

# Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*)

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**Abstract:** We investigated the use and function of coda communication by sperm whales (*Physeter macrocephalus* L., 1758 (= *Physeter catodon* L., 1758)). Codas are stereotyped patterns of clicks often made by sperm whales in social contexts. We used the pulsed structure of coda clicks recorded from socializing female/immature groups to estimate the body-length distribution of the animals producing the codas. Ninety-five percent of the 10 653 codas that we measured were produced by whales measuring from 9 to 11 m. This size range corresponds to the lengths of mature females. We compared these data to a length distribution calculated from photographic measurements of individuals from the same groups encountered during the same studies. There were more whales shorter than 8.5 m (10.0%) and longer than 12.5 m (2.7%) in the photographic length distribution than in that of the coda producers (0.30% and 0.08%, respectively). Since males leave their natal group when they are shorter than 9 m and return to breeding areas when they measure 13 m or more, our data show that the codas were produced almost entirely by mature females. We suggest that coda communication serves several functions, including social bonding.

**Résumé :** Nous avons étudié l'utilisation et les fonctions de la communication par « codas » du cachalot (*Physeter macrocephalus* L., 1758 (= *Physeter catodon* L., 1758)). Les codas sont formées d'une série de cliquetis qui possèdent un pattern stéréotypé. Nous avons suivi des groupes sociaux de femelles et de jeunes et enregistré leurs codas afin d'estimer la distribution des tailles des cachalots qui les produisent à partir de la structure pulsée des cliquetis. Quatre-vingt-quinze pour cent des 10 653 codas analysées ont été produites par des cachalots mesurant de 9 à 11 m. Ces longueurs correspondent à la taille des femelles matures. Nous avons comparé ces résultats avec la distribution des longueurs calculée à partir de photos prises lors des mêmes études. Il y avait plus de cachalots mesurant moins de 8,5 m (10,0 %) et plus de 12,5 m (2,7 %) dans les estimations faites à partir de photos que dans celles réalisées à partir des codas (0,30 % et 0,08 %, respectivement). Les codas semblent émises presque exclusivement par les femelles matures puisque les mâles quittent les groupes de femelles et de jeunes lorsqu'ils mesurent moins de 9 m et y reviennent lorsqu'ils mesurent plus de 13 m. Nous pensons que la communication par codas sert entre autres au renforcement des liens sociaux.

## Introduction

Communication is essential to animal societies. It mediates competition, allows group cohesion, and facilitates reproduction (Bradbury and Vehrencamp 1998). Individuals can use signals to manipulate one another, or signal their identity, status, and mood. They can also share information about their environment.

Some species show sexual dimorphism in their signals. The sexual differentiation is almost always linked to reproduction, territorial defence, infant care, or group coordination. For example, the brown ghost knifefish (*Apteronotus leptorhynchus* (Ellis in Eigenmann, 1912)) produces sexually dimorphic electric organ discharges that are emitted most often during courtship and mating (Bastian et al. 2001). Male fiddler crabs (species of *Uca* Leach, 1814) possess a single enlarged claw that they wave to attract females and repulse neighbouring

males (Crane 1975). Sexual selection and differences in mating and reproductive strategies between sexes resulting from differential investment in offspring are likely behind such divergent communication systems (Alcock 1998).

In species where one sex takes over the care of the offspring, there are often signals unique to that sex which are involved in such care. For example, female mallard ducks (*Anas platyrhynchos* L., 1758) produce a species-specific and sex-specific call to their ducklings before they hatch. When the ducklings emerge from their eggs, they already recognize their species call (Bright 1984).

Differences between the sexes in communication signals related to group coordination may take place in social species with sexual segregation. Female African elephants (*Loxodonta africana* (Blumenbach, 1797)) and their offspring live in matriarchal groups, whereas adult males stay mostly

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solitary (Moss and Poole 1983). Females have a larger vocal repertoire than the males (Poole 1994). Most of the female calls are related to family/bond-group dynamics, cohesion and coordination, or reproduction and communication with males (Poole 1994).

Sperm whales (*Physeter macrocephalus* L., 1758 (= *Physeter catodon* L., 1758)) exhibit extreme physical and behavioural dimorphism. Mature males have three times the mass of females (Rice 1989). Nonbreeding sperm whales are also the most sexually segregated of all species: females tend to stay in tropical or subtropical waters within the 40° parallels, while males separate from their mother's unit and move to colder waters, sometimes up to the polar seas bordering the pack ice (Rice 1989).

