



Short communication

Putative origin and maternal relatedness of male sperm whales (*Physeter macrocephalus*) recently stranded in the North Sea

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ABSTRACT

The globally distributed sperm whale (*Physeter macrocephalus*) has a partly matrilineal social structure with predominant male dispersal. At the beginning of 2016, a total of 30 male sperm whales stranded in five different countries bordering the southern North Sea. It has been postulated that these individuals were on a migration route from the north to warmer temperate and tropical waters where females live in social groups. By including samples from four countries (n=27), this event provided a unique chance to genetically investigate the maternal relatedness and the putative origin of these temporally and spatially co-occurring male sperm whales. To utilize existing genetic resources, we sequenced 422 bp of the mitochondrial control region, a molecular marker for which sperm whale data are readily available from the entire distribution range. Based on four single nucleotide polymorphisms (SNPs) within the mitochondrial control region, five matrilineal lineages could be distinguished within the stranded specimens, four of which matched published haplotypes previously described in the Atlantic. Among these male sperm whales, multiple matrilineal lineages co-occur. We analyzed the population differentiation and could show that the genetic diversity of these male sperm whales is comparable to the genetic diversity in sperm whales from the entire Atlantic Ocean. We confirm that within this stranding event, males do not comprise maternally related individuals and apparently include assemblages of individuals from different geographic regions.

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Despite their high mobility, wide ranging cetaceans often exhibit geographically restricted migration patterns, leading to population structure both among and within ocean basins. Isotope analysis (Borrell et al., 2013; Matthews et al., 2016; Valenzuela et al., 2009), acoustic data (Gero et al., 2016; Rendell and Whitehead, 2004), pollution information (Aguilar et al., 2002; Godard-Codding et al., 2011; Mazzariol et al., 2011), morphological differences (Bolaños-Jiménez et al., 2014; De Luna et al., 2012; Durban et al., 2016) as well as genetic investigations have been performed to define population boundaries, migration routes, and dispersal patterns (Baker et al., 2013; Valsecchi et al., 2010). Due to the difficulty of acquiring samples from free ranging live cetaceans, stranded individuals are frequently used to gain new insights into biolog-

ical and phylogenetic histories (Drouot et al., 2004; Ottewell et al., 2016; Sabatier et al., 2015; Squadroni et al., 2015). As the largest toothed cetacean, the sperm whale (*Physeter macrocephalus*) shows migration patterns and social behaviors similar to some large terrestrial mammals, like Asian elephants (Gero et al., 2015; McComb et al., 2001; Poole, 1989; Stoeger and Baotic, 2016). The females show a strong philopatry to warmer regions around the equator and separate into social groups consisting of one or more matrilineal groups, communicating with specific acoustic codas (Engelhaupt et al., 2009; Lyrholm and Gyllensten, 1998; Richard et al., 1996; Schulz et al., 2008; Whitehead, 1993).

After reaching sexual maturity at ages 18–20 years, males separate from the female groups to form loose bachelor groups, which migrate to colder regions (Whitehead, 2003). Males stay in these bachelor groups until reaching physical maturity at an age of around 35 years, after which they separate into smaller groups or become solitary (Mesnick, 2014). This sex-specific dispersal

