

## Chapter 12

# Sperm Whale: The Largest Toothed Creature on Earth



Mauricio Cantor, Shane Gero, Hal Whitehead, and Luke Rendell

**Abstract** Among large variations in size, habitat use, trophic niche, and social systems of toothed whales, one species—the sperm whale—stands out as an animal of extremes. The world’s largest biological sonar operated by the largest brain on Earth shapes much of sperm whales’ lives as efficient predators, exploiting massive biological resources at great depths. They are nomads with home ranges spanning thousands of kilometers horizontally and more than a kilometer vertically. These three-dimensional movements and extremely low reproductive rates place a premium on cooperative calf care, making it central to the tight matrilineal social units of female sperm whales in tropical and subtropical waters. The social units themselves are elements of sympatric cultural clans with distinctive behaviors and vocal dialects. Males leave their maternal units in their teens, gradually moving to higher latitudes and becoming less social until, when very much larger than the females, they make periodic forays to warmer waters for mating. New technology is beginning to give us insight into the behaviors of this extraordinary animal, but its long life span means that long-term studies using simple methods are still immensely valuable.

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## 12.1 Introduction

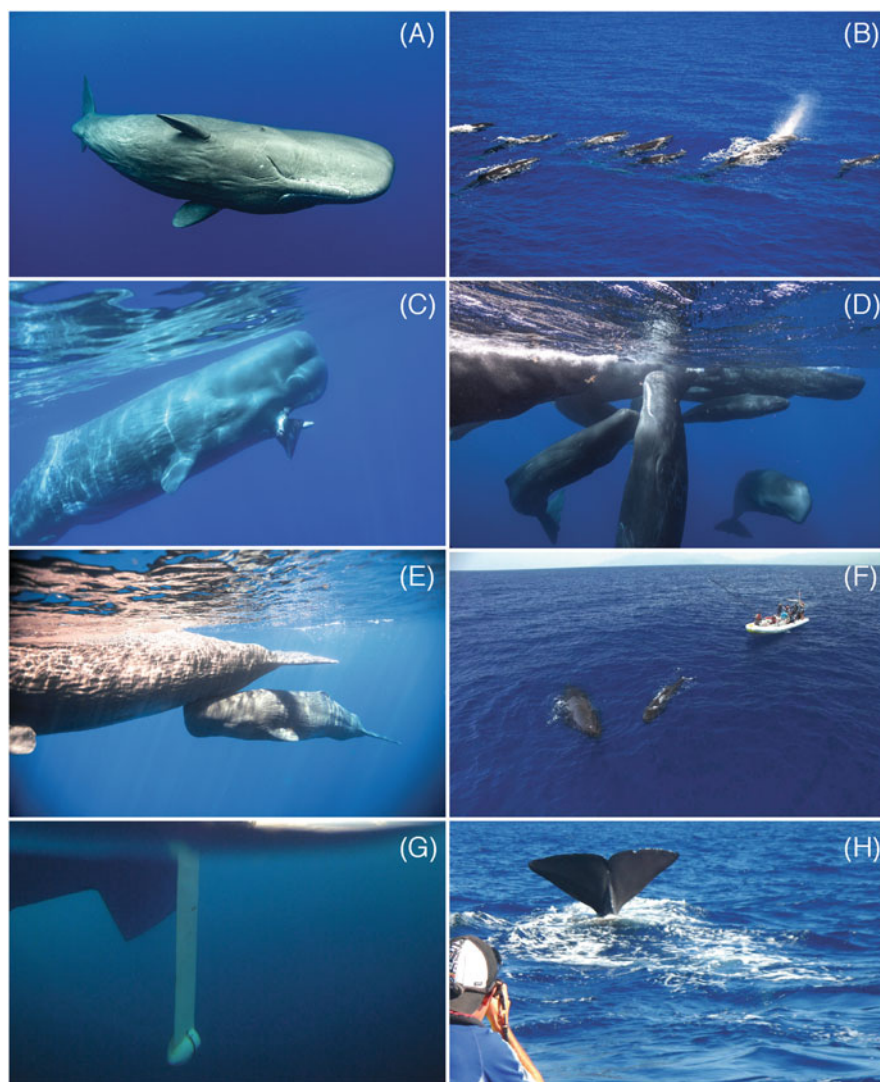
Sperm whales are odd creatures. Their distinctiveness is molded by their surroundings—the deep ocean and their rich social lives. In offshore waters, sperm whales make a living diving to deep strata peppered by unpredictable food patches in an otherwise dark desert. But, for a sperm whale, this desert is a social place.

For most people, they are the archetype of a whale—ask a child to draw a whale and you will likely get a big-headed, out-of-the-ordinary line drawing resembling a sperm whale (Fig. 12.1a). Despite living in an environment unfamiliar to us, sperm whales are engrained in our culture, from starring in one of the most-read novels (Melville 1851) to lubricating the machinery of the industrial revolution (e.g., Whitehead 2002). Thanks to a modern appreciation of the natural world and to increasing research effort, our image of sperm whales has shifted from brutish leviathan to docile giant.

Sperm whales are large-bodied animals—the largest of any toothed predators. Perhaps more arresting than size is the sexual dimorphism in body size and weight, the most marked among cetaceans (Fig. 12.1b). Mature males average about 16 m in length and up to about 45,000 kg compared to the average 11 m, 15,000 kg females. They also have the largest brain in absolute mass (~7.8 kg), but not the largest brain relative to their immense body sizes (see Whitehead and Rendell 2014). Large brains are associated with high cognitive capacities, and sperm whales' rich social lives and complex communication system make excellent use of such abilities.

