Dolphins and whales - taking cognitive research out of the tanks and into the wild

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SPECIES DESCRIPTION

Anatomy

The whales and dolphins (order Cetacea) are a highly diverse group of animals. They have some commonalities (e.g. mammalian body plan and reproductive strategy, complete adaptation to an aquatic lifestyle), but there are several key differences in feeding ecology, social structure and sensory perception that have considerable repercussions on their cognitive abilities.

While the taxonomic position of the cetaceans was disputed for a long time, it now seems reasonably clear that they are located within the superorder Cetartiodactyla, along with the even-toed ungulates (e.g. Price *et al.*, 2005; Agnarsson and May-Collado, 2008). Molecular studies (e.g. Price *et al.*, 2005; Agnarsson and May-Collado, 2008) have confirmed that within the Cetacea, the major taxonomic distinction lies between the toothed whales (suborder Odontoceti) and the baleen whales (suborder Mysticeti), and this distinction is delineated by major behavioural and ecological differences. The taxonomic position of the 3 species of sperm whales (families Physeteridae and Kogiidae) has been subject to some discussion, but they are now generally included within the suborder Odontoceti (e.g. Heyning, 1997; Nikaido *et al.*, 2001; May-Collado and Agnarsson, 2005; Agnarsson and May-Collado, 2008).

The mysticetes range in adult size from 6m (the pygmy right whale, *Caperea marginata*) to over 30m (the blue whale, *Balaenoptera musculus*), and are characterised by their use of baleen plates to filter small prey from the water. Most baleen whales feed in the water column on crustaceans or small schooling fish. However, grey whales (*Eschrichtius robustus*) can also feed on benthic invertebrates by filtering them from the sediment. Ten extant species in 4 major clades (Balaenidae, Neobalaenidae, Eschrichtiidae and Balaenopteridae) are currently recognised.

With the exception of the sperm whale (*Physeter macrocephalus*), with an adult male size of up to 20m, the odontocetes tend to be smaller, with adult sizes ranging from 1.4m (the vaquita or Gulf of California porpoise, *Phocoena sinus*) to 13m (Baird's beaked whale, *Berardius bairdii*). Diets of odontocetes are varied and range from cephalopods and crustaceans to fish, sea mammals, seabirds or marine turtles. Rather than filter feeding on schools of prey, odontocetes typically single out individual prey animals, which they pursue and capture. Whereas baleen whales are found exclusively in the marine environment and are relatively shallow divers (to 500m), some toothed whales, such as the river dolphin, live exclusively in freshwater habitats, and other species such as beaked whales and sperm whales have evolved a deep-diving lifestyle and are capable of descending to depths of almost 3000m (Schorr *et al.*, 2014). The toothed whales are comprised of 10 major clades (Delphinidae, Phocoenidae, Monodontidae, Iniidae, Pontoporiidae, Lipotidae, Ziphiidae, Platanistidae, Kogiidae, and Physeteridae), with a total of 73 species currently recognised (Nikaido *et al.*, 2001).

Along with the sirenids (manatees and dugongs), cetaceans are the only mammals fully adapted to an aquatic existence. Whereas marine mammals, such as the seals and sealions, return to land for reproduction and essential body maintenance, cetaceans have evolved the physiological adaptations to complete all life processes in the aquatic environment. They are characterised by a more or less torpedo-shaped body and absence of hind legs. The forelimbs have evolved into flippers and most species have a dorsal fin that presumably evolved for stability. A broad tail fluke reinforced by collagen-rich connective tissue, rather than bone, is the primary means of propulsion. Through evolutionary elongation of the premaxillary bones, the entrance of the nasal passage has migrated to the top of the head forming the blowhole (Thewissen, 1994).

Perception

The adaptation to a fully aquatic existence has meant a reduced reliance on the traditional mammalian sensory systems of vision and olfaction, and an evolution towards using sound as the primary means of perception and communication. Whereas light is absorbed quickly in the aquatic environment, sound waves transmit freely through water, travelling at greater speed and experiencing less attenuation than in air. Underwater, vision is limited to distances of approximately 100m in the best conditions, and not useful at depths below 200m. Sound, on the other hand, allows cetaceans to sense their environment and communicate over distances for tens if not hundreds of kilometres (e.g. Madsen *et al.,* 2002; Janik, 2005).

Many mysticetes and odontocetes use sound extensively for communication. Some baleen whales produce highly structured songs, thought to function in mate attraction and/or male-male competition (e.g. humpback whales, *Megaptera novaeangliae*: Helweg *et al.,* 1992; bowhead whales, *Balaena mysticetus*: Stafford *et al.*, 2008), and various sounds related to feeding and social behaviour have also been described (e.g. Cerchio and Dahlheim, 2001; Dunlop *et al.*, 2008). Toothed whales use a variety of tonal sounds mostly for social communication (e.g. May-Collado *et al.*, 2007). However, in addition to social sounds, all odontocete species studied so far have been shown to produce broadband clicks for echolocation. True echolocation has not been documented in baleen whales (but see Stimpert *et al.*, 2007).

Sound production in mysticetes remains poorly understood, but at least some species appear to use the larynx as their main sound-generating organ (Reidenberg and Laitman, 2007). Odontocetes, on the other hand, have evolved an independent sound production mechanism: sound is generated by nasal plugs located at the junction between the nasal passage and adjacent air sacs (Madsen *et al.*, 2013). This system allows the recycling of air between the different air sacs, while diving rather than expelling it into the water. Except for the sperm whales, these nasal plugs are paired structures, and studies using animal-attached hydrophones or small catheters to measure air pressure in different parts of the nasal passage suggest that echolocation clicks are generated with the right nasal plug, whereas the left one serves to produce tonal sounds (Cranford *et al.*, 2011; Madsen *et al.*, 2013).

In toothed whales, outgoing sound passes though the melon, an organ comprised of fatty tissue overlying the premaxillary bones, thought to function to focus the sound. The shape of the melon is controlled by various muscles, which allows the animal to modify the structure of the sound beam (Harper *et al*., 2008).

Resonant volumes in the trachea, nasal passage and adjacent air sacs are subject to pressure-related change, as animals ascend and descend in the water column. This means that acoustic features related to resonance, such as formants, important in the communication of many terrestrial mammals, do not provide reliable markers to encode information such as individual identity.

Sound reception in baleen whales remains poorly understood. However, in toothed whales, incoming sounds are thought to be received by the jaws, and conducted directly to the inner ear via special fatty channels (Ketten, 2000). The oral cavity and gular region may also play a role in conducting sound to the inner ear (Cranford *et al.*, 2008). Echolocating species are able to use the returning echoes to identify objects, including prey or underwater features for orientation. The functional range over which echolocation provides useful information remains unclear, but is bound to vary depending on the echolocation task. Prey detection is thought to be possible over a few hundred metres (e.g. Au *et al.*, 2004, 2010). Some species may be able to obtain useful information for navigation (e.g. depth of the water column) over a few kilometres. The echolocation signals of some species are audible to conspecifics over tens of kilometres (thus providing potentially useful information on prey aggregations; Madsen *et al*., 2002).