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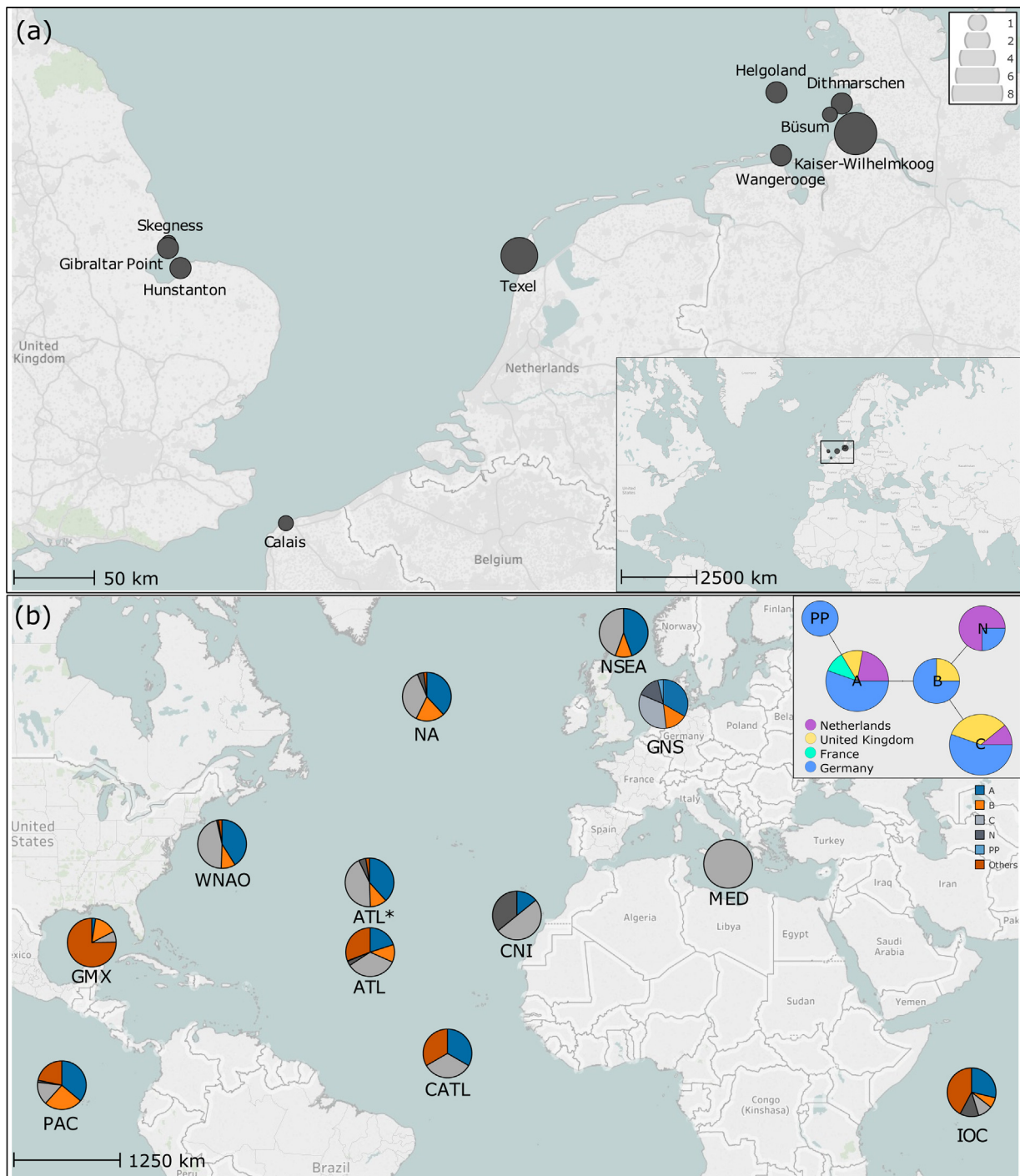


Fig. 1. (a) Sperm whale stranding sites (Jan-Feb 2016). Size of circle equals number of individuals stranded at that site. (b) Haplotype network for this study and worldwide distribution of the sperm whale mtDNA control region haplotype frequencies (from Alexander 2016 and references therein). Pie charts indicate frequency of the five haplotypes found within our bachelor group (“A”, “B”, “C”, “N”, “PP”) and “others” (all remaining); exact number of individuals see Table 1. Locations: “GNS” = German North Sea; “NA” = Northern North Atlantic; “NSEA” = Northern North Sea; “WNAO” = Western North Atlantic; “CATL” = central Atlantic; “GMX” = Gulf of Mexico; “MED” = Mediterranean Sea; “ATL” = all Atlantic regions; “ATL*” = Atlantic regions without GMX and MED; “PAC” = overall Pacific; “IOC” = Indian Ocean.

