

cover over the last 30 years and, as I write this, another large-scale bleaching event is starting to accelerate, the first time this reef system, the world's largest, has bleached two years in a row. Coral is now second on the animal-type endangered list after frogs, with losses of coral species recorded every year. All too often forgotten about, the reef fish, reef invertebrates, including crustaceans and cephalopods, and the other animals that rely on corals are being lost at an alarming rate along with their remarkable visual systems.

Conclusions

The design of visual systems in the ocean is more diverse than on land, the variability driven by a greater range of light habitats. This includes a variety of unique optical mechanisms to optimise light capture at various light levels and in various light habitats. While most animals in the ocean as a whole are colour-blind monochromats, just because of the volume of habitat, colour vision systems up to the twelve-channel stomatopod retina exist. Even in surface waters, however, many species, including the dominant fish and crustaceans, are dichromatic, probably reflecting the rapid and wavelength-specific attenuation of light and therefore information over any distance. Two channel systems may also be useful in flicker reduction and reduce intensity ambiguity that a monochromat suffers from.

Fish colour vision systems on the reef, and in the ocean in general, are remarkably variable with number and peak sensitivity placement of cones following few discernible trends other than staying within light availability windows. Smaller fish do tend to have ultra-violet-dedicated spectral sensitivities while the larger predators are often ultra-violet-insensitive dichromats. There are specific colour-codes for both communication and camouflage in the ocean, again reflecting light availability and driven by wavelength-selective attenuation in this habitat.

Polarisation vision and specific body reflections are a new currency of information transfer while fluorescent signalling in fish and 'polarocrypsis' require further evidence. Perhaps the largest unknown, aside from trying to

find trends or rules within fish colour vision, is what information is passed (or hidden) by particular colours or indeed polarisation reflections? Is one fish that is yellower or redder than the next more viable as a mate as some freshwater systems suggest? For many reasons, including keeping a watchful eye on our oceans and their crumbling ecosystems, it is time we returned to the ocean to actually see what is in the sea.

FURTHER READING

- Cott, H.B. (1940). *Adaptive Coloration in Animals*. (London: Methuen & Co. Ltd).
- Cronin, T.W., Johnsen, S., Marshall, N.J., and Warrant, E.J. (2014). *Visual Ecology*. (Princeton and Oxford: Princeton University Press).
- Jerlov, N.G. (1976). *Marine Optics*. (Amsterdam: Elsevier).
- Johnsen, S. (2012). *The Optics of Life: A Biologist's Guide to Light in Nature*. (Princeton and Oxford: Princeton University Press).
- Johnsen, S., Gagnon, Y.L., Marshall, N.J., Cronin, T.W., Gruev, V., and Powell, S. (2016). Polarization vision seldom increases the sighting distance of silvery fish. *Curr. Biol.* **26**, 752–754.
- Land, M.F., and Nilsson, D.-E., (2002). *Animal Eyes*. (Oxford: Oxford University Press).
- Levine, J., and MacNichol, E. (1982). Color vision in fishes. *Sci. Am.* **246**, 108–117.
- Lythgoe, J.N. (1979). *The Ecology of Vision*. (Oxford: Clarendon Press).
- Lythgoe, J.N., Muntz, W.R.A., Partridge, J. C., Shand, J., and Williams, D.M. (1994). The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef. *J. Comp. Physiol. A.* **174**, 461–467.
- Marshall, N.J., Jennings, K., McFarland, W.N., Loew, E.R., and Losey, G.S. (2003). Visual biology of Hawaiian coral reef fishes. III. Environmental light and an integrated approach to the ecology of reef fish vision. *Copeia* **3**, 467–480.
- Marshall, N.J., and Arikawa, K. (2014). Unconventional colour vision. *Curr. Biol.* **24**, 1150–1154.
- Marshall, N.J., Roberts, N.W., and Cronin, T.W. (2014) Polarisation signals. In *Polarized Light and Polarization Vision in Animal Sciences* G. Horvath ed. (New-York: Springer), pp. 407–442.
- Marshall, N.J., Carleton K.L., and Cronin, T.W. (2015). Colour vision in marine organisms. *Curr. Opin. Neuro.* **34**, 86–94.
- Phillips, G.A., Carleton, K.L., and Marshall, N.J. (2015). Multiple genetic mechanisms contribute to visual sensitivity variation in the Labridae. *Mol. Biol. Evol.* **33**, 201–215.
- Porter, M.L., Blasic, J.R., Bok, M.J., Cameron, E.G., Pringle, T., Cronin, T.W., and Robinson, P.R. (2012). Shedding new light on opsin evolution. *Proc. R. Soc. B* **279**, 3–14.
- Siebeck, U.E., Losey, G.S., Marshall, N.J. (2006). UV communication in fish. In *Communication in Fishes*, Volume 2. F. Laddich, S.P. Collin, P. Moller, B.G. Kapoor eds. (Science Publications Inc.), pp. 423–455.
- Stieb, S.M., Carleton, K.L., Cortesi, F., Marshall, N.J., and Salzburger, W. (2016). Depth-dependent plasticity in opsin gene expression varies between damselfish (Pomacentridae) species. *Mol. Ecol.* **25**, 3645–3661.