A glance at sperm whale external morphology reveals odd adaptations for a deep-sea life (Fig. 12.1a). Their blow does not come from the top of their heads, but is left-skewed, coming from a single asymmetric blowhole. About one quarter to one third of the animal's body makes up the barrel-shaped head, which is largely composed of the spermaceti organ (Clarke 1970). This organ is packed with spermaceti oil that has physical properties of wax, from which the whales get their name. That massive head houses the world's largest biological sound generator. At both ends are air sacs, and air from distal sacs at the tip of their noses is forced through the cartilaginous phonic lips (or *museau du singe*) to produce a click. The click is directed backward to the frontal sac placed in front of the skull and then reverberates forward, through a mass of connective tissue and oil termed the junk that lies underneath the spermaceti and serves to direct sounds from the head into the environment. The resulting bursts of high-pressure sounds—the clicks—are loud (236 dB *re*: 1  $\mu$ Pa rms; Møhl et al. 2003) and forward-directional (Møhl et al. 2000).

Loud clicks allow sperm whales to “see” much further than the end of their noses. In this three-dimensional aquatic world, sound travels about 4.5 times the speed that it does in air. Because sound does not attenuate quickly in the dense medium of



**Fig. 12.1** Morphology, behavior, and methods for studying sperm whales, *Physeter macrocephalus*. (a) A close encounter highlights the distinctive massive head and its powerful biosonar (©Amanda Cotton). (b) A traveling social unit of females in the company of a mature male highlights the sexual dimorphism in body sizes (©Marina Milligan). (c) A whale with squid in mouth in a rare glimpse of prey brought to the surface (©Robyn and Wade Hughes). (d) While resting and socializing, females are relatively active at the surface with social unit members (©Patrick Dykstra). (e) A suckling calf illustrates how maternal and allomaternal care of young is a strong force within social units (©Patrick Dykstra). (f) Methods for studying sperm whale behavioral ecology include DTags to record dive profiles (©Keri Wilk), (g) arrays of omni- and directional hydrophones (©Marina Milligan), and (h) individual photo identification via natural marks in longitudinal studies (©Dominica Sperm Whale Project)

water—while light travels only a few hundred meters at most—it is especially efficient for sensing the physical environment while scanning for prey, predators, and peers (Madsen et al. 2002). From echolocation to communication, theirs is a world of sound.

Sperm whales are ecologically important throughout much of the deep oceans. They are distributed circumglobally (Jaquet 1996) and eat a worldwide biomass comparable to that of all human fisheries combined, roughly 100 million tons per year (Whitehead 2003). This enormous consumption helps to regulate mesopelagic food webs via top-down control of mesopredator numbers directly and of producers and detritivores indirectly. It also acts as a “biological pump” that counteracts the downward flow of carbon through migration and sinking of organic matter. Sperm whales contribute to nutrient cycling by feeding at the typically dark but nutrient-rich depths and defecating at the sea surface where nutrients may be in short supply. The fecal plumes rich in nitrogen and iron content promote plankton growth and primary productivity, when brought to the euphotic zone where the sun penetrates, especially in the iron-depleted waters in the southern hemisphere, contributing to an estimated removal of 200,000 tons more carbon from the atmosphere than they produce through respiration (Lavery et al. 2010).

By occupying such a niche, where few other animals venture, they largely escaped competition, except from each other. Sperm whales live long, grow slowly, and mature late; females produce few energy-expensive offspring; high calf survival rates are vital to population growth (Whitehead 2003). By being large-bodied animals that behave cooperatively, they also largely escape predation, except from killer whales (*Orcinus orca*) and humans. Much of this ecological success is mediated by their acoustic sensory capabilities that drive their foraging skills and social lives.

Here, we revisit the classic and recent findings on the behavioral ecology of sperm whales to illustrate the lives of deep-diving odontocetes and discuss how well general principles of behavioral ecology hold up in this species. Our goal is to offer an overview of sperm whales as important predators and as a cooperative, social, and cultural species. We dive into their adaptations to mesopelagic habitats, assessing their foraging and movement behaviors; then we surface to assess their social lives and learned traditions. We close the chapter by raising some challenging questions we hope the next technological advances will help to answer.

## 12.2 Foraging

Sperm whales are the largest toothed predators, but it is not their teeth that make them efficient hunters. Their mouths are impressive for the nearly 90-degree wide gape and large jaws; but they have only vestigial maxillary teeth and no proper oral cavity, lips, or cheek (Werth 2004; Fig. 12.1a). The mandibular teeth are fully exposed along the lower jaw, but may not even be used to capture or handle prey (Werth 2004). What makes sperm whales efficient predators are their noses. Scientists