Female sperm whales reach sexual maturity when they measure 8.3–9.2 m (around 7–13 years old) and are physically mature at 10.4–11.0 m (Rice 1989). They form, with their immature offspring, social “units” of ca. 10–12 individuals with nearly permanent membership (Whitehead and Weilgart 2000). Most of the male sperm whales leave their mother's unit at around age 6 (Whitehead and Weilgart 2000), when they would measure roughly 8.5 m (from the growth curve of Rice 1989). Mature males return to the female – immature unit areas to breed when they measure around 13 m, and are in their late 20s (Best 1979). There is little evidence of any form of long-term associations among males (Lettevall et al. 2002), although males are known to mass-strand on beaches together (Rice 1989).

Male and female sperm whales emit sharp, impulsive, broadband clicks (Backus and Schevill 1966). They produce several types of clicks with an assortment of repetition rates ranging from 220 clicks per s to 1 click every 5–7 s (for a review see Jaquet et al. 2001). They also make codas that are short, stereotypically patterned series of 3–40 clicks which are thought to function in communication (Watkins and Schevill 1977). Codas are principally produced during periods of social behaviour (Whitehead and Weilgart 1991), but are also heard in small numbers during foraging dives (Madsen et al. 2002).

In the present study, we investigate which sperm whales produce codas, using the inter-pulse intervals (IPIs) of clicks within codas. These intervals are proportional to the physical dimensions of the click-producing apparatus, and thus are monotonically related to the length of the producer (Adler-Fenchel 1980; Møhl et al. 1981; Gordon 1991; Pavan et al. 2000; Rhineland and Dawson 2004). By this method, we are able to estimate the size of sperm whales and infer which age and sex classes produce the codas.

## Materials and methods

### Recordings

The data for this analysis were collected in the tropical and subtropical South Pacific Ocean during the years 1985–2000 from 10 to 13 m auxiliary sailing vessels. Groups of female and immature sperm whales were tracked and followed visually and acoustically (see Appendix of Whitehead 2003). Acoustic recordings of coda vocalizations were made using omni-directional hydrophones (Offshore Acoustics, frequency response 6 Hz – 10 kHz,  $\pm 3$  dB, with no pre-amplifier, or Benthos AQ17/modified AQ21B, frequency response 1–10 kHz,  $\pm 3$  dB connected via Barcus-Berry “Standard” or Ithaca 453

pre-amplifiers), recorded either on a cassette recorder (Sony TC-D5M) or a reel-to-reel tape recorder (Uher 4000, Sony TC770 or Nagra IV-SJ), and digitized at 44.1 kHz. The maximum depth of recording was 10 m and the range to the whales was estimated to be between 50 and 500 m, although the ranges were not measured. Codas were extracted using the software package Rainbow Click (Gillespie 1997) for analysis (for more detail see Rendell and Whitehead 2003). Fifteen thousand and seventy nine codas recorded on 111 different days were extracted and available for analysis.

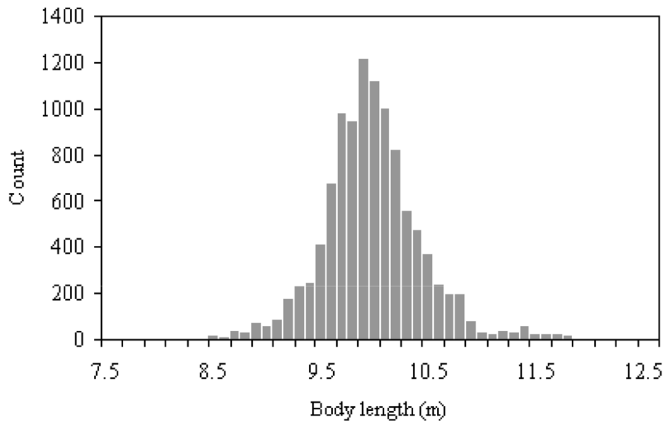
### IPI measurements

We used automated routines written in MATLAB® version 6.1.450, release 12.1 (MathWorks Inc. 2001) to implement Goold's (1996) cross-correlation and cepstrum methods for estimating the inter-pulse interval (IPI) of each click in each coda (as in Rendell and Whitehead 2004). Both methods fail when the IPI signal is not clear in the waveform owing to, for example, interference from other sounds, surface or other reflections of pulses, directionality of emission effects, or overloading. One particular problem for both methods was spurious low IPI values caused by the routine becoming confused by clicks that had an extended first pulse, thus we had to introduce a minimum IPI below which estimates were rejected. We set this limit at 2 ms, which corresponds to a body length of 7.7 m; a size that male and female sperm whales attain at around 4 and 6 years old, respectively (from the growth curve in Rice 1989). Thus, our method could not have measured codas from animals aged 3 or less. We set an upper limit of 9 ms, which corresponds to a body length of 17.8 m; a size that is larger than any of the mature males measured by Rhineland and Dawson (2004). Thus, estimated body lengths were constrained within the limits of 7.7 and 17.8 m.

