congener species show evidence for conservation or divergence in temporal and spectral features of sounds: centrarchid sunfishes (Gerald, 1971), coral reef chaetodontid butterflyfishes (Tricas and Boyle, 2015a), African cichlids (Amorim et al., 2004, 2008; Lobel, 1998), gobies (Lugli et al., 1997), mormyrid elephantfish (Crawford et al., 1997; Crawford and Huang, 1999) and pomacentrid damselfishes (Kenyon, 1994; Lobel and Mann, 1995; Myrberg and Riggio, 1985; Myrberg et al., 1993; Spanier, 1979). Yet comparisons of sound production by sympatric species in large aquatic communities are limited. Several recent studies used passive acoustic monitors to characterize sound production by multiple fish species in different shallow marine communities. These studies have identified peak frequency differences between diurnal and nocturnal sonic activity (Ruppe et al., 2016), seasonal variations in sound pressure and spectral features (Buscaino et al., 2016), acoustic complexity indicators (Pieretti et al., 2017) and differences between acoustic features in different habitats (Ricci et al., 2016). However, fish soundscape studies often must infer the sonic activity to selected species observed in the study area without direct information on the repertoires of species-specific sounds. When the sound repertoires of individual species are known, this can lead to the use of acoustic estimates of daily, lunar, and reproductive variations in numerous species-specific sounds (Nelson et al., 2011; Casaretto et al., 2014; Schärer et al., 2014; Monczak et al., 2017). However, many passive acoustic monitoring studies are selective for species that produce loud sounds that travel over large distances, and do not detect sounds that are of low intensity.

Coral reefs are among the most ecologically diverse habitats on the planet, with at least 4000 species estimated to inhabit coral reefs worldwide (Lieske and Myers, 2002). A recent meta-analysis reported that sound production was known for about 300 species (48 families) of coral reef fishes, with the majority of families remaining to be examined (Lobel et al., 2010). On Hawaiian reefs, researchers have more recently used underwater rebreathers (which unlike scuba do not produce noise from bubbles), cameras, and audio recorders to screen for the bioacoustic activities of 96 species (45 families) in a reef fish community (Tricas and Boyle, 2014). They found that 45 (47%) of these species in 12 families produced 85 different sound types. In addition to identifying each sonic species, they also documented the behavioral contexts in which sounds were produced (Fig. 5A). The largest number of sounds occurred during agonistic interactions with other fish during aggressive encounters, territory defense and nest defense. This was followed by a high number of sounds associated with courtship/spawning behavior and vigilance (an acoustic response to predators or divers). The sounds were primarily solitary pulses or blended pulse sounds that include single pulses, pulse trains, rasps, growls, hums, etc (Fig. 6). Pulsed sound events were <100 ms long with most peak frequencies near 200 Hz across a range from <100 to 1000 Hz (Fig. 5B). Sounds were also highly diverse in bandwidth, with several sound types extending into the infrasound range near the lower 10 Hz limit of the recording hydrophone. This study provides the first approximation that sound production occurs in at least half of the conspicuous fishes, and confirms that single coral reefs offer a rich acoustic environment for the study of sound production and communication in a diversity of fish taxa. It also confirms that the behavioral contexts of sound production are shared among many sympatric species within a single community.
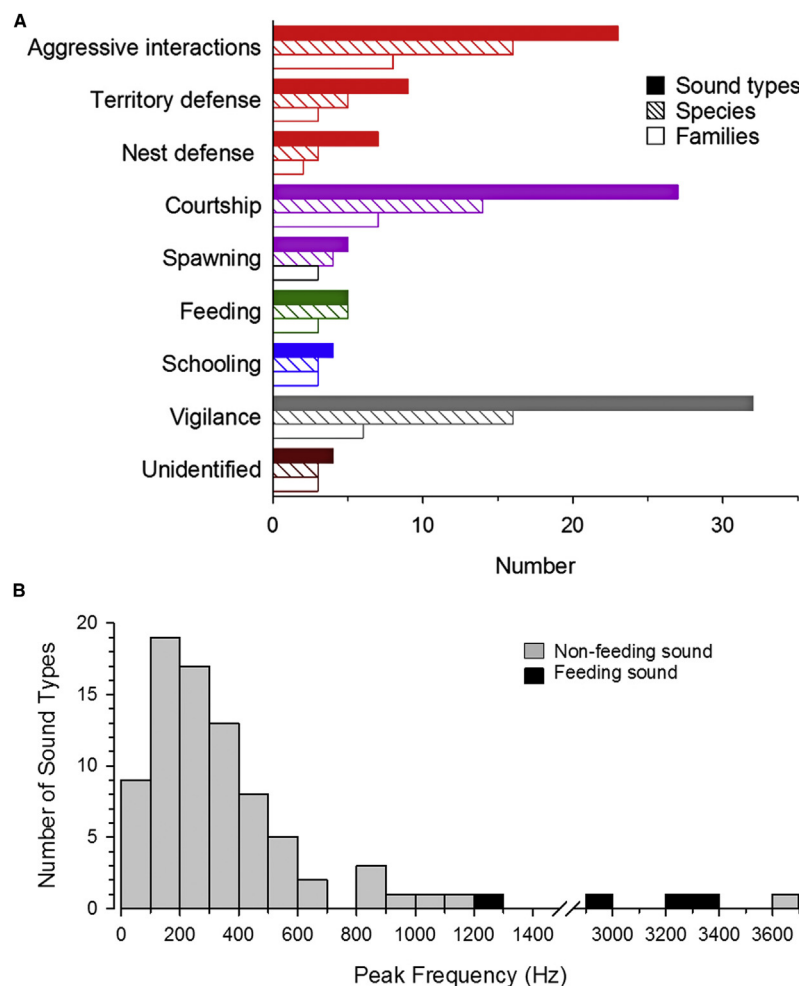


**Figure 5** **Acoustic behaviors and peak sound spectrum of 45 species of Hawaiian coral reef fishes.** (A) Behavioral contexts of 85 sound types observed in the field. Data are shown for the total number of sounds produced by all species (*solid bars*), number of species that produced sound associated with a behavior category (*hatched bars*), and number of fish families the produced sound associated with a behavior category (*open bars*). Fish sound categories are agonistic behaviors separated into aggressive interactions among individuals and defense of territories or nests (*red bars*), reproductive interactions separated into courtship and spawning behaviors (black), feeding (green), schooling (blue), vigilance (gray), and unidentified behavioral contexts (burgundy). Several sound types were produced in multiple behavior categories. (B) Average peak frequency of each sound made by the 45 species. Sounds were produced during non-feeding behaviors shown above (*gray bars*) and scraping of reef substrate during feeding by parrotfish, black durgon triggerfish, and barred filefish (*black bars*). Note that the frequency distribution for most non-feeding sounds is ≤ 1200 Hz with a peak between 100 and 300 Hz. Sounds produced during feeding by parrotfish and black durgon are of higher peak frequency. (A) From Tricas and Boyle (2014). (B) From Tricas and Boyle (2014).

