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Whalewatcher Sperm Whale

Whale of Extremes

Photo: Flip Nicklin/Minden Pictures

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Dear ACS member,

It is a tremendous honor to share this issue of *Whalewatcher*, devoted exclusively to sperm whales, with you. Sperm whales - the mythological leviathan of Biblical lore and fabled subject of the epic struggle between man and beast in Herman Melville's *Moby Dick*. Of all the cetaceans, this fascinating denizen of the deep looms large in our collective imagination.

Today, sperm whales are protected, and we now see them as beautiful giants – the most complex mind in the waters. But not so long ago, the view was very different; they were fierce monsters to be exploited for profit. Though the "monstrously ferocious" exploits of sperm whales were greatly exaggerated for the effect of literary value or hunting

braggadocio in whaling literature, in reality they are a far cry from the vengeful leviathan that stalked Captain Ahab and his crew.

We now know that sperm whales, along with at least two other species of "great whales," have spindle neurons – specialized brain cells credited with the ability to interact socially and form long-lasting bonds, experience love, and suffer emotionally. Once thought to be unique to humans, elephants, and great apes, the discovery of spindle neurons in whales should stimulate a vigorous debate about the breadth of whale cognition and the ethics of hunting and confining them.

These gentle behemoths communicate through extensive song repertoires, recognize the songs of individual whales within their pod, improvise new songs, and transmit pod-specific dialects to their progeny. Similar to higher primates and humans, they have evolved closely-knit, complex social and family units, form alliances to develop sophisticated foraging strategies, and teach these strategies to their young. In short, sperm whales excel at the cognitive trait to which our own species attributes "intellect" – language.

This brings us to an interesting question - what makes us human? Humans possess the capacity for not only language, but also empathy, feeling and expressing emotion, and forming long-lasting family and social bonds. If these traits are the markers by which we gauge intellect and 'personhood,' how are we now to engage the largest 'mind in the water' through meaningful, thoughtful (or at least, non-destructive) human-whale interactions? I posit that it is no longer sufficient to study sperm whales through abstract reasoning as a sole means of inquiry. We may never know what they know; but we certainly feel what they feel.

On behalf of the staff and National Board of Directors of the American Cetacean Society, I would like to extend my sincere gratitude and appreciation to Dr. Hal Whitehead, whose candid enthusiasm for his work has earned him the fervid admiration of colleagues and enthusiasts worldwide. Be inspired!

Very McCarmuch

Executive Director American Cetacean Society

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Sperm Whales in the Mediterranean:

The Difficult Art of Coexisting With Humans in a Crowded Sea

by Giuseppe Notarbartolo di Sciara, Alexandros Frantzis, Luke Rendell

In this article we tell the story of a population of sperm whales that happens to have elected the Mediterranean, a semi-enclosed sea, as their residence. Many find it surprising that sperm whales, so typically oceanic, are capable of making a living in a relatively small marine basin such as the Mediterranean, locked within the landmasses of three continents, and affected by human activities of many types. In fact, in spite of its small size compared to the oceans, the Mediterranean Sea offers abundant habitat suitable to sperm whales'



A leisure boat observed harassing a sperm whale in the Mediterranean - an increasing threat. Photo courtesy Alexandre Gannier / Groupe de recherche sur les cétacés.

needs – in particular the steep continental slopes that plunge to depths sometimes exceeding 5000 meters where the whales can find the squid on which they subsist. Human presence, as we shall see, causes considerable problems to sperm whales in the Mediterranean, however it hasn't managed to extirpate the whales from the region. Not yet, at least.

In geological terms, the history of sperm whales' presence in the Mediterranean is relatively recent; the Mediterranean itself, as it appears today, is a recent sea. Between six and five million years ago the landmasses of Africa and Europe, in their converging motion, had squeezed the ancient Tethys Sea to the point of severing completely its connections with the world's oceans, thereby causing most of the water to evaporate and transforming the region in a desert interspersed by series of shallow, hypersaline lagoons. This upheaval, known as the Messinian Salinity Crisis, obliterated most of the Tethys' ancient marine life forms. Subsequent tectonic readjustments eventually recreated an opening between Europe and Africa, in the site known today as Gibraltar, and sea water roared back in from the Atlantic Ocean in an event known as the "Zanclean Deluge." Thus was the modern Mediterranean Sea formed, thereby creating the conditions for the today's cetacean fauna – sperm whales included – to colonize the new marine region, and call the Mediterranean home.

Knowledge About Sperm Whales in the Mediterranean Dates Back More Than Two Millennia

The earliest knowledge of Mediterranean sperm whales coincides with the oldest written knowledge for all cetaceans worldwide. Aristotle, who lived and worked on a Mediterranean shore, provided the first reference to cetaceans, with amazing descriptions of the morphology and natural history of dolphins, porpoises and, of course, the sperm whale. In his work *Historia Animalium*, written 2360 years ago, Aristotle stated, "...the dolphin has its blowhole dorsally, but that of the whale is found at the front." By "whale" he clearly means sperm whale, which is different from baleen whales, since "...the mysticete has no

teeth in its mouth, but hard hair." Although Aristotle made no reference of the exact location of the observations that he reported, his knowledge was likely to originate mainly from the north Aegean Sea. He was born in Stageira, on the Chalkidiki Peninsula, where sperm whales can still be found today.

Not much scientific progress was made on sperm whale knowledge in the Mediterranean between Aristotle's times and the mid-20th century, except for studies performed by anatomists and zoologists on stranded animals. The observations by Arturo Bolognari of the University of Messina in Italy, are a notable exception. He recorded frequent sightings of large sperm whale herds off the coast of north-eastern Sicily, and published his observations in a series of papers that appeared between 1949 and 1957. In Bolognari's times, sightings of social units up to 30 individuals were not unusual, something unheard of today. Sadly, Bolognari also reported on the frequent killings of sperm whales by fishermen, as they stranded alive or were seen near the coast. It is not clear why the animals were killed; the carcasses were often left decomposing on the beach. Sperm whales were injured and killed with a variety of means: tied and dragged ashore, shot, and injured by explosives. Calves, rather than inspiring compassion, were often the first to be slaughtered. Bolognari's observations of useless massacres prompted him to question the contemporary Melvillian idea that sperm whales were ferocious sea monsters. Noting that sperm whales are "a highly significant artwork of Nature," capable of altruistic behaviors, Bolognari was among the first to formulate a compelling wish that these animals - notwithstanding the ruthless persecution he witnessed - may avoid extinction and rightfully keep thriving undisturbed throughout the world's oceans.

What is Special about Mediterranean Sperm Whales?