Audiogram data are available for many odontocete species, but limited for mysticetes. However, hearing sensitivity at different frequencies has been estimated from the dimensions of the ear bones and the basilar membrane in the inner ear (e.g. Ketten, 1997, 2000; Hemilä *et al.*, 1999). Most toothed whales have sensitive hearing between 10 and 100kHz (Au, 2000), although for some porpoises and small dolphins, the range of sensitive hearing extends considerably above 100kHz (e.g. Kastelein *et al.*, 2002). Baleen whales are thought to hear best at frequencies below 10kHz, with some species adapted to hearing at very low frequencies of a few tens of Hz (Ketten, 2000).

Cetaceans are not thought to have sensitive chemosensory abilities (Kremers *et al.*, 2016), although taste buds and chemoreceptor cells have been found in some species, and bottlenose dolphins have been shown to be able to perceive sour, bitter and sweet tastes (Kremers *et al.*, 2016)

Most cetaceans have well-developed eyes, which are generally located on the side of the head, rather than facing forward. Whales and dolphins were originally thought to be colour blind, but at least some species of delphinids appear to have basic colour vision (Mobley and Helweg, 1990; Kremers *et al.*, 2016). Visual acuity is high among marine delphinids, whereas some river dolphins appear to have limited capability or are even functionally blind (e.g. Mass and Supin, 1990, 1999).

The skin of cetaceans has rich innervation and may be capable of sensing fine differences in water pressure (Ridgway and Carder, 1990). This may aid in maintaining laminar flow around the body, but also help sense approaching conspecifics, predators, or prey at close range. While the body of adult cetaceans largely lacks hair, many species have hairs as embryos and neonates, and some species retain functional sensory hairs into adulthood, which appear to play a role in prey sensing and capture (e.g. Pyenson *et al.*, 2012; Drake *et al.*, 2015).

Life cycle

All cetaceans are slow reproducing, with females giving birth to single calves. In most species, birthing appears to occur at specific times of year. While the females of some small odontocetes are able to reproduce annually, most whales and dolphins have inter-birth intervals of multiple years, with females of some species only reproducing every 5 years (Whitehead and Mann, 2000). Lactation ranges from 6 months in some baleen whales to several years in sperm whales (Best *et al.*, 1984; Whitehead and Mann, 2000), and the young of several toothed whale species appear to remain dependent on their mother beyond the age of weaning (e.g. Bigg *et al.*, 1990; Olesiuk *et al.*, 1990).

Reproduction is costly in terms of energetic resources: female cetaceans mobilise a large amount of their body fat to produce a foetus and nurse a young calf. Females of migratory baleen whale species do not feed during this time, and rely entirely on stored fat reserves to sustain themselves and their offspring. However, reproduction also has cognitive costs, because breathing in cetaceans is a voluntary response and the animals need to be conscious to breathe, so that both mothers and newborn calves of some species appear not to sleep during the first month after birth (Lyamin *et al.*, 2005).

Some toothed whale species have been shown to undergo menopause, with the females of some delphinids living almost half of their lives in a post-reproductive state. For example, female resident killer whales (*Orcinus orca*) typically stop reproducing around age 45, but may live well into their 90s (Olesiuk *et al.*, 1990). The presence of post-reproductive females has a significant effect on the survival probability of their sons (Foster *et al.*, 2012), either because they act as repositories for ecological knowledge (Brent *et al.*, 2015), or through active provisioning of food (Wright *et al.*, 2016).

Cetaceans are generally long-lived, with large overlaps between generations. With a maximum longevity of 22-23 years (Koschinski, 2001), the harbour porpoise (*Phocoena phocoena*) is probably on the lower end of cetacean life expectancies. Killer whales are thought to live for a maximum of 80-90 years for females, and a maximum of 50-60 years for males (Olesiuk *et al.*, 1990). Maximum longevity for Atlantic bottlenose dolphins has been estimated at 50 and 30 years for females and males, respectively (Stolen and Barlow, 2003). Female narwhals (*Monodon monoceros*) are thought to reach at least 115 years of age (Garde *et al.*, 2007). Life expectancy data for baleen whales is scarce, but photographic and morphological data suggest maximum longevity of 60-90 years for most baleen whale species (e.g. Hamilton *et al.,* 1998; Arrigoni *et al.*, 2011). However, novel molecular aging methods suggest longevity exceeding 200 years for bowhead whales, *Balaena mysticetus* (George *et al.*, 1999).

Individual identification

Photographic identification of cetaceans using natural marking was first pioneered in the late 1970s (Hammond *et al.*, 1982) and has been used effectively in studies of population structure, social behaviour and cognition. While in some species every individual can be reliably identified from high-quality photographs (e.g. killer whales: Bigg, 1982; Bain, 1990; humpback whales: Stevick *et al.*, 2001), populations of other species, especially the smaller odontocetes, typically contain a proportion of poorly marked individuals (e.g. Wilson *et al.*, 1999), so that conclusions are often drawn from a sample of well-marked individuals that may not be representative of the population as a whole.

A number of long-term studies using photographic identification have now been running for several decades, yielding a wealth of social information. These studies have largely focused on bottlenose dolphins (*Tursiops* spp.; e.g. Wells, 1991; Wilson *et al.*, 1997; Connor *et al.*, 2001) and killer whales (e.g. Bigg *et al.* 1990; Similä *et al.*, 1996), providing valuable baseline information, on which to base research into the social cognition of these species (e.g. Sayigh *et al.,* 1999; Deecke *et al.*, 2010).

Other marking techniques, such as roto- or spaghetti-tags, tags bolted through the dorsal fin or freeze brands, were explored in the 1970s and 1980s (e.g. Irvine *et al.*, 1982), but largely abandoned once photo-ID became established. Small satellite tags, deployed using a crossbow or air rifle and embedded into the animals' blubber or dorsal fin with barbs, are also used to track movement patterns of some of the larger cetaceans (e.g. Mate *et al.*, 2007).