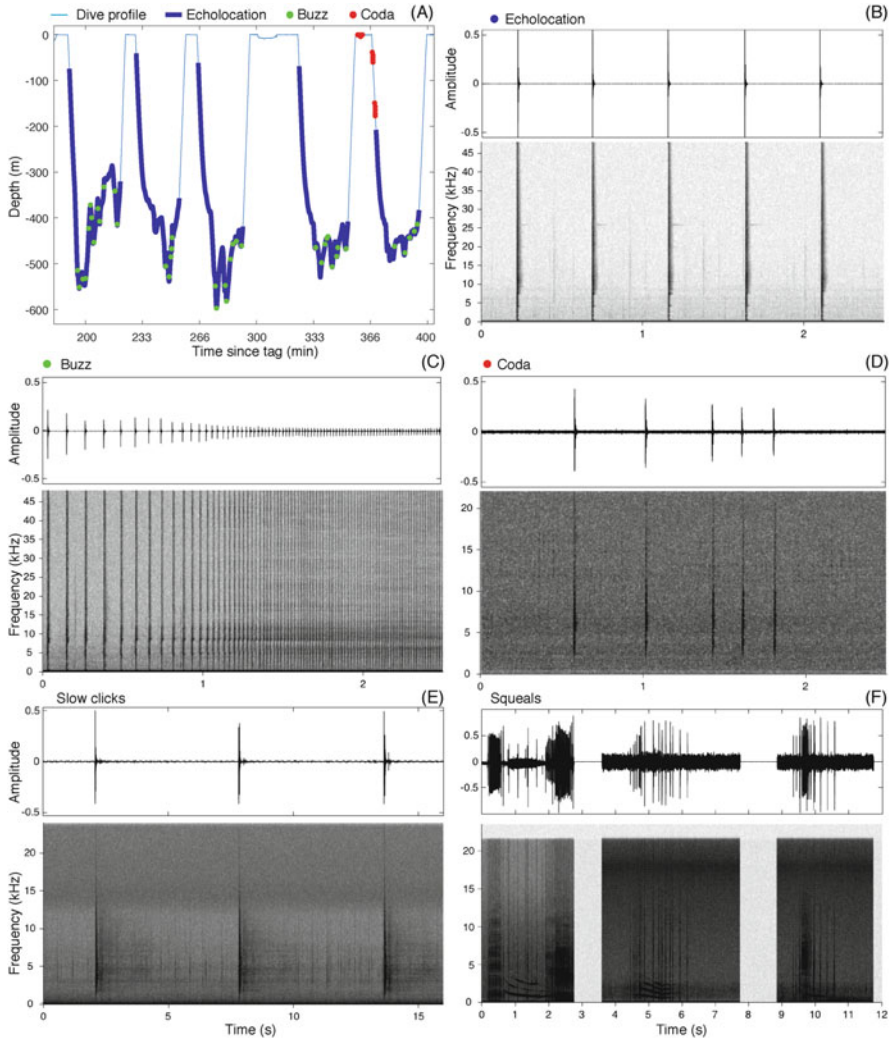
have come up with a variety of theories for the evolution of the sperm whale head, from buoyancy control (Clarke 1970) to battering ram (Carrier et al. 2002), but the only explanation that does not sink under the weight of its own contradictions is that it is uniquely adapted to produce highly focused echolocation clicks from the largest biosonar on Earth.

Foraging sperm whales dive after a range of large food items that dwell in deeper waters—mainly deep-sea squids, but also fishes (Kawakami 1980). Stomach contents suggest that preferred prey are gelatinous cephalopods of the Histioteuthidae family, but those of at least other five families, including the giant (*Architeuthis* spp.) and jumbo squids (*Dosidicus gigas*), are also consumed. To find prey in dark deep waters, sperm whales echolocate. The challenge of directly observing foraging has led to many hypotheses about how whales capture and consume prey. For instance, their whitish outer mouth lining—in sharp contrast with their otherwise largely dark bodies—suggests that sperm whales could lure bioluminescent squid (Beale 1839). Stomach contents reveal that prey are captured with few bite marks and suggest suction feeding (Werth 2004). It is now clear that sperm whales do not acoustically stun their prey with intense clicks (Fais et al. 2016), as previously suggested (Norris and Møhl 1983). However, it was not until the advent of animal-borne technologies that could dive along with the whales that we began to understand the finer mechanics of their deep foraging behaviors.

The overarching challenge for predators is maximizing net energy, that is, accruing higher intake via prey capture than the energy spent searching for and handling them. For air-breathing predators foraging with a restricted oxygen supply, underwater time must be spaced out by breaks at the surface. Sperm whales perform deep and long dives of ~400–1200 m for ~40–50 min and split up with short breaks of ~9 min at the surface to load up their blood and muscles with oxygen (Watwood et al. 2006). Typical sperm whale dives are “U-shaped” (Fig. 12.2a). When foraging, sperm whales use their long-range biosonar through ~80% of the dives (Watwood et al. 2006). They produce predictable and characteristic long series of regularly spaced clicks at 0.5–2 s intervals (Fig. 12.2b). When homing in on and capturing prey, sperm whales produce “buzzes” (or “creaks”; Fig. 12.2c) that are rapid accelerating sequences of clicks (Fais et al. 2016; Miller et al. 2004).

There are some sex differences in foraging behavior. Females focus on cephalopods about 0.1–1.0 kg (Fig. 12.1c), but males show greater variation in foraging strategies, in part due to their wider ranging habits. In colder high-latitude waters, males hunt the colossal squids (*Mesonychoteuthis hamiltoni*) and a selection of mesopelagic and demersal fish in Antarctic/Arctic waters (Teloni et al. 2008; Hanselman et al. 2018). This variation in prey and habitats enables at least two distinct types of foraging dives: shallower dives with fewer and longer buzzes suggesting evasive and larger prey and deeper dives with relatively more but shorter buzzes suggesting denser and less evasive prey (Teloni et al. 2008; Fais et al. 2015).

There is still much to learn about sperm whale foraging. Very little is known about the ontogeny of diving, foraging, and echolocation; but calves can make long (up to 44 min) and deep (down to 662 m) dives prior to age 1, producing echolocation clicks and, rarely, buzzes at this young age (Tønnesen et al. 2018). The role of



**Fig. 12.2** The diverse acoustic behavior of sperm whales, *Physeter macrocephalus*. (a) Dive profile of a tagged sperm whale showing the typical "U shape". Foraging sounds, such as (b) echolocation clicks and (c) buzzes, are produced in the deeper phases of the dive. Social sounds are mostly produced in the shallower phases, here illustrated by (d) the 1 + 1 + 3 coda type recorded in Dominica and typically heard in the Caribbean; (e) slow clicks recorded from males in the Gulf of Alaska (note the energy emphasis at 2–4 kHz and the reverberations; courtesy L. Wild/SEASWAP); and three "squeals" (f) recorded in the southeast Pacific (note that they overlap other social sounds, both codas and chirrups). Waveforms and spectrograms were produced with 1024 point FFT, 50% overlap, Hanning window



learning in the development and tuning of diving behaviors remains poorly understood. We are largely prevented from studying optimal foraging in sperm whales because mapping prey distribution at such depths is currently prohibitively expensive. Behavioral decisions on habitat use and with whom to forage are also important factors in foraging success. On this topic, we know much more.