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Primer

Marine bioacoustics

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The marine environment is the planet's largest, yet in many respects the least accessible. Our human sensory repertoire, with its emphasis on vision and air-adapted hearing, does not serve us well underwater. Underwater vision is often limited and as divers we find hearing of little, or no, use. Yet we know from the physics that underwater sound has properties well suited to serve as sensory and communication channels for suitably-adapted marine animals. The rapidly developing area of marine bioacoustics seeks to characterise underwater sound in relation to the acoustic capability of particular species (acoustic habitat), and discover the role of acoustics in the lives of marine animals (acoustic ecology) (Clarke *et al.*, 2011).

Although the physics of underwater sound may be well characterized for ideal conditions, we still have much to learn about: the detail of biologically relevant sound; the diversity and performance of sound reception across marine animals; and the importance of sound in behaviour and ecology. Observation of *in situ* behaviour is essential for a satisfactory understanding of bioacoustics, yet is difficult underwater. Hence, we are still well short of an adequate understanding of both acoustic habitat and acoustic ecology. New approaches and technologies are opening up exciting opportunities and accelerating progress. In turn, better understanding of the biological dimensions of marine acoustics will open up possibilities for passive remote sensing of marine ecosystems; better characterization of the impacts of rising levels of anthropogenic noise; improved technology for biological investigation and autonomous underwater vehicles; and it may even lead to the development of augmented-reality options for human divers to enhance our experience of the underwater acoustic world.

The basics of underwater sound

The physical properties of underwater sound and the characteristics of ambient

noise in the sea are well known (Rodgers and Cox, 1988). Although the physics is interesting in its own right, for the biological perspective of this Primer we do not need to go much beyond the basics of how sound is generated underwater, how it propagates, and how, and what, we should measure to get a sense of the biologically relevant sound, hearing capabilities, underwater acoustic habitats, and acoustic ecology.

Consideration of the physics typically starts with the idealised situation of a water body with no boundaries, or obstructions, before it can be extended to more complex acoustic environments of biological relevance, such as shallow coastal waters. In the idealised situation the sound from a specified source can be precisely defined at any location within the sound field. The sound field consists of an oscillating pressure wave that propagates radially from the source. The pressure wave is directly linked to back-and-forth radial particle motion that also propagates outward from the source. Close to the source there may be hydrodynamic flow driven by movement of the source, but out beyond a wavelength or two is the acoustic farfield, where the pressure fluctuation dominates the sound field. The pressure component decreases largely due to radial spreading (R^{-1}), and is directly related to the particle velocity component ($p = \rho cv$, where p = pressure, ρ = density, c = speed of sound in water, v = particle velocity). For these conditions to apply, the distance from the source, R , needs to be greater than a few wavelengths and also much greater than the source dimension. At 30 Hz, the wavelength of sound is 50 m, at higher frequencies the wavelengths are correspondingly less (10 m at 150 Hz and 1 m at 1500 Hz; $\lambda = c/f$, where λ = wavelength, c = speed of sound in water, f = frequency in Hz).

To describe sound intensity and compare sounds, the convention is to use decibels (dB). The level in decibels of a sound with intensity I is defined with respect to a reference intensity, I_0 , as $10 \log_{10}(I/I_0)$. Sound intensity is proportional to the square of the acoustic pressure. Because most hydrophones measure the acoustic pressure, rather than the intensity, it is more convenient in underwater acoustics to measure the sound pressure level as $20 \log_{10}(p/p_0)$, where p_0 is the reference pressure level of $1 \mu\text{Pa}$. The sound pressure used in