results in the males being the major drivers of gene flow across geographic regions and social assemblages (Lyrholm et al., 1999). Although a sex-specific dispersal pattern is found in all sperm whales around the globe, there are some differences between geographic regions. Different substructuring and organization of social groups is observed among the three large oceans (Atlantic, Pacific and Indian): While there are distinct subpopulations in the Atlantic and Indian Ocean, the Pacific population is more homogeneous (Alexander et al., 2016). Atlantic and Pacific populations have been

thoroughly studied and different home ranges of female groups as well as differences in the composition of social groups have been found. In the Atlantic, females show smaller home ranges (400 km² as opposed to 1500 km² in the Pacific) and social groups are clearly distinct from one another and only rarely mix or meet, as opposed to the situation in the Pacific (Gero et al., 2008). In the Atlantic, up to three different subpopulations have been proposed, with one of them, the Mediterranean, considered resident (Borrell et al., 2013; Drouot et al., 2004; Engelhaupt et al., 2009; Winsor and Mate, 2016).

Table 1
Arlequin and AMOVA analysis of mtDNA data of stranded male sperm whales, compared to existing mtDNA data. Haplotype diversity H and nucleotide diversity are shown with standard deviation. Significant difference ($p < 0.05$; t -test) from our bachelor group (GNS) is indicated by * and bold script. F_{ST} values are shown in comparison to the bachelor group (GNS); Significance was evaluated by permutation test. Haplotype frequencies are given in total numbers of individuals (see also Fig. 1).

	# indiv.	Haplotype diversity H	Nucleotide diversity (%)	F_{ST}	Exact test p value	Haplotype Frequencies					
						A	B	C	N	PP	others
GNS	27	0.761 ± 0.043	0.337 ± 0.243	–	–	9	4	9	4	1	–
NA	47	0.698 ± 0.033	0.287 ± 0.213	–0.014	0.439 ± 0.011	18	9	17	2	–	1
NSEA	18	0.628 ± 0.062	0.275 ± 0.214	–0.012	0.399 ± 0.002	8	2	8	–	–	–
WNAO	87	0.616 ± 0.028*	0.281 ± 0.208	0.011	0.022 ± 0.002*	36	8	40	1	–	2
CNI	14	0.648 ± 0.081	0.3412 ± 0.255	0.022	0.181 ± 0.003	2	–	7	5	–	–
CATL	3	1.000 ± 0.272	0.526 ± 0.496	–0.019	0.269 ± 0.004	1	–	1	–	–	1
GMX	153	0.500 ± 0.044*	0.222 ± 0.175	0.490*	<0.001 ± 0.000*	4	23	11	–	–	115
MED	40	0.000 ± 0.000*	0.000 ± 0.000*	0.501*	<0.001 ± 0.000*	–	–	40	–	–	–
ATL	362	0.748 ± 0.010	0.345 ± 0.239	0.133*	<0.001 ± 0.000*	69	42	124	8	–	119
ATL#	169	0.654 ± 0.020*	0.294 ± 0.213	–0.003	0.160 ± 0.009	65	19	73	8	–	4
PAC	1096	0.775 ± 0.008	0.375 ± 0.253	0.043*	0.070 ± 0.013	396	281	167	17	–	235
IOC	247	0.807 ± 0.012	0.454 ± 0.294	0.091*	<0.001 ± 0.000*	71	17	24	31	–	104

Abbreviation: "GNS" = German North Sea (this study); "NA" = Northern North Atlantic; "NSEA" = Northern North Sea; "WNAO" = Western North Atlantic; "CNI" = Canary Islands; "CATL" = central Atlantic; "GMX" = Gulf of Mexico; "MED" = Mediterranean Sea; "ATL" = overall Atlantic; "ATL#" = overall Atlantic without GMX and MED; "PAC" = overall Pacific; "IOC" = Indian Ocean (Alexander et al., 2016, Supplementary Material 2, and references therein).