**A** *Cephalopholis argus*                     pulses

**F** *Stegastes marginatus*              half pulse train

**B** *Chaetodon multicinctus*                     pulse

**G** *Melichthys niger*                            rasp

**C** *Abudefduf vagiensis*           high frequency pulse

**H** *Sufflamen bursa*                      pulse train

**D** *Plectroglyphidodon johnstonianus*     pulse train

**I** *Xanthichthys auromarginatus*          pulse train

**E** *Plectroglyphidodon johnstonianus*       growl 2
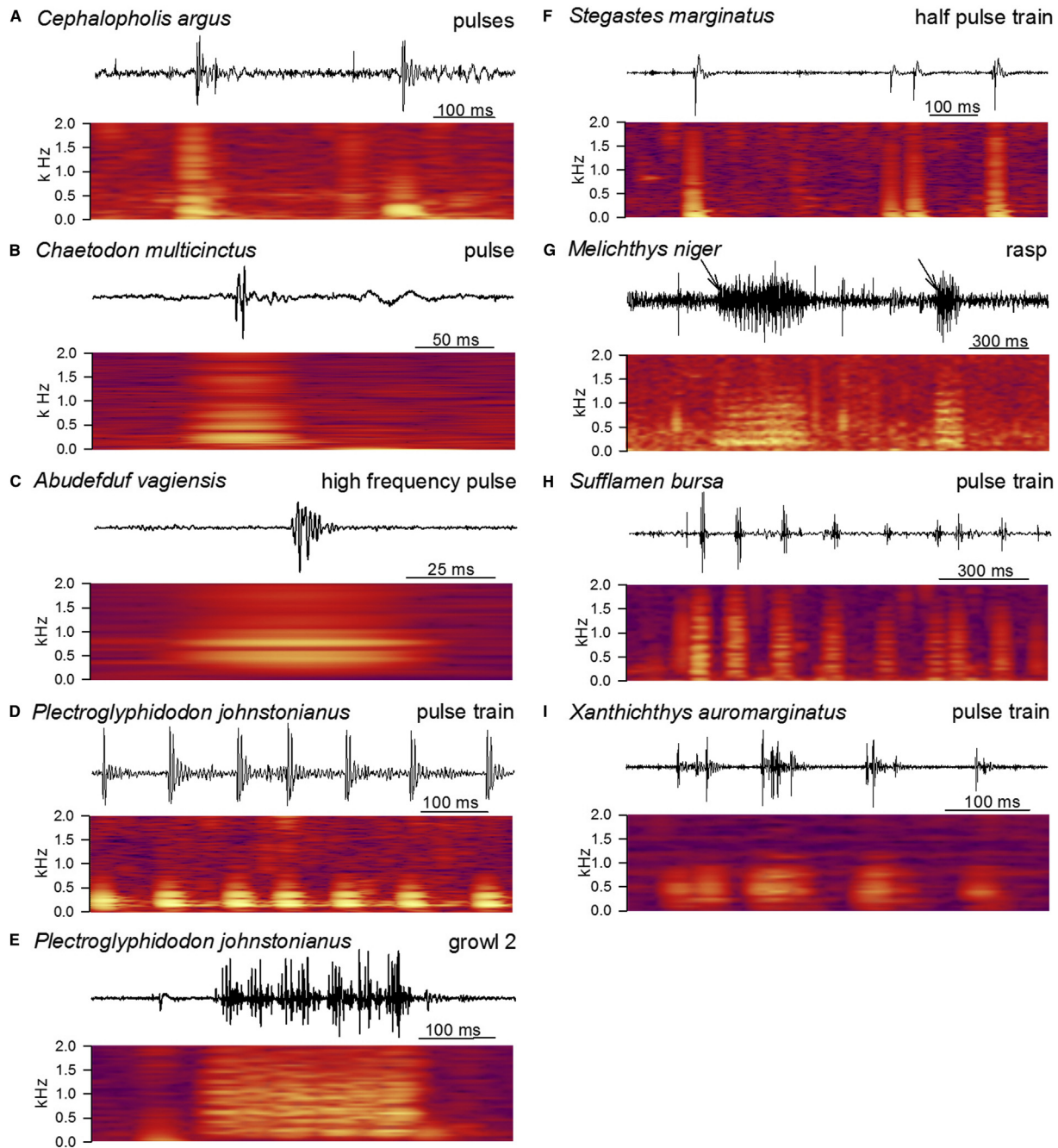
**Figure 6**    Waveforms and spectrograms of agonistic sounds produced by fish at Puako reef, Hawai'i, HI, USA Scientific names are given in the figure (A) peacock grouper pulse sounds during social interactions with conspecifics (B) multiband butterflyfish pulse sound during agonistic bouts with a conspecific (C) high-frequency pulse sound by the Indo-Pacific sergeant during nest defense (D, E) pulse train and growl 2 sounds by the blue-eye damselfish during defense of coral territory (F) half pulse sound by the Hawaiian gregory during defense of feeding territory (G) rasp sound produced by the black durgon triggerfish during social interactions (H) pulse train sound by the lei triggerfish during social interactions, and (I) pulse train sound of gilded triggerfish social interactions. Relative intensity of sounds across the frequency spectrum is indicated from low (*dark purple*) to high (*bright yellow*) in spectrograms. From Tricas and Boyle (2014).

## 2.09.6    Hearing and Neural Encoding of Sound Stimuli

### 2.09.6.1    The Fish Ear

There are many excellent and detailed reviews of the morphology of the fish inner ear and the detection of sound, and the primary mechanisms for the encoding of sound by the fish ear are provided below. The ear of most jawed fishes has three semicircular canals and three otolithic organs (Popper, 2011; Popper and Fay, 2011; Schulz-Mirbach and Ladich, 2016; Schulz-Mirbach et al., 2019;

Popper and Hawkins, 2018) (**Fig.** 7A–C). The semicircular canals provide information on the angular rotation of the head in three orthogonal planes during swimming, angular movements, and are not involved in hearing (Boyle and Highstein, 1990; Highstein et al., 2004). The other organs include the utricle, saccule and lagena with sensory maculae that are loaded by a lapillus, sagitta, or asteriscus otolith, respectively. These otolithic organs serve vestibular functions for posture, balance and primary orientation as well as auditory functions (Popper and Fay, 1993; Popper and Platt, 1993). In teleost fishes, the otoliths develop from a calcium carbonate (aragonitic/protein) accretion in the ear (Mugiya et al., 1981; Campana and Neilson, 1985), and have a density about three times that of water and the surrounding soft body tissues. Each otolith is coupled to the respective underlying sensory macula of hair cells by an intervening otolith membrane (Platt and Popper, 1981). The ciliary bundle and single kinocilium on the apical surface of each sensory hair cell projects into the otolith membrane and are therefore coupled to shearing motions between the otolith and sensory macula. The hair cell resting potential is depolarized when the stereocilia are deflected toward the kinocilium, and hyperpolarized in the opposite direction. These mechanical deflections modulate the release of excitatory neurotransmitters onto the terminals of primary afferent neurons of the eight nerve that project to the CNS. Thus the ear of the fish is modeled as an inertial accelerometer that detects motions caused by shearing forces between the sensory epithelium and the otolith.

The paired saccular otoliths and vertical maculae of teleosts project laterally from the midline axis of the fish body by about 20–40° (Sand, 1974; Lu and Xu, 2002; Schellart and Buwalda, 1990; Schulz-Mirbach et al., 2011a), and are oriented at reflective angles within an acoustic field. The axis of best hair cell sensitivity is determined by subpopulations of hair cells with different vertical orientations. Bidirectional vertical patterns predominate in pre-teleosts as found in the saccular maculae of extant cartilaginous, rayed-fin and lungfishes that show no well-defined horizontal populations and likely represent the basic vertebrate pattern (Popper and Fay, 1993; Popper and Platt, 1983; Mathiesen and Popper, 1987). In the teleost, five patterns of hair cell orientations in the saccule are recognized, four of which include both horizontally and vertically oriented populations (Popper and Coombs, 1982; Popper and Fay, 1993; Popper and Schilt, 2008) recently reviewed by Ladich and Schulz-Mirbach (2016) (**Fig. 8**). The response of these hair cells to a sound wave varies with their relative orientation and collectively provides information about the sound source to the central nervous system (Enger et al., 1973; Popper et al., 1988, 2003). Acoustic information from the saccule, which is considered to be the main acoustic organ (Popper and Fay, 1999), may also be enhanced by input from the utricle and lagena (see Rogers et al., 1988). These multiple auditory channels project to specific regions of the medulla with subsequent connectivity to the midbrain as in tetrapods (see reviews by McCormick, 1999; Bass et al., 2005; Bass and Lu, 2007). Of note, the macula communis in the inner ear of the jawless lamprey has a small vertical macula with dorsal and ventral orientations of hair cells, and two maculae in the horizontal plane with hair cells oriented in the forward direction on the anterior and backward direction on the posterior end (Lowenstein et al., 1968; Popper and Hoxter, 1987; Maklad, 2014)). Recent work shows that the developing lamprey ear closely resembles that of the zebrafish otic vesicle, indicating a possible shared common ancestor that had a defined otic anteroposterior asymmetry and that otic Otx1 expression is likely to account for the separation of the zones of the single macula into distinct regions (Fritzsch et al., 2001, Hammond and Whitfield, 2006). More experimental molecular and developmental studies are needed to resolve the shared and convergent features of the fish ear.

### 2.09.6.2    Physiological Investigations of Hearing

#### 2.09.6.2.1    Auditory Evoked Potentials and Fish Hearing

The auditory evoked potential (AEP), which is detected by subdermal electrodes placed over the brain and ear, is a slow-wave of the bioelectric field produced during early activation of the auditory system by an acoustic stimulus. This non-invasive technique is used widely to rapidly estimate relative response thresholds to different sound frequencies (usually tone pips) for diverse fish taxa. However, there are several criticisms for use of this technique such as the underestimation of neural thresholds, non-standardized methods among labs, sensitivity to electrical/background noise, a lack of correlation with behavioral/psychophysical thresholds, and others (Ladich and Fay, 2013; Maruska and Sisneros, 2016; Sisneros et al., 2016). Therefore, while the AEP technique has provided much insight to the hearing capabilities of fishes, it is considered not to be a useful tool for determining or comparing absolute hearing thresholds widely among taxa. It is better applied to experiments such as those that test the pre and post effects of manipulations to the auditory system of experimental subjects (Popper et al. 2019).