With a 44.1 kHz sample rate, our maximum time resolution was 0.02 ms; in terms of estimated body length, an increase of 0.02 ms from a 4 ms IPI changes the body length estimate by about 3 cm. For each coda and each IPI estimation method, we estimated the IPI of each of its constituent clicks, and the proportion of clicks with identical IPI estimates (to within 0.02 ms). Codas with 50% or more identical IPI estimates (from either method) were retained for further analysis, since we assumed that repeatedly obtaining an IPI estimate identical to within the limits of our sampling rate from one coda was reasonable evidence that this modal value was the true IPI of the vocalizing animal. Another source of variation in IPI measurement may be due to the orientation of the whale in relation to the hydrophone, since off-axis clicks recorded ahead of whales present varying pulse structures (Zimmer et al. 2005). However, these confused structures (Fig. 4 in Zimmer et al. 2005) would likely give rise to variation in the IPI estimates and reduce the probability of multiple identical estimates as required by the above condition. Furthermore, the field protocols used for this study — specifically the animals being approached from behind — led to most recordings being made behind the focal whales and this position seems suitable for size estimation (Zimmer et al. 2005).

We used the equation developed by Gordon (1991) relating body length to IPI to estimate the body length of the vo-

**Fig. 1.** Body length distribution of coda producers estimated from IPI measurements of codas ( $n = 10\,653$ ). Five length estimates  $>12.5$  m are excluded from the figure for visual clarity.



calizing animal. We then compared the length distributions of coda producers in groups off the Galápagos from 1985 to 1987 and off Ecuador during 1991 with photographic measurements of whales from the same groups during these studies (Waters and Whitehead 1990; Kahn et al. 1993). The photographic measurement technique is that of Gordon (1990) and requires photographs being taken perpendicular to the whales that show its back and the horizon. The analytical methods are described and the data summarized by Waters and Whitehead (1990) and Kahn et al. (1993).

**Results**

A total of 10 653 codas out of 15 079 (70.6%) had 50% or more of their IPI estimates identical and were retained in the analysis. The IPI modes of the codas ranged from 2.01 to 8.14 ms, with a mean of 3.52 ms. These translate into a size range of 7.76–16.60 m, with a mean of 9.94 m. Ninety-five percent of the codas were produced by whales 9–11 m long, while 0.54% were from whales 7.7–8.5 m long and 0.07% from whales longer than 12.5 m (Fig. 1).

Length measurement distributions (from 7.7 to 17.8 m) from photographs of sperm whales off the Galápagos from 1985 to 1987 (834 measurements; Waters and Whitehead 1990) and off Ecuador during 1991 (343 measurements; Kahn et al. 1993) were compared with 2641 acoustic length measurements of coda producers from the same areas during the same periods (Fig. 2). A Pearson’s  $\chi^2$  test of the proportions of measurements in 0.2 m bins (from 7.9 to 11.9 m, with outliers included in the extreme categories) showed that the two distributions were different ( $\chi^2_{[20]} = 879.563$ ,  $P < 0.001$ ). There were more whales estimated to be shorter than 8.5 m (10.0%) and longer than 12.5 m (2.7%) in the photographic length distribution than in that of the coda producers for these studies (0.30% and 0.08%, respectively), even though the photographic length measurement method is thought to underestimate the proportion of small animals in the population (Waters and Whitehead 1990). Moreover, 46% of the codas in our sample were recorded in the presence of at least one mature male interacting with the females or within approximately 20 km from the females.

Fifty-eight (0.54%) codas gave IPI estimates smaller than 2.2 ms, which correspond to 8.5 m. After a visual examina-

tion of the waveform of each separate click and manually measuring IPIs where possible, we determined that only 26 were “true” IPIs. The other IPI estimates resulted from the cross-correlation routine becoming confused by clicks that had an extended first pulse ( $>2$  ms) so that the larger correlation between the first pulse and itself obscured the one between the first pulse and the second. The 26 codas with small and reliable IPI estimates were recorded on five different days. The IPI modes of these codas are shown in Fig. 3.

Nineteen of the 26 codas with low length estimates were recorded during 2 days when “juveniles” were noted as being present (20 July 2000: one juvenile; 24 July 2000: two juveniles). The modal IPIs of these codas were 2.33 and 2.52 ms, respectively, and the corresponding body lengths were 8.21 and 8.48 m, suggesting ages of about 8–9 years for a female or 6 years for a male (Rice 1989).

