Underwater Acoustics: Webinar Series for the International Regulatory Community
Marine Animal Sound Production and Reception
Thursday, December 3, 2015 at 12:00pm (US East Coast Time)

Summaries below combine the webinar outline (provided in advance) with each webinar presentation. Content from the **original outline** are indicated in **bold text.**

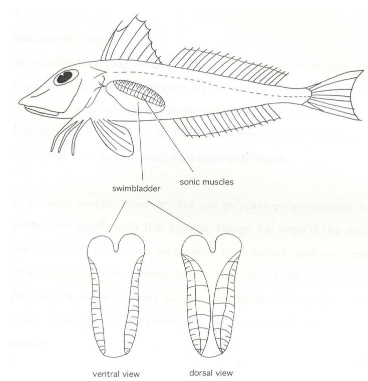
Presentation Summary: Sound Production and Reception in Teleost Fish (M. Clara P. Amorim, Ispa – Instituto Universitário)

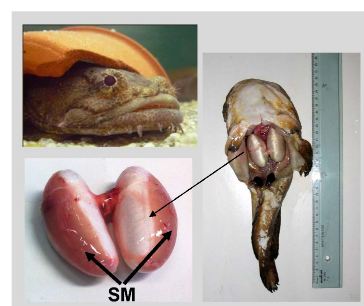
Teleost fish are likely the largest vocal vertebrate group. Sounds made by fish can be an important part of marine soundscapes.

- Fish represent more than half of all vertebrate species; and at least 800 species of fish from over 100 families have been described to produce sound and more vocal species continue to be documented.
- This includes may commercial fish species (cod, croaker, sea bass, grouper)

Fish possess the most diversified sonic mechanisms among vertebrates, which include the vibration of the swim bladder through intrinsic or extrinsic sonic muscles, as well as the rubbing of bony elements (similar to what insects do).

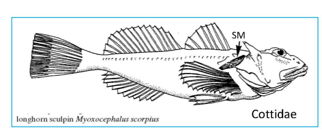
- Sound production mechanisms in many fish species remain unknown, as it is difficult to understand which mechanisms they use to produce sound.
- Two examples of "sonic species" provided: grey gurnard (*Eutrigla gurnardus*) and Lusitanian toadfish (*Halobatrachus didactylus*)
    - o Both of these fish species have swim bladders (sacs filled with air that are used to control buoyancy). Sonic muscles (SM), that have evolved specially for sound production, are attached to their swim bladders. When they contract these [intrinsic] muscles, the swim bladder will vibrate. Each sonic muscle contraction will produce a sound pulse.

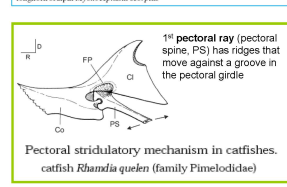




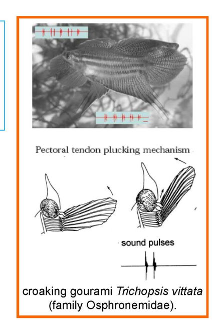
***Halobatrachus didactylus* (Batrachoididae)**

- Swim bladders come in all different shapes, and the sonic muscles attach in different ways
- Sonic muscles can also be extrinsic (in addition to intrinsic)- not directly attached to the swim bladder. In this case, the SM (still specialized muscle), originate in/attached to the skull, pectoral girdle, ribs, and/or vertebrae. When these muscles are contracted, either direct or indirect sound production occurs.
- Sound production via the rubbing of bony elements, especially pectoral structures (pectoral girdle, fin rays, and fin tendons)
    - o Other species use stridulation of the dorsal fin, pharyngeal teeth, or other structures to produce sound
- Herring have an interesting sound production mechanism- bubbles produced through anal pore (may be a defense mechanism)