So far, research has mainly focused on social groups consisting of female sperm whales and calves, while knowledge about behavior and genetic structuring of male groups is still scarce.

Between January and early February 2016, thirty male sperm whales were found live and dead stranded along the North Sea coastline (Fig. 1a; Unger et al., 2016; see supplementary material for details). It has been proposed that these sperm whales may have been on a southern migration from the north towards warmer regions, and accidentally entered the shallow southern North Sea (Schnitzler et al., 2017). Since the strandings co-occurred both locally and temporally in an area where sperm whale strandings are otherwise rare, we do not consider them as multiple independent occasions. On the contrary, such a co-occurrence may indicate that the stranded individuals belong to one or a few associated groups of males on a similar migration route. Male groups have been described to be more dynamic than female groups and can contain up to 40 animals (Mesnick, 2014; Whitehead pers. comm.). Samples collected from these stranded specimens provided the opportunity to investigate the matrilineal relationships and putative origin, as well as the genetic diversity among them, relative to ocean-wide genetic diversity. We analyzed the maternally-inherited mitochondrial control region. We chose this marker because comparable data are available for many regions around the globe with over 40 different mitochondrial DNA (mtDNA) haplotypes (HT) described for sperm whales, providing an extensive database for comparison.

DNA was extracted from skin and muscle samples of 27 available sperm whales using the NucleoSpin® Tissue-Kit from MACHEREY-NAGEL GmbH&Co. KG following the manufacturer protocol. Polymerase Chain Reaction (PCR) was performed on a BiometraT3000 thermocycler, using the MyTaq DNA Polymerase Kit (25 µl reaction volume: 5 µl 5xMyTaq reaction buffer, 0.5 µl of each primer, 0.12 µl MyTaq-DNA-Polymerase, 1 µl sample-DNA, 17.88 µl HPLC-H₂O) with the following cycling: 95 °C for 1 min, 30 cycles (95 °C for 15 s., 55 °C for 15 s., 72 °C for 10 s.), and finally 72 °C for 10 min. Established primers (Engelhaupt et al., 2009) were used (i.e., L15812 5'-CCTCCCTAAGACTCAAGG-3' and H16343 5'-CCTGAGAATGCACTAGAGG-3'). The sequencing reaction was performed with the cleaned PCR product using L15812 primer and the Applied Biosystems BigDye chemistry, and run on an 3130xl Genetic Analyzer (Applied Biosystems).

In total, 422 base pairs (bp) of the mitochondrial control region were sequenced successfully for all samples. Among the sequences, four SNPs were detected and five HT could be distinguished. Four HTs matched the published haplotypes "A", "B", "C" and "N" (Alexander et al., 2016). Worldwide, these are the most frequent

HTs and they have been identified in all three oceans. The fifth HT ("PP"; Genbank accession number KY886371) has not been previously described. In a haplotype network, it is closest to HT "A" (Fig. 1b). Of the five HTs, two ("A" and "B") occur in nine samples each, two ("C" and "N") were identified in four samples, and our newly described fifth HP was identified in one of the 27 samples (Table 1).

To put the genetic composition of these male whales into perspective, we jointly analyzed them together with published haplotype data. Specifically, we compared our haplotype diversity to other postulated subpopulations within the Atlantic, as well as to the Atlantic, Pacific and Indian Oceans, by utilizing the data compiled by Alexander et al. (2016). From that publication, we specifically used Supplementary Material 2 and haplotype data available through datadryad. This dataset comprises 1705 individuals, covering 38 haplotypes and 38 regions compiled from various studies worldwide and covering a time span from 1996 to 2016 (Alexander et al., 2013; Alexander et al., 2016 Engelhaupt et al., 2009; Lyrholm and Gyllensten, 1998; Mesnick et al., 2011; Rendell et al., 2012; Richard et al., 1996; Whitehead, 1998). The program Arlequin3.5 (Excoffier and Lischer, 2010) was used to compute pairwise fixation indices F_{ST} , haplotype and nucleotide diversity, and to construct a minimum spanning tree among haplotypes. The exact test (no. of steps in Markov chain = 100,000; No. of dememorization steps: 10,000; significance level = 0.05) was used to test for significance of population differentiation. For the AMOVA analysis, the 20 regions were assigned to three groups [Pacific (PAC) = 13 regions, Atlantic (ATL) = 6 Regions (including the bachelor group from 2016 analyzed here), Indian Ocean (IOC) = 1 region] (Alexander et al. (2016) Supplementary Material 2).