Using Gordon’s (1991) equation, 7 (0.07%) codas recorded corresponded to a body length longer than 12.5 m. However, for all the values, we manually looked at the waveform and found that they were false measurements resulting from errors in the calculation routines. The routines likely give high estimates when the first and third pulses of a click are more correlated than the first and second.

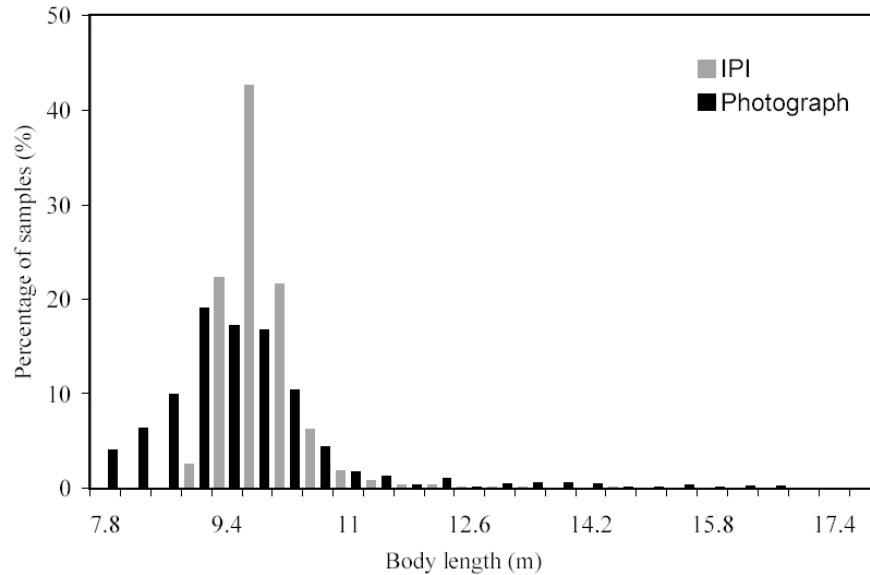
Given the high frequency of errors in the extreme IPI values, we manually calculated IPI values for 201 codas randomly selected from the 10 653 codas used in the analysis. One hundred and eighty-five (95%) of the codas manually analysed had a difference smaller than 5% from the automated calculation.

**Discussion**

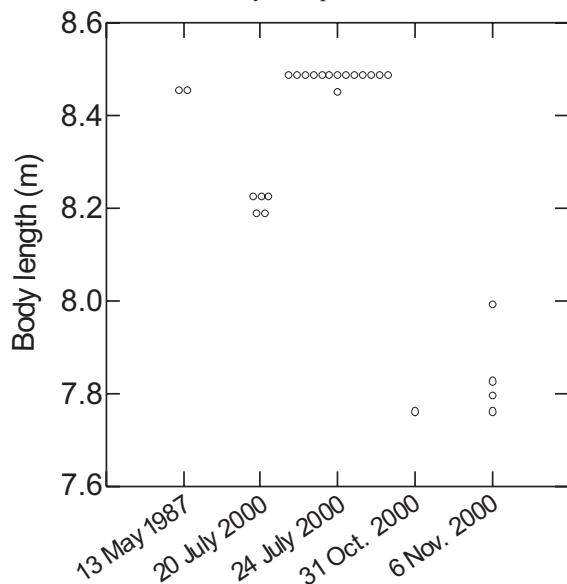
Ninety-five percent of the length measurements calculated with IPI measurements from codas range from 9 to 11 m. These results suggest that the recorded codas were almost exclusively produced by mature females. The codas are not likely to be produced by males, since they leave the female–immature units when they are shorter than 9 m and return to the breeding grounds when they measure around 13 m (Best 1979). Length measurements derived from photographs showed that whales of larger (mature males) and smaller (juveniles of both sexes) sizes were present when the codas were recorded.

There are examples in the literature of male sperm whales producing codas. Pavan et al. (2000) recorded codas from males in the Mediterranean Sea. However, the context of the recordings was different from that of our study. The males sometimes produced a coda at the end of a series of usual (regularly spaced echolocation) clicks (Pavan et al. 2000), thus conforming with the musical definition of “coda”, whereas in our recordings the codas were either part of a coda exchange among whales or heard without other vocalizations. The males in the Mediterranean were found in smaller groups (1–4 whales) than the females of our study (10–30 whales; Whitehead and Waters 1990). One hundred thirty-four of the 138 codas recorded by Pavan et al. (2000) were of only one type (“3+1”), whereas there was a great diversity of types in our recordings (33 types; Rendell and Whitehead 2003). Recent recordings of groups of females in the western Mediterranean Sea show a greater diversity of coda types (L. Rendell, unpublished data). Thus, although males

**Fig. 2.** Body length distributions of sperm whales from the Galápagos, 1985–1987, and Ecuador, 1991, calculated from both acoustic (IPIs of codas,  $n = 2641$ ) and photographic ( $n = 1177$ ) measurements.



