Marine Mammal Acoustic Behavior

Peter L. Tyack

Postal:
Sea Mammal Research Unit
School of Biology
University of St Andrews
St Andrews, Fife KY16 8LB
Scotland
United Kingdom

Email:
plt@st-andrews.ac.uk

Marine mammals exploited acoustic properties of the ocean for tens of millions of years before human acousticians.

Introduction

The species that are called marine mammals actually represent many different lineages of terrestrial mammals that independently adapted to marine life. The terrestrial ancestor most closely related to the polar bear is the brown bear; the sea otter is related to the river otter, and manatees and dugongs are related to elephants. In this article, I discuss pinnipeds (seals, sea lions, and the walrus), whose ancestor diverged from a terrestrial carnivore about 35×10^6 yr ago (Higdon et al., 2007), and cetaceans (whales and dolphins), which separated about 54×10^6 yr ago from a lineage including ungulates such as the hippopotamus (Arnason et al., 2004).

The terminology we use in English for whales and dolphins does not match how biologists distinguish the main division among the cetaceans. For biologists, the two major divisions of the whales are toothed whales and baleen whales, which do not have teeth. Baleen whales are named for the baleen plates that grow down from the upper jaw, forming a sieve that allows baleen whales to engulf whole patches of small prey at one time. The family of toothed whales includes large whales such as pilot, killer, and sperm whales but also includes the smaller dolphins and porpoises. In fact, to a biologist, the killer whale is just a large dolphin.

When mammals evolved a return from terrestrial back to marine life, they were forced to compete with life forms that had been adapting to the ocean since life originated there. Most marine animals take the oxygen they need directly from the water, and most maintain their bodies at the same temperature as the water around them. Mammals would seem at a disadvantage competing against competitors that do not need to ascend to the surface to breathe and that do not need to use metabolic energy to maintain a body temperature tens of degrees above ambient. Was there anything about life on land that could give the returning mammals an advantage as a marine predator?

There does seem to be an advantage for a predator to maintain a body temperature above that of its prey because its responses may be faster and the higher metabolism may give it more power. The costs of needing to generate heat are reduced in larger animals, which have a lower ratio of surface area to volume, and many of the large marine dinosaurs actually maintained body temperatures well above ambient (Bernard et al., 2010). The baleen whales include the largest animals to have evolved on Earth, the blue and fin whales. Their large size makes locomotion so efficient that large baleen whales can spend the winter breeding season in temperate or tropical waters, then migrate thousands of kilometers to more polar waters to take advantage of the pulse of productivity that produces great patches of their prey. The larger an animal is, the more expensive it can be to chase individual prey; baleen whales have solved this problem by being able to engulf thousands of small prey in one gulp. A key to their ecological success lies in their ability to roam the oceans finding and devouring dense patches of prey. However, as we will see, for a social animal to range this far requires a long-range communication system.

Echolocation

The toothed whales have evolved a different formula for ecological success, one that depends directly on acoustic behavior. Many large marine predators such as fish and squid have well-developed eyes and depend on vision for detecting and capturing prey. Vision works well near the surface during the daytime, but much of the ocean is dark and vision can be limited there. Some deep-diving toothed whale species base their remarkable success on using echolocation to detect and capture prey in the dark depths of the ocean. The key to their success is they can use their lungs to make powerful sounds, then use their sophisticated mammalian auditory system to detect echoes from their prey.

Two groups of mammals have evolved sophisticated abilities to locate prey by making sounds and listening for echoes. A brilliant Italian experimentalist named Lazzaro Spallanzani discovered in the eighteenth century that bats need to be able to hear but not to see to orient while flying in the dark (Galambos, 1942). As a biologist, I would hope that such a discovery would lead biologists to have discovered sonar, but actually we did not understand animal sonar until after human engineers developed sonars early in the twentieth century to detect obstacles such as icebergs and military targets such as submarines (an excellent website on ocean acoustics is http://www.dosits.org; their page on this topic is http://www.dosits.org/people/history/early1900/; you can explore underwater sounds at http://www.dosits.org/galleries/audio/interactive/).