There seems to be something different about the Mediterranean sperm whale compared to their brothers and sisters in the large open oceans, but scientists are still trying to put their finger on just what that is. While a natural intuition might be that a population of large whales inhabiting a small enclosed ocean that has been navigated by humans since pre-history should be well known to us by now, the truth is that the sum of our scientific knowledge about these animals could fairly be described as no more than a rough sketch. Almost all our knowledge is driven by self-supported small groups of dedicated researchers whose field data is squeezed from very limited resources, and hence typically concentrated in a locally accessible area. It is amazing and rather depressing that our state of knowledge is such - given all the vessels that use the Mediterranean, the massive impacts humans have had upon this small sea, and populations and resources that crowd its coastlines - that most people are still surprised to learn that sperm whales even exist there. When Luke started his field project in the Balearics for example, the taxi driver that took him from the airport to the harbor, a third generation Mallorcan, confidently asserted that he was wasting his time – there were no sperm whales in the Mediterranean. Perhaps the dedication of these disparate groups of researchers is driven by the fear that unless we are very careful, the taxi driver will in the future be right. There has never been a systematic survey of the entire Mediterranean for sperm whales. We are still grasping for answers to such basic questions as how many sperm whales there are in the region, and whether or not the population is completely isolated from that in the neighboring Atlantic.

Let's start with the isolation question – are sperm whales in the Mediterranean simply a subset of the Atlantic population, taking their holidays basking in the warm waters of Crete and the Balearics, or a "lost tribe," cut off from global sperm whale populations by the narrow straits of Gibraltar? This is a crucial question, because the answer frames the way we should think about managing the way humans are impacting the Mediterranean sperm whale. The short answer is that the evidence at hand points more strongly toward the "lost tribe" than the holiday destination scenario. At the time of the Messinian Salinity Crisis the sperm whale lineage had already clearly separated from other cetacean lines. As mentioned earlier, somewhere in this murky history some sperm whales must have made it into the Mediterranean from the Atlantic at a time when there was a sufficient prey community available for them to prosper, and these whales and their descendants went on to colonize the newly minted sea. The strongest presentday clue to this history is found in the DNA signatures of the sperm whales alive today. Mitochondrial DNA¹ has the convenient property of being passed intact down the maternal line. When scientists have looked at the mitochondrial DNA of sperm whales in the Mediterranean, every single animal sampled has the same mtDNA type, and it is one of several types identified in the Atlantic. These striking facts have two important implications. The first is that all the sperm whales in the Mediterranean originate from the same matriline, possibly even from the same female, a fabled "Mediterranean Eve" who first

¹ Often abbreviated to mtDNA, this is a unique section of DNA found not on the chromosomes in the nucleus of the cell, like most of our genome, but confined in the mitochondria, the chemical powerhouses that provide the basic oomph to drive life's processes. This DNA is passed on intact via the mitochondria in your mother's egg – your father contributes nothing, and there is no mixing up of mitochondrial genes when sperm and egg meet. Therefore your mitochondrial DNA can speak directly about your maternal lineage.

entered from the Atlantic. The second then follows – that the Mediterranean sperm whale population is possibly the result of a single colonization event, and that movements of individuals to and from the Atlantic is either extremely limited (the most probable), or restricted to only members of a single matriline. Hence the support for the "lost tribe" scenario. Further support for this scenario is provided by analysis of DNA from the chromosomes, where Dan Engelhaupt and colleagues have shown that the Mediterranean population is significantly differentiated from all others in the north Atlantic. It follows that the Mediterranean sperm whale has an independent fate from its Atlantic neighbors – we cannot rely on the Atlantic as a source population to furnish ready migrants to replace any losses, so we must take great care in how we treat this population if it is to persist.

Nor can we be entirely confident that the Mediterranean contains a single coherent population – the main basins in the east and west are separated by Italy, Sicily and the shallow waters between there and Africa. Recently some of us and our colleagues have shown that at least some whales from the western basin made it across these barriers.

The evidence comes from a rare, for the Mediterranean, mass stranding of sperm whales that took place on December 10, 2009 on the southern Adriatic coast of Italy. It involved seven sperm whales that stranded alive and died during the following two days. The whales were all male, 10.5 to 12.2m long, and their estimated age was between 15 and 25 years. Complete necropsies were performed on three whales whose bodies were still in good condition at the time of detection. While no evident cause of death could be detected, the concentration of pollutants in the tissues of the animals – in particular organochlorinated compounds - was very high. The stomachs of the animals were empty, and tissue examination showed that the animals had undergone a prolonged starvation, which likely caused, in turn, the mobilization of lipophilic contaminants from the adipose tissue, thereby perhaps affecting immune and nervous functions. In order to learn more about the past of the stranded sperm whales, photos of their flukes and of their characteristic pigmentation patterns were compared with photos of free-ranging sperm whales photographed from all over the Mediterranean. A large collaboration including Italian, French, Spanish, Greek, British and other scientific teams was established. One individual was familiar to Alexandros from the surveys along the Hellenic Trench in Greece. This was a male that had been christened "Zak Whitehead" because of extensive white pigmentation on its head. "Zak Whitehead" had been first photo-identified in 2000 as a six-year old member of a social unit of sperm whales inhabiting the Hellenic Trench in Greece, likely his natal social unit. "Zak Whitehead" was observed seven more times in 2002 and 2005, always among the other members of his social unit (named "Zak"). Eventually, he ended up stranded with the other whales in the SW Adriatic Sea in 2009. He measured 10.5m and his teeth revealed that he was a teenager 15 years old. To reach the stranding location in the Adriatic Sea, "Zak Whitehead" traveled



A young male sperm whale named "Zak Whitehead" was repeatedly observed free ranging within its social unit along the Hellenic Trench from 2000 to 2005 (A). He was recognized by the pigmentation of its upper and lower jaw within a male sperm whale group that mass stranded in 2009 in the Adriatic Sea (B).

at least 630 km (in a straight line). To join the other male sperm whales that stranded in the Adriatic Sea, he apparently left his social unit (which is still observed along the Hellenic Trench) sometime between September 2005 and November 2009 at an age of 11-15. "Zak Whitehead" was not, however, the only old acquaintance among the stranded whales. Two more individuals, "Cla" and "Pomo," had been previously observed and photo-identified by Sabina Airoldi in the western Mediterranean. "Cla" was first photo-identified in 2002 in the NW Ligurian Sea off the Italian coasts, where he was also observed five more times in 2003, 2005 and 2007. He measured 12.1m and was 20-21 years old. The shortest straight line distance (while avoiding land) separating his two last observations made in different basins was 1800-2100 km depending on the four possible paths that the whale could have followed (west or east of Corsica and Sicily, respectively). The history of "Pomo" was very similar: first photo-identified in 2003 in the W Ligurian Sea in a male aggregation, he measured 12.2m and was 19-20 years old.

We suspected that movements of sperm whales from one deep Mediterranean basin to the other through the Strait of Messina or through the Strait of Sicily was happening, but now we have the proof. Although the numbers involved are low, and these events may be rare, they are very important in maintaining connections between the populations, raising the effective population size by maintaining a gene flow and mixing throughout its entire range. Without those links we would be dealing with two smaller and extremely vulnerable populations rather than a single vulnerable one. Keeping these east-west links open is likely to be crucial to the long-term viability of the population, and the potential impact by human activities in the Straits of Messina and Sicily, such as the construction of a bridge between Sicily and the Italian mainland, must be carefully considered.