### 2.09.6.3    Comparative Studies on Hearing Thresholds

Very few studies have investigated the physiological response to acoustic stimuli for relatives of the earliest jawless fishes or members of the sister groups to the tetrapod clade. The most recent work indicates that when tested between 50–800 Hz, the jawless sea lamprey (*Petromyzon marinus*) has equal sensitivities up to 300 Hz but is insensitive at higher frequencies (Mickle et al., 2018). This is consistent with the high sensitivity to very low frequency vibration stimuli down to 10 Hz demonstrated for the river lamprey (*Lamptera fluviatilis*) reduced prep (Lowenstein, 1970). No vibration responses were detected in the eighth nerve of the jawless hagfish (*Myxine glutinosa*) which lacks a well-defined sacculus portion of the macula communi (Lowenstein and Thornhill, 1970). In comparison, the jawed African lungfish (*Protopterus annectens*), which is in the sister group to modern tetrapods, detects underwater sound via particle motion, and also sound pressure via the pressure-to-particle motion transduction mediated by the air-filled lungs (Christensen et al., 2015). This species can also detect airborne sound thorough induced vibrations of the head. The authors propose that early tetrapods had rudimental aerial hearing that preceded evolution of the tympanic middle ear. The inner
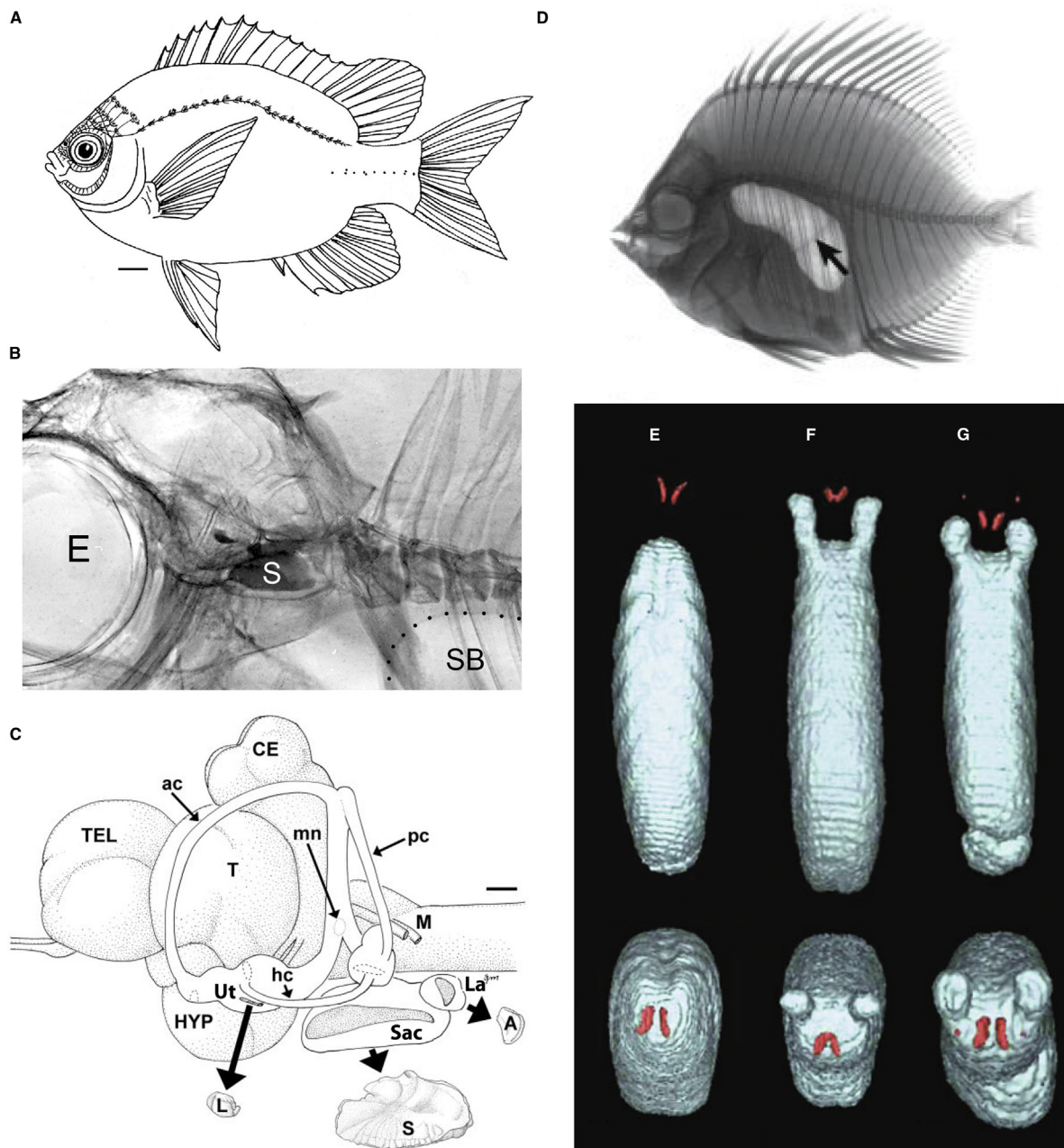
**Figure 7**  **The fish lateral line, ear and morphological diversity of the swim bladder.** (A) Lateral view of the body and lateral line of the Hawaiian sergeant fish, *Abudefduf abdominalis* shows the distribution of lateral line canals (*lines*) and superficial neuromasts (*dots*). The anterior lateral line includes several canals across the surface of the head. The trunk canal extends from the operculum to the caudal edge of the dorsal fin near the tail. Scale bar, 1 cm. (B) Representative inverted xray image of the head shows position of the eye (E), anterior edge (*dotted line*) of the swim bladder (SB), and the sagitta otolith (S) in the saccule of the inner ear. Anterior edge of the swim bladder is located 2–4 mm from the caudal edge of the otic capsule in adults. (C) Diagrammatic lateral view of the inner ear and brain. The saccule and lagena are positioned beneath the brain and oriented in the dorso-ventral plane along the presumed primary axis of particle motion during auditory evoked potential experiments. The position of the sensory macula is outlined and shaded within each otolithic endorgan, while the removed left otolith is illustrated below (*large arrows*). Dashed lines represent the location of the crista ampullaris of each semicircular canal, and the dotted line represents the position of the macula neglecta (mn). *A*, asteriscus otolith of lagena; *ac*, anterior canal; *CE*, cerebellum; *hc*, horizontal canal; *HYP*, hypothalamus; *L*, lapillus otolith of utricle; *M*, medulla; *pc*, posterior canal; *S*, sagitta otolith of saccule; *T*, tectum; *TEL*, telencephalon. Scale bar, 1 mm. B image provided courtesy of K. Maruska. (D) Diversity of the butterflyfish swim bladder. Xray of *Chaetodon octofaciatus* shows the location of the swim bladder and its transverse diaphragm (*arrow*). Lower panel shows 3-D reconstructions of CT images that illustrate the proximity of the saccular otoliths (red) to the associated swim bladder and horns (white). Dorsal (top) and frontal (bottom) views of (E) the bannerfish *Forcipiger flavissimus* which lacks swim bladder horns, (F) *Chaetodon auriga* which has long horn extensions, and (G) *Chaetodon multicinctus* which has short horn extension. Note that in the two species of *Chaetodon* (F, G) the gas-filled cylindrical horns extend rostrally, and are dorsal and lateral to the otic capsules and the saccular otoliths. Smaller utricular otoliths are also visible rostral to the horns in G. Swim bladder diameter = ~1 cm. (A) and (C) modified from Maruska and Tricas (2009). (D) from Webb and Smith (2000). (E–G) from Webb et al. (2010).
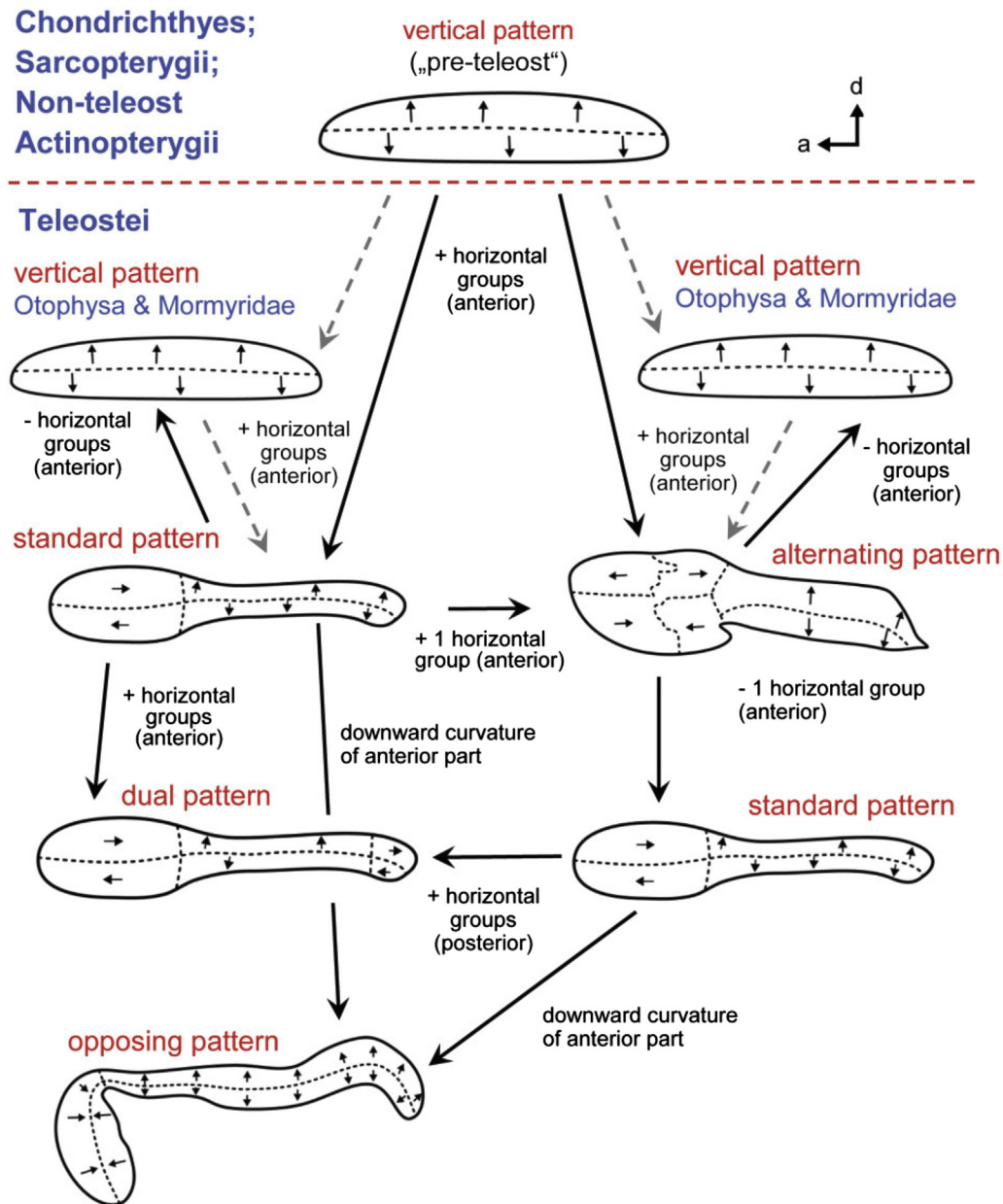
**Figure 8**   The main ciliary bundle orientation patterns on the macula sacculi in teleosts and how the patterns may be derived from one another (see Popper and Fay, 1993). Arrow tips point in the direction of the kinocilia, indicating the orientation of the ciliary bundles in the respective area; the dashed lines separate different orientation groups. Addition of two or three horizontally oriented groups of ciliary bundles results in the standard or alternating patterns, respectively. From the standard pattern the dual pattern can be derived by adding horizontal groups in the posterior region; in the opposing pattern the anterior macula portion is ventrally bent while the orientation of the horizontal groups is retained. The standard pattern may also be obtained by removing one horizontal group from the alternating pattern. The vertical patterns in otophysans and mormyrids may be derived by removing the horizontal groups from the standard or the alternating patterns. The five patterns are modified from Popper and Coombs (1982) and Popper and Schilt (2008). *a*, anterior; *d*, dorsal. From Ladich and Schulz-Mirbach (2016).