The distribution of mtDNA haplotypes was analyzed with regard to the null hypothesis that the males stranded 2016 consist of male offspring from different Atlantic matrilineal lines. Specifically, we investigated the haplotype occurrence and the haplotype/genetic diversity of our bachelor group (GNS) compared to the Atlantic, Pacific and Indian Ocean, as well as to the following subsamples of Atlantic areas: north Atlantic (NA), North Sea (NSEA), western north Atlantic (WNAO), Gulf of Mexico (GMX), and the Mediterranean Sea (MED). The latter two areas are postulated to be subpopulations/resident populations within the Atlantic (Drouot et al., 2004; Engelhaupt et al., 2009; Gero et al., 2007). Mitochondrial genetic diversity in sperm whales is quite low compared to other cetaceans (Alexander et al., 2013). This has been related to matrilineal female association in conjunction with cultural diversification (Whitehead 1998) or environmental perturbation (Tiedemann and

Milinkovitch, 1999) and may further indicate a genetic bottleneck or selective sweep (Alexander et al., 2013). Despite low diversity levels, there are significant differences between the different, postulated subpopulations within the Atlantic as well as differences when comparing the three main ocean basins (Alexander et al., 2016).

The genetic diversity in our group of stranded sperm whales was similar to that observed for the entire Atlantic population. The fit of our group to the Atlantic population's haplotype frequencies was best when the resident subpopulations of the Gulf of Mexico and the Mediterranean Sea were excluded (Fig. 1b). This suggests that (1) our group of stranded male sperm whales is of Atlantic origin and (2) it comprises individuals from disparate regions/subpopulations throughout the entire Atlantic, rather than from a single area. In fact, our stranded animals are genetically even more diverse than a random set of specimens from the Atlantic (excluding the Gulf of Mexico and Mediterranean Sea; see significant difference in haplotype diversity in Table 1).

Male bachelor groups (at least in this case) apparently consist of males descending from different matrilineal lines and thus most probably from different natal social groups. Their maternal relationship is not closer than expected for a random subset of Atlantic Ocean individuals. This high genetic diversity among members of male sperm whale groups is in sharp contrast to the close kin relationships in female-dominated social groups. Whether this large diversity is unique for the sperm whales in our sample or a general pattern of male sperm whale aggregations has to be evaluated in future studies. Our findings can be used in future studies investigating sperm whale aggregations, aiming to increase our knowledge of sperm whale distribution and social behavior.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2017.09.003>.