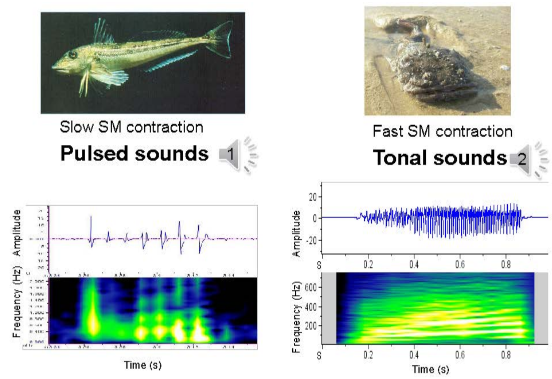


Ladich & Fine (2006)



Fish sounds are usually <u>pulsed</u> (each sonic muscle contraction corresponds to a sound pulse; sounds often consist of repeated pulses), <u>short</u> (typically shorter than 1 s) and <u>broadband</u> (with most energy below 1 kHz- <u>low frequency</u>), although some fish produce tonal sounds.

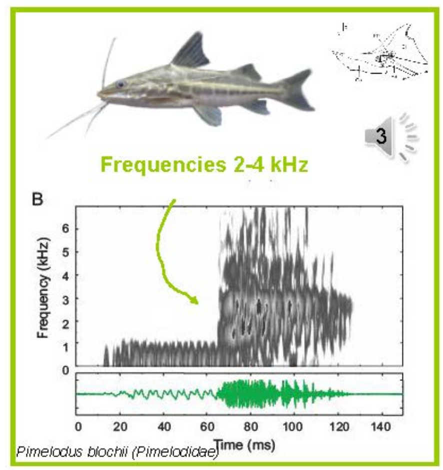
- For some fish species, the muscles contract so rapidly, that the sound pulses fuse together, resulting in a tonal sound (almost like a pure tone).
    - Example sounds played for a grey gurnard (pulsed sound) and a Lusitanian toadfish (tonal)



Sounds generated by bony elements are often higher frequency (up to a few kHz).

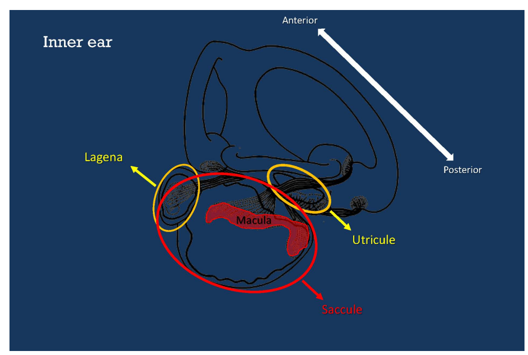
- Catfish example provided. In the beginning, hear a drumming sound, then a stridulatory sound (different sound production mechanisms for each). Stridulatory sounds are at a higher frequency.

- Fish sounds are not as variable as bird songs and other sounds, but still have variability in sound rate, and/or the temporal pattern of pulses. These variations may have breeding/spawning implications.
- Sounds produced by fish are quite stereotyped. Fishes usually only produce 1 or 2 different sound types.



Courtesy of Fritz Ladich

In contrast with terrestrial vertebrates, fish have no external or middle ear. Fish detect sounds with the inner ear, which comprises three semicircular canals (that are perpendicular to each other) and three otolithic end organs: the utricle, the saccule and the lagena.

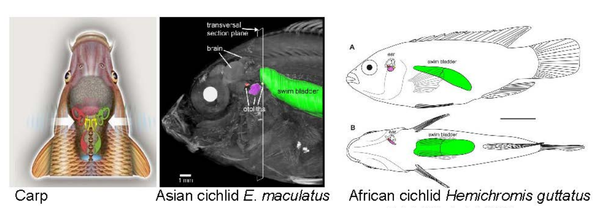


- Each end organ is composed of an "ear stone" or otolith
- Ototliths are much denser than a fish's body (the body has the same density as water and is essentially "transparent to sound"). A sound will propagate through fish tissues, and since the otoliths are denser, they will oscillate [with a phase lag] in relation to the remaining tissues, move against the sensory hair cells, allowing fish to detect particle motion (i.e. detect the movement of sound). All fish can detect the particle motion component of sound but only a few can detect sound pressure.

Some species have evolved accessory auditory structures that serve as pressures transducers and present enhanced hearing sensitivity and increased frequency detection up to several kHz.