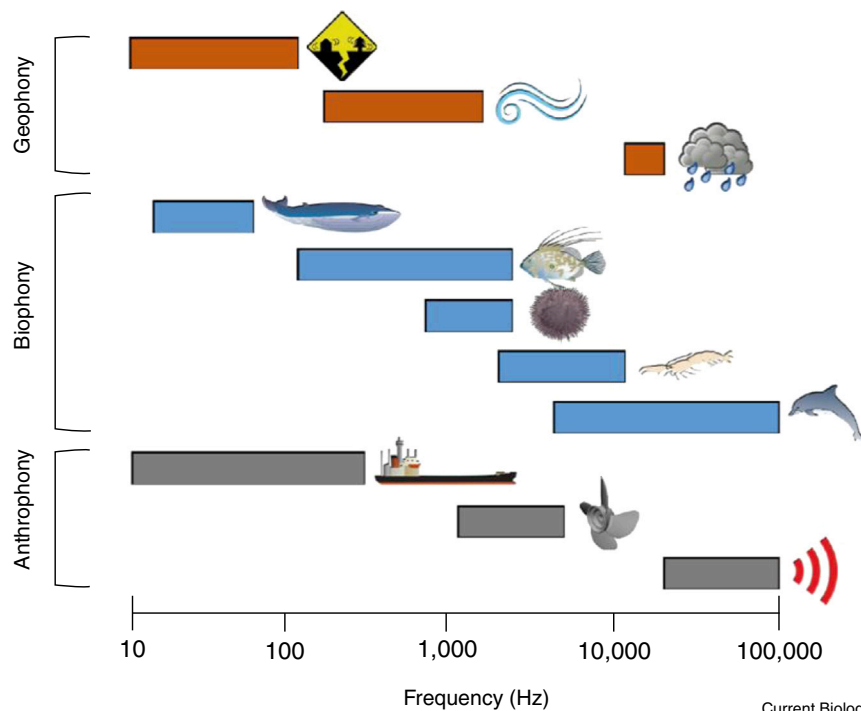


Figure 1. The marine bioacoustic environment.

Diagram of the frequency range of some common sources of abiotic, biotic and anthropogenic sounds: geophony: earthquakes; waves; and rain; biophony: whales; fish; urchin; snapping shrimp; and dolphin; anthrophony: ship; outboard propeller; and sonar. Representative sound intensities include: received level (RL) of an earthquake approximately 700 km away 107 dB re $1 \mu\text{Pa}$ at 100 Hz; blue whale source level (SL) 165 dB re $1 \mu\text{Pa}$ at 1 m; supertanker 190 dB re $1 \mu\text{Pa}$ at 1 m (<http://oceanexplorer.noaa.gov/explorations/sound01/background/acoustics/acoustics.html>); fish range between RL of 100–140 dB re $1 \mu\text{Pa}$ for several NZ fish species, John Dory, two spot demoiselles, gurnard and bigeye; crustaceans RL of 140 dB re $1 \mu\text{Pa}$ for snapping shrimp; paddle crabs 136 dB re $1 \mu\text{Pa}$; urchins RL 140 dB re $1 \mu\text{Pa}$. (Illustration: R. Putland.)

the decibel determination is the root mean square (rms), and the standard reference level is chosen so that for all practical purposes the decibel levels for underwater sound will have positive values. Source level is always quoted at a standard distance of 1 m but can be measured at any convenient distance >1 m that is less than half the distance to the nearest reflector, such as the ocean surface. The level at 1 m can then be calculated. We note in passing that it is not appropriate to compare decibel levels in water and air because the reference levels are very different ($1 \mu\text{Pa}$ versus $20 \mu\text{Pa}$).

Although the intensity of sounds drops as it spreads, there is little attenuation due to absorption. For example, at 500 Hz (within the hearing range of fishes) sound suffers only 1 dB of attenuation due to absorption in 100 km of propagation (Rodgers and Cox, 1988). Low attenuation can result in sounds propagating over large distances, which

can lead to high background sound levels. In addition to low attenuation, other distinctive properties of underwater sound compared with airborne sound include: a much higher speed (1500 m s^{-1} versus 340 m s^{-1}); a greater tendency to refract due to density and temperature gradients; a greater tendency to be scattered by objects, particularly objects containing a gas inclusion; and a smaller particle velocity for a given pressure fluctuation. All of these properties have implications for the way in which sound propagates and for the hearing mechanisms of marine animals.