ear of the coelacanth, a sister group to the lungfish, shares several anatomical features with the tetrapod ear (Fritzch, 1987, 1992) but no physiological work has investigated its hearing mechanisms.

A recent meta-analysis of AEP studies on 111 species in 51 fish families (Ladich and Fay, 2013) provides supportive evidence for a greater hearing bandwidth for taxa that possess accessory hearing structures (see Ladich and Popper, 2004). Species with a gas body near or in contact with the ears had a higher range of best frequencies from 200 Hz – 3 kHz with sound pressure thresholds in the range of 55–83 dB re: 1 µPa. In comparison, those without evident accessory hearing structures had lower best responses from 100 Hz −1 kHz and best frequency thresholds from 78–150 dB re: 1 µPa. Various species also show threshold responses to

measured particle acceleration at best frequency from 30–70 dB re: 1 μm s$^{-2}$. While the absolute sensitivities measured by this technique are not directly comparable (for reasons described above), they are consistent with the idea that coupling of the swim bladder or other gas filled structure with the ear to detect sound pressure enhances hearing bandwidth and sensitivity at higher frequencies.

Comparative AEP experiments on related species have attempted to interpret audiograms in relation to the positioning or morphology of the swim bladder, but the causal factors for sensitivity to sound pressure are not always clear. For example, audiograms for six species of sciaenid croakers and drums show best frequencies in a range of < 100 up to 1000 Hz with a relatively low sensitivity to sound pressure (Horodysky et al., 2008) (Fig. 9A). Among species with swim bladders, thresholds for those with anteriorly projecting diverticulae did not differ statistically from those species without diverticulae. The high thresholds to sound pressure and flat low frequency response to particle motion indicates these species are likely primarily sensitive to particle acceleration (Fig. 9B and C). Of note the northern kingfish, which has a degenerated swim bladder in the adult (Ramcharitar et al., 2001), showed the lowest SPL thresholds at higher frequencies. In comparison, relatively low SPL thresholds were found in prior studies on the silver perch, a sciaenid which has notable rostral swim bladder extensions (Ramcharitar et al., 2004), and the brown meagre, a sciaenid without swim bladder extensions (Wysocki et al., 2009a). Thus given the caveats for comparisons of hearing thresholds within and among laboratories, additional experimental work is indicated to resolve the relationships between swim bladder morphology and hearing sensitivity in some taxa.

Several taxa have evolved accessory hearing structures that enhance sensitivity and range of hearing frequencies (summarized by Ladich and Fay, 2013). For example, representatives of three otophysan orders, which all have specialized Weberian ossicles that mechanically couple the swimbladder and ear for the detection of sound pressure, have similar audiograms in terms of frequency range of best hearing from 600–1000 Hz (Fig. 9D). A relatively high sensitivity to sound pressure at high frequencies is shown in
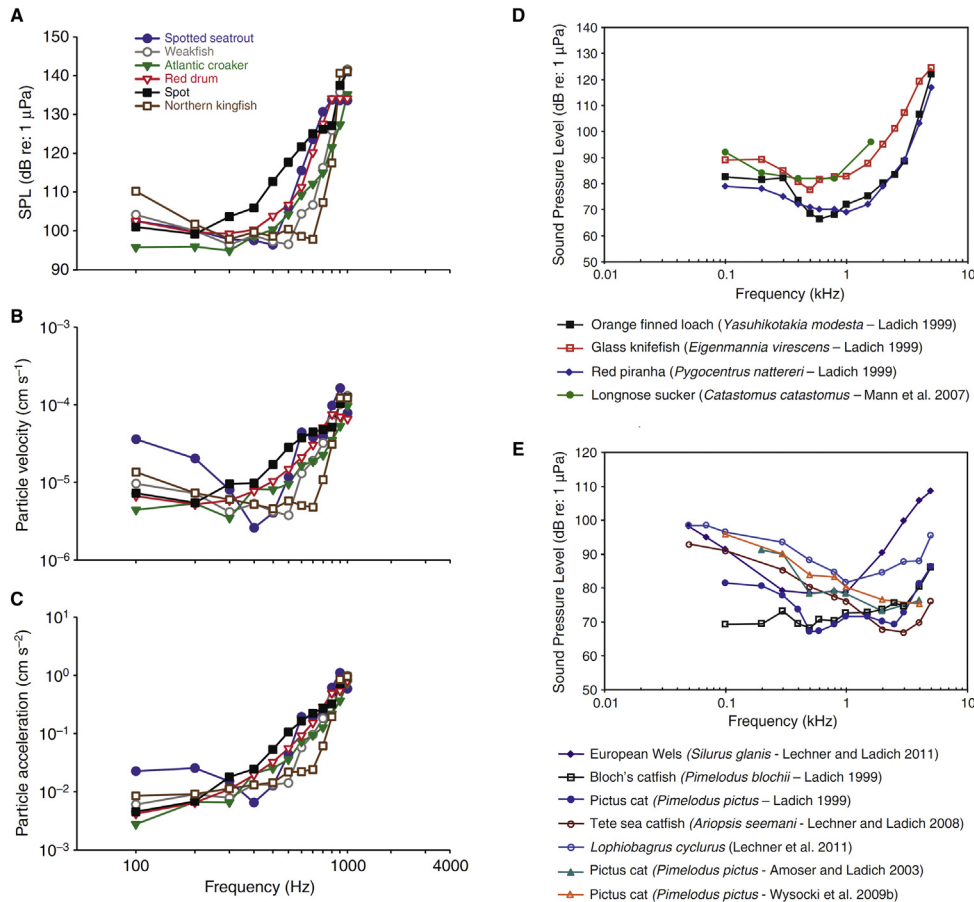