- Some fish have specializations for enhanced hearing: a swim bladder very close to the inner ear, or small ossicles that connect the inner with the swim bladder (Weberian ossicles)

Specialists……. generalists



Schulz-Mirbach et al. (2012)

Fish with hearing specializations (pressure transductors) such as the **Weberian ossicles** or with the **SB in close proximity to the inner ear** can detect the **pressure** component of sound. Fish that lack such specialisations can only detect **particle motion**.

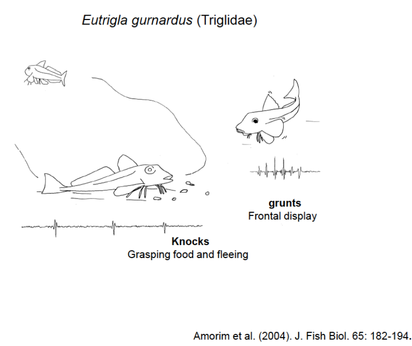
- Some fish have a better ability to hear sound (audiogram shown)
  - A few fish (only some examples) are able to hear a range of frequencies up to several kilohertz and can also listen to sounds at low amplitudes
  - Atlantic salmon has a much lower range of hearing abilities (lower than 1kHz and need sounds to be loud to detect them)

Fish hearing seems to have evolved independently of sound production and is important to detect the 'auditory scene'.

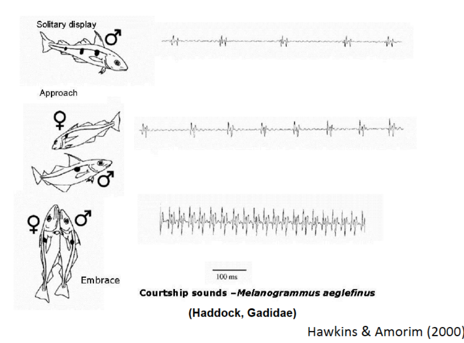
- To detect prey, predators, all sounds they need to be aware of; not just for communication

Acoustic signals are produced during social interactions or during distress situations as in insects or other vertebrates. Sounds are important in mate attraction, courtship and spawning or to defend a territory and gain access to food.

- Alarm sounds made by catfishes (create stridulatory sounds in presence of predators or when in distress; when being held in air)
- Lusitanian toadfish makes distress sounds similar to sounds produced during agonistic interactions (when fish are defending their territories)
- Fishes produce sounds during fights, territorial defense, feeding competition, when obtaining dominance over others
  - Croaking gourami example; when sizes are similar vocal males win more fights than silent males.
  - In some species larger males make higher amplitude and lower frequency sounds (let conspecifics know their fighting ability- that they are big)
  - Several experiments show that sounds can be used as "keep out signals"- territorial deterrents.
  - Competing for resources such as food; several fish arrive to a food source at the same time, display visually and acoustically to keep conspecifics away



- Common context for sound production is during reproduction
  - Mate attraction (e.g. boatwhistle call produced by male Lusitanian toadfish)
    - Calling rate of toadfish is actually related to reproductive success (number of eggs in their nest); important behaviour for their reproductive fitness
  - Courtship and spawning
    - Can stimulate females and synchronize release of gametes; increase chances of fertilization (e.g. haddock)



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Animals and Sound > How do fish hear?
(http://www.dosits.org/animals/soundreception/fishhear/)

Animals and Sound > Advanced Topic > What components of sound are used for hearing?
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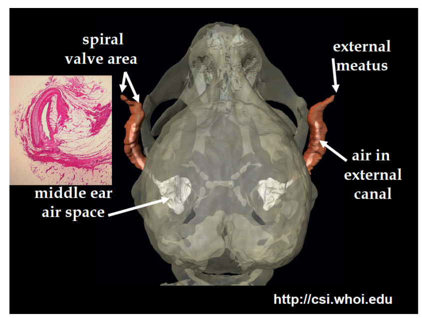
Presentation Summary: Marine Mammal Underwater Hearing: Sound Production, Sound Reception, and Sound Impacts (Dr. Darlene Ketten, Jefferson Science Fellow, National Academy of Sciences and U.S. Dept. of State, Harvard University Medical School, Woods Hole Oceanographic Institution)

What is a Marine Mammal?