A fundamental problem when studying cetacean behaviour and cognition is that direct observation is only possible when the animals are at the surface to breathe, but most behavioural responses to social or environmental stimuli happen underwater out of our sight. In the last 20 years, miniaturisation of technology has permitted the development of on-animal data loggers (e.g. Johnson and Tyack, 2003; see Fig. 7.1), which have provided fascinating insights into the underwater lives of whales and dolphins. Such tags are typically attached with suction cups and remain on the animal for hours or day. Most tags contain accelerometers, magnetometers and pressure sensors, which allow researchers to reconstruct the detailed underwater movement of the tagged individuals in 3 dimensions. In addition, some tags also contain hydrophones and sufficient storage capacity to record high-quality underwater sound, which allows the study of echolocation behaviour, and the responses to anthropogenic noise and communicative events (e.g. Johnson *et al.*, 2009). Digital archival tags have so far mostly been used to investigate foraging behaviour and responses to anthropogenic sounds. However, they present valuable tool investigate other aspects of cognition (particularly social ones), as well.

Ecological characteristics

Baleen and toothed whales differ fundamentally in the way they obtain food, and this distinction has shaped their cognitive evolution. Mysticetes typically feed on small schooling prey, engulfing a large number of prey items in a single gulp. Their sensory systems are therefore adapted to effectively detect such large aggregations, and to sense their density and profitability. Odontocetes, on the other hand, typically feed on individual prey items, which they must detect, pursue and capture. They have therefore evolved sensory capability to detect and track fast-moving and manoeuvrable prey, presumably using their echolocation (e.g. Au *et al.*, 2004).

Aside from some river dolphins, which appear to have few predators other than humans, most cetaceans are subject to predation by sharks and killer whales. Anti-predator strategies include morphological adaptations (e.g. counter-shading: Caro *et al.*, Whitehead, 2011; false gill slits in dwarf and pygmy sperm whales, *Kogia simus* and *K. breviceps*: Bloodworth and Odell, 2008), as well as behavioural strategies such as vertical and horizontal avoidance, aggression and mobbing (Ford and Reeves, 2008). Playbacks of killer whale sounds to various cetacean species have provided valuable insights into such behavioural anti-predator strategies (e.g. Tyack *et al.,* 2011; Curé *et al*., 2012, 2013).

The movement ecology of baleen and toothed whales shows fundamental differences, and these are likely to affect spatial cognition and memory. Many odontocetes remain in the same habitats year-round or follow movements that are not seasonally defined, whereas most mysticetes follow a clear seasonal migration. Baleen whales typically give birth on low-latitude breeding grounds, which they

Fig. 7.1: Photograph of a juvenile killer whale (*Orcinus orca*) carrying an archival digital recording tag (Dtag; Johnson & Tyack, 2003). The tag is attached by 4 suction cups and records the animal's underwater movements, as well as any sounds it hears or emits. It was used to study the echolocation behaviour and hunting strategies of killer whales while feeding on Pacific salmon (*Oncorhynchu*s spp.; Wright et al., 2017). Photograph by Volker Deecke.

visit in the winter months, but then migrate to high-latitude feeding grounds, where they spend the summer. In some species, feeding activity appears to be entirely limited to the summer months. This migratory behaviour may be due to the lower thermoregulatory capacity and higher predation risk of calves (Corkeron and Connor, 1999; Clapham, 2001).

Social characteristics

Photographic identification has played a critical role in identifying the social structure of many species. Like other mammals, cetaceans have strong bonds between mothers and dependent young. In many species, however, such bonds can persist beyond independence. Odontocetes exhibit a variety of social structures (Connor *et al.*, 1998), ranging from closed groups in killer whales (Bigg *et al.*, 1990) and sperm whales (Whitehead *et al.*, 1991), to fission-fusion societies (e.g. bottlenose dolphins, *Tursiops aduncus*: Smolker *et al.,* 1992; Möller *et al.*, 2006) or stratified societies (e.g. Risso's dolphins, *Grampus griseus*: Hartman *et al.*, 2008). Social behaviour varies between age and sex groups, but can also exhibit pronounced differences between populations of the same species (e.g. killer whales: Bigg, 1990; Baird, 2000; Tavares, 2017)

Several species of toothed whales have been shown to have a distinct matrilineal social organisation, with closed groups consisting of individuals from 3 or 4 generations, related through matrilineal descent. Matrilineal social structure has so far been documented in sperm whales (Richard *et al.,* 1996; Lyrholm and Gyllensten, 1998), killer whales, and long-finned pilot whales (*Globicephala melas*: Amos *et al.*, 1993), but is probably also found in other species, particularly in the subfamily Globicephalinae.

The social structure of both Atlantic and Indo-Pacific bottlenose dolphins is characterised by weak and/or temporary associations between females, but remarkably strong and lasting associations between adult males (Wells, 1991; Smolker *et al.,* 1992; Möller *et al.,* 2006). Such male alliances have been documented in all bottlenose dolphin populations studied to date. Alliance members are sometimes, but not always, close relatives (e.g. Möller *et al.*, 2001; Parsons *et al.*, 2003) and maintain very high levels of association, sometimes for the majority of their lives. These male alliances are thought to increase access to females in reproductive condition. In Shark Bay, higher-order alliances of several groups of males, joining forces against rivals in contests for females, have also been documented (Krützen *et al.*, 2003; Connor *et al.,* 2010).

The social structure of baleen whales remains poorly understood, but is thought to be more fluid than that of odontocetes. The period of dependency is generally much shorter in baleen whales. Calves of many baleen whale species are weaned and independent after 6-7 months (Whitehead and Mann, 2000). Little is currently known about adult association behaviour in baleen whales, although long-term association between individuals do exist in at least some species (e.g. Weinrich, 1991; Ramp *et al.*, 2010).

STATE OF THE ART

In captivity, most species of odontocetes appear to respond readily to training, if using positive reinforcement and acoustic or visual bridges, so that fundamental aspects of cognition, such as perception and memory, can be readily assessed. The challenges of a comprehensive assessment of cetacean cognitive abilities lie principally in the fact that many species are difficult or impossible to maintain in captivity, and that captive animals are unlikely to express the full cognitive repertoire of their wild counterparts. This is particularly problematic in studies of social cognition and communication. Most of our knowledge on cetacean cognition comes from toothed whales, and much of this research has been done in a captive setting. Bottlenose dolphins (*Tursiops* spp.) have received the vast majority of research attention, with only a handful of cognitive studies on a few other species (belugas, *Delphinapterus leucas*. killer whales, harbour porpoise and Pacific white-sided dolphins, *Lagenorhynchus obliquidens*).

Because sound is the principal means by which most cetacean species receive and transmit information, playback experiments are the primary research tool by which cetacean cognition has been assessed in the field (Deecke, 2006). Playbacks offer an effective way to present controlled stimuli to wild whales and dolphins, in order to assess their response. So far, playback has been used primarily to understand social cognition in toothed whales, including individual and group recognition. With the exception of research on the production, perception and learning of song in humpback whales, very little cognitive research has been done on baleen whales - these species are almost impossible to maintain in captivity and present substantial challenges for research in the wild.