The sperm whales of the Mediterranean are also distinctive in their behavior. In the open oceans, male sperm whales move during their maturation to high latitude waters, presumably to access abundant prey resources and attain the growth needed to be competitive in the breeding game. Males that remain in the Mediterranean don't have that option. Genetic and behavioral evidence suggests that most males do stay - for example, Alexandros has documented males in the Hellenic Trench with residency times of three to five years, indicating a degree of philopatry seen nowhere else. Another colleague, Alexandre Gannier, has suggested that Mediterranean males, at least in the Western basin, may show a kind of miniaturized version of the more common male movement pattern by preferentially heading to the north of the basin, and it does seem that social groups are less likely to be encountered in those regions. However, for all its attractions, the Cote d'Azur cannot offer the feeding riches of the polar regions, and it is rare to see a truly massive male, suggesting that they simply cannot attain the size of their open ocean counterparts.

Finally, there is something different happening in the vocal dialects of sperm whales in the Mediterranean. This was first noticed by Gianni Pavan, Fabrizio Borsani and colleagues who pointed out that the vast majority of codas they heard were of a single type - three regular clicks and then a longer pause before the fourth, a pattern termed '3+1'. This picture has since been broadly confirmed every study of sperm whale codas in the Mediterranean confirms the 3+1 as very, if not the most, common. It has however been importantly refined with the observation that other coda types are heard in different behavioral contexts, by the French researchers Violaine Drouot and Alexandre Gannier, as well as Luke and Alexandros. Nonetheless, the situation is very different from other oceans where coda diversity is much greater. Alexandros has also found evidence that coda types can be correlated with behavioral contexts such as alarm, which has not been reported anywhere else. Human cultural diversity around the Mediterranean is ancient and vastly diverse - in contrast, sperm whale culture appears to be restricted. This pattern mirrors that seen in bird populations on islands, where their culturally transmitted song is often much restricted in diversity, and these observations further strengthen the



A previously unknown resident sperm whale population unit was discovered in 1998 off SW Crete, Greece. It turned out that the entire Hellenic Trench is the most important habitat for sperm whales in the eastern Mediterranean. In 2007 it was proposed as a Marine Protected Area for this species. Photo by Pelagos Cetacean Research Institute/A. Frantzis.

picture of the Mediterranean sperm whale as an isolated, and hence very vulnerable, lost tribe.

So, to our best knowledge, the Mediterranean sperm whale population is small and isolated. The first preliminary abundance estimates indicate a total at the very low thousands if not just hundreds of individuals. The eastern Mediterranean sub-population seems to contain only a few hundred individuals. During 12 years of surveys, the Pelagos Cetacean Research Institute has photo-identified only 181 individuals (at least 17 of which are known to or considered to have died). All available evidence points to a total of 200-250 whales. This is a very small population. The size of the population in the western basin is even less well known, but is unlikely to be more than 2,000 and may be less than 1,000. Small populations do, however, mean frequent resightings and therefore a great opportunity to start entering into the private lives of the whales. Sometimes, there are amazing personal whale stories in these lives that come to the surface as we follow their social units year on year.

One of these stories concerns "Zakob" and "Zakobino." "Zakob" is a mature female whale, 9.5m long now, who was first observed in 2002 and has been encountered fourteen times since then. In 2002, she was member of the "Zak" social unit, one of the 16 social units that are known in the eastern Mediterranean and seem to be resident along the Hellenic Trench, in Greece. The "Zak" social unit had twelve members in 2002, but in 2003 it split into two subgroups of six whales; "Zakob" remained in the "Zak1" social unit at least until 2005. On June 25, 2007 we encountered a social unit of seven whales which was new to us, and we gave it the name "Kythira." However, later in the evening of that day, when we analyzed the photos taken, we were surprised to find out that this new social unit was composed of five whales previously unknown to us, plus a wellknown female - "Zakob!" Furthermore, "Zakob" had a young calf that we named "Zakobino." We considered this a nice surprise. Heading southeast along the Hellenic Trench eight days later, we again met the "Kythira" social unit, but now missing "Zakob" and "Zakobino." Where had they gone? A sperm whale mother with her calf were wandering somewhere alone? The mystery was solved the next day when we encountered a well-known social unit - "Palaio" - off southern Crete. The group contained fifteen individuals, a record for the population that we are studying. When the photo-identification analysis was completed, "Zakob" and "Zakobino" were found among them! They had recently changed social unit. The story however continues. A few days later we left Crete to start moving north-west, e.g. in the opposite direction. On August 19 we met another well-known and apparently very stable social unit - the "Pylos," containing ten individuals. However that day they had three visitors! A visiting sub-adult male ("Ermis") was among them just for the day, and guess who else ... "Zakob" and "Zakobino!" Exactly like we did, they had changed heading when they reached south Crete and moved north-east, but the amazing fact was that they had changed social unit once more! "Zakob," with her young and unprotected calf "Zakobino," had changed social units three times in just 25 days, and none of the units was her own original "Zak" social unit! Anyway, the story has a happy end. "Zakob" and "Zakobino" were both encountered several times in 2008, still with the "Pylos" social unit. It seems that they had been accepted in a new social unit at last. However, "Zakob" might be one of those individuals who keeps provoking social changes (we all know at least one!). In 2009 we met her once more together with her "Zakobino." She was still with other whales of the "Pylos" social unit, but now only with half of them. The stable "Pylos" social unit had split in two! Was "Zakob" the "agent provocateur" of this change?

The adventure of "Zakob" and "Zakobino" reminds us that the highly social animals that we meet out there in the ocean or in nature

in general are persons and personalities. They are not just whales, dolphins, elephants, wolves or gorillas. They have their characters, their relatives, their beloved ones, their own culture and their own objectives. They have their own personal lives! These kinds of insights lead some to question whether there is anything scientific or ethical that allows us to consider that their lives are less important than the life of each one of us. The small size of the Mediterranean sperm whale population, although of conservation concern, also allows us to understand not just its biology, but to build up (as in Shane Gero's work off Dominica; see his article) a history of a sperm whale society.

What is Threatening Sperm Whales in the Mediterranean?

Fishing: Driftnets, the so-called "walls of death," have been deadly to many large marine fauna in the Mediterranean for decades, and they have taken their toll on sperm whales. Giuseppe and colleagues have compiled records that show that at least 229 sperm whales were reported carrying evidence of entanglement with driftnets, or being found dead tangled in nets, between 1971 and 2003. In 2006, six sperm whales stranded in the Balearic Islands alone; of these, three were bearing nets or scars indicating contact with driftnets, with the others too decomposed to ascertain cause of death, although driftnets would be a highly likely cause. Bear in mind, these are only the ones that were reported – these numbers can be multiplied by some unknown factor to account for those whale carcasses that never made it to shore. Such mortality is devastating for a population of sperm whales that might only have a maximum potential growth rate of <1% per year, and it simply must be stopped if the Mediterranean sperm whale is to survive. Since 2002 driftnets have been outlawed by the European Union, and later by the International Commission for the Conservation of Atlantic Tuna (ICCAT), but the law and reality can come adrift as often as the nets themselves, and it is only in the last couple of years that even rich European nations like France have begun seriously enforcing the law. In southern Italy significant driftnet fishing still occurs illegally. Without continued and increasing enforcement, driftnets pose an existential threat to Mediterranean sperm whales. It is now a race against time to eradicate these nets before they eradicate the sperm whales.