- Marine mammals evolved from primitive land mammals
- **Marine mammals belong to five vertebrate groups: cetaceans (dolphins and whales), pinnipeds (seals, sea lions, and walruses), sirenians (manatees and dugongs), mustelids (sea otters) and ursids (polar bears).**
- **Cetaceans are divided into the odontocetes (toothed whales and dolphins) and the mysticetes (baleen whales). Pinnipeds are divided into the phocids (true seals), the otariids (eared seals and sea lions), and the odobenids (walrus).**
- **Cetaceans and sirenians are air breathers but in terms of body shape, limbs, etc., are completely aquatic adapted; the other groups are amphibious, adapted in varying degrees to living on land and in water.**

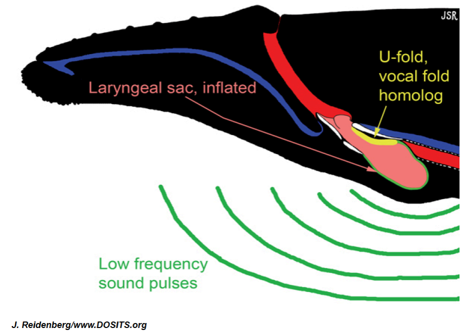
Marine Mammal Sound Production

- In order to understand how marine mammals produce sound in water, we need to understand the functional anatomy of the head and throat in each group
    - One way to examine head anatomy in marine mammals is by using biomedical imaging methods (CT and MRI scanning):

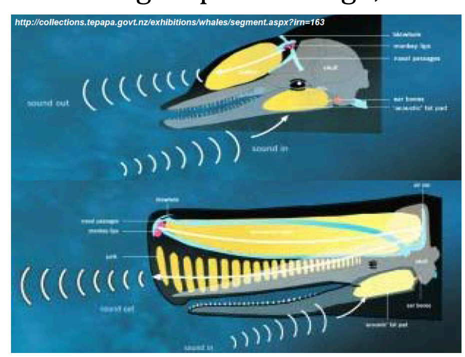


        - Some groups (polar bears, otters) have ears and head anatomy with very minor differences from their land counterparts.
        - Pinnipeds have varying degrees of adaptations (harbour seal at right) - and generally look overtly very similar to land carnivores (such as dogs and cats) but they do have some aquatic specializations
            - Pinnipeds retained the basic structure for sound production as land mammals (the larynx), but for sound reception, they have some specializations like a cartilaginous, spiral valve (red insert) at the external end of the ear canal, which can contract to prevent water from entering when in choppy water when at the surface. We do not know if they flood the canal or not during dives.
        - By comparison, cetacean heads have considerable differences from land mammals (beaked whale CT scan at right) and scientists see something that is entirely different (from land mammals/pinnipeds). The whole anterior skull is elongated (referred to as telescoping) with the frontal bones and sinuses pushed backwards and up. This creates a scoop or cavity at the front of the head, which holds the melon, a large, ovoid, fat-filled body that sits atop the long jaw area, creating the characteristic bump of dolphin heads. The nares (nose passage opening) are found just behind the melon, having been shifted through evolution from the anterior to the dorsal surface of the head. This new dorsal nostril position is the “blowhole” and allows whales to breathe at the surface without exposing more than the very top of their heads.

- **Like land mammals, all marine mammals have a larynx which is used to produce vocalizations.**
    - Baleen whale sound production depends upon a larynx like most mammals, including humans. In baleen whales, the larynx has U-shaped vocal folds (similar to our vocal cords) over which air passes to produce the basic sounds. In most species there is also an extra laryngeal sac that may amplify those sounds. The very large larynx and sac common in most baleen whales accounts for the extremely low frequency sounds characteristic of many baleen whales (in some species at infrasonic frequencies).