Many marine animals are sensitive to sound, but do not have the capacity to detect sound pressure. Their hearing is mediated by sensors that respond to the movements of the animal in the sound field. In effect they are detecting the particle motion component of the field. This distinction between pressure and motion sensing is important, in part because pressure sensing hydrophones

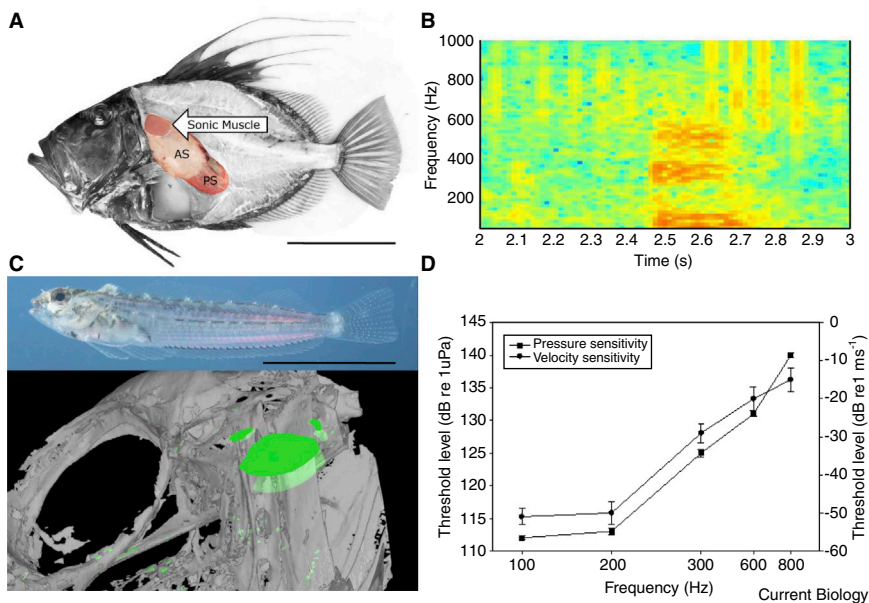


Figure 2. Fish sound production and hearing.

(A) John Dory (*Zeus faber*) sonic muscle (AS, anterior swimbladder; PS, posterior swimbladder; scale bar: 0.1 m). (B) John Dory sound spectrogram. (C) Pre-settlement triple fin (*Forsterygion* sp.) and microCT image of the head showing the location of the three pairs of otoliths in the skull behind the orbit (colour coded green; scale bar for the fish picture, 0.01 m). (D) Triple fin audiogram showing best hearing sensitivity in the 100–200 Hz range. (Photographic credits: John Dory, J Montgomery; triplefin, I. Macdonald; triplefin CT scan I. Anderson.)

are much more readily available than adequately sensitive vector motion sensors. Although acoustic pressure and motion are directly related in the ideal situation, this is not necessarily the case in more complex scenarios, such as where there are surface or sea floor reflections. In practice this means that, when using conventional hydrophones, the acoustic habitat is being characterised by pressure sensors and may not match the acoustic environment being experienced by those inhabitants that detect the particle motion component of the acoustic field (Nedelec *et al.*, 2016).

The more complex acoustic environments of biological relevance take account of the properties of sound propagation in shallow water, and the effects of temperature and salinity gradients in open ocean areas. For example, where the range between the source and the receiver is greater than the water depth, surface and bottom reflection retain the sound within the water column, giving rise to cylindrical spreading. With cylindrical spreading, the amplitude of the sound decreases as $1/(\sqrt{R})$ and this can increase the effective range of sound in comparison

with the spherical spreading of sound in a free-field situation. However, shallow water also limits the propagation of low-frequency sound; for example, it has been estimated that sounds at frequencies of less than about 70 Hz will be lost to a fine sand seafloor in water depth of 10 m.

One of the conclusions to draw from our consideration of the properties of underwater sound is that, because of real-world complexities, there is no real substitute for direct measurement. Moreover, this should be done in a manner appropriate to determining its suitability as a biologically useful cue, taking account of the hearing capabilities and mechanisms of the species of interest. To appreciate this point, it may be helpful to consider a visual analogy: to understand the biological function and relevance of body coloration in fish, not only is it important to establish the colour properties in natural underwater light, but also how this would appear to the biologically relevant observer given their visual capabilities.

Finally, it is worth thinking about signal and noise in underwater sound. For example, in many studies, ‘reef sound’ produced by biological or

physical sources may be considered as background ‘noise’ and a nuisance. But from the perspective of an animal, or even a diver trying to locate the reef, ‘reef sound’ may indeed be the ‘signal’ that we would like to characterise. In relation to acoustic habitat and acoustic ecology, what is signal and what is noise will depend on our interpretation of the biological relevance and use of the sound. Sound generated by sea state or rain on the surface of the sea is most likely to be noise that masks, or interferes with, the biologically valuable sound. Anthropogenic sources may or may not contain useful directional information and may represent either signal or noise depending on circumstances. Standard deep-water noise spectra (Knudsen curves; see Urlick, 1983) show that, in the range 50–1000 Hz, noise due to shipping and wind-generated surface waves can significantly raise the ‘noise floor’ and potentially mask the detection of biologically relevant signals. It seems that anthropogenic sound levels have risen significantly over time and concerns have been raised that this may have a negative impact on fish (Hawkins *et al.*, 2015) and other marine animals (Erbe *et al.*, 2016).