Echolocation was first discovered in bats a few decades after engineers developed sonars (Griffin, 1958) and in toothed whales decades later (Au, 2015). Bats and toothed whales force air from their lungs past phonic lips to generate high-frequency click sounds whose energy is directed forward toward targets. Echolocation has allowed both of these groups to specialize in hunting prey in conditions where darkness hampers visual hunters, such as at night or in the dark depths of the sea. Even during the day, light does not penetrate far in most seawater, so echolocators can often detect their prey at much greater ranges using sound than is possible using vision.

The sperm whale is perhaps the most specialized echolocator. Sperm whales devote about a third of the volume of their large body (up to 16 m in length) to the spermaceti organ, which lies above the skull and is filled with a specialized wax. Biologists have argued that the spermaceti organ functions as a battering ram or to regulate buoyancy, but most modern biologists have reached a consensus that this large organ evolved to generate the loudest sonar signals of any animal (Møhl et al., 2003).

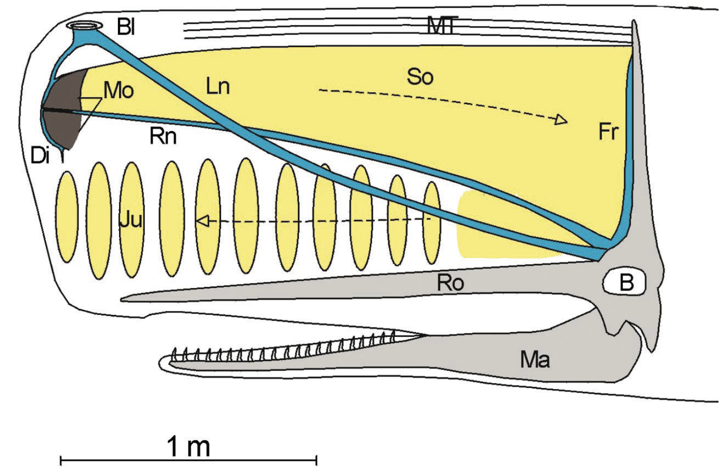

Figure 1. Illustration of the "bent horn" model of sound production in the sperm whale proposed by Møhl et al. (2003). The initial sound of a sperm whale click is generated by the passage of air from the right nares (Rn) through the phonic lips (also known as the monkey lips; Mo). Most of this sound energy passes backward through the spermaceti organ (So), reflects off the frontal sac (Fr), and forms a forward-directed beam as it passes through the junk (Ju). B, brain; Bl, blow hole; Di, distal air sac; Ln, left naris; Ma, mandible; MT, muscle/tendon layer; Ro, rostrum. From Madsen et al. (2002).

Figure 1 illustrates the sound production anatomy of the sperm whale. When sperm whale clicks are measured in the beam, they are as loud as the most intense naval sonars deployed on warships. This powerful sonar is estimated to allow sperm whales to detect a squid as far away as 300 m or more (Madsen et al., 2007). The ability of deep-diving toothed whales to use sonar to detect, select, and capture prey is a prime factor for their evolutionary success, supporting prewhaling populations of more than a million sperm whales (Whitehead, 2002) and supporting a radiation of many species of deep-diving toothed whales.

When a dolphin or toothed whale is echolocating on prey, the best sonar targets are features such as dense bone or a gas-filled cavity that have densities very different from those of seawater. When a sonar signal hits a hard target, it does not reflect very efficiently if the wavelength of the sonar signal is larger than the circumference of the target. A dense bone in a prey fish for a dolphin might be about 2 cm in circumference. The speed of sound is about 1,500 m/s, so a wavelength of 2 cm (or 0.02 m) would correspond to a sonar frequency of 1,500/0.02 = 75 kHz. Thus, if the dolphin sonar needed to resolve objects about 2 centimeters in size in order to select prey, it would need to use a high-frequency sonar signal and have an auditory system capable of detecting frequencies more than four times higher than those humans can hear. These remarkable capabilities of bats and toothed whales to produce and to hear signals of unusually high frequency are thought to have evolved in response to the need for their sonars to resolve small targets.

Some fish have a gas-filled swim bladder that is used to maintain buoyancy. This gas-filled bladder is an excellent sonar target, especially when ensonified with sound at the resonant frequency of the bladder. This is much lower in frequency than for a solid target of the same size, with swim bladders typically having resonance frequencies of a few kilohertz. At the higher frequencies of toothed whale clicks, each size and kind of fish reflect different patterns of sound, allowing echolocating whales to select prey.