Ship Strikes: Ship strikes of sperm whales in the Mediterranean Sea are frequent, and represent one of the main anthropogenic threats for the species, with unusually high fatal rates reported every year. The Mediterranean Sea is particularly susceptible to ship-associated impacts due to the high-density of shipping routes over sensitive deep sea ecosystems. Over the past half century, shipping has greatly expanded in the Mediterranean Sea. About 220,000 vessels greater than 100 tons cross the Mediterranean each year. This sea, although only 0.8% of the world's surface oceans, was estimated ten years ago to carry 30% of the world's total merchant shipping and 20% of its oil shipping. At any time, there are more than 2000 large cargo vessels cruising the Mediterranean Sea. Furthermore, a total of over 9,000 vessels, including ferries, fast ferries and hydrofoils, as well as military, fishing, pleasure and whale-watching boats, navigate the waters daily of the Western Basin alone.



A sperm whale with propeller marks on its body stranded in W Peloponnese (Hellenic Trench) after a collision with a large vessel. Ship strikes seriously threaten the endangered Mediterranean sperm whales. Photo by Pelagos Cetacean Research Institute/A. Frantzis

Propeller marks or cut flukes have been observed on several photo-identified sperm whales in both the western and eastern Mediterranean basins. The known number of sperm whale ship strikes in Greece depicts well the size of the problem. Of the 19 sperm whales examined out of the 23 stranded since 1997, at least 11 (58%) had collision marks on their bodies indicating a ship strike as the likely cause of death. As with driftnets, this figure does not include animals killed by ships whose carcasses never reached the coasts. Such a high death toll is likely to be unsustainable for a sub-population that may not contain more than 200-250 individuals.

The only management measure taken nowadays in the Mediterranean Sea is the recommendation for speed reduction in the Strait of Gibraltar. A Notice to Mariners was published on January 2007 by the "Instituto Hidrográfico de la Marina" in Spain. This Notice establishes a security area characterized by high densities of sperm whales, where crossing ships have to limit maximum speed to 13 knots, and to navigate with particular caution.



Following the recent findings on the high sperm whale mortality rates due to ship strikes in Greece, international efforts are now focusing on the reduction or elimination of ship strikes along the Hellenic Trench. This is the area with the highest sperm whale density in the eastern Mediterranean basin (see distribution map below). Luckily, sperm whale density in the area reaches a clear peak at a particular distance from the coasts, while it drops quickly when we move further offshore. While this density peak currently coincides with the most common routes selected by the large vessels navigating the area, it would be relatively easy to reduce the local ship strike problem by moving shipping lanes a few miles offshore. The scientific work of modeling sperm whale distribution and ship routes is already in progress. Upon its completion the conservation goal is to submit an official proposal for moving the shipping lanes to the International Maritime Organization (IMO). There is hope that if this conservation battle can be won, it will inspire similar modifications in other important habitats for sperm whales in the Mediterranean and elsewhere. The recent successes achieved by Spain in changing the shipping lanes in the Alborán Sea and in applying specific traffic regulations in the Straits of Gibraltar demonstrate that noise and ship strike reduction in critical areas is not impossible.

Marine Debris: Marine debris is defined as any manufactured or processed solid

Map of the distribution of sperm whales in the Mediterranean Sea, including all locations mentioned in the text.1: Strait of Messina, 2: Gargano Peninsula, 3: Hellenic Trench, 4: Chalkidiki Peninsula, 5: Corsica, 6: Strait of Gibraltar, 7: Cyprus, 8: Zakynthos Island, 9: Aegean Sea, 10: Crete, 11: Adriatic Sea, 12: Atlantic Ocean, 13: Sicily, 14: Africa, 15: Ligurian Sea, 16: Cote d'Azur, 17: Greece, 18: Ionian Sea, 19: Italy, 20: France, 21: Spain, 22: Strait of Sicily, 23: Mallorca and Balearic Islands, 24: Thessaloniki, 25: Alboran Sea. waste material that enters the marine environment from any source. It is a particular problem for the Mediterranean Sea, given the densely populated coasts that surround it. Huge quantities of plastic debris reach the Mediterranean every year. Floating marine debris, especially plastics (synthetic organic polymers) can be ingested by sperm whales, mainly because of misidentification with their natural prey. This is likely to occur more often in juveniles, probably due to ignorance and investigation of inappropriate prey items. However, sub-adult and adult whales have also been found with plastic debris in their stomachs, and this has occasionally been the apparent cause of their stranding and death. Once ingested, plastic debris can disrupt digestion, diminish the whale's appetite and finally reduce its growth rate. However, in the worst cases they block the digestive tract or, when sharp enough, cause internal injuries including the rupture of the stomach. In such cases the whale dies emaciated and with a lot of suffering and pain.

While examining stomach contents of stranded sperm whales in Greece, we found plastic debris in four out of eight whales. For some of them this is a fatal mistake. The most dramatic and extreme case so far was that of a male calf only 5.3m long. This poor whale was found floating dead very close to the coasts of the famous Mykonos Island in the Cyclades in the Aegean Sea. When we saw the carcass it was obvious that something had gone wrong with that whale because it was very emaciated. However, it was difficult even to imagine what we were about to discover while performing the necropsy. Reaching the stomach of a sperm whale is not an easy task, even for a young whale. However, in that particular case the stomach was pretty visible and almost came out by itself, just after the first cuts on the whale's body. It was disproportionately big and full for such a young whale. We started imagining that we might be in front of the first record of a giant squid in the Mediterranean Sea... What else could be such a big prey item in the stomach of a sperm whale? The reality was truly disappointing, and above all very shameful for our own "wise" species: the *Homo* supposed to be "*sapiens*" (i.e. with wisdom).



A young sperm whale was found floating dead off Mykonos Island in Greece. Its stomach was completely full with almost one hundred plastic bags and other debris. Photo by Pelagos Cetacean Research Institute / A. Frantzis.

All our "civilization" was in the stomach of this whale. Tens of big compacted plastic bags used for garbage or construction materials, all kinds of plastic cover for anything we can buy in a supermarket, plastic ropes, pieces of nets, even a plastic bag with full address and telephone number of a souvlaki restaurant in the town of Thessaloniki (located some 500 km further north). Unfortunately, the whale could not call them to complain about the damage caused by their product.

Noise Pollution: Noise pollution is produced by many and various human activities in the Mediterranean Sea. Its direct and indirect impact on sperm whales is not yet well understood, and it is difficult to quantify. Nevertheless, there is evidence suggesting that it is important, especially for a small and fragile

population like the Mediterranean one. The most important sources of anthropogenic noise in the Mediterranean are: heavy maritime traffic (the sheer volume of this means that no silent areas exist anymore in the region), seismic surveys, military sonar, drilling operations, coastal construction works and underwater explosions originating from military exercises and illegal dynamite fishing.

Military sonar occurs much less frequently than shipping noise, but when active it produces extremely high levels of noise known to be harmful for deep diving whales, such as the beaked whales. Its effect on sperm whales has not been assessed yet, although at least in one case, sperm whales showed strange behaviors when exposed to military sonar emissions. Sea areas with steep underwater cliffs, trenches and canyons, are perfect habitats for the deep diving whales, and unfortunately, are preferred by those who plan anti-submarine military exercise. The latter has been shown to be incompatible with the former, and can only be an additional concern for sperm whales.