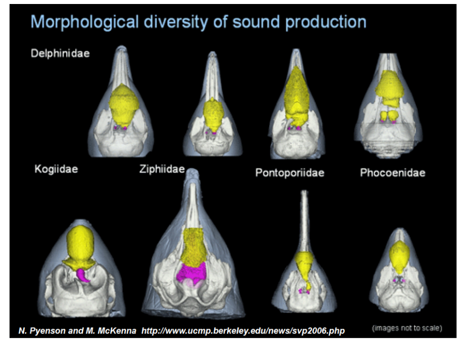
    - Odontocetes may produce mid to high frequency sounds with their larynx but they also produce a range of ultrasonic signals (clicks, burst pulses, and buzzes), which are used for echolocation.
    - Echolocation (also called biosonar) means the sounds that some animals produce in order to generate echoes from objects in their sound path. These echoes are detected by the animal and analysed by its brain to determine the objects characteristics, such as shape, density, or direction and speed if it is moving.
    - These ultrasonic signals are generated by manipulating air in specialized sacs located along the air passages of the nares. As air travels along the narial passages, the buzzes and clicks are produced as air passes in and out of these sacs and through a pair of tough, muscular valves, called the museau de singe, near the blowhole. These sounds are directed into the water through the fatty melon (diagram at right). Therefore dolphins/toothed whales produce sounds by pushing air up through the narial passages and the melon acts somewhat like an acoustic lens to focus or direct the outgoing sound. Typical ultrasonic signals of odontocetes range between 30-70kHz range, but some go as high as 150-160kHz..



    - In all odontocetes, and at least some mysticetes, there are also specialized fat bodies aligned with the lower jaw that are important for whales to hear underwater. The fatty bodies along the jaw connect to the middle ear and because they have acoustic characteristics similar to those of water they are the most efficient channels for sound to reach the ear, in the same way as air filled external canals work for land mammals.
    - Sperm whales have an even more elaborate and specialized sound production system. As with other odontocetes, they have a dorsal narial opening, but sperm whales have one narial passage closed off, which results in sounds being guided to the frontal scoop of the skull and then bounced back and forth, so that they are amplified and then emitted through the large specialized fatty block of the sperm whale head referred to as the "junk"

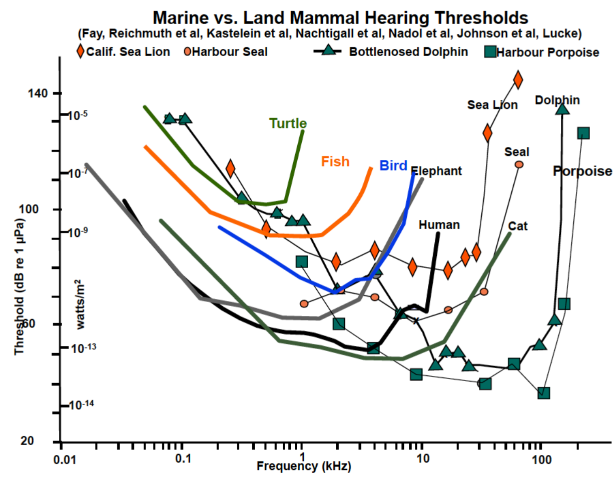
- **Peak spectra of lower frequency vocalizations and ultrasonic echolocation signals are correlated with the size of the animal, the distance over which it expects to signal or communicate, and, for echolocators, the type of prey and complexity of the habitat. Species that hunt small fish in complex environments use higher frequencies at lower intensities while offshore species communicating across long distances use relatively low frequencies, sometimes at high intensities.**

- The melons and jaw fats in toothed whales vary widely and are related to the species differences in what sounds are produced and what frequencies are used for echolocation.



Marine Mammal Sound Reception

- Jaw fats are found in all cetaceans. The jaw fats act effectively as pinna- the external flaps that we refer to as the outer ear, and as the channels to the middle ear, an analogue of our external auditory canal.
- Examples of Vertebrate Audiograms (hearing curve) shown at right. Humans are not specialized for any particular type of hearing but are fairly sensitive across a broad range (hearing measured in air). The elephant is a low frequency specialist. Amphibious animals that can hear underwater and in air (sea lion and seal) also have a broad range and can often hear higher frequencies than humans but their dual adaptation makes them less sensitive underwater than the highly adapted odontocetes (toothed whales). Currently, we do not have a baleen whale curve, but their hearing sensitivity is estimated to be best at lower frequencies, like that of elephants. Like bats, another echolocator, odontocetes, have very acute hearing at ultrasonic frequencies. They also have a wide hearing range (humans can hear~8 octaves, odontocetes hear ~10-12 octaves). However, they have poor low frequency hearing. .