The range at which an echolocator can detect a target depends on the intensity of the sonar signal, on how much sound energy is lost as it propagates from the echolocator to the target and back, and on how much of the sound energy hitting a target reflects back. Sound energy is absorbed by seawater molecules either by viscous or chemical interactions, especially at higher frequencies. For example, a sonar signal at 100 kHz loses between a quarter and a half of its energy as it passes through 100 m of seawater. Absorption thus limits the effective range of high-frequency echolocation from tens to a few hundreds of meters.

Communication

Long-Range Propagation of the Low-Frequency Calls of Fin Whales

In contrast to the absorption of high-frequency sound in seawater, low-frequency sound can travel over much longer ranges than we are used to for sound in air. Low-frequency sounds below about 100 Hz have negligible absorption even when traveling thousands of kilometers through the ocean. In addition, in the deep ocean, there is a special sound channel that allows sound to spread with little loss over great ranges. When a sound is made in the open ocean, downward heading sound rays will refract back upward as they encounter water that is denser due to hydrostatic pressure. And upward heading sound rays refract downward as they near warmer surface waters in most of the ocean. These two phenomena cause sound energy to concentrate at depths where the sound speed is at a minimum, around 1,000 m in temperate and tropical seas, leading this to be called the deep sound channel.

The physics of sound propagation in the deep sound channel was understood by the end of World War II. During the start of the Cold War in the 1950s, the US Navy developed an underwater listening system codenamed "Jezebel" to take advantage of the deep sound channel to detect low-frequency sounds at great ranges (Nishimura, 1994; http://www.dosits.org/people/history/SOSUShistory/). As soon as the Navy was able to listen to low frequencies, Navy acousticians often heard low-frequency sounds that they called the "Jeze monster." This discovery of an unknown sound source in the ocean led marine bioacousticians on a search for the Jeze monster, which finally was identified as the 20-Hz calls of fin whales (Schevill et al., 1964; http://www.dosits.org/files/dosits/fin7.mp3). This kind of detective work formed the basis of the first generation of marine mammal bioacoustics during the 1950s and 1960s.

Payne and Webb (1971) used early data on the low-frequency calls of finback whales to report that if finback sounds spread evenly in all three dimensions, they would be detectable out to about 100 km but that spreading in the deep sound channel would enable these calls to be detected at ranges of 1,000 km or more. Despite such a compelling prediction, it was not until after the end of the Cold War that biologists were able to demonstrate such long-range propagation of whale calls.

The problem was one that is common in ocean science: how to develop appropriate scales of measurement. During the 1960s and 1970s, marine mammal bioacousticians learned how to record the sounds of marine mammals from small vessels, where they could get close enough to link a call to an animal under visual observation. We knew that these whales swam thousands of kilometers, and Payne and Webb (1971) had hypothesized that their sounds could travel over similarly large ranges. But it was not until naval technologies for tracking underwater sounds were made available to whale biologists that investigators could actually test long-range detection of whale calls.

Fin and blue whales tend to disperse into deep oceanic areas where they produce these calls during the winter breeding season. Stafford et al. (1998) used Navy listening stations to locate blue whale calls far out to sea (http://www.dosits.org/files/dosits/blue1.mp3). They then sent a naval air patrol to the site 400-600 km from their receiver locations. It dropped buoys that could record underwater sound and transmit the signal via radio, confirming the location of the calling whale. An observer was able to sight a large whale but was not able to confirm the species identification. **Figure 2** shows a 1,700-