## 12.3 Traveling

Sperm whales are nomadic, with home ranges that can span thousands of kilometers. In the mesopelagic world, food resources are patchy, usually short-lived and unpredictable in space and time. So, sperm whales can be almost anywhere that there are deep ice-free waters, and they are usually on a constant search.

There are marked differences in distribution between the sexes. Females, often with young, concentrate in lower-latitude waters, generally less than 40° north or south (Whitehead et al. 2008; Mizroch and Rice 2013). Females roam more widely in the Pacific than they do in the Atlantic, where only males have been documented traveling long distances (Gero et al. 2007). Males in general show a wider range of movements than females, sometimes traveling thousands of kilometers across ocean basins and at other times staying resident in rather small coastal areas for months or years (Mizroch and Rice 2013; Rødland and Bjørge 2015). There is little evidence that sperm whales follow regular migration routes or clear seasonal agendas, as do most baleen whales.

Sperm whales likely use information on relevant environmental conditions, gleaned directly or through conspecifics (e.g., eavesdropping on the click patterns of other sperm whale groups), to update knowledge about habitat and food patch quality. Their movements are typically a relatively straight track at about 4 km/h (Fig. 12.1b), which means they may cover about 90 km, horizontally, in a day. When food abounds, however, paths are more convoluted, so that displacements are restricted to about 10–20 km (Whitehead 2003). Over larger spatiotemporal scales, we know much less about the decisions sperm whales make about movements, but we suspect that habitat knowledge handed down over generations plays an important role.

In social animals such as sperm whales, a consensus must be reached on movement decisions if a group is to remain together. Foraging groups of female sperm whales often make long and seemingly disorganized turns that may be indicative of shared decision-making (Whitehead 2016). In the Pacific, a typical group containing 30+ individuals can take 1 h or more to complete a turn, and within this period there is much individual variation in heading (Whitehead 2016). The precise mechanics of female group decisions remain poorly understood, and we do not know the extent to which an individual plays a leading role, perhaps a matriarch, with a long life span of experience to draw upon (as in killer whales; Brent et al. 2015). Female sperm whales can be slow and seemingly disorganized when deciding where to go; but the same is not true about deciding with whom they travel.

## 12.4 The Social Sperm Whale

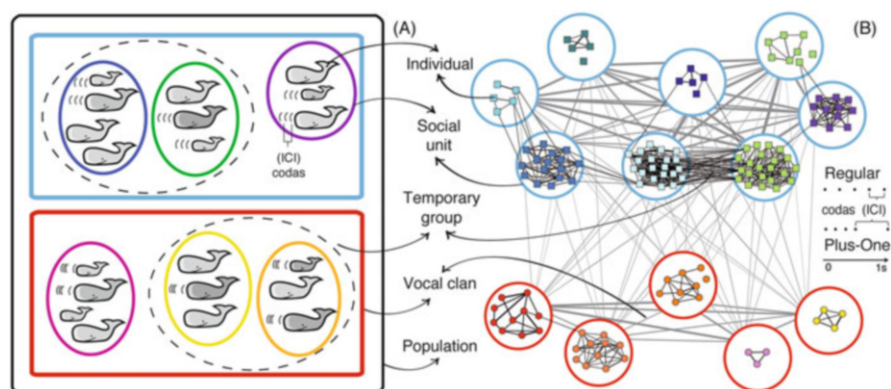
The social behavior of sperm whales follows their sexual divergences in lifestyles. Adult males are generally solitary. In their teens, males depart from their natal groups to move poleward. After leaving their female relatives, they live quasi-solitary lives in polar or near-polar waters where they feed, grow, and mature, only returning to the tropical and subtropical breeding grounds in their late 20s to search for receptive females (Best 1979). In warmer waters, the now large males roam around, apparently avoiding one another while visiting groupings of females for periods of minutes to hours (Fig. 12.1b). But males can engage in social gatherings among themselves. In low latitudes, younger and smaller males may form loose aggregations—bachelor groups (Best 1979); in high latitudes, they occasionally cluster (Curé et al. 2013). The drivers of male clustering are not understood—perhaps protection against larger predators or feeding/mating competitors, perhaps simply a relict sociality from their nursery years.

Females are deeply social beings, always in the company of others. Together with calves and juveniles, they spend most of their lives in stable, nearly matrilineal familial units (Fig. 12.1d). Such social units range in membership from 3 to over 20 close relatives as well as unrelated individuals (Lyrholm et al. 1999; Konrad et al. 2018). Social units make up the primary tier of female sperm whale societies (Fig. 12.3), within which individuals move and feed together and share knowledge. However, there are social preferences, partially driven by kinship such that strict matrilineal lines appear to structure relationships among unit members (Gero et al. 2013; Konrad et al. 2018). Females cooperatively raise and defend their calves; they may also find food together by eavesdropping on each other or sharing information about food patches (Whitehead 2003). The absence of territoriality and within-unit mating suggests reduced competition among unit members (Christal and Whitehead 2001). More strikingly, within the social units (and in rare cases between), females can suckle each other's calves (Gero et al. 2009; Fig. 12.1e).