The aim of this section is to review the research on cetacean cognition with a focus on studies conducted in the wild. This will help identify future approaches using the novel technologies now available and can also inform strategies to study cognition in the more challenging species, such as the deep-diving odontocetes and the baleen whales.

Perception and attention

Studies on perception have investigated hearing abilities in toothed whales, and behavioural or neurophysiological audiogram information is available for several species (e.g. Thomas *et al.,* 1988; Sauerland and Denhardt, 1998; Szymanski *et al.*, 1999; Kastelein *et al.*, 2002; Houser *et al.,* 2008; Branstetter et al., 2017). Studies on baleen whale perception are currently limited to a few preliminary studies on grey whales (*Eschrichtius robustus*; Dahlheim and Ljungblad, 1990; Ridgway and Carder, 2001).

The echolocation abilities of toothed whales have been largely studied in captivity, and have shown to provide very detailed resolution of size, shape and texture (e.g. Herman *et al.,* 1998; DeLong *et al.*, 2006), as well as cross-modal transfer between echoic and visual recognition (e.g. Harley *et al.*, 2003). Whereas in visual cognition tasks, gaze direction can provide information where an animal focuses its attention, the rate and direction of echolocation can provide this information in echoic cognition of toothed whales (e.g. Wisniewska *et al.*, 2012). Few studies have looked at echoic perception in the wild. Studies on free-ranging bottlenose dolphins show that the animals adjust both inter-click intervals and source levels to ensure good signal-to-noise ratios and effective signal processing with varying range to the echolocation target (Jensen *et al.*, 2009). Wild bottlenose dolphins appear to be able to echolocate through sandy sediments to detect visually hidden fish (Herzing, 2004). The fact that individual echolocation rates decrease with increasing group size in many species may mean that toothed whales are able to extract information from echoes returning from clicks of other group members (Götz *et al.*, 2006). Madsen and colleagues (2005) present exciting insights into the echoic perception of Blainville's beaked whale (*Mesoplodon densirostris*). They show that strategically placed acoustic tags can not only be used to record outgoing echolocation clicks, but also their returning echoes. Using echograms, they were able to visualise the echoic information obtained by the tagged whale, as it homed in on individual targets or schools of prey.

In addition to active use of echolocation to obtain information about objects in their environments, some toothed whales have been shown to use passive listening, for example, for sounds produced by prey animals (e.g. Gannon *et al.*, 2005). Because baleen whales are not known to echolocate, passive listening may be their primary way of orientation and prey detection.

Physical cognition: spatial relationships, numerical competence and tool-use

While there has been a fair amount of research into echolocation (the primary method by which most toothed whales obtain information about their environments), we know very little about how cetaceans integrate spatial information and use it for orientation and navigation, or to remember and localise food sources. Studies from the wild are largely limited to mapping movement patterns and migratory routes. Bottlenose dolphins appear to be able to use their echolocation to detect fish hidden from view and buried in sediments (Herzing, 2004). When it comes to tracking objects that are hidden both visually and acoustically, studies in captivity suggest that, like many terrestrial mammals, bottlenose dolphins (*Tursiops truncatus*) are able to identify the location of objects that they are able to track visually, but perform poorly when tracking hidden objects (i.e. the object is placed in a secondary container before being moved to a hiding place: Jaakkola *et al.*, 2010).

Only a few studies have so far investigated numerical competence in cetaceans, and none of these were conducted in the wild. Captive bottlenose dolphins, which were trained to choose sets of fewer items physically presented in their tank, were able to generalise this response to novel numbers and items, thus suggesting that the animals had a sense of the numerical concept "less" (Kilian *et al.*, 2003). Dolphins exhibit similar performance when presented with visual representations, rather than physical items, suggesting that their numerical competence does not require echolocation, but is expressed equally well in the visual domain (Kilian *et al.,* 2003; Jaakkola *et al.*, 2005). Similarly, captive bottlenose dolphins are also able to generalise the concept of "same" and "different" (Mercado *et al.*, 2000).

Tool use may be defined as the use of a freely manipulable object to modify the physical properties of a target object, through some form of complex mechanical interaction (e.g. Seed and Byrne, 2010). Bottlenose dolphins (*Tursiops* sp.) in Shark Bay are known to pick marine sponges off the sea floor and carry them on their rostrum, while probing in the substrate for fish (Smolker *et al.*, 1997). The precise function of sponging remains unclear, but it may serve to protect the rostrum from physical injury or harmful fish, such as stingrays. The behaviour is more common in females and appears to be transmitted through social learning along maternal lines (Krützen *et al*., 2005). Many species of baleen and toothed whales emit bubbles as part of the foraging process, and this can be interpreted as tool use in the widest sense. The most complex use of bubbles comes from humpback whales: some northeast Pacific populations exhibit a feeding behaviour, where up to 20 individuals feed cooperatively on schooling herring (*Clupea pallasii*; e.g. D'Vincent *et al.*, 1985). One group member swims in a circle below the school, exhaling air and thus creating a curtain of bubbles that encircle the fish. All group members then swim upwards through the bubble net, engulfing the fish. These feeding groups are stable over the years, and show a remarkable level of coordination (D'Vincent *et al*., 1985). During the herding phase, one or two individuals emit a series of low-frequency calls that may serve to manipulate the schooling behaviour of the fish (Cerchio and Dahlheim, 2001). Similar feeding vocalisations have also been documented in killer whales in the Northeast Atlantic (Simon *et al.,* 2006; Deecke *et al.*, 2011). Because a physical structure, a sound, is apparently being used to modify the behaviour of the prey, such herding calls can also be seen as tool-use in the widest sense.

Learning and memory

In captivity, odontocetes can readily be trained to learn associations between different visual, acoustic or echoic stimuli in their environment, or to respond with conditioned behaviours (see Schusterman *et al.*, 1986; Jaakkola, 2012). In captivity, novel associations or behavioural responses can also be socially transmitted through observational learning (e.g. Yeater *et al.*, 2010). There is limited, mostly anecdotal, evidence for associative and social learning in the wild (e.g. Guinet, 1991; Guinet and Bouvier, 1995; Yeater *et al*., 2010). Some of the best field evidence for complex associative learning in odontocetes comes from the social transmission of sponging (Krützen *et al.*, 2005), as well as associations of killer whales and bottlenose dolphins with artisanal fisheries, where certain individuals have learned to cooperate with fishermen in often complex behavioural interactions, in order to increase their own foraging success (e.g. Wellings, 1944; Pryor and Lindbergh, 1990; Neil, 2002). At least some species of mysticetes are similarly capable of complex social learning: in humpback whales, novel feeding behaviours are far more likely to spread between frequent social associates (Allen *et al.*, 2013).