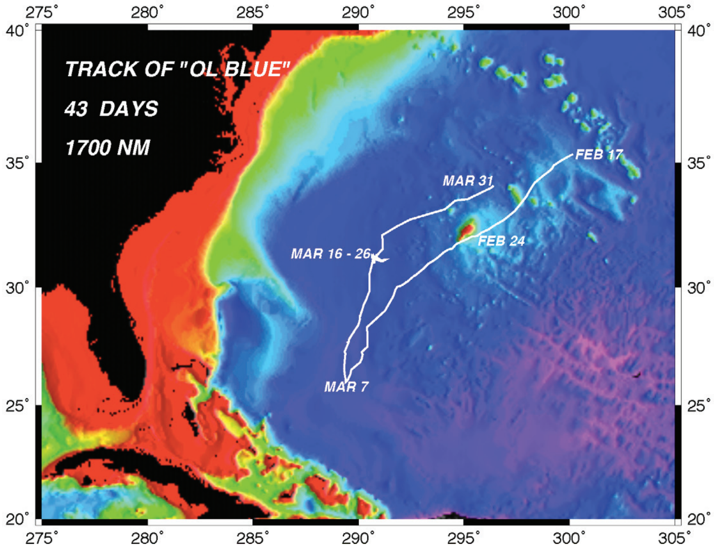

Figure 2. *Track of a calling blue whale. This individual whale had a distinctive call that allowed US Navy acoustics expert Chuck Gagnon to track it as it swam >3,000 km in the North Atlantic over 43 days. Courtesy of Christopher Clark, Cornell University, and Clyde Nishimura, US Naval Research Laboratory.*

km track of a blue whale whose distinctive call was localized over 43 days using Navy listening stations.

These studies of long-range propagation of whale calls were a technological *tour de force*, but we still do not know much about the effective range of communication when the whales are the receivers. Fin whales on the feeding ground have been observed from an airplane rapidly swimming toward a group of whales that were feeding 10 km away (Watkins and Schevill, 1979); they might have been responding to calls, but this could not be measured from the plane. Tyack and Whitehead (1983) used several boats, each following a different group of humpback whales on the Hawaiian breeding grounds to show that one whale accelerated and made a beeline for a large active group 9 km away. These observations represent the limit of our observations of potential call and response in whales. We still do not have good methods for determining whether a whale is hearing and responding to calls of another at ranges of tens or hundreds of kilometers.

Song of Humpback Whales

Unlike the low-frequency calls of fin and blue whales, humpback whales produce sounds with a broad frequency band, up to several kilohertz (http://www.dosits.org/files/dosits/hump1.mp3). The high-frequency components of the humpback sounds have higher rates of absorption as they pass through seawater. In addition, humpback whales tend to congregate in shallow coastal waters where propagation is not as advantageous as in the deep sound channel. These factors limit the detection range of the full frequency bandwidth of humpback song to a few tens of kilometers compared with hundreds of kilometers for the fin and blue whale calls.

Humpback songs are complex not only in their broadband frequency structure but also in having a long complex sequence of sounds that may continue for 5-15 min before repeating (link to file http://acousticstoday.org/hbksong). Another form of complexity is that the song is always changing throughout the singing season. At any one time, most singers within a population sing very similar songs, but the song changes over time. Different parts of the song come and go at different times, but often the changes are clear enough to define new song types for different years. The only way this process of change can occur is if humpback males copy the songs they hear around them, all tracking the changes together. This kind of vocal learning is common among songbirds but rare among mammals (Tyack, 2016).

Since the 1970s, bioacousticians have recorded the songs of humpback whales from local populations in tropical breeding grounds. Comparisons showed that songs were similar from different sites within an ocean basin, such as the West Indies and Cape Verde Islands in the North Atlantic or Hawaii and the Pacific coast of Mexico, but songs differed across different ocean basins, such as the North Atlantic, North Pacific, or South Pacific. Not only are the songs similar within an ocean basin, but the trends of song change also are similar (Cerchio et al., 2001). Because the full bandwidth of the songs does not propagate farther than tens of kilometers, the assumption was that whales must mix across breeding sites separated by thousands of kilometers within an ocean basin.

If humpback males learn their song by listening to those of other males, then it qualifies as a form of cultural transmission, a trait shared through social learning. For nearly a century, anthropologists and other social scientists jealously reserved the word "culture" for humans alone, but evidence of tool making and other cultures in anthropoid apes have led to more acceptance of the idea of animal cultures. Learned vocal traditions such as song dialects qualify as forms of animal culture, and the constant change of the songs of humpback whales facilitates the study of cultural transmission of song. Interest in transmission of animal cultures led bioacousticians working in 6 humpback breeding grounds spanning a distance of more than 6,000 km in the South Pacific to