Signals, by definition, have some biological value to either the sender or the receiver. Biologically produced sound may be inadvertent (of no value to the sender) as in the case of urchin noise, but still provide useful proxy signal for receivers interested in the presence of urchin habitat, such as larval fish looking for a place to settle. Most biologically produced sound, though, will also be of direct value to the sender through a role in either echolocation or intraspecific communication. Biologically important sounds are characterized by their frequency range, intensity, and information content (Figure 1).

Acoustic adaptations of marine species

Sound production

Biological value is encapsulated in adaptation. Sound may be produced inadvertently, as for example by sea urchins scraping their teeth on the rocks, or by the muscle contraction produced by a fish as it makes a rapid turn. But where the sound being produced is of direct adaptive value to the sender, then evolution captures biological value through overt mechanisms to enhance

and control the sound production. So the diversity and prevalence of sound production mechanisms attest to the wider biological value of underwater sound.

It used to be thought that sound production was not that common in invertebrates, but with technological advances, such as more sensitive hydrophones, more and more sound-producing invertebrates are being discovered. The mechanisms by which they produce sound are also more diverse than previously thought. They range from stridulatory mechanisms that include the rubbing of body parts (lobsters) to specialised muscles that vibrate the exoskeleton (mantis shrimps). The stand-out example of sound production in these groups is the mechanism found in snapping shrimp: modified claws in the shrimp produce a pulsed water jet of sufficient speed to cause a cavitation bubble (Versluis *et al.*, 2000). The collapse of the bubble generates the distinctive snap from which these shrimp derive their name. The sound of snapping shrimp is often the dominant sound emanating from reefs worldwide. The snap is sufficiently intense that it can be used to stun prey, but it is likely to have other additional biological functions. Interestingly, the intensity of the combined sound of snapping shrimp shows strong diurnal fluctuations generating part of what has been called the dawn and dusk chorus.

Fish are the most diverse of any equivalent vertebrate clade, and have a corresponding diversity of independently evolved sound production mechanisms (Parmentier and Fine, 2016). Stridulation is common, often generated by mechanisms involving the pectoral fins and girdle. But even more common are sound production mechanisms using specialized sonic muscles to vibrate a gas-filled swim-bladder. These too have evolved multiple times; sonic muscles are found directly inserted on the swim-bladder (Figure 2), others connect the swim-bladder wall to other outside structures, and some vibrate the swim-bladder indirectly via tendons or bony plates without any direct swim-bladder attachment.

Being air-breathing, marine mammals also have the option to use air movement to generate sound. Their repertoire includes both intense and richly varied vocalizations ranging from songs of