Cetaceans are one of only a few mammalian taxa capable of complex vocal learning. Captive odontocetes can be trained to copy sounds in their environment, and to associate existing vocal patterns and sound stimuli with novel contexts (Janik and Slater, 1997). Captive animals will furthermore spontaneously copy each other's vocalisations (e.g. Crance *et al.*, 2014). There is also good evidence for complex vocal production learning, from both toothed and baleen whales in the field: modifications to stereotyped call types of killer whales are transferred between groups that do not interbreed (Deecke *et al.*, 2000). In Sarasota, Florida, pairs of male bottlenose dolphins in an alliance converge on a common signature whistle pattern (Watwood *et al.*, 2004). Wild bottlenose dolphins are able to copy the signature whistles of close social associates (King *et al.,* 2013), and killer whales occasionally appear to copy call types of other social groups (Weiß *et al.*, 2011). All male humpback whales on a common breeding ground typically share the same song type, which changes within and between seasons (e.g. Cerchio *et al.*, 2001), and song changes can propagate very rapidly throughout a population (Noad *et al.*, 2000) and even across ocean basins (Garland *et al.* 2011).

Field playbacks to wild bottlenose dolphins have shown that the animals are able to recognise the signature whistles of relatives, including offspring that have been independent for several years (Sayigh *et al.*, 1999). Playback experiments have furthermore shown that wild bottlenose dolphins recognise the structural properties of their own signature whistle, and typically respond by matching it (King and Janik, 2013). Humpback whales show different behavioural responses to playbacks of song and social sounds (Tyack, 1983; Mobley *et al.*, 1988), suggesting different functions of the sounds. While recognition of individual or group identity or behavioural context from vocalisations is well established, both in captivity and the wild, the evidence for categorical matching is limited and controversial. Vergara and Barrett-Lennard (2017) trained a captive beluga to match two sound categories (screams and pulse trains): while the individual eventually achieved a high degree of accuracy on the training set, it failed to generalise the discrimination to novel exemplars. Reverting to an achievable training task showed that the poor performance was not due to lack of motivation, but may suggest a fundamental difference in the way humans and cetaceans perceive tonal and pulsed sounds.

In captivity, cetaceans have shown good capacity for both short-term and long-term memory. Bottlenose dolphins can be successfully trained to respond to a specific command by repeating the last behaviour exhibited (Mercado *et al.*, 1998), and to repeat actions performed with specific objects (Mercado *et al.*, 1999), which shows that they maintain a working memory of their behaviour. Captive bottlenose dolphins, furthermore, recognised playbacks of signature whistles of former social associates, even after decades of separation (Bruck, 2013). The results of field playbacks, showing that wild dolphins recognise the signature whistles of their offspring that have been independent for several years (Sayigh *et al.*, 1999), is also suggestive of long-term social memory.

Social cognition and communication

Cetaceans live in complex social environments, and the evidence suggests that they have evolved complex social cognitive faculties to guide social decisions. Long and stable associations between individuals have been shown among both mysticetes and odontocetes. There is solid evidence for recognition of individuals from signature whistles in bottlenose dolphins (e.g. Sayigh *et al*., 1999), but such individual recognition is probably more wide spread, especially among the toothed whales. Playback experiments in the field (King and Janik, 2013; King *et al*., 2013) and captivity (King *et al*., 2014) further suggest that bottlenose dolphins copy the signature whistles of other individuals, and may effectively use them as labels to address specific individuals. Quick and Janik (2012) showed that usage of signature whistles increased in situations when individuals rejoined after some period of separation.

In contrast to the individual signatures of bottlenose dolphins, many killer whale populations exhibit group-specific variation in their vocalisations that identifies social groups rather than individuals. Resident killer whales in the northeast Pacific live in stable matrilineal social groups that typically consist of 3 or 4 generations of animals, related through matrilineal descent. All members of such a matriline share the same vocal repertoire of 8-15 highly stereotyped call types (Ford, 1991). Some of the call types may be shared with other, presumably related, matrilines, however, the population also contains matrilines that frequently associate, yet have no call types in common. All groups that share at least one call type are grouped together into a common acoustic clan. The Northern Resident population of killer whales contains 3 such clans (Ford, 1991). Examples of repertoires from matrilines belonging to different clans are given in Fig. 7.2. Call types that are shared among matrilines often show subtle structural differences between groups. Weiß and colleagues (2006) showed that usage of matriline-specific call types increased after the birth of a new calf.

Comparisons with microsatellite DNA data suggest that structural variation of at least some call types reflects genetic relatedness, as well as social affiliations (Deecke *et al.*, 2010). The vocal dialects, therefore, may allow resident killer whales to identify maternal relatives with a high degree of precision. Like bottlenose dolphins, killer whales occasionally mimic call types of another acoustic clan (Weiß *et al*., 2011). Whether such copied calls also function in labelling has yet to be established.

While the social cognition and communication systems of a few odontocete species are relatively well understood, we are a long way from a comprehensive understanding of the acquisition, processing and transmission of social information for the taxon as a whole. Many oceanic dolphin species habitually live in groups of hundreds and in some cases thousands of individuals. Living in groups of such size likely requires constant processing of social information and behavioural decision-making, yet studying individual behaviour in such large groups is extremely challenging. Some beaked whale species appear to have very unusual social structures and mating systems (e.g. Connor *et al*., 1998), yet due to their pelagic habitat and deep-diving lifestyles, their social cognition is very difficult to study. Finally, we know very little about the social lives of mysticetes, even though some species clearly show long-term social association between individuals, and a high degree of behavioural cooperation. New technologies (such as animal attached recording tags that can record behavioural and acoustic responses to social stimuli) promise to be extremely helpful in providing novel insights into the complex social lives of a large number of cetacean species.