**Figure 9** Teleost AEP audiograms (A) Audiograms for six sciaenid species in relation to mean sound pressure (SPL) in dB re: 1·μPa (B) mean velocity in cm·s−1 and (C) mean acceleration in cm·s−2 for six sciaenid species: spotted seatrout (*filled blue circles*), weakfish (*open gray circles*), Atlantic croaker (*filled green triangles*), red drum (*open red triangles*), spot (*filled black squares*) and northern kingfish (*open brown squares*). (D) AEP audiograms from otophysan fishes that have the Weberian apparatus which transfers sound pressure sensitivity from the swim bladder to the ear: the longnose sucker *Castotomus catostomus*, orange finned loach *Yasuhikotakia modesta*, the red piranha *Pygocentrus* (formerly *Serrasalmus*) nattereri, and the glass knifefish *Eigenmannia virescens*. After Ladich (1999) and Mann et al. (2007) (E) Audiograms for seven representatives of the otophysan catfish families Siluridae, Pimelodidae, Ariidae and Claroteidae. After Ladich (1999), Lechner and Ladich (2008, 2011), Wysocki et al. (2009b) and Lechner et al. (2011). From Horodysky et al. (2008). Figures from Ladich and Fay (2013).

a variety of catfishes, some with best frequencies above 1000 Hz and thresholds below 70 dB re: 1 μPa (**Fig. 9**E). AEP studies have also provided physiological evidence for a high hearing threshold to frequencies extended to the ultrasonic range (90 kHz) for the clupeid American shad and gulf menhaden (subfamily Alosinae) but not in the related clupeid sardine, anchovy or herring of other subfamilies which have hearing thresholds limited to lower frequencies (100–5000 Hz) (Mann et al., 1998, 2001, 2005). It is proposed that this sensitivity to ultrasound sound pressure may have evolved to detect the high intensity ultrasonic clicks used by potential predators such as the bottlenose dolphin, *Tursiops*, for echolocation in their natural environment (Plachta and Popper, 2003). This sensitivity to ultrasound at high SPL thresholds is proposed to be mediated by a unique morphological specialization in the utricle but awaits an experimental test (Higgs et al., 2004).

Other fish groups have reduced the distance between portions of the gas-filled swim bladder (a hydrostatic organ for buoyancy) and the inner ear that enhance hearing capabilities (reviewed by Schellart and Popper, 1992; Braun and Grande, 2008). Comparative behavioral and physiology studies show a general trend for enhanced sensitivity or extended high frequency range of hearing that is associated with the presence of rostral extensions of the swim bladder toward or directly coupling with the ear that include some holocentrid squirrelfishes (Tavolga and Wodinsky, 1963; Coombs and Popper, 1979), the Atlantic cod *Gadus morhua* (Chapman and Hawkins, 1973), *Chaetodon* butterflyfishes (Tricas and Boyle, 2015a), several distant and sister cichlid genera (Schulz-Mirbach et al., 2012), the otic capsule in some mormyrids (McCormick and Popper, 1984; Yan and Curtsinger, 2000; Fletcher and Crawford, 2001), sciaenid drums and croakers (Ramcharitar et al., 2006; Horodysky et al., 2008), the geriid mojarra (Parmentier et al., 2011b) and others (reviewed in Braun and Grande, 2008).

### 2.09.6.4    Experimental Studies on Accessory Hearing Structures

The non-invasive AEP technique is also used to experimentally demonstrate the effect of accessory auditory structures on hearing sensitivity and bandwidth. Deflation of the goldfish swim bladder, which is mechanically coupled to the ear by the Weberian apparatus, increased hearing thresholds by about 50 dB at frequencies up to 1.5 k Hz, but not in the toadfish and blue gourami which lack swim bladder accessory hearing structures (Yan et al., 2000). Removal of the tripodes ossicles from the Weberian apparatus of the goldfish produce a frequency dependent increase in thresholds from 7 dB at 100 Hz up to 35 dB at 2 k Hz (Ladich and Wysocki, 2003). Sensitivity also decreased after filling of the gas bullae of the clupeid menhaden for ultrasound hearing (Wilson et al., 2009), the suprabranchial air-breathing chambers of gouramis (Yan, 1988), and blocking of the specialized lateral trunk channels of the swim bladder in the loach (Kratochvil and Ladich, 2000) confirming their contributions to enhanced hearing.

Recent studies have experimentally confirmed that extensions of the swim bladder toward the ear enhance hearing ability. Butterflyfishes (family Chaetodontidae) have a well-developed swim bladder (**Fig. 7**D–G). Members of the genus *Chaetodon* are distinguished by the presence of a laterophysic connection, which is a unique morphological association between rostral projections of the swim bladder and the lateral line at the posterior margin of the skull (Webb, 1998). *Chaetodon* subgenera differ with respect to the dimensions of the horns (length and width) and their proximity to the adjacent lateral line and ear (Webb et al., 2010) (**Fig. 7**D,F,G). AEP experiments show that the bannerfish butterflyfish *Forcipiger*, which lacks swim bladder horns, is sensitive only to particle acceleration at relatively high stimulus thresholds at all frequencies (Tricas and Boyle, 2015b). In this species hearing thresholds did not change after deflation of the swim bladder, which would be required for the transduction of sound pressure stimuli to the ear (**Fig. 10**A). In contrast, audiograms of *Chaetodon* species, which have rostral swim bladder horns, show much lower thresholds to sound pressure and an extended high frequency range of hearing up to 1.3–2 kHz (**Figs. 10**B–D). Experimental displacement of gas by the injection of gel into fish with long the swim bladder horns (*Chaetodon multicinctus* and *Chaetodon auriga*) decreased auditory sensitivity (increased thresholds) in the low pass 200–600 Hz frequency range by 5–10 dB and variably among species at higher frequencies. Removal of all gas from the swim bladder body decreased baseline hearing sensitivity in *Chaetodon* by 10–20 dB, and to near that of *Forcipiger*. This study experimentally demonstrates that all butterflyfishes are primarily sensitive to particle acceleration, and that hearing sensitivity and frequency range are enhanced by the transduction of sound pressure stimuli mediated by the swim bladder and horns.

#### 2.09.6.4.1    *Single Cell Recordings and Encoding of Particle Motion*
Recent advances in single cell techniques have provided great neurophysiological demonstrations of how the sensory macula of the inner ear detects and transforms particle motions into neural codes to provide temporal, spectral and directional information to higher processing regions of the brain. The development of a three-axis mini shaker system (Fay, 1984; Fay and Edds-Walton, 1997) allowed for single cell recordings of auditory primary afferents during controlled movements of the fish body and ear in translational oscillatory motions in the horizontal and mid-sagittal planes.