References

- Aguilar, A., Borrell, A., Reijnders, P.J.H., 2002. Patterns in geographical and temporal variation of organochlorine pollutant concentrations in marine mammals. *Mar. Environ. Res.* 53, 425–452, [http://dx.doi.org/10.1016/S0141-1136\(01\)00128-3](http://dx.doi.org/10.1016/S0141-1136(01)00128-3).
- Alexander, A., Steel, D., Slikas, B., Hoekzema, K., Carraher, C., Parks, M., Cronn, R., Baker, C.S., 2013. Low diversity in the mitogenome of sperm whales revealed by next-generation sequencing. *Genome Biol. Evol.* 5, 113–129, <http://dx.doi.org/10.1093/gbe/evs126>.
- Alexander, A., Steel, D., Hoekzema, K., Mesnick, S., Engelhaupt, D., Kerr, I., Payne, R., Baker, C.S., 2016. What influences the worldwide genetic structure of sperm whales (*Physeter macrocephalus*)? *Mol. Ecol.*, 2754–2772, <http://dx.doi.org/10.1111/mec.13638>.
- Baker, C.S., Steel, D., Calambokidis, J., Falcone, E., González-peral, U., Barlow, J., Burdin, A.M., Clapham, P.J., Ford, J.K.B., Gabriele, C.M., Mattila, D., Rojas-Bracho, L., Straley, J.M., Taylor, B.L., Urbán, J., Wade, P.R., Weller, D., Witteveen, B.H., Yamaguchi, M., 2013. Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Mar. Ecol. Prog. Ser.* 494, 291–306, <http://dx.doi.org/10.3354/meps10508>.
- Bolaños-Jiménez, J., Mignucci-Giannoni, A.A., Blumenthal, J., Bogomolni, A., Casas, J.J., Henríquez, A., Iñiguez Bessega, M., Khan, J., Landrau-Giovanetti, N., Rinaldi, C., Rinaldi, R., Rodríguez-Ferrer, G., Suty, L., Ward, N., Luksenburg, J.A., 2014. Distribution, feeding habits and morphology of killer whales *Orcinus orca* in the Caribbean Sea. *Mamm. Rev.* 44, 177–189, <http://dx.doi.org/10.1111/mam.12021>.
- Borrell, A., Vacca, A.V., Pinela, A.M., Kinze, C., Lockyer, C.H., Vighi, M., Aguilar, A., 2013. Stable isotopes provide insight into population structure and segregation in eastern North Atlantic sperm whales. *PLoS One* 8, e82398, <http://dx.doi.org/10.1371/journal.pone.0082398>.
- De Luna, C.J., Goodman, S.J., Thatcher, O., Jepson, P.D., Andersen, L., Tolley, K., Hoelzel, A.R., 2012. Phenotypic and genetic divergence among harbour porpoise populations associated with habitat regions in the North Sea and adjacent seas. *J. Evol. Biol.* 25, 674–681, <http://dx.doi.org/10.1111/j.1420-9101.2012.02461.x>.
- Drouot, V., Bérubé, M., Gannier, A., Goold, J.C., Reid, R.J., 2004. A note on genetic isolation of Mediterranean sperm whales (*Physeter macrocephalus*) suggested by mitochondrial DNA. *J. Cetacean Res. Manag.* 6, 29–32.
- Durban, J.W., Fearnbach, H., Burrows, D.G., Ylitalo, G.M., Pitman, R.L., 2016. Morphological and ecological evidence for two sympatric forms of type B killer whale around the Antarctic Peninsula. *Polar Biol.* 40, 1–6, <http://dx.doi.org/10.1007/s00300-016-1942-x>.
- Engelhaupt, D., Rus Hoelzel, A., Nicholson, C., Frantzis, A., Mesnick, S., Gero, S., Whitehead, H., Rendell, L., Miller, P., De Stefanis, R., Cañadas, A., Airolidi, S., Mignucci-Giannoni, A.A., 2009. Female philopatry in coastal basins and male dispersion across the North Atlantic in a highly mobile marine species, the sperm whale (*Physeter macrocephalus*). *Mol. Ecol.* 18, 4193–4205, <http://dx.doi.org/10.1111/j.1365-294X.2009.04355.x>.
- Excoffier, L., Lischer, H.E.L., 2010. Arlequin suite ver3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* 10, 564–567, <http://dx.doi.org/10.1111/j.1755-0998.2010.02847.x>.
- Gero, S., Gordon, J., Carlson, C., Evans, P., Whitehead, H., 2007. Population estimate and inter-island movement of sperm whales, *Physeter macrocephalus*, in the eastern Caribbean Sea. *J. Cetacean Res. Manag.* 9, 140–150.