While sperm whale calves may be physiologically capable of following their mothers during long deep dives (Tønnesen et al. 2018), calves usually remain near the surface, following other adults of the social unit when the adults emerge to breathe (Whitehead 2003). A sperm whale calf represents a significant energy investment in terms of gestation, lactation, and long periods of care. Maturation is slow. Females mature sexually at about 9 years old and reproduce until their 40s, while males attain sexual maturity later (the prolonged puberty can last until their 20s) and grow for longer (into their 30s to reach full physical maturity near their 50s). Throughout their lives, females give birth to a single calf at a time, following a gestation of 14–16 months, at about 5-year intervals (Best 1979). Thus, each calf matters, and the structure of female sperm whale society revolves around them (Gero et al. 2013).

Female social units often associate temporarily with other such units, to form groups—the reasons behind this behavior are poorly understood, but may relate to increased protection from predators. Where studied well, such as off Dominica in the





**Fig. 12.3** Social patterns and culture in sperm whales, *Physeter macrocephalus*. **(a)** Schematic of sperm whale multilevel social structure. Females and young live in nearly permanent social units of tens of members (colored ellipses) for many years. Social units form temporary groups (dashed ellipses) that last from a few hours to a few days; these groups are preferentially formed among social units that share coda repertoires, forming vocal clans (colored rectangles) within the same population (black rectangle). **(b)** Empirical data from sperm whales in the Eastern Pacific. In the social network, modules of individual females (small colored nodes) are connected by social relationships (black links whose thicknesses are proportional to the time that individuals were seen together) and define social units (open colored circles). Note that in some occasions members of different social units occur together, representing temporary groups. In the overlaid acoustic network, modules of social units connected by acoustic behavioral similarity (gray links whose thicknesses are proportional to the similarity of their coda repertoires) represent vocal clans. Black dots represent clicks, and spaces represent inter-click intervals (ICI), illustrating the rhythm of typical codas of each clan. Figure adapted from Cantor et al. 2015

Caribbean, there is evidence for “bond groups,” pairs of units that show social preferences for each other enduring across decades, possibly for life (Gero et al. 2015). Wherever studied, these temporary groups are composed of social units that share similar vocal repertoires (Fig. 12.3), which we return to later. Thus, we currently understand sperm whale social structure as complex and hierarchical.

Social structure is also apparently flexible, varying considerably from place to place. For example, estimates of both group and social unit sizes (excluding calves) are larger in the Pacific (groups, 25–50; units, around 12) than in the Atlantic (groups, 5–18; units, 5–6). Calves are more abundant per group in the Atlantic than in the Pacific, and this could lead to, or perhaps result from, differences of intensity and strategies of within-unit maternal and allomaternal care (Whitehead et al. 2012). The matrilineal structure of the social units tends to be less marked in the Pacific than in the Atlantic (Whitehead et al. 2012; Konrad et al. 2018). In the Pacific, groups with different vocal dialects are sympatric (Rendell and Whitehead 2003), which appears to be the case in the Atlantic as well (Gero et al. 2016b). The causes of such large-scale variation in social structure are, again, poorly understood. It is possible that elevated predation pressure by killer whales in the Pacific has selected larger group sizes (Whitehead et al. 2012).

Variations in sperm whale social structure give insight into the ecological and evolutionary forces, namely, predation pressure and the need to forage while caring for vulnerable calves that promote complex social structure. Such highly organized societies are expected to use more diverse communication signals, stemming from the need to identify themselves as individuals and as members of higher level social groups (Freeberg et al. 2012). In the next section, we explore how, among sperm whales as in humans, social complexity is mediated by communication.

## 12.5 Communication

The classical behavioral ecology account of the evolution of communication starts with *cues*, by-products of some activity that nonetheless provide reliable information for others to use. In sperm whales, the obvious example would be the production of echolocation buzzes indicating to a listener that the producer has encountered prey. If the use of that information by others then has selective consequences for the cue producer, the behavior can evolve into a *signal*, selected because its production changes the behavior of receivers. The sperm whale click generator evolved to form a crucial element of sperm whale sensory biology, but its inadvertent role as a producer of cues has led to it being pressed into service as a producer of communication signals.

While sperm whales could plausibly communicate using a range of modes—chemical, visual, and so forth—in the marine habitat, the acoustic modality has several advantages. Sound can propagate over hundreds of kilometers in the right conditions. By comparison, chemical communication is slow and short range, and we do not have evidence of its use among sperm whales. While visual communication is also limited underwater, sperm whales often come within visual range of each other. Such proximity associates with intense social behavior, so it is possible that body posture and movements such as jaw opening could have communicative function. Sperm whales also display aerial behaviors such as breaching and lobtailing (striking the water with the tail flukes) that result in visual and acoustic cues that appear to play a role in communication (Waters and Whitehead 1990).

Nonetheless, it is vocal communication that has been best studied and that we focus on here. Despite tens of thousands of vocalizations having been analyzed, there has been no experimental demonstration of responses in other sperm whales, through the types of playback studies that are the gold standard for research into animal communication (e.g., King and Janik 2013). Thus, while our level of knowledge about the nature and function of such interactions is below that of other species on which experiments have been performed, we still have good evidence that sperm whales pay attention to each others' vocal production.