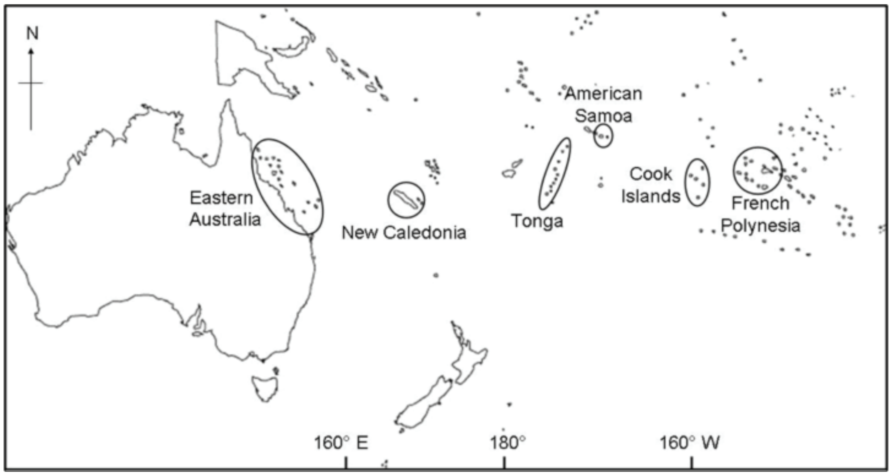

Figure 3. *Map of the South Pacific showing the humpback breeding grounds from which song was recorded by Garland et al. (2011).*

compare song data recorded over a period of 11 yr (Garland et al., 2011). **Figure 3** shows the locations of the six breeding grounds.

When the song data from the different breeding grounds were analyzed, song types were found to be shared across the full 6,000-km span from Eastern Australia to French Polynesia (**Figure 4**). However, the song was never the same across all sites during the same year. Rather, each song type (represented by a color in **Figure 4**) originated in East Australia and then spread from west to east, taking 2-3 yr to reach French Polynesia. This process represents a particularly large scale for repeated cultural diffusion from a population where new material originated in east Australia to breeding grounds farther to the east.

Functions of Marine Mammal Calls

The first phase of marine mammal bioacoustics focused on which species made which sounds. This is still an active research question today, but by 1980, interest in marine mammal behavior broadened to also focus on the contexts in which animals make a call, how others respond, and how calls function in communication. In many whale and seal species, adult males repeat complex vocalizations, called songs, during the breeding season. In many seal species and some cetaceans such as the humpback whale discussed in the *Song of Humpback Whales*, males congregate during the breeding season in traditional areas where females come to mate. The complex songs males produce advertise their readiness to compete with other males and to mate with females. Female vocalizations also play a role in reproduction for some species. For example, female northern right whales produce a scream call that is thought to attract males (Parks and Tyack, 2005; http://www.dosits.org/files/dosits/egscream.mp3).

Some seals breed on beaches where interactions can be observed relatively easily by terrestrial human observers; other species breed at sea where observations are more difficult. All seals can vocalize in air and under water, and in all species observed, vocal communication plays a role in breeding behavior. Elephant seals are one of the species that mate on land; males use vocalizations to assess the fighting ability of other males, and females compare different males by listen-