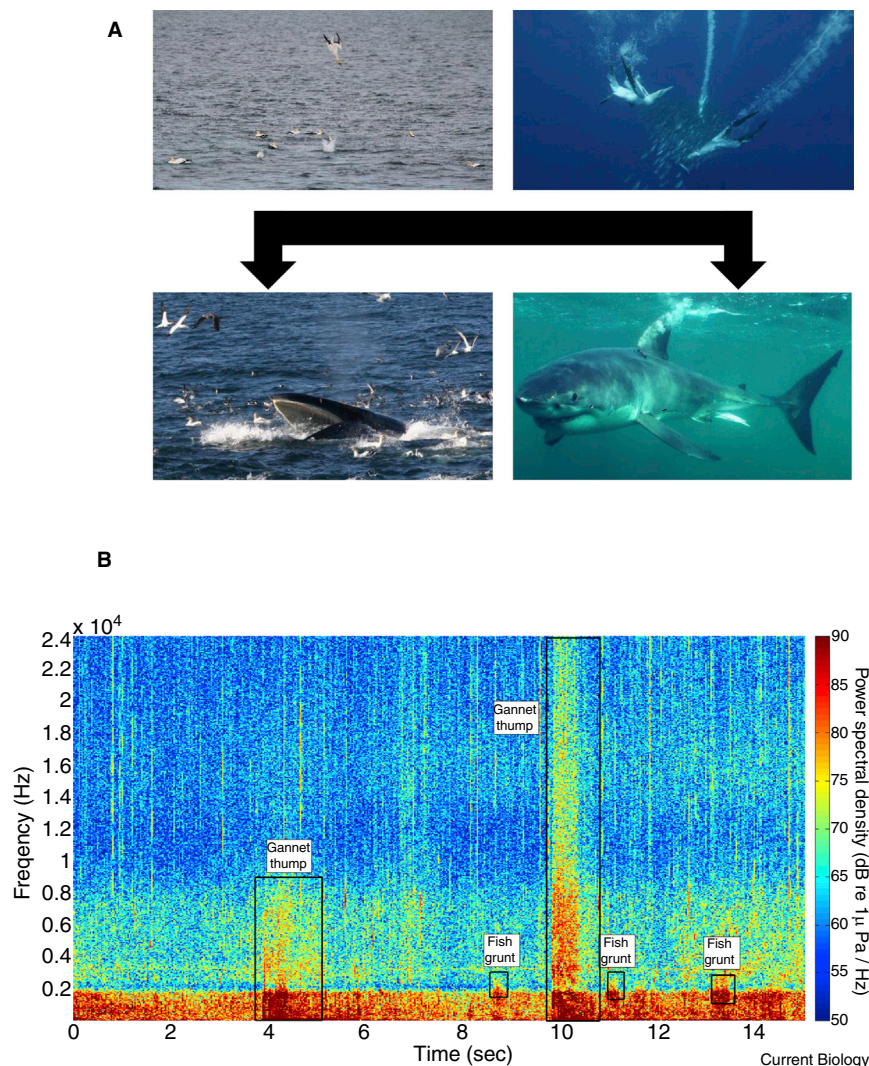


Figure 3. Acoustic ecology.

(A) Sound produced by food patches and associated predators may provide a cue for pelagic predators to locate food sources. For example seabirds may locate food patches through olfactory or visual cues and then the sounds they produce through diving, or calling while sitting on the sea surface, may alert pelagic predators to the food patch. (B) Spectra of recorded sounds from the Hauraki Gulf, showing gannet diving and fish grunts. Photographic credits: gannet diving, P. Low; underwater gannet, S. Hathaway (www.stevethathaway.com); Brydes whale, S. Behrens; shark, K. Scollay, Department of Conservation, New Zealand.

humpback whales to the intense and precisely controlled echolocation clicks of dolphin and toothed whales. The vocalization songs of baleen whales are particularly interesting for the intensity of the sounds they produce and their ability to take advantage of sound transmission properties of seawater to project their song over ocean-scale distances.

Recent developments in tagging technology now allow for the deployment on whales of tags with GPS, accelerometers, and hydrophones. The movement data from these tags

can track behavioural states such as diving and feeding, and align these behaviours not just with the whales own vocalization, but also with the sounds that make up its wider acoustic habitat. In the specific case of beaked whales, this has provided fascinating insights into their use of echolocation, and their acoustic interaction with their prey (Johnson *et al.*, 2009).

Hearing

Underwater sound can be detected by sensors that respond to either the

particle motion or the sound pressure of the propagating sound wave. Many invertebrates and fish are small relative to the wavelengths of low-frequency sound (<1000 Hz), and if they are neutrally buoyant and floating in the water column, they will move with the same motion as the surrounding water particles. Many of these species have acceleration detectors to determine their own movements and enable them to detect gravity, and these same detectors are relatively easily modified to respond to sound (Figure 2). The extent to which an acceleration detector can serve for underwater hearing depends on both its sensitivity and its frequency response characteristics. The characterization of particle motion hearing is challenging, so it is still very much a work-in-progress to ascertain the capabilities for the wide range of invertebrates and fish that likely depend on this means of sensing sound. Likewise, the default use of pressure-sensitive hydrophones to characterize acoustic habitat can create problems reconciling the two defining components of acoustic habitat: sound characterization and hearing capability.

With the provision of a gas-filled chamber, like the swim-bladder in fishes, the compression and rarefaction produced by a passing sound wave causes the chamber to vibrate in the sound field due to the differing acoustic impedance of water and gas. Across different fish species, there are a wide range of sensory adaptations that assist with the detection of swim bladder vibrations (Ladich and Schulz-Mirbach, 2016). Perhaps best known are the mechanical linkages, not dissimilar to our own middle ear ossicles, which transmit swim-bladder vibrations into the inner ear of the fish. Known as Weberian ossicles, these linkages are found in freshwater species, including catfishes, electric (knife) fishes, and carp, and a few marine species. In other marine species adaptive specializations linking swim-bladder vibration to mechanical sensors in the ear and the lateral line include anterior extensions of the swim-bladder into the inner ear (herring) and specialized ligaments that may connect with both the inner ear and lateral line (bigeye).