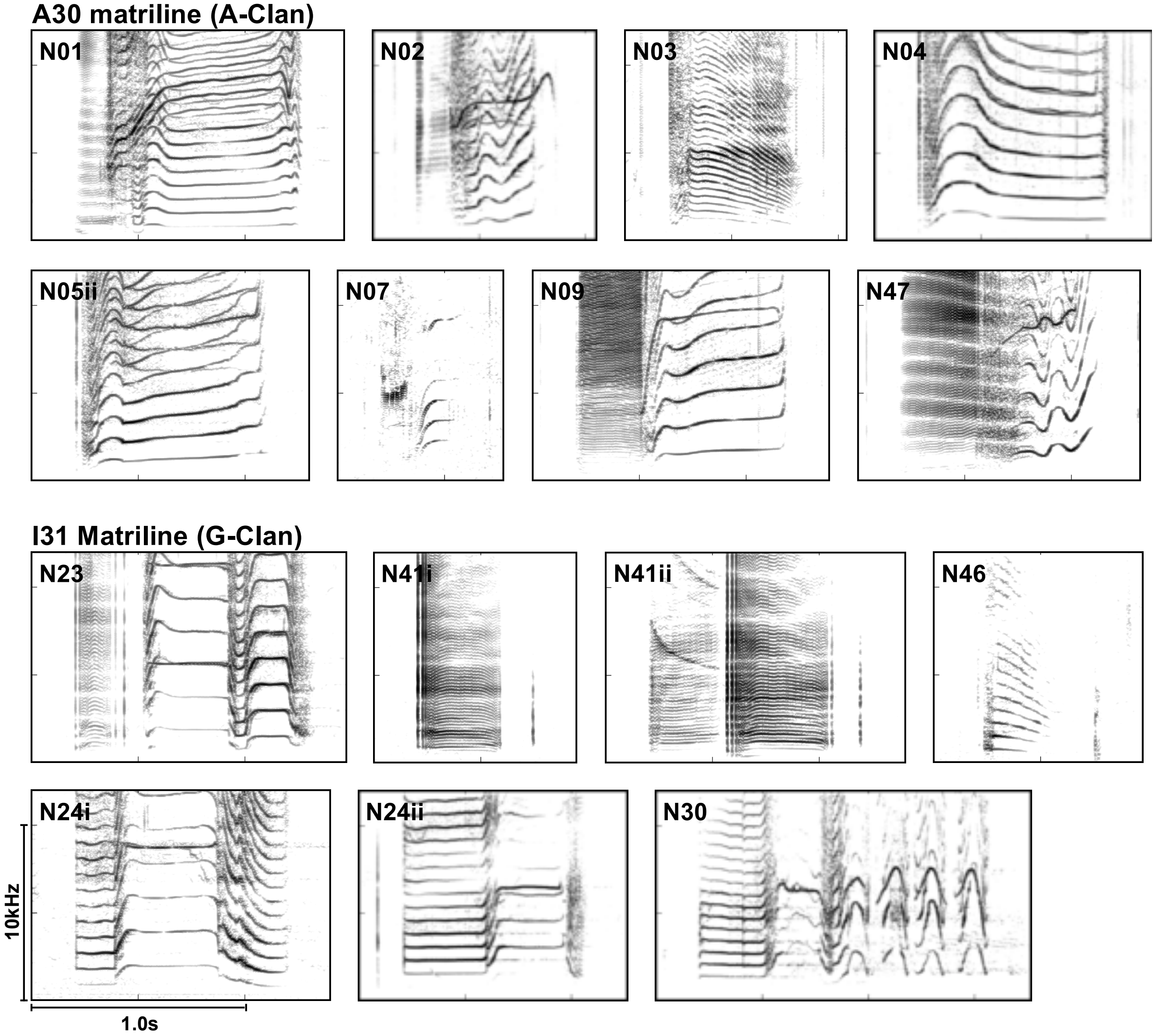

Fig. 7.2. Spectrograms of the most common call types from recordings of two matrilines of Northern Resident killer whales (*Orcinus orca*) belonging to different acoustic clans. In spite of the fact that these groups associate frequently, they do not share any stereotyped call types.

Future directions

Cetaceans are long-lived species, and it can therefore take decades to build up informative social histories of individuals. Long term studies, such as those conducted on bottlenose dolphins in Sarasota Bay, USA (e.g. Wells, 1991), and Shark Bay, Australia (e.g. Connor *et al.* 2001), or on killer whales in British Columbia, Canada, and Washington State, USA (e.g. Bigg *et al.* 1990), are therefore invaluable to provide the background of social information against which complex questions of social cognition can be framed. In addition to information on maternal (and in some cases also paternal) genealogies, these studies have provided records of social associations for large numbers of individuals, often for the entirety of their lives. Because of such wealth of social information, we are now in a position to address fine scale questions on the manifestation and evolution of social cognition in these species.

Captive research has provided valuable insights into the cognitive abilities of toothed whales. Some aspects of perception, physical cognition and learning do not lend themselves to be studied in the field. On the other hand, research into many aspects of social cognition can only be valid if conducted on functional social groups in the wild. Aside from a few juvenile grey whales, baleen whales have not been held in human care, and captive research is therefore not an option for this clade. Ultimately, we will need to arrive at an integrative approach, where an understanding of cognitive mechanisms elucidated from captive studies can be complemented by rigorously designed experiments on wild animals, providing ecological validity. The ability to obtain long-term acoustic data sets using autonomous recorders, and to reconstruct underwater movements from animal-borne tags, and thus analyse the fine-scale behavioural responses to playbacks or to natural social and communicative events, finally gives us the ability to complement captive studies with data of similar quality and detail from the field.

(BOX Ch7_Deecke_BoxO SHOULD BE INSERTED HERE)

FIELD GUIDE

It is an overcast and calm day in late August in Goletas Channel, off the north-eastern coast of Vancouver Island, Canada. After initial light fog in the morning, the air is now clear and the sea only slightly rippled - ideal fieldwork conditions. We are following a group of 10 killer whales, as they are travelling northwest in the channel, in a loose formation. The group is led by its matriarch, A30, thought to be around 60 years old. With her are her adult sons A38 (aged 38 years) and A39 (aged 34). A30 also has two adult daughters accompanying her: A50 (aged 25) and A54 (aged 20). Both now have offspring of their own: A50 is the mother of the 10 year-old female A72 (characterised by a very distinctive nick in the leading edge of her dorsal fin) and A84, a 4-year old juvenile, whose sex is yet to be determined. A54 gave birth to female A75 seven years ago, and to A86 (sex unknown) 3 years ago. She also has a new calf, A93, who is only a few months old and typically swims in echelon formation, close to her mother. All individuals in the group can be readily identified from photographs or by trained eye, based on the shape and size of their dorsal fin and nicks in the fin, as well as pigmentation patterns and scars in the saddle, the grey patch behind the fin.

A30 and her matriline are members of the Northern Resident population of killer whales, and typically range from central Vancouver Island north to the border with Southeast Alaska. Like other members of their population, the A30s frequent the waters off northern Vancouver Island in late summer and autumn to intercept Pacific salmon (*Oncorhynchus* spp.), passing through the straits and fjords on their way to the spawning rivers. Northern Resident killer whales have been the subjects of a systematic study into killer whale life history and social behaviour since 1972, for which group composition is documented on a regular basis. Because A30 matriline is one of the most commonly encountered groups, we have a plethora of information on association patterns, social interactions and life-history data for this group (e.g. Bigg *et al*., 1990; Olesiuk *et al*. 1990).