In the Mediterranean, drilling activity is taking place exclusively in the eastern basin to date, but our unquenchable thirst for oil is driving an increase in seismic surveys in recent years. Many countries, especially Italy, Cyprus and Greece have

planned or started both exploration and drilling within sperm whale habitat, often in critical areas for the species.

Finally, two major types of underwater explosions often occur in the region: routine military exercises and illegal dynamite fishing. Although marine mammal deaths caused by dynamite have been reported, their impact is difficult to assess, and is largely ignored by policy makers and enforcement authorities.

Mediterranean sperm whales are living in an environment where they are exposed to significant levels of anthropogenic noise 24 hours a day. There are no silent oases anywhere in the Mediterranean anymore, and anthropogenic noise is something new for their bodies and their brains. It was completely absent two centuries ago, and this period seems very short for a long-lived mammal to adapt.

The live stranding in southern Italy in December 2009 of seven sperm whales in an apparent state of starvation is at the same time puzzling and worrisome. Puzzling because although not much is known about biomass and distribution of mesopelagic squid in the Mediterranean, which constitute most of the diet of sperm whales in the region, until now there never was reason to doubt that there was ample availability of these mollusks. Worrisome because of the suspicion that there might be a connection between dearth of squids and the intense seismic surveys that had been conducted in area at the time of the stranding, coupled with the notion that seismic surveys can have detrimental effects of squid in a wide area. Unfortunately, the abundance and distribution of deep water squid are difficult and expensive to investigate, and current knowledge and research



Dorsal fins of four sperm whales members of the same social unit that are resting at surface. Calluses are visible on the top of the three largest fins that belong to mature females. Photo by Pelagos Cetacean Research Institute/A. Frantzis.

means are clearly insufficient to know what the situation is. Such concerns should prompt study of the sperm whale – squid relationship through the monitoring of sperm whales' acoustic foraging behavior (creaks) which is indicative of feeding activity, and defecation rates, which are indicative of feeding success.

Harassment: The number of small pleasure boats traversing the inviting blue waters of the Mediterranean increases year upon year, and with this increase comes an increase in casual boaters encountering sperm whales at sea. For most, this is a wonderful and exhilarating experience that is enjoyed with a respectful attitude toward the whales concerned and all go on their way unharmed. For some, however, this is not enough - for whatever reason, be it ego, bravado, or a misplaced "love" for the animals, watching from a distance is not enough and they must get closer, even into the water with the animals. Then the situation has changed from observation to harassment. Nearly all researchers who have followed sperm whales for appreciable amounts of time in the Mediterranean have seen this unfortunate behavior. It is unfortunately almost impossible to quantify, or to assess its impact, even though the avoidance behavior is obvious to those who have spent days and weeks observing the natural behavior of sperm whales. The only real medicine for this problem is not legal. In most cases such harassment is illegal, but enforcement impossible. It seems to be a case of educating owners and captains of pleasure boats about the risks of harassment to both the whales and, for those foolhardy enough to enter the water, themselves.

Clearly, sperm whales in the Mediterranean are in danger of extinction due to a number of threats deriving from human activities, such as fishing, shipping, marine pollution including plastic, noise pollution, and disturbance. Luckily, the list of threats no longer includes deliberate attacks by humans. Our wish is that, like with direct killings, also the other threats will be mitigated in the future – for example, by having driftnet fleets disappearing completely - so that sperm whales will continue to exist in this marine region. If we can prove that sperm whales can coexist with humans in the small, overcrowded Mediterranean, this will be a demonstration that such coexistence will be possible everywhere on the planet.

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Hal Whitehead (Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1) uses a 40-foot ocean-going sailing boat to study the deep-diving whales of offshore waters, the sperm (since 1982) and northern bottlenose (since 1988). His research focuses on the behavior, social organization and transmission of culture among these animals, as well as on their ecology, population biology, and conservation. The principal research tools that he uses are photoidentification, acoustic tracking, and genetic analysis. He also works on general methods of analyzing animal societies and cultural evolution. Hal is a University Research Professor at Dalhousie University, in Halifax, Nova Scotia. For more information see: whitelab.biology.dal.ca.

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Shane Gero (Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1) mentored under Hal Whitehead through his masters and doctoral work at Dalhousie University in Halifax, Canada, the latter of which he is currently concluding. The Dominica Sperm Whale Project, a long-term behavioral study of sperm whale families, grew from this partnership and has collaboratively made advances in our understanding of sperm whale social relationships, babysitting, diet, movement and communication. Learn more about Shane and the whale families at www.thespermwhaleproject.org.

Luke Rendell (MASTS Lecturer in Marine Biology, University of St Andrews, Fife, KY16 9TS, UK) has studied sperm whales around the world since 1993. After obtaining a Ph.D. on sperm whale vocal dialects in 2003 from Dalhousie University, Canada, he returned to the UK as a NERC Postdoctoral Fellow in the Sea Mammal Research Unit at the University of St Andrews, where he was appointed MASTS (masts.ac.uk) Lecturer in 2012. His research interests encompass ecology, behavior and conservation of marine mammals, and the evolution of social learning and culture in humans and other animals.

Giuseppe Notarbartolo di Sciara (Ph.D. marine biology, University of California San Diego, 1985) started as a species-oriented marine ecologist (marine mammals, sharks and manta rays, of which he described a new species, Mobula munkiana), progressively moving towards place-based marine conservation. In 1986 he spearheaded the creation of the Italian National Cetacean Stranding Network, which he coordinated until 1990. In 1986 he funded the Tethys Research Institute in Milano, which he directed until 1997 and now again since 2010. In 1991 he proposed the creation of the Pelagos Sanctuary for Mediterranean Marine Mammals, which was established in 1999 by a treaty amongst Italy, France and Monaco. In 1996 he was nominated president of the Central Institute for Applied Marine Research in Rome, where he served for seven years. He served from 1999 to 2003 as Commissioner or Alternate Commissioner for Italy at the International Whaling Commission, and from 2002 to 2010 as Chair of the Scientific Committee of ACCOBAMS. Current activities include: Regional Coordinator for the Mediterranean and Black Seas, IUCN WCPA - Marine; Deputy Chair, IUCN Species Survival Commission - Cetacean Specialist Group; teacher of science and policy of the conservation of marine biodiversity at the University of Milan. For more details: www.disciara.net.

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Jan Straley has studied the behavior and population dynamics of large whales in the North Pacific for over thirty years. Her early research on humpbacks has provided insight into why some whales linger in the colder waters of the North Pacific during the fall and winter, when most whales, and sensible Alaskans, migrate to the warmer climates of Mexico and Hawaii. Her research today involves interactions among large whales and human activities, primarily with fisheries. She is currently an Associate Professor at the University of Alaska Southeast, a founder of Sitka Whalefest and the Sitka Sound Science Center. Jan lives in Sitka, Alaska with her husband John, a novelist, poet and criminal investigator. Her son, Finn, born in 1988, lives in Los Angeles.