The nasal click generator produces a diverse range of acoustic signals, including “slow clicks,” “squeals,” and “codas.” Slow clicks (Fig. 12.2e) are intense slow-repetition clicks associated with mature males. They are more than just slow echolocation clicks, showing reverberations that give them a “ringing” quality,

hence the alternative term “clang.” First recorded when mature males were consorting with female groups on breeding grounds (Whitehead 2003), hypotheses about their function have revolved around mating competition. The spermaceti organs of mature males comprise up to one third of their body length compared to around one quarter in females and thus represent an exponentially greater physiological investment. Arguments have been made that this morphological and behavioral sexual dimorphism results from sexual selection “on a grand scale” (Cranford 1999). But slow clicks are also produced by males at high latitudes, where females are rare (Jaquet et al. 2001; Oliveira et al. 2013). In these contexts, slow clicks do not overlap with foraging; they tend to be produced at or near the surface (Jaquet et al. 2001, Oliveira et al. 2013), features that suggest communicative function. Thus, perhaps male-male competition cannot completely explain slow click production, and it may be that while the sexual selection hypothesis is broadly correct, the signals have also been co-opted for communication at high latitudes. By contrast, “squeals” are short bursts of clicks produced at such high repetition rates that they take on a low tonal mewling quality (Fig. 12.2f). Their production is relatively rare and strongly associated with social behavior or high arousal behavioral states (Weir et al. 2007). If squeals are a signal, they must function in particularly close range interactions. While rare, squeals could turn out to be a significant part of sperm whale communication repertoire. Squeals and slow clicks are not, however, the entire story for sperm whale acoustic communication.

Codas are stereotyped patterns of clicks that can be grouped into recognizable “types.” (Coda types are distinguished based on the temporal patterning of the clicks they contain; e.g., five regularly spaced clicks are termed a “five-regular,” or 5R, type; the 4 + 1 type contains four regularly spaced clicks followed by a longer pause before the final click, while a “1 + 1 + 3” coda contains longer gaps between the first two clicks followed by three clicks in quick succession.) Codas were first reported in the scientific literature by Watkins and Schevill (1977), who noted stereotyped patterns of clicks produced at the end of dives—thereby forming “codas” to the dive in the musical sense of the term.

Codas are also produced at the beginning, not just the end, of dives (e.g., Schulz et al. 2011) and most prolifically during periods of social behavior at the surface (Whitehead and Weilgart 1991; Fig. 12.2d). In tropical waters, codas are produced almost exclusively by animals in the size range consistent with mature females and immature males, rather than mature males (Marcoux et al. 2006), although males can produce them at high latitudes (Curé et al. 2013). The clicks that make up codas are also markedly different to those typically used in echolocation, as they are less powerful and more omnidirectional than echolocation clicks (Madsen et al. 2002); this is expected of a signal selected for communication as opposed to echolocation. These changes could result from inflation of air sacs within the spermaceti complex (Madsen et al. 2002). This, along with clear separation in time and space between foraging and coda production (Watwood et al. 2006)—and the prolific production during periods of close-quarter surface interactions (Weilgart and Whitehead 1993)—is why codas are generally considered to be a principal form of acoustic communication in sperm whales.

More insight into individual coda production came when acoustic size measurement methods linked the production of coda types to specific individuals (Schulz et al. 2011). The whales in one Caribbean social unit share production of the single coda type that dominates their unit's repertoire, the 1 + 1 + 3 type. Most units in this population share the 1 + 1 + 3 type, and neither individuals nor units can be identified by the way they produce this coda type (Gero et al. 2016b). Thus, the coda repertoire of a sperm whale social unit is a shared group-level signal, with sharing extending beyond the immediate social unit. This supports the notion that they are learned signals, given the presence of both closely related and unrelated individuals in these units, with learning of the 1 + 1 + 3 type influenced by individuals other than the mother (Gero et al. 2008).

There is another layer of complexity in one coda type, the 5R. This type is common around the world—it is the second most common type heard in the Eastern Caribbean (Gero et al. 2016b) and widely used in the Pacific (Weilgart and Whitehead 1993; Amano et al. 2014) and the Azores (Oliveira et al. 2016). Furthermore, it appears to be produced at the start of sequences of codas more often than expected by chance (Weilgart and Whitehead 1993). In multiple social units in the Eastern Caribbean (Gero et al. 2016b), and in different groups encountered around the Azores (Oliveira et al. 2016), whales produce this 5R coda in individually distinctive ways—with subtle variations in rhythm and tempo.

Studies of how coda vocalization varies between oceans, regions, social units, and individuals have given us new windows into sperm whale social structure at spatial scales that are difficult to observe otherwise. “Vocal clans” of sperm whales are collections of social units that share a part of the repertoire that forms a large proportion of their coda production and is readily distinguishable from the repertoires of units from other clans (Rendell and Whitehead 2003; Fig. 12.3b). The sharing of coda repertoires—belonging to a vocal clan—appears to be a significant structuring factor in sperm whale society worldwide. Coda repertoires may therefore serve as vocal markers of clan membership (Rendell and Whitehead 2003). Two of the largest clans in the Eastern Tropical Pacific were those characterized by the production of “+1” codas (all with a longer final interval at the end), and hence termed the “*Plus-One*” clan, and the production of codas in which clicks are regularly spaced, hence termed the “*Regular*” clan (Rendell and Whitehead 2003; Cantor et al. 2016). In the Eastern Caribbean, a single coda type is sufficient to discriminate between the two sympatric clans—the *EC1* clan produces primarily 1 + 1 + 3 codas, while the *EC2* does not and produces predominantly 5R3 codas instead (Gero et al. 2016a). Similarly, a single coda type, the 3 + 1, dominates the coda repertoire in the Mediterranean sperm whale population (Pavan et al. 2000). Most significantly, when social units form temporary associations with other units in the Pacific, they do so with units of the same vocal clan, even though the clans are sympatric (Rendell and Whitehead 2003). This pattern is reflected in the Atlantic Ocean, where sympatric clans have been confirmed in the Eastern Caribbean (Gero et al. 2016a). But, there is variation—contrasting evidence from the North Pacific suggests that clans off Japan are more consistent with geographic rather than sympatric dialect variation (Amano et al. 2014).