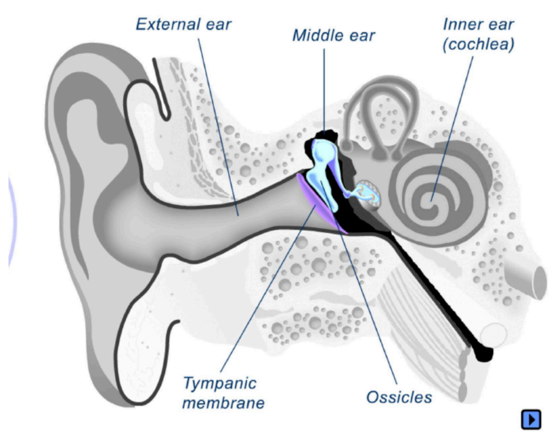


How does hearing work in marine mammals?

- **The most important adaptations in marine mammal ears for hearing underwater are in the outer and middle ears. Many have outer canal valves and specialized middle ear tissues to assist with pressure equalization during diving and extremely dense ear bones that are resistant to breakage from extreme ambient pressures. The outer ears of cetaceans have unique fats that receive and channel underwater sound to the middle and inner ear.**

- **Marine mammals, like land mammals, have a three-part auditory system: Outer Ear (sound collection and transmission); Middle Ear (amplification and mechanical transduction) and Inner Ear (neurotransduction).**

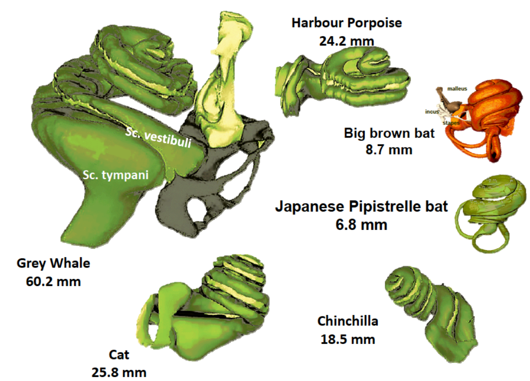
(animation of how hearing works in mammals)



- The external ear and external auditory canal collects the sound and channels it to the middle ear, where the ossicles amplify and transduce the sound waves into a mechanical pressure wave with a velocity component. The sound then is processed by the components of the inner ear, a spiral shaped organ found in all mammals, the cochlea. The cochlea is responsible for much of what we think of as our hearing ability, such as determining your hearing range (lowest to highest frequencies you can hear) and your sensitivity (how well you can hear across that range of frequencies). As sound wave moves through the cochlea, the basilar membrane suspended along the cochlear canal vibrates at different points as a result of differences in its resonance characteristics along its length. As the membrane moves, hair cells with fine stereocilia are pushed against a second membrane which has a different mass and stiffness than the basilar membrane, causing the stereocilia to bend, and triggering a chemical release that results in a nerve impulse that travels to the brainstem and then on to the auditory cortex of the cerebrum.

- **The inner ear (cochlea) of all marine mammals is similar to land mammals but in many species it can receive and transduce a greater range of frequencies. Cetacean inner ears also have double to triple the innervation density of those of other mammals, and they are capable of better detection of signals in noise and better sound localization than most mammals.**

  Marine mammal ears vary in size (see images at right, drawn to scale). Within the cochlea of each species, the resonating membranes also differ in their size and stiffness, which results in the differences between species in hearing ranges and sensitivities.



Marine Mammals and Sound Impacts

- Noise can have multiple deleterious effects on communication and behaviour without having a direct impact on hearing.
  - Masking, which impacts communication and detection of important environmental cues.
  - Noise can affect critical behaviours, such as mating and foraging.