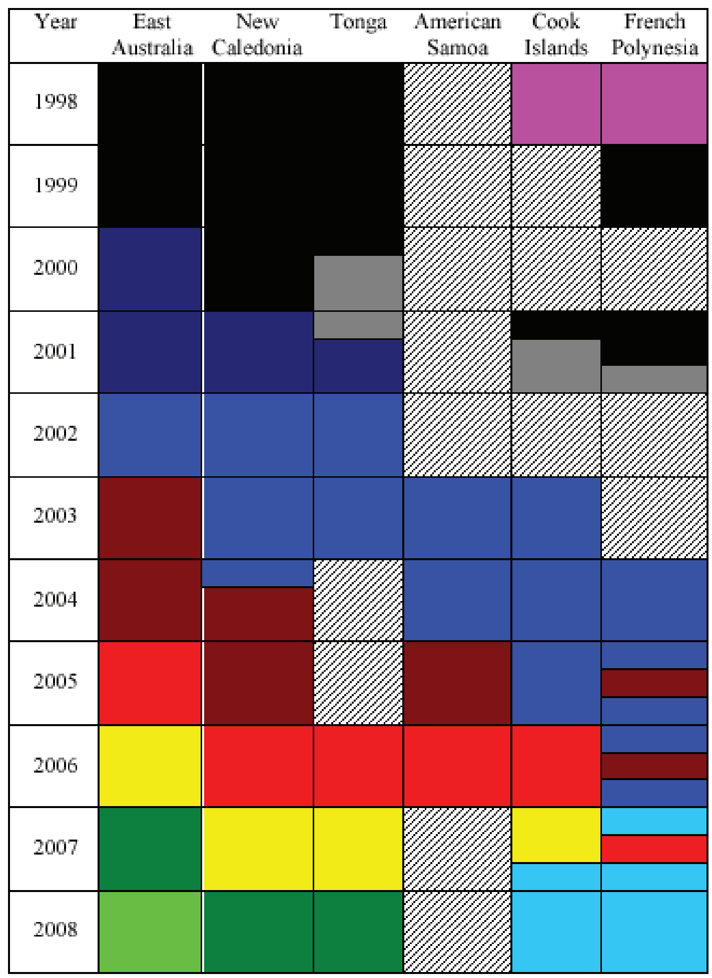

Figure 4. *Song types identified by Garland et al. (2011) in the South Pacific from 1998 to 2008. Each color represents a song type. If two colors are listed for 1 yr at one site, both song types were recorded during that year.*

ing to their vocalizations. In many species of seals that live in polar waters, both Arctic and Antarctic, males produce complex songs that can be a dominant part of the acoustic soundscape during the breeding season. Bearded seals in the Arctic (http://www.dosits.org/files/dosits/bseal1.mp3) and Weddell seals in the Antarctic (http://www.dosits.org/files/dosits/wed222.mp3) produce trilling songs and harbor seals in temperate latitudes produce underwater roars that function in defense of territories (http://www.dosits.org/files/dosits/hbseal.mp3).

Another important function of vocalizations among seals involves parental behavior. Seal pups are often born on crowded beaches, and in many species, the mother leaves the pup so that she can forage at sea to gain nutrition for lactation. Here when the mother returns to the beach, the mother and pup face the problem of identifying one another. In many of the species tested, females make a pup attraction call that the pup learns to use to identify its mother and mothers learn to identify vocalizations of their pup (Trillmich, 1981). The vocal identification system along with visual and olfactory cues can help a mother and pup to reunite, even in a large beach with many mother-pup combinations.

Individual Identification in Dolphins

This problem of individual identification is just as important for cetaceans where strongly bonded individuals may routinely separate out of sight of one another. Unlike seals where the pup may wean after just a few months, young bottlenose dolphins typically suckle for 3-5 yr, and suckling has been reported in pilot and sperm whales older than 10 yr of age (Kasuya and Marsh, 1984). A newborn calf bottlenose dolphin (from now on, I am using “dolphin” for “bottlenose dolphin”) will swim very close to the mother, but by 1 yr of age, mother and calf frequently separate out of sight of one another for many minutes at a time. Dolphins maintain contact by using an individually distinctive signature whistle (Janik and Sayigh, 2013; http://acousticstoday.org/whistle). When wild dolphins separate, they are more likely to produce signature whistles, and they increase their whistle rate at the maximum separation and as they reunite.

Dolphin whistles are tonal signals where the frequency is modulated from about 2-20 kHz, usually in a complex and distinctive pattern. Female dolphins in the wild develop a distinctive and stereotyped whistle by 1 yr of age, and this whistle is stable for decades. Males also develop a stereotyped whistle by 1 yr of age, but as they mature and leave their mother, many will form an alliance with another adult