Clans are not static. There were dramatic changes in population composition off the Galápagos Islands from the 1980s to the 2010s, with extensive turnover of individuals. By the end of the twentieth century, sperm whales had all but disappeared from these waters, for reasons that are not understood. After a period of absence, they came back in the early 2010s—but these were not the same sperm whales. The incomers had the vocal dialects of two other clans—one that had previously only been heard once before around the Galápagos and another that was previously known only from Chilean waters—suggesting a large-scale displacement of clans (Cantor et al. 2016). By contrast, the same coda dialect has been recorded in the Eastern Caribbean over the past 30 years, indicating that at least one of the clans present in those waters has remained in that area for the same 30-year period (Gero et al. 2016a, b). By the nature of nomadic behavior of sperm whales, clan structure can be spatially flexible; but its dialect and membership remain stable over time. While individuals, and units, may roam widely; social identity does not change.

Sperm whale codas are rich in information about the producer's identity. We understand some diversity and patterns of variation in coda production but do not understand the communication function of codas. The most direct evidence of communication may come from a study of coda exchanges, matching, and overlapping in two social units—one from the Pacific and one from the Caribbean (Schulz et al. 2008). These exchanges form duet-like sequences, in which whales synchronize timing of coda production (Schulz et al. 2008). In some birds, such overlapping is thought to be an aggressive signal (e.g., Dabelsteen et al. 1997). This does not seem to be the case here, because there were no other signs of aggressive interactions, and overlapping occurred between individuals from the same social unit that we would expect to also engage in cooperative caring of calves. Instead, these vocal exchanges could function to affirm the shared unit and/or clan membership of the whales involved (Schulz et al. 2008), in a similar manner as affiliative signals in birds (Kelley et al. 2008). Rapidly and synchronously matching a shared coda type effectively signals a shared repertoire and hence probable social affiliation (Schulz et al. 2008). There is a potential parallel between the sense of connection and belonging provoked by shared rhythmic behavior in humans (drumming, clapping, dancing) and the notion that shared rhythmic codas in sperm whales may communicate the message “we belong.”

## 12.6 Social Learning

Rendell and Whitehead (2003) suggested that variations of sharing codas represented learned and culturally transmitted group-level vocal signatures. However, evidence for vocal learning is difficult to test in sperm whales. There are weak relationships between maternal lineage (as indicated by mitochondrial DNA that is passed down the maternal line) and coda repertoires (Whitehead et al. 1998), but these are not strong enough to explain vocal variation as a product of genetic differences. Furthermore, this correlation disappears when genetic sequence

divergence is measured (Rendell et al. 2012). Therefore, the most likely explanation for coda dialect variation between groups is that coda repertoires are learned by young sperm whales, generally from their mother, who is also the source of their mitochondrial DNA. However, off Dominica, fine-scale similarity of coda repertoire is not correlated within kinship within or between social units, suggesting that if a mother's codas are the prime dialect model for the young sperm whale, then her influence is diluted by unit- or clan-level conformity (Konrad et al. 2018).

More direct evidence in favor of learning comes from the acoustic repertoire of calves, which often produces a greater diversity of, and low consistency within, coda types (Schulz et al. 2008; Gero et al. 2016a, b). This is perhaps indicative of "babbling" as in humans and other species (Gero et al. 2016a). Among the community off Dominica, calves take at least 2 years to learn to produce the stereotyped patterns of the coda types in their natal dialect (Gero et al. 2016a). Therefore, over many generations, repeated learning could have introduced small copying errors that accumulated down lineages, giving rise to the patterns of dialect diversity of today.

If divisions appear so critical to sperm whale society, how did they come to be? It is impossible to investigate historical processes empirically, but recent modeling work used populations of virtual whales with characteristics informed by known parameters of sperm whale life history. The models showed that clans with different dialects, resembling real-world ones, emerged when virtual whales learned from each other in a specific manner, conforming to the most similar individuals around them (Cantor et al. 2015). Similar processes explain vocal dialect diversity in birds and humans, and such repeated episodes of social learning (from others as opposed to individual trial and error) can give rise to a second cultural inheritance system based on information held in brains rather than genes (Whiten 2017). So, we argue, it is appropriate to describe sperm whale vocal dialects as cultural traditions.

Vocal dialects do not appear to be the only traditions in sperm whale societies, and vocal learning is not the only form of sperm whale social learning. The best evidence for nonvocal learning comes not from female groups, but from the rise of a new tradition among males foraging at high latitudes. This is the taking of fish from longlines set by fishers in the waters off south Alaska that began in the late 1990s in one place (West Yakutat). This behavior subsequently spread east and west along almost the entire south Alaska seaboard by 2010, in a pattern that fits to "wave-of-advance" models originally formulated for describing the dynamics of prehistoric human groups (Schakner et al. 2014).

While female-based clans have distinctive repertoires of coda vocalizations, they also show variation in other behavioral patterns. Groups of the most well-known clans of the Pacific—*Regular* and *Plus-One*—consistently vary in movement patterns and use of habitat and also forage and socialize differently (Whitehead and Rendell 2004; Marcoux et al. 2007a; Cantor and Whitehead 2015). Likewise, social behavior varies between clans: individuals of the *Regular* clan dive more synchronously and show briefer associations that are more evenly distributed across individuals than the members of the *Plus-One* clan (Cantor and Whitehead 2015). Thus, clan membership has implications for more than vocal dialect; clans are repositories of multiple traditions, incorporating ways of communicating, knowledge about



habitats and their features, and knowledge about how to manage social relationships. Multiple traditions make a culture. It therefore seems reasonable to describe clans as cultural groups. Those populations where multiple clans occur in sympatry may be termed a multicultural society.

Cultural variation can have implications for the fitness of clan members (Marcoux et al. 2007b). Since social units are driven by care of young (Gero et al. 2013), differences in social relationship quality and duration among social unit members—and surface time between foraging dives—could affect the quality of allomaternal care, and this could lead to differences in calf survival between clans (Cantor and Whitehead 2015). Likewise, differences in diet, movements, and foraging styles result in some clans having higher feeding success than others but also in being affected differently by ecological shifts, such as El Niño-Southern Oscillation events (Whitehead and Rendell 2004). Thus, cultural variations between clans could represent alternative strategies for dealing with the challenges of survival in a changing ocean.