- Gero, S., Engelhaupt, D., Whitehead, H., 2008. Heterogeneous social associations within a sperm whale, *Physeter macrocephalus*, unit reflect pairwise relatedness. *Behav. Ecol. Sociobiol.* 63, 143–151, <http://dx.doi.org/10.1007/s00265-008-0645-x>.
- Gero, S., Gordon, J., Whitehead, H., 2015. Individualized social preferences and long-term social fidelity between social units of sperm whales. *Anim. Behav.* 102, 15–23, <http://dx.doi.org/10.1016/j.anbehav.2015.01.008>.
- Gero, S., Whitehead, H., Rendell, L., 2016. Individual, unit and vocal clan level identity cues in sperm whale codas. *R. Soc. Open Sci.* 3, 1–12, <http://dx.doi.org/10.1098/rsos.150372>.
- Godard-Coding, C.A.J., Clark, R., Fossi, M.C., Marsili, L., Maltese, S., West, A.G., Valenzuela, L., Rowntree, V., Polyak, I., Cannon, J.C., Pinkerton, K., Rubio-Cisneros, N., Mesnick, S.L., Cox, S.B., Kerr, I., Payne, R., Stegeman, J.J., 2011. Pacific ocean-wide profile of CYP1A1 expression, stable carbon and nitrogen isotope ratios, and organic contaminant burden in sperm whale skin biopsies. *Environ. Health Perspect.* 119, 337–343, <http://dx.doi.org/10.1289/ehp.0901809>.
- Lyrholm, T., Gyllensten, U., 1998. Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. *Proc. R. Soc. – Biol. Sci.* 265, 1679–1684, <http://dx.doi.org/10.1098/rspb.1998.0488>.
- Lyrholm, T., Leimar, O., Johanneson, B., Gyllensten, U., 1999. Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proc. R. Soc. – Biol. Sci.* 266, 347–354, <http://dx.doi.org/10.1098/rspb.1999.0644>.
- Matthews, C.J.D., Longstaffe, F.J., Ferguson, S.H., 2016. Dentine oxygen isotopes (δ18O) as a proxy for odontocete distributions and movements. *Ecol. Evol.* 6, 4643–4653, <http://dx.doi.org/10.1002/ece3.2238>.
- Mazzariol, S., Guardo, G., Di Petrella, A., Marsili, L., Fossi, C.M., Leonzio, C., Zizzo, N., Vizzini, S., Gaspari, S., Pavan, G., Podestà, M., Garibaldi, F., Ferrante, M., Copat, C., Traversa, D., Marcer, F., Airolidi, S., Frantzis, A., de Beraldo Quirós, Y., Cozzi, B., Fernández, A., 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, <http://dx.doi.org/10.1371/journal.pone.0019417>.
- McComb, K., Moss, C., Durant, S.M., Baker, L., Sayialel, S., 2001. Matriarchs as repositories of social knowledge in African elephants. *Science* 292, 491–494.
- Mesnick, S.L., Taylor, B.L., Archer, F.I., Martien, K.K., Treviño, S.E., Hancock-Hanser, B.L., Moreno Medina, S.C., Pease, V.L., Robertson, K.M., Straley, J.M., Baird, R.W., Calambokidis, J., Schorr, G.S., Wade, P., Burkanov, V., Lunsford, C.R., Rendell, L., Morin, P.A., 2011. Sperm whale population structure in the eastern and central North Pacific inferred by the use of single-nucleotide polymorphisms, microsatellites and mitochondrial DNA. *Mol. Ecol. Resour.* 11, 278–298, <http://dx.doi.org/10.1111/j.1755-0998.2010.02973.x>.
- Mesnick, S., 2014. Family *Physeteridae* (sperm whale). In: Wilson, D.E., Mittermeier, R.A. (Eds.), *Handbook of the Mammals of the World, Vol. 4. Lynx Edicions, Barcelona*, pp. 300–317.
- Ottewell, K., Coughran, D., Gall, M., Irvine, L., Byrne, M., 2016. A recent stranding of Omura's whale (*Balaenoptera omurai*) in western Australia. *Aquat. Mamm.* 42, 193–197, <http://dx.doi.org/10.1578/AM.42.2.2016.193>.
- Poole, H., 1989. Mate guarding, reproductive success and female choice in African elephants. *Anim. Behav.* 37, 842–849.
- Rendell, L., Whitehead, H., 2004. Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurement. *Anim. Behav.* 67, 865–874, <http://dx.doi.org/10.1016/j.anbehav.2003.04.018>.
- Rendell, L., Mesnick, S.L., Dalebout, M.L., Burtenshaw, J., Whitehead, H., 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter*