A72, the 10 year-old female, is wearing a digital recording tag (Dtag; Johnson & Tyack, 2003; Johnson *et al*., 2009; see Fig. 7.1), attached below her dorsal fin with 4 suction cups. The tag has a magnetometer, accelerometers, and a depth sensor to record A72's underwater movements with very high resolution. In addition, the tag also contains two hydrophones to record high-quality underwater sounds, including the echolocation clicks and communicative calls and whistles of A72 and the other members of her group, but also the noise generated by passing vessels. All data are stored on the tag. To aid in tracking the whale and recovering the tag, the tag sends out VHF radio signals that we can pick up, using our antenna array every time A72 surfaces and the antenna clears the surface. We have programmed the tag to detach from the animal at 7PM. At this point, the tag will shunt its remaining battery power to two loops of galvanic wire, causing them to corrode in the seawater over the next 20min or so. This will open up 4 small rubber tubes, each leading to one of the suction cups, and break the vacuum, causing the tag to float free.

The whales are heading northwest in the channel, in a loose formation. A72 is with A30, A50 and A84, travelling within 50m of the shoreline. A54 and her offspring A75, A86 and A93 are swimming in a tight subgroup behind them, while the two adult males A38 and A39 are paralleling them mid-channel. We encountered the whales earlier this morning, some 12km to the southeast. It took us just over an hour to deploy the Dtag. This was done by slowly paralleling the group with one team member on the bow of the vessel, holding a 5m carbon fibre pole with the tag attached to its end. Eventually, A72 surfaced close to the boat and the tag was deployed. The animal gave a short flinch as the tag attached, but quickly resumed her previous behaviour. The vessel we are using for this research is a 10m aluminium-hulled vessel, specially designed to minimise disturbance to the animals: the vessel is powered by a surface-drive propulsion system, which is extremely quiet. In addition, the engines are mounted on rubber shock-absorbers, to limit sound propagation through the hull, and the exhaust is expelled through two water-filled mufflers. In addition, we are using a 21m steel-hulled sailboat for cooking and accommodation.

We are following the whales at a distance of 50-100m, looking for signs of feeding activity. The aim of our study is to use the tag data, to gain a better understanding of the behavioural strategies deployed by resident killer whales to detect, pursue and capture their primary prey, Pacific salmon. Northern resident killer whales preferentially feed on Chinook salmon (*Oncorhynchus tshawytscha*), but will also take chum (*O. keta*) and other salmon species (Ford and Ellis, 2006). The health of the population appears intricately linked to Chinook salmon returns to the major river systems within the animals' range (Ford *et al.*, 2010), and by better understanding their foraging process we hope to be able to ultimately minimise anthropogenic influences on their feeding success. If we find evidence that A72 may have caught a salmon, we will take the boat closer and look for fish scales near the surface where the animal surfaced. These will help us confirm a salmon capture, but also provide information on the species and age of the fish taken, and allow us to determine later how the whale used its echolocation to detect and track the fish. The results of this study have since been published by Wright and colleagues (2017).

Table 1. Essential experimental equipment required to study cetaceans in the field.

Tool	**Function**
Digital SLR camera	A high-quality camera with telephoto lens is essential for identifying individuals from natural markings. A 300mm or 400mm image stabilised lens works best on small boats. Choose a fixed lens

	for larger species, but an adjustable zoom lens (e.g., 80-300mm) preferable for smaller species that have a tendency to approach the boat for bow-riding.
Boats	A good research boat must be stable, fast and manoeuvrable enough to keep up with the animals, and capable of handling the sea conditions where the animals live. Power supply and space for research equipment that is protected from the elements are additional considerations. Any boat used for cetacean research should be designed with the reduction of underwater noise output in mind to minimise disturbance to the animals.
Hydrophone	Hydrophones are required to monitor and record underwater vocalisations and should be sensitive in the full frequency range produced by the study species. Simple hydrophones deployed over the side of the boat are useful while the boat is stationary, but need to be retrieved before the boat moves. Towable or hull-mounted systems allow monitoring and recording while underway as well (but may receive interference from engine noise)
Digital recorder	A sound recorder should be capable of capturing the full range of sound frequencies produced by the species studied. Standard systems sampling at 48kHz are adequate for baleen whales, but most toothed whales require sampling rates of 96kHz or higher. Two-channel recorders are adequate for general recording, but projects where identifying the direction of localisation of sounds is important require multi-channel recorders.
Acoustic analysis software	Several programmes are available. Adobe Audition (Adobe Systems, San Jose, USA) or Audacity (Audacity Development Team) work well for rapidly scanning large sound files. Sound analysis programmes such as Raven (Cornell Lab of Ornithology, Ithaca USA), Avisoft (Avisoft Bioacoustics, Glienicke Germany) allow more detailed measuring of sounds and also some simple manipulations. MATLAB (The Math Works, Natick, USA) is useful for more complex signal processing tasks.
Theodolite	A theodolite can be useful in situations where animal movements need to be tracked from shore (e.g., to document movements towards or away from a sound source).
Underwater loudspeaker	Realistic playback experiments require a high-quality sounds source. Underwater loudspeakers developed for synchronous

	swimming (e.g., Lubell Labs LL916, Columbus, USA) are adequate in some circumstances. However, for playback of ultrasonic vocalisations systems with better high-frequency response are required.
Digital recording tags	Accelerometry tags are invaluable to record the underwater movement of animals and some tags are able to also record underwater sound (e.g., Dtag, Johnson & Tyack, 2003) and GPS location. Tags attached with suction cups are minimally invasive and if applied correctly can remain attached for hours or days. Various propulsion systems (crossbows, pneumatic devices) have been used for deployment, but a long light-weight carbon fibre pole works best for species that are reasonably habituated to boats
Autonomous recorders	In situations where long-term records of communication signals are required, autonomous recorders can be helpful. These are deployed on the ocean floor and can be set to record continuously or on a duty cycle (e.g., 5 min every hour). Deployments of several weeks of continuous recording are possible, whereas duty-cycling can extend recording time to over a year.

However, today we have a second objective to our research: having a tag on a killer whale and being able to track its underwater movements in response to sound stimuli gives us the opportunity to test whether playback experiments can be used to address questions about social cognition in this species. Specifically, we want to see whether killer whales extract social information from the call types of other clans in their population, call types that they are presumably familiar with, but which they do not usually produce themselves. A30 matriline is a member of the A-clan, an assemblage of several dozen matrilines that all share at least one call type. The Northern Resident population contains two other clans, G-clan and R-clan, and members of different clans do not share any call types (Ford, 1991). We have therefore prepared a short playback sequence containing 8 calls produced by members of the I31 matriline. This matriline forms part of the G-clan, occasionally associates with A30 matriline, but does not share any of its call types (see Fig. 7.2, for an illustration of the vocal repertoires of both groups). Playing back calls of a different acoustic clan can rule out call-type matching as the primary reason for a vocal response. As a control, we can then use recordings from another killer whale population (e.g. Icelandic or Norwegian killer whales) containing call types that the A30s will also not produce themselves, but will also be unfamiliar with.