### 2.09.6.5    The Saccule

Primary afferents of the saccule in the goldfish, toadfish and sleeper goby are sensitive to directional features of particle motion displacement thresholds as low as 0.1 nm RMS (Fay, 1984; Fay and Edds-Walton, 1997; Lu et al., 1998; Fay and Ream, 1986). Primary afferent fibers show cosinusoidal (circular) directional response patterns (determined by locking of spikes with the phase of the sinusoidal oscillation of the body) with nearly all best axes in the horizontal plane near the same angle from the midline of the fish, which is approximately equal to the orientation of the saccular maculae (**Fig. 11**A and B). Saccular units of the toadfish also show best directions in the mid-sagittal plane that range from strong horizontal to all vertical elevations in accordance with its wide
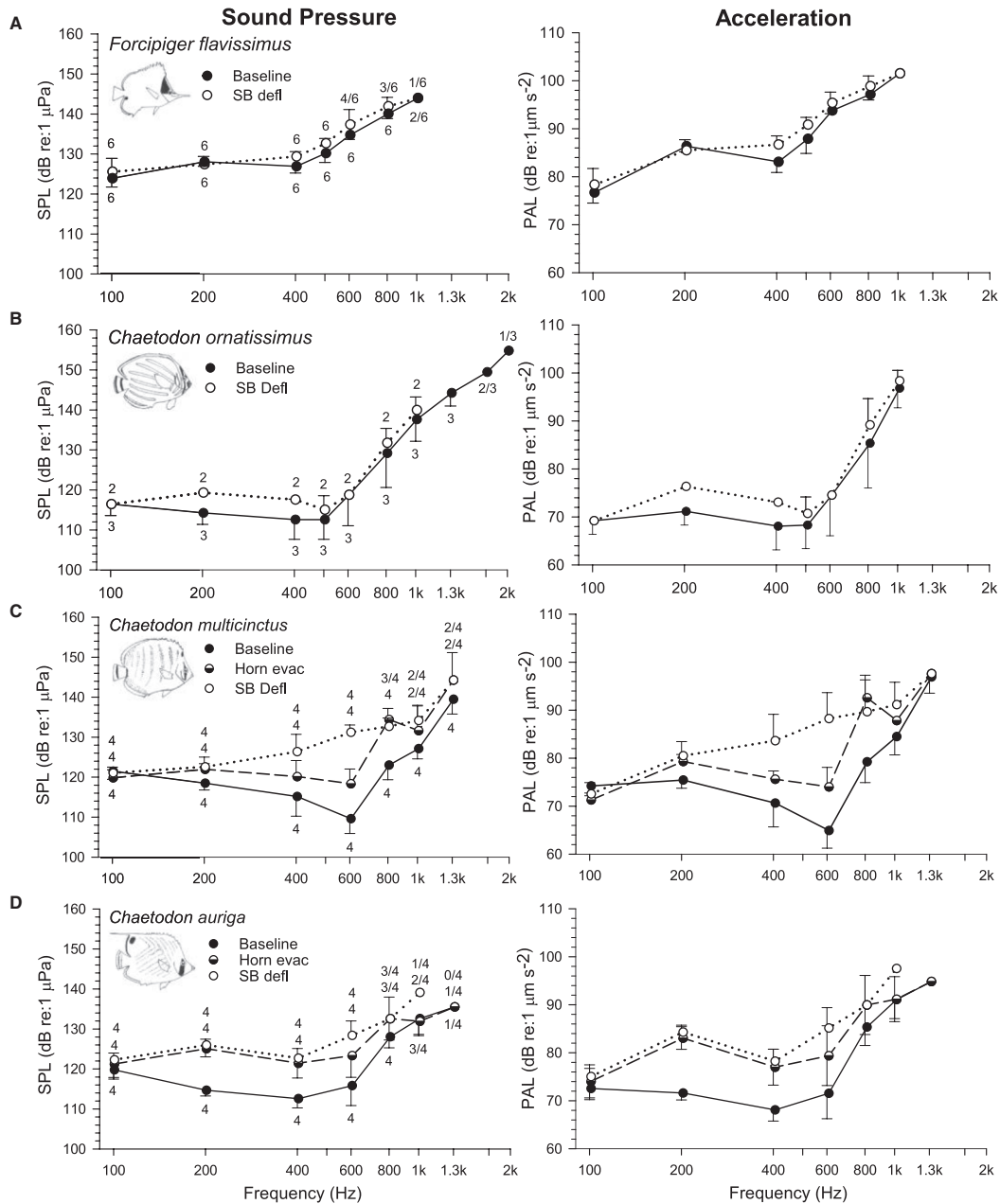
**Figure 10** The effect of the gas-filled swim bladder horns and chamber on hearing sensitivity in *Chaetodon* butterflyfish with different laterophysic morphologies as determined by the AEP technique (A) *F. flavissimus*, which lacks an LC and swim bladder horns shows no change in normal AEP threshold (black circles) following deflation of the swim bladder (open circles) (B) *C. ornatissimus* has short swim bladder horns with an indirect connection to the LC that we were not able to manipulate. The baseline thresholds extended to 2000 Hz and appear to increase by approximately 5 dB in the 200–400 Hz band following deflation of the swim bladder (C) *C. multicinctus* has long swim bladder horns with an indirect connection to the LC. Baseline thresholds increased in the 200–600 Hz band after gas was evacuated from the swim bladder horns (half-filled circles) with a maximum increase of 10 dB at 600 Hz. Subsequent deflation of the swim bladder demonstrated further threshold increases most notable at 600 Hz (D) *C. auriga* has long swim bladder horns with a direct connection to the LC. Baseline thresholds increased by about 10 dB at 200–600 Hz after gas was evacuated from the swim bladder horns and swim bladder. AEP threshold data are provided in relation to sound pressure level (left column) and particle acceleration level (right column). Data are means and s.e. among individuals. Numbers at data points indicate sample size at each test frequency, or fraction of test subjects for which an AEP was recorded. From Tricas and Boyle (2015b).

range of hair cell orientations found on the macula (Fay and Edds-Walton 1997). In contrast, the goldfish saccule, which has the majority of saccular hair cells oriented in the dorsal ventral axis, shows a much narrower range of vertical sensitivity and likely does not resolve well the elevation of acoustic particle motions (Fig. 11A). These significant studies demonstrate that the saccule of the fish ear responds to very small inertial displacements of the otolith, extracts frequency and amplitude from particle motions, and has varying capabilities associated with the macula morphology for encoding information about the axis of a sound source.
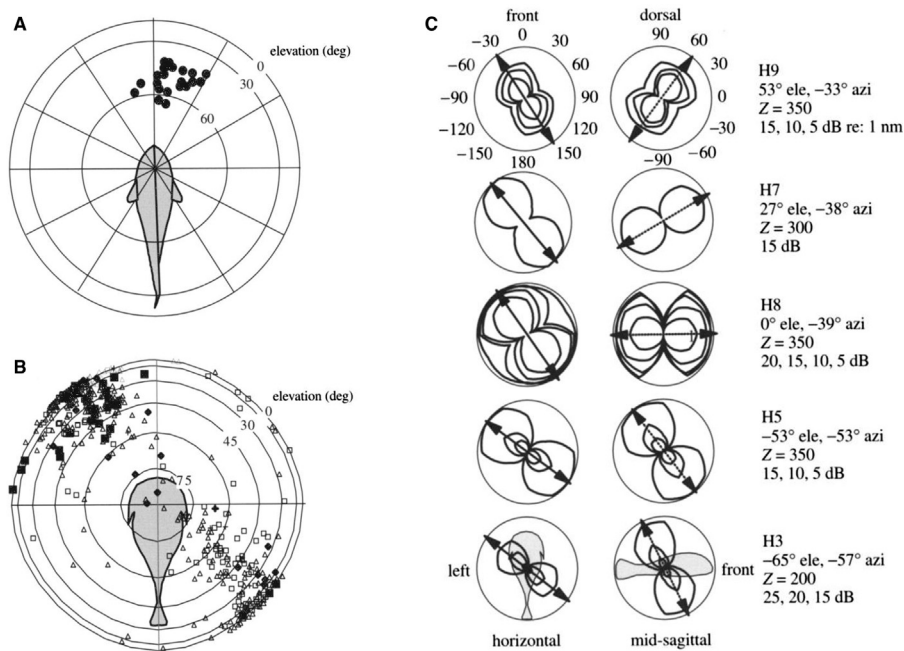
**Figure 11    Directional sensitivity of the teleost fish ear.** (A) Representations of a globe, with the fish at the center, showing the location on the Northern Hemisphere at which the most effective axis for each afferent penetrates the surface. An afferent's azimuth is plotted on the circular axis as in a polar plot. Elevation is represented on the radial axis. Twenty-one right saccular afferents from the goldfish (upper panel). Four hundred and forty-three left saccular afferents from the toadfish (lower panel). The differing symbols in indicate data sets from different research seasons. (B) Directional responsiveness patterns for five saccular afferents from the left ear of a toadfish. Each is a polar plot of phase-locked spike rate (4-statistic) as a function of stimulus axis angle, usually at several fixed displacement amplitudes (given in dB re: 1 nm). The afferent identity is given in the column on the right (e.g. H9), the most effective axis of stimulation in the mid-sagittal plane (ele) and the horizontal plane (azi) are given along with the phase-locked spike rate (4) indicated by the maximum radius of the circular axes. The best direction in the horizontal plane (plots on left) and the mid-sagittal plane (plots on right) are shown for each afferent by the double-headed arrows, which also illustrate the 180 ambiguity inherent to these measurements. The stimulus angles are shown around each circle. To make these figures, the lines connect data points (not printed), each of which is plotted twice for clarity once at the nominal axis angle, and once again at that angle plus 180°. The cartoon of the toadfish in the bottom panels indicates the plane represented. (A) From Fay and Edds-Walton (2000). (B) From Fay and Edds-Walton (2000).