- Noise can also have both hearing and non-hearing physiological impacts
  - Temporary or permanent threshold shifts from sound exposures
  - Other physiological effects such as stress in high noise environments

- **Like land mammals, marine mammals are subject to hearing loss from sound impacts but also from disease, aging, and trauma. Captive animals tested over several years have been shown to lose high frequency hearing as they age in a process similar to that known for humans (presbycusis). This suggests they are also subject to Noise Induced Hearing Loss (NIHL) if exposed to sounds in their hearing range for long periods of time and at high intensities.**
  - The ocean is not quiet. There are natural, biological and physical noises. When looking at Wenz curves, what we find is that marine animals evolved to exploit sound ranges based on this natural background noise. Ovals shown for each group approximate the vocalization and hearing ranges of species that have been measured or estimated for each group. Most fishes hear reasonably well at mid to low frequencies at levels consistent with moderate sea states. So far we know very little about turtle hearing; those that have been tested have a narrow hearing range and sensitivities similar to those of fish. As stated above pinnipeds have ranges similar to many land mammals but on average poorer sensitivity than some mammals, particularly for their hearing in air. Finally, odontocetes exploit very high frequencies at which there is little natural background noise, while mysticetes use lower frequencies, but that may be an unavoidable result of their very large structures.
  - Humans add sound to the marine environment for all of our activities. As shipping or other activities increase, so does noise in the ocean. Most of our activities produce noise at lower

frequencies. Therefore, we expect that many of our activities may result in long term impacts on baleen whales rather than the higher frequency adapted odontocetes. However, some impacts, like those from impulse noise and explosives, can affect a very wide range of species.

    - Technologies such as D-tags are used to monitor animals while diving and can detect sounds that they produce as well as sounds in the environment around them
        - Sonar sounds affecting echolocation activity was described
        - Beaked whale strandings have occured coincident with some naval and seismic exercises
            - **The exact effect of the sonar exercise that results in the strandings is still unknown**
            - Part of the problem may be stress effects from the noise or ship activities

- Every ear is different in its sensitivity and every species is different in its hearing range, so impacts are not identical for all species for any given sound. There can also be gender and age differences in susceptibility to noise impacts in addition to species differences.

Terminology

audiogram: A graph of hearing ability conventionally displayed as frequency vs. sensitivity measured as sound pressure or intensity

cochlea: the inner ear spiral which contains cells that transform sound energy into neural impulses.

decibel (dB): a scale based on the log ratio of two quantities. It is commonly used to represent sound pressure level. The value of the decibel depends upon the reference pressure, which differs in air vs. water. The decibel level of sound is properly stated in the form of n dB re n microPa . The microPascal is a unit of pressure. In terms of intensity, 100 dB re 20 microPa in air equals approximately 160 dB re 1 microPa in water.

infrasonic: below 20 Hz, the lower limit of human hearing

kHz: kilo Hertz. A Hertz (Hz) is a measure of sound frequency equal to 1 cycle/sec. A kHz is one thousand cycles per second

nares/narial: air passages that connect the throat area with the external opening of the nose.

octave: An octave is broadly defined as a doubling of frequency. Thus, a one octave shift from 500 Hz is 1,000 Hz; from 3,000 Hz, it is 6,000 Hz. Adult humans have on average an 8 octave functional hearing range of 32 Hz to 16 kHz

ossicles: the middle ear bones that act as levers to mechanically transform sound waves into pressure, frequency, and velocity components transduced by the inner ear.

ultrasonic: above 20 kHz, the upper limit of human hearing.

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Hearing in Cetaceans and Sirenians, the Fully Aquatic Ear
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(http://www.dosits.org/animals/effectsofsound/marinemammals/behavioralchanges/)
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Hearing Loss (http://www.dosits.org/animals/effectsofsound/marinemammals/hearingloss/)

Animals and Sound > Advanced Topic > What components of sound are used for hearing?
(http://www.dosits.org/animals/advancedtopics/componentsofsound/)

Animals and Sound > Advanced Topic > Hearing Loss
(http://www.dosits.org/animals/advancedtopics/hearingloss/)

Technology Gallery > Passive Acoustic Recording Tags
(http://www.dosits.org/galleries/technology/observermarineanimals/passiveacousticrecordingtags/)