Richard Ellis is one of America's leading marine conservationists, and one of the foremost painters of marine natural history subjects. His research has taken him all over the world. In addition to painting, Richard is the author of more than eighty magazine articles. His books include The Book of Whales, Dolphins and Porpoises, Great White Shark, co-authored by John McCosker, Men and Whales, Physty (his first children's book), Monsters of the Sea, Deep Atlantic, Imagining Atlantis, The Search for the Giant Squid, Encyclopedia of the Sea, Aquagenesis: The Origin and Evolution of Life in the Sea, The Empty Ocean, Sea Dragons: Predators of Prehistoric Oceans, No Turning Back: The Life and Death of Animal Species, Singing Whales and Flying Squid: The Discovery of Marine Life, Big Fish (a book of his drawings and paintings), On Thin Ice: The Changing World of the Polar Bear. And most recently, The Great Sperm Whale – A Natural History of the Ocean's Most Magnificent and Mysterious Creature."

Selected References

Books on the Sperm Whale

Beale, T. 1839. The natural history of the sperm whale. John van Voorst, London.

Bennett, F. D. 1840. Narrative of a whaling voyage around the globe from the year 1833 to 1836. Richard Bentley, London.

Berzin, A. A. 1972. The sperm whale. Israel Program for Scientific Translations, Jerusalem.

Ellis, R. 2011. The great sperm whale. A natural history of the ocean's most magnificent and mysterious creature. University of Kansas Press, Lawrence, KS.

Gordon, J. 1998. Sperm whales. Colin Baxter, Grantown-on-Spey, Scotland.

Melville, H. 1851. Moby Dick or the whale. Harper &Brothers, New York.

Starbuck, A. 1878. History of the American whale fishery from its earliest inception to the year 1876. Government Printing Office, Washington, DC.

Tønnessen, J. N., and A. O. Johnsen. 1982. The history of modern whaling. University of California Press, Berkeley, California. Whitehead, H. 2003. Sperm whales: social evolution in the ocean. Chicago University Press, Chicago, IL.

Scientific Papers on the Sperm Whale

Antunes, R., T. Schulz, S. Gero, H. Whitehead, J. Gordon and L. Rendell. 2011. Individually distinctive acoustic features in sperm whale codas. Animal Behaviour 81:723-730.

Arnbom, T., V. Papastavrou, L. S. Weilgart and H. Whitehead. 1987. Sperm whales react to an attack by killer whales. Journal of Mammalogy 68:450-453.

Ashford, J. R., P. S. Rubilar and A. R. Martin. 1996. Interactions between cetaceans and longline fishery operations around South Georgia. Marine Mammal Science 12:452-456.

Backus, R. H., and W. E. Schevill. 1966. *Physeter* clicks. Pages 510-527 in K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley.

Bearzi, G., N. Pierantonio, M. Affronte, D. Holcer, N. Maio and G. N. Di Sciara. 2011. Overview of sperm whale *Physeter macrocephalus* mortality events in the Adriatic Sea, 1555-2009. Mammal Review 41:276-293.

Bearzi, G., N. Pierantonio, S. Bonizzoni, G. N. di Sciara and M. Demma. 2010. Perception of a cetacean mass stranding in Italy: the emergence of compassion. Aquatic Conservation-Marine and Freshwater Ecosystems 20:644-654.

Bel'kovich, V. M., and A. V. Yablokov. 1963. The whale - an ultrasonic projector. Yuchni Teknik 3:76-77.

Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 in H. E. Winn, and B. L. Olla, eds. Behavior of marine animals. Volume 3. Plenum, New York.



A sperm whale skeleton, Lithograph by Delahaye, in van Beneden and Gervais, Osteographie des Cétacés vivants et fossiles,1880.

Best, P. B., P. A. S. Canham and N. Macleod. 1984. Patterns of reproduction in sperm whales, *Physeter macrocephalus*. Reports of the International Whaling Commission (Special Issue) 6:51-79.

Bolognari, A. 1957. Sulla biologia del capodoglio. Atti Della Società Peloritana Di Scienze Fisiche, Matematiche e Naturali 3:143-156.

Caldwell, D. K., M. C. Caldwell and D. W. Rice. 1966. Behavior of the sperm whale *Physeter catodon* L. Pages 677-717 in K. S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley.

Christal, J., H. Whitehead and E. Lettevall. 1998. Sperm whale social units: variation and change. Canadian Journal of Zoology 76:1431-1440.

Clarke, M. R. 1970. The function of the spermaceti organ of the sperm whale. Nature 228:873-874.



Photo by Flip Nicklin/Minden Pictures.

Clarke, M. R. 1978. Buoyancy control as a function of the spermaceti organ in the sperm whale. Journal of the Marine Biological Association of the United Kingdom 58:27-71.

Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. Discovery Reports 37:1-324.

Clarke, M. R., and N. MacLeod. 1976. Cephalopod remains from sperm whales caught off Iceland. Journal of the Marine Biological Association of the United Kingdom 56:733-749.

Cranford, T. W. 1999. The sperm whale's nose: sexual selection on a grand scale? Marine Mammal Science 15:1133-1157.

Dillon, M. C., K. R. Richard, H. Whitehead and J. M. Wright. 2002. Social and population genetic structure of sperm whales assessed by molecular genetic analyses. Pages 43-52 in C. J. Pfeiffer, ed. Molecular and cell biology of marine mammals. Malabar, Florida.

Drouot, V., J. Goold and A. Gannier. 2004. Regional diversity in the social vocalizations of sperm whale in the Mediterranean Sea. Revue D Ecologie-La Terre Et La Vie 59:545-558.

Dufault, S., H. Whitehead and M. Dillon. 1999. An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide. Journal of Cetacean Research and Management 1:1-10.

Engelhaupt, D., A. R. Hoelzel, C. Nicholson, A. Frantzis, S. Mesnick, S. Gero, H. Whitehead, L. Rendell, P. Miller, R. De Stefanis, A. Canadas, S. Airoldi and A. A. Mignucci-Giannoni. 2009. Female philopatry in coastal basins and male dispersion across the North Atlantic in a highly mobile marine species, the sperm whale (*Physeter macrocephalus*). Molecular Ecology 18:4193-4205.

Frantzis, A., and P. Alexiadou. 2008. Male sperm whale (*Physeter macrocephalus*) coda production and coda-type usage depend on the presence of conspecifics and the behavioural context. Canadian Journal of Zoology 86:62-75.

Gannier, A., V. Drouot and J. Goold. 2002. Distribution and relative abundance of sperm whales in the Mediterranean Sea. Marine Ecology-Progress Series 243:281-293.

Gero, S., D. Engelhaupt, L. Rendell and H. Whitehead. 2009. Who Cares? Between-group variation in alloparental caregiving in sperm whales. Behavioral Ecology 20:838-843.

Gero, S., D. Engelhaupt and H. Whitehead. 2008. Heterogeneous social associations within a sperm whale, *Physeter macro-cephalus*, unit reflect pairwise relatedness. Behavioral Ecology and Sociobiology 63:143-151.

Gordon, J. C. D. 1987. Sperm whale groups and social behaviour observed off Sri Lanka. Reports of the International Whaling Commission 37:205-217.

Gordon, J. C. D., A. Moscrop, C. Carlson, S. Ingram, R. Leaper, J. Matthews and K. Young. 1998. Distribution, movements, and residency of sperm whales off the Commonwealth of Dominica, Eastern Caribbean: implications for the development and regulation of the local whale watching industry. Reports of the International Whaling Commission 48:551-557.