### 2.09.6.6    The Lagena and Utricle

Although the saccule is considered the primary auditory organ in the fish ear, single cell recordings show that both the vertically-oriented lagena and horizontally-oriented utricle also encode frequency and directional information of particle motion (Fay, 1984). Recent experiments on primary afferents from the lagena of the sleeper goby show units with strong phase-locking responses to a bimodal range of low stimulus frequencies: < 50 and 80–125 Hz (Lu et al., 2003). As for saccular units, lagenar afferents responded best in the direction of the longitudinal axis of the macula in the horizontal plane and show a wide range of vertical sensitivities in the mid-sagittal plane. However, lagenar units were less sensitive to particle motions than saccular units by about an order of magnitude (Lu et al., 2003). These experiments confirm that the lagena contributes information to the CNS on the direction and elevation of a sound source, and its relative low sensitivity to particle motions in the goby may extend the range of hearing to higher stimulus levels after when responses from the saccule are saturated.

Neurophysiology experiments on the utricle show that many primary afferent fibers have strong-phase locking responses and low characteristic frequencies centered around 80 Hz (range < 50–400 Hz) (Lu et al., 2004). Most fibers were directionally sensitive over a wide range of horizontal angles (153°) with best responses clustered around the main longitudinal axis of the fish body. Recent chronic recording experiments on free-swimming toadfish confirm that utricular primary afferents respond best at low stimulus frequencies (80–200 Hz) as well as to playbacks of conspecific boatwhistles and grunts of similar fundamental frequencies (Maruska and Mensinger, 2015). Most toadfish utricular afferents also showed clear directional responses, with the largest population responding best to stimuli delivered along the longitudinal axis of the fish body. Combined, these neurophysiological studies indicate that the teleost lagena and utricle extend the dynamic response range and provide important azimuth and elevation information to the brain about the direction of an acoustic source.

### 2.09.7    Sound Source Localization

Sound localization from binaural time delays in particle motion would be physically challenging for most fish species. The high velocity of underwater sound impinges on the small and juxtaposed inner ears of the fish (separated by only mms to a few cms

depending on size and species) with interaural time delays of only several microseconds which is below the neural delay thresholds for frogs and toads, mammals and birds (see Olsen et al., 1989; Grothe et al., 2004, 2010). Furthermore, the high acoustic transparency of the fish body to sound pressure would produce little difference in the associated particle motions detected by each ear. Thus in fishes directional information is mediated by the particle motion vectors, and in some species may be used in conjunction with sound pressure to enhance localization of the source.

Recent experimental studies on the plainfin midshipman have provided critical understanding to the importance of particle motion vectors for localization of a biologically-relevant sound source. This species inhabits shallow coastal reefs of the northeast Pacific during the reproductive season where Type I males establish adjacent nests in rocky shelters. Here males advertise their nest location by the production of a continuous hum with a fundamental frequency of about 90–140 Hz (Brantley and Bass, 1994). In this system, gravid females are highly motivated to approach advertising males, and can be readily attracted to sinusoidal-like hums produced by an underwater loudspeaker (McKibben and Bass, 1998). In choice experiments where two artificial hum sources were played, females were able to discriminate between overlapping acoustic signals that differed in duration, frequency, amplitude, fine temporal content, and approach the source.

These studies showed that reproductively active females could differentiate among and approach different sound signals, but the relevant acoustic stimulus remained elusive. What followed was a series of significant phonotaxis experiments to determine whether sound pressure, particle motion, or a combination of both provided the relevant stimulus that guide females to the location of the male's nest. From a behavioral ecology perspective, this was an important question because midshipman males are not visually conspicuous when vocalizing at the nest site, unlike many mobile reef fishes that also use visual displays in courtship and attraction behaviors.

### 2.09.7.1    Localization by Particle Motions in a Monopole Field

The hypothesis that particle motion from a pulsating swim bladder is the relevant attraction stimulus was tested on the plainfin midshipman. In a series of behavior experiments Zeddies et al. (2010) generated a 90 Hz acoustic field from a monopole projector placed in a shallow 4-m diameter cement tank. They then mapped the pressure and particle motion field across the tank floor with a spatial resolution of 5 cm (Fig. 12A). When gravid females were released in the monopole field, the majority (73%) swam in straight or slightly curved paths toward the sound source that were in line with the particle motion vectors (Fig. 12B and C). These experiments demonstrated that female midshipman move to a biologically-relevant monopole sound source by following the particle motion vectors back to the source. However, both the particle motion and sound pressure gradients project radially from the source and presented a most basic problem for the fish with a unidirectional approach solution. Would females be able to locate a sound source where particle motion vectors and sound pressure did not point directly to and away from a source?

### 2.09.7.2    Localization by Particle Motions in a Dipole Field

The importance of particle motion for sound source localization to a dipole acoustic source was tested on midshipman females (Zeddies et al., 2012). A dipole projector was placed near the center of the tank and the particle motion vectors mapped near the bottom. This dipole field was more spatially complex, and the particle motion vectors point directly toward the source only along the dipole axis. Females which were released at points near the dipole axis, where particle motion is aligned, made a direct or slightly curved approach to the source along the dipole axis (Fig. 12D). Another group of females was released at locations approximately 90° from the dipole axis where sound pressure was low and particle motion was parallel but offset from the dipole axis. The majority of these females was also able to locate the source, but swam in a curved path that approximately followed the particle motion vector from their point of release back toward the source. In addition, a few females swam directly toward the dipole source without following the particle motion vector track almost in line with the sound pressure null. The main approach path used by most females to arrive at the dipole source was generally consistent with the vector approach model by Kalmijn (1997) which postulates that fish maintain a constant angle with the axis of particle vibration even when it does not point directly to the source.