Hearing in marine mammals has been extensively studied for some families, such as dolphins and seals. In dolphins, the reception of sound

pressure depends on the lower jaw and associated fatty tissue. For a limited number of species within these groups, sound reception has been characterized by both auditory evoked potentials and behavioural audiograms showing hearing sensitivity and range strongly related to communication and echolocation vocalizations (Pacini and Nachtigall, 2016). Hearing is not just about acoustic reception: new approaches are now opening up the fascinating study of acoustic behaviour and perception. Examples include: how acoustic information is used to achieve sophisticated echolocation capability; the development of a bite-plate hydrophone for dolphins that show bio-sonar strategies used by free-swimming animals differ from those used by restrained dolphins performing a similar target discrimination task; and observations of free-swimming dolphins fitted with cameras to record video and sound that document their ability to simultaneously co-ordinate communication signals and prey capture echolocation.

Acoustic ecology

Given the potential for sound to propagate over large distances, it is not surprising to find sound being used for distance-related interactions between individuals and their acoustic habitat, and interactions within and between species (Figure 3). The potential use of sound for habitat selection has been a topic of intense research for the last decade. Individual reef habitats have been shown to have distinctive acoustic signatures that vary with time (diurnal, lunar, and seasonal cycles), spatially (reefs >2 km apart can sound completely different) and with reef health. A range of reef species both invertebrate and vertebrate have been shown to be attracted to settlement habitat on the basis of sound. Reef sound has also been shown to propagate many kilometres from the reef, but effective distance at which pre-settlement larvae can be attracted is still a matter of debate. Better characterization of the particle motion component of these reef sound fields and related hearing capabilities of the larvae, and ultimately better behavioural studies, will be required to resolve the ecological scale of acoustic habitat selection.

Fish vocalization is often associated with territorial defence and mate selection. Female fish can localize, and are attracted to male calls, and characteristics of the courtship acoustic signals, such as dominant frequency, amplitude, and fatigue resistance, are used by females to assess male quality (Amorim *et al.*, 2015). Contact calls have also recently been discovered in a nocturnal planktivorous fish species, and are thought to maintain a loose group cohesion during nocturnal feeding (van Oosterom *et al.*, 2016). Not surprisingly, more complex social acoustic communication occurs in marine mammals, and there are active research efforts to study individual whistle signatures and decipher information transfer in marine mammal acoustics.

Active sound production, either for intraspecific communication or for echolocation, carries with it the risk of interception by potential prey or predators. Killer whales shift to a more cryptic form of echolocation when they feed on prey attuned to their echolocation clicks, and it appears that dolphins reduce click level to maintain a constant (and presumably inaudible) level at the prey. It is also interesting that noise-producing fish make up a large part of the diet of some dolphins. Eavesdropping may also extend to the inadvertent sound produced by prey aggregations and their predators, such as diving birds (Radford and Montgomery, 2016). It seems highly likely that underwater sound provides a rich set of acoustic cues, comparable to the developing understanding of terrestrial acoustic ecology.

Future prospects

We have highlighted how new approaches and technologies are opening up exciting opportunities and accelerating progress in our understanding of the marine bioacoustic environment. In turn, our prediction is that better understanding of the biological dimensions of marine acoustics will open up numerous further possibilities. As we better understand reef sound production, the full context of active sound production, and ecological interactions in the pelagic zone driven by sound, we will enrich the potential for passive remote sensing of marine ecosystems.

Similar understanding will also allow us to better characterize the impacts of rising levels of anthropogenic noise. Particle motion sensors based on the model of a fish ear and dolphin-inspired sonar will provide opportunities for improved sensing technology for instrumentation, autonomous underwater vehicles, and perhaps even augmented reality options for human divers to enhance our direct experience of the underwater acoustic world.