The whales have reached the western end of Nigei Island, where Bate Passage meets Goletas Channel from the north. After some milling and foraging activity at the junction, they start heading north in Bate Passage, and we decide that this is a good time for the playback experiment, as this is a location where other groups could be approaching from the west. The whales have gone into resting behaviour: the group members are lined up beside each other in a line, almost touching. They are diving for 3-4min and moving very slowly. We ask the sailboat to assume a position approximately 1.5km behind the whales, and lower the playback speaker into the water, while we continue to follow the group in the smaller boat and monitor their underwater vocalisations, using a hydrophone array towed behind the boat. Currently, the whales are largely silent, except for the occasional N03 call (Fig. 7.2).

We start the playback at 5:11PM. The playback system had been calibrated to transmit the calls with a source level of 152dB, the typical source level of stereotyped call for this population (Miller, 2006). After the first few playback calls, the members of A30 matriline that had been silent for the last 20min, start vocalising prolifically. Interestingly, they are producing N47 calls, the signature call type of this particular matriline (Weiß *et al*., 2006). A spectrogram showing the vocal response recorded on A72's Dtag is given in Fig. 7.3. Later, analysis of the tag data also shows rapid acceleration and a 180º turn towards the playback source. The whales remain agitated for the next 30min, frequently changing direction, although little further vocal behaviour is recorded on the tag. Eventually, they resume their resting behaviour and slowly continue northwards in Bate Passage. We continue to follow them through the Passage and into Gordon Channel. The tag detaches on time at 7:30PM. and we manage to recover it within minutes. We head for anchorage to get some food and rest, and to begin the long process of downloading the tag data.

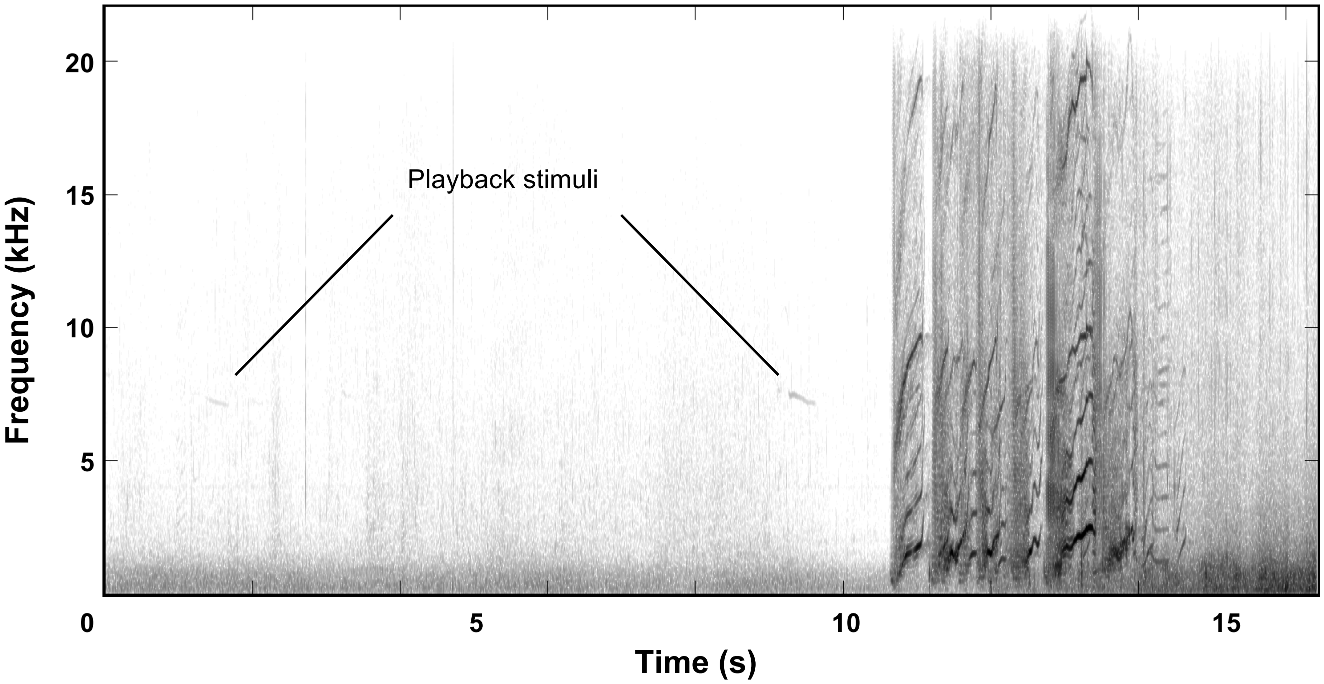

Fig. 7.3. Spectrogram of the vocal response of A30 matriline of the Northern Resident population of killer whales to the playback of G-clan calls. The recording was made on an archival digital recording tag (Dtag; Johnson & Tyack, 2003) deployed on one of the group members. The playback was conducted from a distance of approximately 1.5km. The playback stimuli are faintly visible.

This experiment illustrates the value of conducting cognitive research on cetaceans in the field, but also some of its challenges. Many replicates will be necessary to draw firm conclusions about call recognition in killer whales, and opportunities to conduct playback trials under similarly ideal conditions and appropriate contexts can be hard to come by. However, the preliminary data suggest that the members of A30 matriline responded to the playback, by orientating towards the source, communicating their presence, and signalling their identity by producing the one call type most useful for identifying this group. The experiment was only made possible by the long-term data available for Northern Resident killer whales. Without an understanding of the animals' association patterns and repertoire variation within the population, choosing appropriate playback stimuli and interpreting responses would have been impossible. With several long-term studies on free-ranging cetaceans now having reached maturity, and with new technologies that allow us to obtain detailed behaviour data from free-ranging unrestrained animals, we now have the ability to tackle fine-scale questions and to finally take cognitive research on whales and dolphins out of the tanks and into the field.

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- European Association for Aquatic Mammals: https://eaam.org

PROFILE

Volker was born far from the sea in southern Germany and grew up in landlocked Austria. An interest for wildlife and human languages led him to study animal behaviour and communication. He started studying biology in Berlin, Germany but soon transferred to Vancouver, Canada where he eventually acquired the necessary boating skills and completed a master's degree at the University of British Columbia investigating the evolution of vocal dialects in fish-eating Northern Resident killer whales. He received his doctorate from the University of St. Andrews in Scotland focused on the vocal behaviour of mammal-eating killer whales in British Columbia and Alaska and the response of harbour seals to killer whale calls. After post-doctoral research at the University of British Columbia's Marine Mammal Research Unit, Volker returned to the United Kingdom, where he is currently associate professor in wildlife conservation at the University of Cumbria. Volker has studied the acoustic communication and population structure of killer whales in Canada, Alaska, Shetland and Iceland and has also been involved in behavioural and cognitive research on grey whales, humpbacks, brown bears and snow leopards.

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