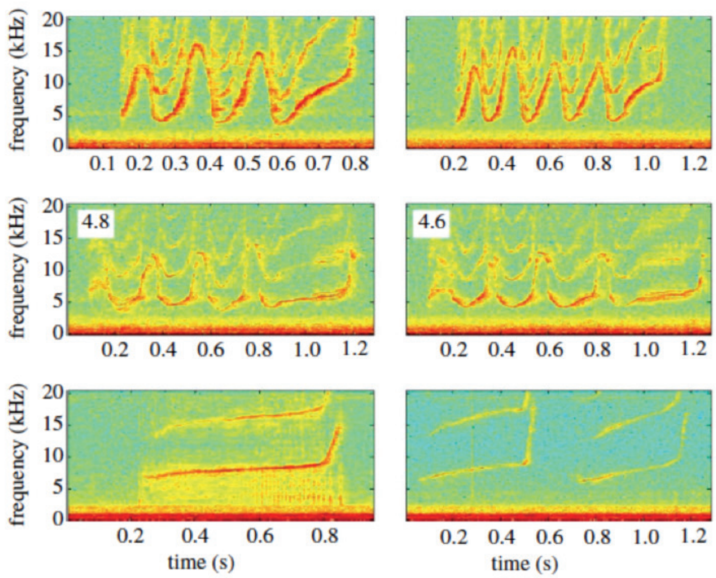

Figure 5. *Examples of signature whistles of a bottlenose dolphin whose whistle was imitated **(top row)**, of imitations of this signature whistle (**middle row**), and the signature whistle of the dolphin making the imitation (**bottom row**). The number in the upper left of each imitation is the average similarity score given by human judges on a scale of 1 (not similar) to 5 (very similar). From King et al. (2013).*

male. As the alliance forms, the whistles of the alliance partners tend to converge and become more similar (Watwood et al. 2004), although they still retain individually distinctive features.

Dolphins do not just produce their own signature whistle, but they also produce a variety of other whistles. The function of most of these is poorly defined, but there is a distinctive pattern where dolphins that share a strong bond, either male alliance partners or mother-calf pairs, may occasionally imitate one another’s signature whistle (King et al., 2013; **Figure 5**). After a dolphin produces its own signature whistle, it is more likely to whistle back to playback of a whistle that matches its signature whistle than to control whistles. These results suggest not only that dolphins use their signature whistles to maintain contact, but they can also initiate an interaction by imitating the signature whistle of a partner.

This pattern of dolphins copying individually distinctive signature whistles appears to involve the skill of vocal learning described for humpback song, but it is difficult to prove with just observations of natural calls. Richards et al. (1984) trained bottlenose dolphins in the laboratory to imitate synthetic whistle-like signals generated by a computer. Their demonstration of imitation of a broad range of these arbitrary signals demonstrated clear abilities for vocal learning of whistle sounds in dolphins.

Killer Whales

Bottlenose dolphins have a social organization in which one animal may maintain strong associations with a few others but within an otherwise very fluid pattern of grouping in which groups are only stable for a few minutes at a time. By contrast, killer whales have the most stable groups known for any mammal. Neither sex disperses from its natal group as they mature. Closely related groups of killer whales that are matrilineally related (called a matriline) and that associate most of the time together are called pods. Each pod has a unique group-distinctive repertoire of stereotyped calls, which are thought to be used to maintain group cohesion (http://www.dosits.org/files/dosits/orca5.mp3; http://acousticstoday.org/kwhale). If a pod grows too big, it may separate into several different matrilineally related pods. Pods that have some overlap in their repertoire of stereotyped calls are described as an acoustic clan, and acoustic clans tend to share mitochondrial DNA, suggesting that they descended from the same matriline (Yurk et al., 2002).

The calls of killer whales do not change as rapidly as the songs of humpback whales, but some calls do change over the course of a decade or so. There appears to be variability in the rate of change in different call types, with some showing divergence between matrilines over a period of a decade and others showing little change and divergence (Deecke et al., 2000). This suggests that the pattern of acoustic clans may result from cultural drift of the acoustic features of calls coupled with vocal matching of calls from matrilines that regularly associate with one another. This kind of matching across matrilines is called horizontal transmission of information, in contrast to vertical transmission that goes from parent to offspring.

Within the same geographical area, different ecotypes of killer whale may have completely different foraging patterns. For example, in the Pacific Northwest, there are populations of killer whales that specialize in foraging on salmon in the same area as populations of killer whales that specialize in foraging on marine mammals. When killer whales use echolocation to hunt marine mammal prey that have good hearing, they are much more cryptic in their use of echolocation and calling than killer whales that are hunting less acoustically sensitive salmon. Even when these different ecotypes of killer whale live in the same place, they have no overlap in their repertoires of stereotyped calls, indicating that horizontal transmission of calls requires social association and interaction.