### 2.09.7.3    Localization with Sound Pressure Cues

Subsequent studies attempted to determine the contribution of sound pressure and the lateral line to the localization of the hum sound source by female midshipman (Coffin et al., 2014). In these experiments, females with a presumed surgically deflated swim bladder showed no difference in the ability to approach a monopole sound source compared to sham surgery controls. However, it was discovered post-trial that 88% of the surgical deflated females had a near fully or partially 're-inflated' the swim bladder. Subsequent post hoc analysis of the data showed that a very low number (11%) of the fully deflated fish exhibited positive phonotaxis compared to the post-surgery re-inflated subgroup, and that 95% of all fish that localized the source had at least a partially inflated swim bladder. In lateral line experiments, females with an ablated mechanosensory lateral line system showed no difference in phonotaxis behavior compared to sham-ablated controls, indicating that the lateral line is not involved in sound source localization at
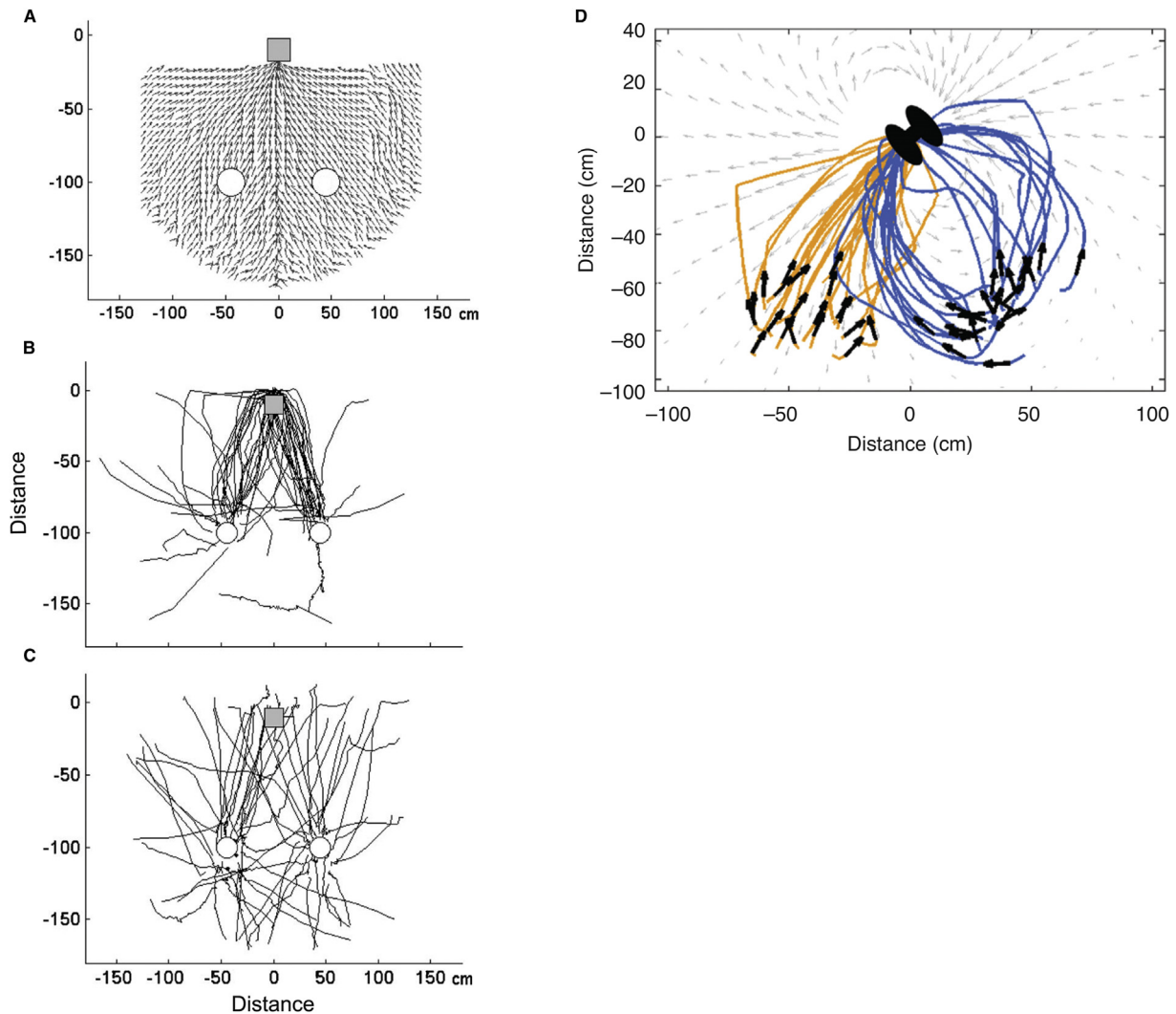
**Figure 12**  **Sound localization by gravid plainfin midshipman females to a monopole and a dipole sound source.** (A) Particle displacement vector field in the XY plane as measured at 4.5 cm above the tank floor. Monopole projector (square) is near center of the tank. Fish were released at sites (circles) 100 cm from the sound source. (B) Response pathways of fish released at one of two sites in front of the active monopole sound source. (C) Pathway of fish released in front of inactive projector. The axes are the distance from the center of the tank in cm. Note that the phonotaxic responses of the gravid females in the test (sound on) group consisted primarily of straight to slightly curved tracks to the sound source. (D) Response pathways of gravid plainfin midshipman females as they approach a dipole sound source. Orange traces show tracks of fish released near the dipole axis. Blue traces show tracks of fish released away from the dipole axis and near the plane orthogonal to the axis of vibration. Gray arrows indicate the particle velocity vectors. Black arrows show the initial directions of the fish as they leave the release sites. Note that fish follow lines of particle motion. (A - C) From Zeddies et al. (2010). (D) From Zeddies et al. (2012).

large distances from the source (Coffin et al., 2014). Thus the results of these experiments are consistent with the idea that sound pressure mediated by the swim bladder may also be important for sound source localization in the midshipman, and further investigation is needed.

The above experiments put back into focus several theoretical models of sound source localization that address the 180° ambiguity of particle motion vectors, in which the direction of the sound source cannot be determined from only the axis of linear acceleration. Several of these models require that the fish is able to detect both sound pressure and particle motion including the phase model (Schuijf, 1975; Schuijf and Buwalda, 1975), the orbital model (Shellart and de Munck, 1987), and computational model (Rogers et al., 1988), although the shallow environment of the midshipman mating may not present an optimal experimental system for direct tests. The system might be evaluated in relation to other models that do not require the use of sound pressure information including the constant angle of approach model (Kalmijn, 1997), the multipole model (Rogers and Zeddies, 2008), and the time averaged intensity model (Sisneros and Rogers, 2016). These models also await future empirical tests on other fish groups, most of which do not produce continuous acoustic stimuli to attract mates and may require serial sampling of particle motion or pressure fields over time and space.

## 2.09.8    Future Directions

Classic studies on fish hearing and sound production have focused largely on the proximate mechanisms of sound communication. Below are some possible areas for future research to better understand fish acoustic behavior in their natural environment.

1. **What are the spatial features of biologically-relevant sounds?** More research is needed to quantify the polarity, directionality and intensity of biologically-relevant acoustic fields. Characterization of sounds from environmental background noise, natural prey and predators, or behaving conspecifics can be used to better interpret the function and evolution of fish auditory systems.

2. **Is perception of low frequency acoustic bands biologically important?** Many fish produce low frequency sound fields (<20 Hz) during their normal behaviors. However, the vast majority of studies address the acoustic spectrum above 80–100 Hz. Future work should investigate this orphaned low frequency spectrum to describe the natural sources of infrasound stimuli and processing by the fish ear.

3. **How are biologically-relevant acoustic stimuli processed by the auditory system?** Physiology experiments that use short tone pips to characterize hearing bandwidth and encoding are generally limited to proximate questions about auditory function. More neurophysiology research is needed to determine how biologically-relevant stimuli (e.g. natural defense and mating calls) are encoded at the level of the ear and processed at different levels of the central nervous system.

4. **How are biologically-relevant signals and cues processed in the behaving fish?** Laboratory neurophysiology experiments rely primarily on a reduced or immobile fish prep. There is very little information on how the nervous system of a behaving fish processes and integrates acoustic and other stimuli in natural settings. Collaborative development of new micro-miniaturized technologies would allow long-term recording from multiple processing centers in fish, other small aquatic vertebrates, and invertebrates. Recent advances in microcircuit data acquisition, processing, and storage, which currently is widely applied to rodents and primates, make this seemingly impossible goal now more achievable.

5. **What are the soundscapes of fish communities?** Many marine and freshwater organisms are experiencing serious environmental challenges from climate change. Recent studies have used passive acoustic remote monitoring techniques to characterize the long-term soundscapes in fish communities (see Lindseth and Lobel, 2018; Desjonquères et al., 2019). The recording of acoustic soundscapes and fish sound libraries can become a useful tool to monitor the state of fish populations and ecosystems without direct human observation.

6. **How can we control the effects of anthropogenic noise on wild fish populations and communities?** Harmful high-intensity acoustic noise in the aquatic environment can be produced by large ships, small boats, sonar, seismic exploration with air guns, underwater explosions, and pile driving (see Carroll et al., 2017, Popper and Hawkins, 2019). Broad integrative approaches by sensory biologists and ecologists can model the effect of noise on impacted fish populations and communities, rather than laboratory studies on a single test species. These are needed to provide a sound basis for future conservation and management of these important resources.

## 2.09.9    Summary

Fishes are found in nearly all aquatic environments, and many species use acoustic communication during social interactions. Fish have several different sound production mechanisms that involve motions of the swim bladder or other morphological structures. Natural sources of sound are primarily multipolar in nature, although monopole-like sounds (e.g. a vibrating swim bladder) also occur. Some species produce sustained courtship hums, but most produce short sound pulses primarily during reproductive and agonistic interactions that span the frequency range of $< 20$ to $> 1000$ Hz. Particle motion, and in some cases sound pressure, are the two primary acoustic stimuli that are detected. The inner ear is of the basic vertebrate plan, and is sometimes associated with accessory hearing adaptations such as the Weberian apparatus, swim bladder extensions, or other gas-filled structures that impart sensitivity to sound pressure. Sensitivity to particle motion is usually <1000 Hz, with a higher sensitivity and frequency range for species sensitive to sound pressure. Single cell experiments confirm that the saccule encodes frequency, intensity and directional information with smaller contributions from the utricle and lagena. Recent behavioral studies confirm that fish can follow particle motion vectors to localize a relevant sound source, but the role of sound pressure for sound localization is still in debate.

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