FURTHER READING

- Amorim, M.C.P., Vasconcelos, R.O., and Fonseca, P.J. (2015). Fish sounds and mate choice. In *Sound Communication in Fishes* F. Ladich, ed. (Vienna: Springer), pp. 1–33.
- Clark, C.W., Rice, A.N., Ponirakis, D.W., and Dugan, P.J. (2011). Marine acoustic ecologies and acoustic habitats: concepts, metrics, and realities. *J. Acoust. Soc. Am.* 130, 2320–2320.
- Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., and Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Poll. Bull.* 103, 15–38.
- Hawkins, A.D., Pembroke, A.E., and Popper, A.N. (2015). Information gaps in understanding the effects of noise on fishes and invertebrates. *Rev. Fish Biol. Fish.* 25, 39–64.
- Johnson, M., de Soto, N.A., and Madsen, P.T. (2009). Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review. *Mar. Ecol. Prog. Ser.* 395, 55–73.
- Ladich, F., and Schulz-Mirbach, T. (2016). Diversity in fish auditory systems: one of the riddles of sensory biology. *Front. Ecol. Evol.* 4, 2–28.
- Nedelec, S.L., Campbell, J., Radford, A.N., Simpson, S.D., and Merchant, N.D. (2016). Particle motion: the missing link in underwater acoustic ecology. *Methods Ecol. Evol.* 7, 836–842.
- Pacini, A.F., and Nachtigall, P.E. (2016). Hearing in whales and dolphins: relevance and limitations. In *The Effects of Noise on Aquatic Life II* (New York: Springer), pp. 801–807.
- Parmentier, E., and Fine, M.L. (2016). Fish sound production: insights. In *Vertebrate Sound Production and Acoustic Communication* (Springer International Publishing) pp. 19–49.
- Radford, C.A., and Montgomery, J.C. (2016). Potential competitive dynamics of acoustic ecology. In *The Effects of Noise on Aquatic Life II* (New York: Springer) pp. 895–900.
- Rodgers, P.H. and Cox, M. (1988). Underwater sound as a biological stimulus. In *Sensory Biology of Aquatic Animals*, J. Atema, R.R. Fay, A.N. Popper and W.N. Tavolga, eds. (New York: Springer-Verlag), pp. 131–149.
- Urick, R.J. (1983). *Principles of Underwater Sound*. (New York: McGraw-Hill).
- van Oosterom, L., Montgomery, J.C., Jeffs, A.G., and Radford, C.A. (2016). Evidence for contact calls in fish: conspecific vocalisations and ambient soundscape influence group cohesion in a nocturnal species. *Sci. Rep.* 6, 19098.
- Versluis, M., Schmitz, B., von der Heydt, A., and Lohse, D. (2000). How snapping shrimp snap: through cavitating bubbles. *Science* 289, 2114–2117.

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Primer

Marine ecosystem services

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Coastal and marine environments can begin up to 100 kilometers inland, extend to the continental shelf, and include ocean systems with waters up to 50 meters in depth. The distinct marine ecosystems found in these environments include estuarine and coastal wetlands, such as marshes and mangroves, sand beaches and dunes, seagrass beds, and coral and oyster reefs.

Marine ecosystems represent some of the most heavily exploited ecosystems throughout the world. For example, coastal zones make up just 4% of the earth's total land area and 11% of the world's oceans, yet they contain more than a third of the world's population and account for 90% of the catch from marine fisheries. However, human activities are now threatening many of the world's remaining marine ecosystems and the benefits they provide. Due to coastal development, population growth, pollution and other human activities, 50% of salt marshes, 35% of mangroves, 30% of coral reefs, and 29% of seagrasses have already been lost or degraded worldwide over several decades. As much as 89%

of oyster reefs may also have been lost globally. Overfishing has been a persistent and growing problem in marine environments, and loss of fisheries is also linked to declining water quality through the increasing occurrence of harmful algal blooms, offshore pollution and oxygen depletion (hypoxia). Given the current rapid loss of coastal and marine environments, it is important to understand what is at stake in terms of the foregone economic benefits and values as marine ecosystems disappear.

In this Primer, I provide an overview of some of the key benefits, or 'services', provided by marine ecosystems before going on to discuss some of the key challenges in quantifying and valuing marine ecosystem services. One important feature of these critical habitats is that they are interconnected from the land to the ocean. Thus, the challenge for future research is to assess the benefits that arise from such an interconnected seascape.

Marine ecosystem services

Collectively, the benefits provided to humans by ecosystems are referred to as *ecosystem services*. Table 1 provides some examples of marine ecosystem services, which comprise various goods, services and cultural or other benefits. The goods produced by marine ecosystem services are the products obtained from these habitats, such as fish

Table 1. Examples of marine ecosystem services.

Goods	Services	Cultural benefits
• Fish harvests	• Recreation and tourism	• Carbon sequestration
• Wild plant and animal resources	• Transportation	• Bequest for future generations
• Raw materials	• Scientific and educational opportunities	• Religious significance
• Genetic material	• Flood control	
• Water	• Storm protection	
	• Pollution control	
	• Breeding and nursery habitats	
	• Shoreline stabilization and erosion control	
	• Carbon sequestration	