Gosho, M. E., D. W. Rice and J. M. Breiwick. 1984. The sperm whale *Physeter macrocephalus*. Marine Fisheries Review 46(4):54-64.

Healy, S. D., and C. Rowe. 2007. A critique of comparative studies of brain size. Proceedings of the Royal Society B: Biological Sciences 274:453-464.

Jaquet, N., and H. Whitehead. 1999. Movements, distribution and feeding success of sperm whales in the Pacific Ocean, over scales of days and tens of kilometers. Aquatic Mammals 25:1-13.

Jaquet, N., H. Whitehead and M. Lewis. 1996. Coherence between 19th century sperm whale distributions and satellitederived pigments in the tropical Pacific. Marine Ecology Progress Series 145:1-10.

Kawakami, T. 1980. A review of sperm whale food. Scientific Reports of the Whales Research Institute 32:199-218.

Kock, K., M. Purves and G. Duhamel. 2006. Interactions between cetacean and fisheries in the Southern Ocean. Polar Biology 29:379-388.

Lavery, T. J., B. Roudnew, P. Gill, J. Seymour, L. Seuront, G. Johnson, J. G. Mitchell and V. Smetacek. 2010. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. Proceedings of the Royal Society B: Biological Sciences 277:3527-3531.

Lyrholm, T., O. Leimar, B. Johanneson and U. Gyllensten. 1999. Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. Proceedings of the Royal Society of London, B 266:347-354.

Madsen, P. T., D. A. Carder, W. W. L. Au, P.E. Nachtigall, B. Møhl and S.H. Ridgway. 2003, Sound production in neonate sperm whales (L.). Journal of the Acoustical Society of America 113: 2988-2991.

Madsen, P. T., R. Payne, N. U. Kristiansen, M. Wahlberg, I. Kerr and B. Møhl. 2002. Sperm whale sound production studied with ultrasound time/depth-recording tags. Journal of Experimental Biology 205: 1899-1906.

Madsen, P. T., M. Wahlberg and B. Møhl. 2002. Male sperm whale (*Physeter macrocephalus*) acoustics in a high latitude: implications for echolocation and communication. Behavioural Ecology and Sociobiology 53:31-41.

Malloy, M. 1989. Whalemen's Perceptions of "The High and Mighty Business of Whaling". The Log of Mystic Seaport 41:56-67.

Marcoux, M., L. Rendell and H. Whitehead. 2007. Indications of fitness differences among vocal clans of sperm whales. Behavioural Ecology and Sociobiology 61:1093-1098.

Marcoux, M., H. Whitehead and L. Rendell. 2006. Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology 84:609-614.

Marino, L., R. C. Connor, R. E. Fordyce, L. M. Herman, P. R. Hof, L. Lefebvre, D. Lusseau, B. McCowan, E. A. Nimchinsky, A. A. Pack, L. Rendell, J. S. Reidenberg, D. Reiss, M. D. Uhen, E. Van der Gucht and H. Whitehead. 2007. Cetaceans have complex brains for complex cognition. PLoS Biology 5:e139.

Mathias, D., A. Thode, J. Straley and K. Folkert. 2009. Relationship between sperm whale (*Physeter macrocephalus*) click structure and size derived from videocamera images of a depredating whale (sperm whale prey acquisition). Journal of the Acoustical Society of America 125:3444-3453.

Mazzariol, S., G. Di Guardo, A. Petrella, L. Marsili, C. M. Fossi, C. Leonzio, N. Zizzo, S. Vizzini, S. Gaspari, G. Pavan, M. Podesta, F. Garibaldi, M. Ferrante, C. Copat, D. Traversa, F. Marcer, S. Airoldi, A. Frantzis, Y. De Beraldo Quiros, B. Cozzi and A. Fernandez. 2011. Sometimes sperm whales (*Physeter macrocephalus*) cannot find their way back to the high seas: A multidisciplinary study on a mass stranding. Plos One 6:e19417.

Mesnick, S., K. Evans, B. L. Taylor, J. Hyde, S. Escorza-Treviño and A. E. Dizon. 2003. Sperm whale social structure: why it takes a village to raise a child..*in* F. B. M. de Waal, and P. L. Tyack, eds. Animal social complexity. Intelligence, culture and individualized societies. Harvard University Press, Cambridge, Massachusetts.

Mesnick, S. L. 2001. Genetic relatedness in sperm whales: evidence and cultural implications. Behavioral and Brain Sciences 24:346-347.

Mesnick, S. L., B. L. Taylor, F. I. Archer, K. K. Martien, S. E. Treviño, B. Hancock-Hanser, S. Moreno Medina Carolina, V. L. Pease, K. M. Robertson, J. M. Straley, R. W. Baird, J. Calambokidis, G. S. Schorr, P. Wade, V. Burkanov, C. R. Lunsford, L. Rendell and P. A. Morin. 2011. Sperm whale population structure in the eastern and central North Pacific inferred by the use of

single-nucleotide polymorphisms, microsatellites and mitochondrial DNA. Molecular Ecology Resources 11:278-298.

Miller, P. J. O., K. Aoki, L. E. Rendell and M. Amano. 2008. Stereotypical resting behavior of the sperm whale. Current Biology 18:R21-R23.

Miller, P. J. O., M. P. Johnson and P.L. Tyack. 2004. Sperm whale behaviour indicates the use of rapid echolocation click buzzes 'creaks' in prey capture. Proceedings of the Royal Society of London, Series B. 271: 2239-2247.

Møhl, B., M. Wahlberg, P. T. Madsen, A. Heerfordt and A. Lund. 2003. The monopulsed nature of sperm whale clicks. Journal of the Acoustical Society of America 114:1143-1154.

Møhl, B., M. Wahlberg, P. T. Madsen, L. A. Miller and A. Surlykke. 2000. Sperm whale clicks: directionality and source level revisited. Journal of the Acoustical Society of America 107:638-648.

Møhl, B., E. Larsen and M. Amundin. 1981. Sperm whale size determination: outline of an acoustic approach. FAO Fisheries Series 5:327-332.

Norris, K. S., and G. W. Harvey. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). Pages 397-417 in S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville, eds. Animal orientation and navigation. NASA Special Publications, Washington, D.C.

Norris, K. S., and B. Møhl. 1983. Can odontocetes debilitate prey with sound? American Naturalist 122:85-104.

Pavan, G., T. J. Hayward, J. F. Borsani, M. Priano, M. Manghi, C. Fossati and J. Gordon. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985-1996. Journal of the Acoustical Society of America 107:3487-3495.

Pirotta, E., J. Matthiopoulos, M. MacKenzie, L. Scott-Hayward and L. Rendell. 2011. Modelling sperm whale habitat preference: a novel approach combining transect and follow data. Marine Ecology-Progress Series 436:257-272.

Pouchet, G., and H. Beauregard. 1885. Note sur "L'organe des Spermaceti". Compt. Rend. Hebdomadaires des Séances et Mém. De la Soc. De Biol., vol. 8, II, pp. 342-344

Pouchet, G.: and H. Beauregard. 1892. Recherches sur le cachalot. Nouv. Arch. du Mus. d'Hist. Nat., vol 3, IV, 1892, pp. 1-86.