- macrocephalus*? Behav. Genet. 42, 332–343, <http://dx.doi.org/10.1007/s10519-011-9513-y>.
- Richard, K.R., Dillon, M.C., Whitehead, H., Wright, J.M., 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proc. Natl. Acad. Sci. U. S. A. 93, 8792–8795, <http://dx.doi.org/10.1073/pnas.93.16.8792>.
- Sabatier, E., Pante, E., Dussud, C., Canneyt, O., Sabatier, Van, Pante, E., Dussud, E., Canneyt, C., Van, O., Simon, B., 2015. Genetic monitoring of pilot whales, *Globicephala* spp. (Cetacea: Delphinidae), stranded on French coasts. Mammalia 79, 111–114.
- Schnitzler, J.G., Frédérich, B., Früchticht, S., Schaffeld, T., Baltzer, J., Ruser, A., Siebert, U., 2017. Size and shape variations of the bony components of sperm whale cochleae. Sci. Rep. 7 (46734), <http://dx.doi.org/10.1038/srep46734>.
- Schulz, T.M., Whitehead, H., Gero, S., Rendell, L., 2008. Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. Anim. Behav. 76, 1977–1988, <http://dx.doi.org/10.1016/j.anbehav.2008.07.032>.
- Squadrone, S., Brizio, P., Chiaravalle, E., Abete, M.C., 2015. Sperm whales (*Physeter macrocephalus*), found stranded along the Adriatic Coast (southern Italy, Mediterranean Sea), as bioindicators of essential and non-essential trace elements in the environment. Ecol. Indic. 58, 418–425, <http://dx.doi.org/10.1016/j.ecolind.2015.06.016>.
- Stoeger, A.S., Baotic, A., 2016. Information content and acoustic structure of male African elephant social rumbles. Sci. Rep. 6, 27585, <http://dx.doi.org/10.1038/srep27585>.
- Tiedemann, R., Milinkovitch, M.C., 1999. Culture and genetic evolution in whales. Science 284, 2055a, <http://dx.doi.org/10.1126/science.284.5423.2055a>.
- Unger, B., Wohlsein, P., Herr, H., 2016. Large amounts of marine debris found in sperm whales stranded along the North Sea coast in early 2016. Mar. Pollut. Bull. 112, 134–141, <http://dx.doi.org/10.1016/j.marpolbul.2016.08.027>.
- Valenzuela, L.O., Sironi, M., Rowntree, V.J., Seger, J., 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). Mol. Ecol. 18, 782–791, <http://dx.doi.org/10.1111/j.1365-294X.2008.04069.x>.
- Valsecchi, E., Corkeron, P., Galli, P., Sherwin, W., Bertorelle, G., 2010. Genetic evidence for sex-specific migratory behaviour in western South Pacific humpback whales. Mar. Ecol. Prog. Ser. 398, 275–286, <http://dx.doi.org/10.3354/meps08280>.
- Whitehead, H., 1993. The behaviour of mature male sperm whales on the Galapagos Islands breeding grounds. Can. J. Zool. 71, 689–699.
- Whitehead, H., 1998. Cultural selection and genetic diversity in matrilineal whales. Science 282, 1708–1711.
- Whitehead, H., 2003. Sperm Whales: Social Evolution in the Ocean. The University of Chicago Press, Chicago, Illinois.
- Winsor, M.H., Mate, B.R., 2016. Seismic survey activity and the proximity of satellite-tagged sperm whales *Physeter macrocephalus* in the Gulf of Mexico. Bioacoustics 17, 191–193, <http://dx.doi.org/10.1080/09524622.2008.9753813>.