Questions and Answers (asked during the webinar)- Transcript

The fish sounds that were played, were the recorded in the wild (a lot are recorded in tanks with isolated fish)? Are there differences between recordings in the lab and in the wild?
Sounds played, with the Lusitanian toadfish, were recorded in the wild. The other sound played from the Sciaenids, those were also recorded in the wild (in an estuary). The other sounds, for the gurnards, were recorded in quite large tanks. And the others, I believe, were recorded in tanks. Tanks can have an influence on the sounds that are recorded because they have a resonance, but usually when you record/study sound in the lab (which is good since you can set up and control experiments), you can insulate the tanks that you use to record the fish and also take into account the resonance so that it doesn't interfere with the fish sounds.

How does the lateral line come into play with sound reception in fish, or is part of another sensory reception mechanism? How does the lateral line work?
It is another sensory mechanism but it is integrated; the lateral line also has hair cells that are neuromasts, but they work more or less in the same way, and can detect particle motion of sound (vibration, etc.), and can be useful for schooling behaviour. But they can also detect low frequency sound, and can be integrated with the inner ear to detect low frequency sound.

Sturgeon vocalizations?
Dr. Amorim was checking on this, and they do make sounds during spawning.

How do the fat channels function like pinnae?
There is a lot of variability amongst species. Acoustic impedance- as we are listening now, air is conducting sound through our ear. The ossicles conduct the airborne sound back through the water and transduces it. One of the catches with hearing underwater, is that you need an air canal that can conduct underwater sound. The fats have two things. One, they are matched to the acoustic characteristics of water, and then they also have multiple shapes and lobes. Where our ears have cartilage and different shapes, this effects what sounds you can hear best. Think of the huge ears of bats- the size of ears determines what frequencies of sounds are best received. A dolphin will rotate its head to turn its fatty "pinnae" to get better orientation to the sound it wants to pick up.

How are higher frequencies detected in the first, thicker and shorter parts of the cochlea, and lower frequencies detected in the thinner and wider parts of the cochlea (basic mechanics)?
Compared to a violin/ guitar- thicker, tighter strings have a higher frequency when you pluck them. Same idea applies to the basilar membrane. Think of them as a tight guitar string. Every band of the basilar membrane has a different stiffness and mass. The higher the stiffness (the membrane gets thicker but narrower, and has bony shelves attached to it) the stiffness is very great. But at the other end of the cochlea, where it is very broad and thin, it is "floppy", like the loosest string on a guitar. Same concept, it's resonance. Increase in stiffness gives a higher resonant frequency; less stiffness gives a lower resonant frequency. Balance of stiffness and mass.

On the spectrogram presented on effects of sonar and dolphins, there was a stop or a gap once noise level reached a certain level. Do we commonly see this in cetaceans when exposed to anthropogenic noise?
We can't say we "commonly see it" in cetaceans. There have been very few studies targeted at this. Studies have focused on beaked whale because of the strandings associated with it (sonar). Scientists have found in both Pacific and Atlantic waters, that there was this response from sonar. But when tried other stimuli, it was realized that it was novel sounds in general that would cause beaked whales to stop clicking, and also cut off their foraging dives (why DTags were important- could look at diving

behaviour), gradually, but at some distance, surface. However, it is not generalized because they found in the same experiments that the beaked whales were distributed by the sounds (stopped clicking, and in some instances, moved away), pilot whales were attracted to the sounds. We do know that the animals that have been observed in the vicinity of controlled tests with sound have varying responses (by species, different behaviors, etc.)

What is the role of tip links in sound impacts?
The tip links join the various stereocilia, holding them together to work in tandem. In normal or some extreme sounds, it is possible that the stereocilia will move differentially, and the tip links will be overstretched and break. If they break, they do not re-heal. This will cause permanent damage to the stereocilia to work together/in tandem, and the signal is not transduced. This would then cause a major threshold shift. Now that will not be true for every sound throughout the entire cochlea- it will only be certain parts of the cochlea that any given sound could effect, depending on the frequency, relative sensitivity, type of noise, how intense it is, etc.