The behavioral diversity embedded in sperm whale clans highlights an important point. If conservation has as its focus the preservation of diversity, a substantial amount of the behavioral diversity of sperm whales, and the knowledge that underpins it, might be held among the culturally defined clans, as opposed to genetic populations or arbitrary management stocks. The maintenance of such diversity could be important in the long-term resilience of sperm whale populations. These cultural traditions, honed by the environment in which they were innovated and passed on across generations of mothers, may be a significant reason why sperm whale societies survive. Thus, our long-term conservation plans should take sperm whale cultural factors into account (Whitehead 2010; Brakes et al. 2019).

We return to the notion of belonging. Belonging to a clan is crucial for a sperm whale—whether in a region inhabited by just one, or in one of the multicultural zones, belonging defines much of how sperm whales live their lives. Clans may contain tens of thousands of individuals, thus featuring among the largest mammalian cultural groups outside humans (Whitehead and Rendell 2014). The question remains unanswered of why some populations contain multiple sympatric clans and some do not. When we eventually answer this question, we may understand something quite profound about the societal essence of being a sperm whale.

## 12.7 Outstanding Questions

Some behavior of sperm whales fits predictions from behavioral ecology. That they stay when feeding is good and move when it is poor (Whitehead 2003) is classical optimal foraging. The fission of particularly large social units of females (Christal et al. 1998) and the fusion of small ones (Konrad et al. 2018) similarly fit theories of optimal group size. Male dispersal is the norm among mammals, and male sperm whales disperse. However, other elements of sperm whale life do not fit so neatly with the expectations of a behavioral ecologist. Why do males head for the far ends

of the Earth, thousands of kilometers from the nearest female? And why are they so big? Extreme male-biased sexual dimorphism in mammals is presumed to be the result of important intermale competition for, or defense of, resources or females or young. But it is hard to envisage serious competition for, or defense of, resources by male sperm whales. There is no evidence of them defending females or young, and physical competition seems rare. So why are male sperm whales so massive? Could it be female choice?

For females, cooperative, long-term groupings seem to make sense in the difficult and dangerous world of animals always on the move in the pelagic zone. Females of many other mammalian species form cooperative groups, helping each other survive and reproduce (Clutton-Brock 2016; Lukas and Clutton-Brock 2018). The nature of cooperative groups of female mammals can be arranged on a continuum indexed by female relatedness within groups, and the position along this continuum predicts many social attributes (Lukas and Clutton-Brock 2018). With little relatedness among group members, females tend to be arranged in a dominance hierarchy, mediated by aggression. Conversely, when most group members are close kin, there tends to be division of labor, reproductive suppression, infanticide by females, and considerable alloparental care. Sperm whales, with a mean within-social-unit relatedness of about 0.14 (Konrad et al. 2018), are at the lower end of the continuum and, as with other mammals at this general level of within-group kinship, do not seem to have female infanticide, reproductive suppression, or division of labor. But they may be unusual in their apparent lack of female-female aggression and in the importance of alloparental care. Why?

The study of sperm whale behavior is undergoing a technological revolution, affording us data-rich perspectives on what they do over short timescales. Drones document social behavior at the surface, as well as measuring size, health, and collecting biological samples; tags detail each movement and each sound underwater (Fig. 12.1f); acoustic arrays (including those on animal-borne tags) capture their world of sound (Fig. 12.1g) and infer deepwater foraging behavior, communication interchanges, and maybe even prey fields; high-resolution molecular genetics allow detailed measures of kinship and pedigree; and artificial intelligence processes such as machine learning and computer vision are enabling computers to recognize individual whales from photographs or clans from acoustic recordings. These new methods allow us to address the problems of vast geographic scales and to penetrate the depths of the oceans to discern what sperm whales do below the surface, where direct observation is not currently possible, but where they spend most of their time. Methods are improving in reliability, output, ease of use, and reduced cost.

Despite new technologies, however, long-term observational studies (Fig. 12.1h) continue to provide crucial insights. Much of what we know about the lives of sperm whales come from data painstakingly collected in often very simple ways of observing, sound recording with simple hydrophones, and photographing, data amassed over years of expeditions (e.g., Whitehead 2003; Gero et al. 2016a, b; Cantor et al. 2016). These efforts plus the new ones are essential for interpreting increasingly detailed and powerful analytical methods of processing new data, with computer tools for realistically simulating the behavior of the whales.

## 12.8 Closing Remarks

Today we can appreciate that sperm whales, with their familial ties, learned traditions, and social organization, draw some parallels with our own societal and cultural lives. Today's researchers still face unanswered questions about the behavior of sperm whales. Today's oceans are different from those in which sperm whale foraging strategies, roaming habits, social structures, and cultures arose. Today's sperm whales, the relics of two massive hunts in the past two centuries (Whitehead 2002), are faced with increasing human presence, are confronted with entanglement in fishing gear, are run down or harassed by shipping fleets, encounter plastics masquerading as prey, and are subject to the changes brought about by a warming, acidified ocean.

Tomorrow's ecology will be different, but tomorrow's sperm whales will still be the largest toothed creature on Earth. How much will their ways of life change because of our behavior? Tomorrow's researcher will not only be charged with figuring out what it means to be a sperm whale but also, and perhaps more importantly, what it is like to live as our neighbors on this shared planet. Armed with knowledge born of necessity, tomorrow's researchers will need to find collaborative solutions to enable sperm whale survival so that this generation's whales can pass on their cultural inheritance to their calves in a healthy ocean.

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