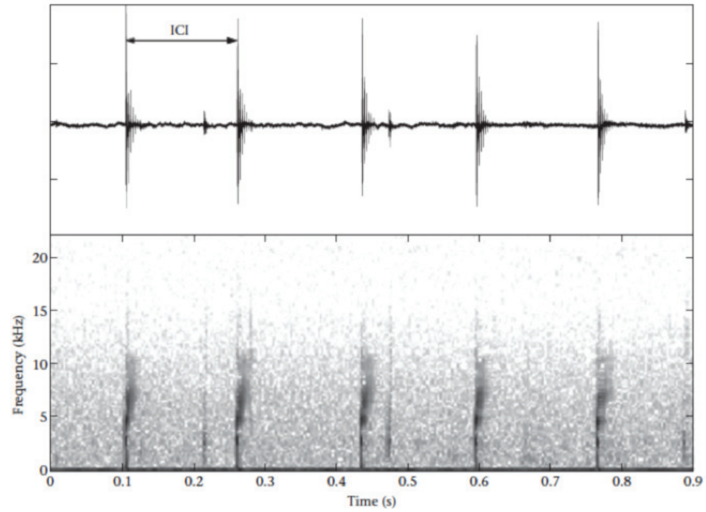

Figure 6. *Waveform (**top**) and spectrogram (**bottom**) of a sperm whale coda containing 5 clicks (from Rendell and Whitehead, 2005). Note how each coda click contains a series of pulses. ICI, interclick interval.*

Sperm Whale Vocalizations

Sperm whales do not make vocalizations as complex as the songs of humpback whales or the stereotyped calls of killer whales. Their communication signals, called codas (Figure 6), are formed of rhythmic repetitions of an altered version of their echolocation click (Madsen et al., 2002; audio file, http://acousticstoday.org/swhale). Analysis of the coda repertoires of groups of sperm whales from the Caribbean and the South Pacific revealed vocal clans. Each vocal clan is a set of sperm whale groups that share the same coda repertoire (Rendell and Whitehead, 2003). Only one vocal clan was recorded in the Caribbean, but five different clans were recorded in the South Pacific. Each clan is composed of thousands of whales spread over thousands of kilometers. Different clans could share the same geographical region, but groups producing one set of codas have only been observed joining with other groups that produced the same codas.

Codas are not the only tradition passed down within a sperm whale clan. Different clans had different movement and feeding patterns even when they co-occurred in the same area; different clans also had better foraging success at different phases of the El Niño oceanographic cycle (Whitehead and Rendell, 2004). These results suggest that cultural differences allow multiple social groupings of sperm and killer whales, each with specific ecological and foraging adaptations, to coexist using the same habitat in different ways. A fascinating feature of the culture of whales is that it is cumulative; the cultural traits such as vocalizations build on the features of earlier versions. In humans, this accumulation of culture has led to the development of complex knowledge and technology, building from generation to generation over time. We now know that whale culture can involve thousands of animals within a cultural group, with traditions spreading over thousands of kilometers and developing over decades or more, increasing in diversity over time. These cultural traditions involve communication, echolocation, and foraging behaviors, but we have little evidence for an increase in complexity for the short time periods over which they have been observed. There is little evidence for marine mammal culture involving technology; rather, it is social behaviors that appear to be especially important.

When you listen to sperm whale codas, they are not acoustically as striking and complex as killer whale calls or as musical as humpback song (although they certainly are rhythmic). But when you think about codas as a cultural tradition, I hope that you agree that a relatively simple acoustic signal can actually represent a complex and fascinating communication tradition.

Conclusion

Marine mammals brought mammalian sound production and hearing capacities to life in the ocean, which enabled them to exploit the favorable physics of sound in the sea. This enabled them to find prey and orient in the dark using echolocation and to communicate over ocean basin scales. Some marine mammals evolved remarkably sophisticated abilities to learn vocalizations, modifying the sounds they produce based on vocalizations they hear from conspecifics. This led to the development of fascinating animal cultures whose complexity we are only just beginning to understand.

Biosketch

Peter Tyack is professor of marine mammal biology at the University of St Andrews, St Andrews, Scotland, UK. He is a behavioral ecologist who studies acoustic communication, vocal production learning, and social behavior in marine mammals, including reproductive advertisement in baleen whales, individually distinctive contact calls in delphinids, and echolocation in deep-diving toothed whales. In collaboration with engineer Mark Johnson, he has developed sound-and-orientation recording tags. He has developed a series of studies on the responses of marine mammals to anthropogenic sounds, including the effects of naval sonar and oil exploration on baleen and toothed whales.

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