Rendell, L., S. L. Mesnick, M. L. Dalebout, J. Burtenshaw and H. Whitehead. 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? Behavior Genetics, 42:332-343.

Rendell, L., and H. Whitehead. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society of London, B 270:225-231.

Rendell, L., and H. Whitehead. 2004. Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurement. Animal Behaviour 67:865-874.

Rendell, L. E., and H. Whitehead. 2005. Spatial and temporal variation in sperm whale coda vocalisations: stable usage and local dialects. Animal Behaviour 70:191-198.

Richard, K. R., M. C. Dillon, H. Whitehead and J. M. Wright. 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proceedings of the National Academy of Sciences of the United States of America 93:8792-8795.

Ruiz-Cooley, R. I., D. Gendron, S. Aguíñiga, S. Mesnick and J. D. Carriquiry. 2004. Trophic relationships between sperm whales and jumbo squid using stable isotopes of C and N. Marine Ecology Progress Series 277:275-283.

Santos, M., G. Pierce, P. Boyle, R. Reid, H. Ross, I. Patterson, C. Kinze, S. Tougaard, R. Lick, U. Piatkowski and V. Hernandez-Garcia. 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990-1996. Marine Ecology-Progress Series 183:281-294.

Schulz, T. M., H. Whitehead, S. Gero and L. Rendell. 2010. Individual vocal production in a sperm whale (*Physeter macro-cephalus*) social unit. Marine Mammal Science 27:149-166.

Schulz, T. M., H. Whitehead, S. Gero and L. Rendell. 2008. Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. Animal Behaviour, 76:1977 1988.

Sigler, M. F., C. R. Lunsford, J. M. Straley and J. B. Liddle. 2008. Sperm whale depredation of sablefish longline gear in the northeast Pacific Ocean. Marine Mammal Science 24:16-27.

Teloni, V., M. P. Johnson, P. J. O. Miller and P. T. Madsen. 2008. Shallow food for deep divers: Dynamic foraging behavior of male sperm whales in a high latitude habitat. Journal of Experimental Marine Biology and Ecology 354:119-131.

Thode, A., D. Mellinger, S. Stiensessen, A. Martinez and K. Mullin. 2002. Depth-dependent acoustic features of diving sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico. Journal of the Acoustical Society of America 112:308-321.

Thode, A., J. Straley, C. O. Tiemann, K. Folkert and V. O'Connell. 2007. Observations of potential acoustic cues that attract sperm whales to longline fishing in the Gulf of Alaska. Journal of the Acoustical Society of America 122:1265-1277.

Tiemann, C. O., A. M. Thode, J. Straley, V. O'Connell and K. Folkert. 2006. Three-dimensional localization of sperm whales using a single hydrophone. Journal of the Acoustical Society of America 120:2355-2365.

Townsend, C. H. 1935. The distribution of certain whales as shown by the logbook records of American whaleships. Zoologica 19:1-50.

Waters, S., and H. Whitehead. 1990. Aerial behaviour in sperm whales, *Physeter macrocephalus*. Canadian Journal of Zoology 68:2076-2082.

Watkins, W. A. 1980. Acoustics and the behavior of sperm whales. Pages 291-297 in R. Busnel, and J. F. Fish, eds. Animal sonar systems. Plenum Press, New York.

Watkins, W. A., K. E. Moore and P. Tyack. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. Cetology 49:1-15.

Watkins, W. A., and W. E. Schevill. 1977. Spatial distribution of *Physeter catodon* (sperm whales) underwater. Deep-Sea Research 24:693-699.

Watkins, W. A., and W. E. Schevill. 1977. Sperm whale codas. Journal of the Acoustical Society of America 62:1486-1490.

Watwood, S. L., P. O. Miller, M. Johnson, P. T. Madsen and P. L. Tyack. 2006. Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). Journal of Animal Ecology 75:814-825.

Weilgart, L., and H. Whitehead. 1993. Coda vocalizations in sperm whales (*Physeter macrocephalus*) off the Galapagos Islands. Canadian Journal of Zoology 71:744-752.

Weilgart, L., and H. Whitehead. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behavioural Ecology and Sociobiology 40:277-285.

Weilgart, L., H. Whitehead and K. Payne. 1996. A colossal convergence. American Scientist 84:278-287.

Weilgart, L. S., and H. Whitehead. 1986. Observations of a sperm whale (*Physeter catodon*) birth. Journal of Mammalogy 67:399-401.

Weilgart, L. S., and H. Whitehead. 1988. Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology 66:1931-1937.

Whitehead, H., A. Coakes, N. Jaquet and S. Lusseau. 2008. Movements of sperm whales in the tropical Pacific. Marine Ecology Progress Series 361:291-300.

Whitehead, H. 1993. The behaviour of mature male sperm whales on the Galapagos breeding grounds. Canadian Journal of Zoology 71:689-699.

Whitehead, H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioural Ecology and Sociobiology 38:237-244.

Whitehead, H. 1996. Variation in the feeding success of sperm whales: temporal scale, spatial scale and relationship to migrations. Journal of Animal Ecology 65:429-438.

Whitehead, H. 1998. Cultural selection and genetic diversity in matrilineal whales. Science 282:1708-1711.

Whitehead, H. 1999. Variation in the visually observable behavior of groups of Galápagos sperm whales. Marine Mammal Science 15:1181-1197.

Whitehead, H. 2002. Estimates of the current global population size and historical trajectory for sperm whales. Marine Ecology Progress Series 242:295-304.

Whitehead, H. 2005. Genetic diversity in the matrilineal whales: models of cultural hitchhiking and group-specific non-heritable demographic variation. Marine Mammal Science 21:58-79.

Whitehead, H., J. Christal and S. Dufault. 1997. Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. Conservation Biology 11:1387-1396.

Whitehead, H., M. Dillon, S. Dufault, L. Weilgart and J. Wright. 1998. Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. Journal of Animal Ecology 67:253-262.

Whitehead, H., and J. Gordon. 1986. Methods of obtaining data for assessing and modelling sperm whale populations which do not depend on catches. Reports of the International Whaling Commission (Special Issue) 8:149-166.

Whitehead, H., and L. Rendell. 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. Journal of Animal Ecology 73:190-196.

Whitehead, H., S. Waters and T. Lyrholm. 1991. Social organization in female sperm whales and their offspring: constant companions and casual acquaintances. Behavioural Ecology and Sociobiology 29:385-389.

Whitehead, H., and L. Weilgart. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour 118:275-296.

Whitehead, H., and L. Weilgart. 2000. The sperm whale: social females and roving males. Pages 154-172 *in* J. Mann, R. C. Connor, P. Tyack, and H. Whitehead, eds. Cetacean Societies. University of Chicago Press, Chicago.

Worthington, L. V., and W. E. Schevill. 1957. Underwater sounds heard from sperm whales. Nature 180:291.

Zimmer, W. M. X., P. T. Madsen, V. Teloni, M. P. Johnson and P. L. Tyack. 2005. Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. Journal of the Acoustical Society of America 118:3337-3345.

Zimmer, W. M. X., P. L. Tyack, M. P. Johnson and P. T. Madsen. 2005. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. Journal of the Acoustical Society of America 117:1473.



Whales logging off Dominica. Photo by Marina Milligan.



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