**Fig. 3.** Body length measurements <8.5 m calculated from “true” IPI measurements (see text) of codas by date of recording. Identical measurements on the same day are spread out on the x axis.



have the ability to produce codas, they made hardly any in the social contexts in which we made our recordings.

Fifty-four percent of the codas in our sample were recorded when there were no mature males interacting with the females; they were not even within a few tens of kilometres from the females. In addition, 73% of our codas were recorded when there was no calf in the group. Therefore, coda production can neither be solely related to mate attraction nor to the care of calves.

The main threat for female sperm whales (other than anthropogenic impacts such as whaling) is predation by killer whales, *Orcinus orca* (L., 1758) (Whitehead 2003; Pitman et al. 2001). Sperm whales defend themselves communally (Whitehead 2003) and seem to participate in allomaternal

care of the calves (Whitehead 1996). In addition, they might increase their feeding success through group foraging (Best 1979). If these are the major driving forces behind sperm whale sociality, then forming associations with other females becomes crucial. Our current understanding of coda production suggests that they may be important in forming and maintaining these associations. For example, the production of codas is correlated with other social behaviours (Whitehead and Weilgart 1991) and they are often heard in exchanges between socializing animals (Whitehead 2003). Moreover, the nonrandomized order of the codas in exchanges may suggest a type of conversation (Weilgart and Whitehead 1993).

Mature male sperm whales might not need to be social in the same way as females. Maturing males form bachelor schools (Gaskin 1970), although there is no evidence that these include long-term bonds (Lettevall et al. 2002). Therefore, unlike the females, they may not need to use coda communication to the same extent. Investigation of vocal behaviour within these bachelor schools could help assess the functions of codas with respect to sociality.

Finally, our observation that coda production seems restricted largely to mature females suggests a parallel with communication in African elephants (Weilgart et al. 1996; Whitehead 2003), where females have a larger vocal repertoire than males (Poole 1994). Female elephants live in matriarchal groups (Moss and Poole 1983) where the older females lead the family units and are sources of important social knowledge (McComb et al. 2001). More work detailing coda production at the individual level is needed to explore this further.

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## References

- Adler-Fenchel, H.S. 1980. Acoustically derived estimate of the size distribution for a sample of sperm whales (*Physeter catodon*) in the Western North Atlantic. *Can. J. Fish. Aquat. Sci.* **37**: 2358–2361.
- Alcock, J. 1998. *Animal behaviour: an evolutionary approach*. Sinauer Associates, Inc., Sunderland, Mass.
- Backus, R.H., and Schevill, W.E. 1966. *Physeter* clicks. In *Whales, dolphins and porpoises*. Edited by K.S. Norris. University of California Press, Berkeley. pp. 510–527.
- Bastian, J., Schniederjan, S., and Nguyenkim, J. 2001. Arginine vasotocin modulates a sexually dimorphic communication behavior in the weakly electric fish *Apteronotus leptorhynchus*. *J. Exp. Biol.* **204**: 1909–1923. PMID: 11441033.
- Best, P.B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. In *Behavior of marine animal*. Vol. 3. Cetacea. Edited by H.E. Winn and B.L. Olla. Plenum Press, New York. pp. 227–289.
- Bradbury, J.W., and Vehrencamp, S.L. 1998. *Principles of animal communication*. Sinauer Associate, Inc., Sunderland, Mass.
- Bright, M. 1984. *Animal language*. British Broadcasting Corporation, London, UK.
- Crane, J. 1975. *Fiddler crabs of the world*. Ocypodidae: genus *Uca*. Princeton University Press, Princeton, N.J.
- Gaskin, D.E. 1970. Composition of schools of sperm whales *Physeter macrocephalus* Linn. east of New Zealand. *N.Z. J. Mar. Freshw. Res.* **4**: 456–471.
- Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the R/V *Aurora Australis*. *Rep. Int. Whal. Comm. No. 47*. pp. 897–908.
- Goold, J.C. 1996. Signal processing techniques for acoustic measurement of sperm whale body lengths. *J. Acoust. Soc. Am.* **100**: 3431–3441. doi:10.1121/1.416984. PMID: 8914321.
- Gordon, J.C.D. 1990. A simple photographic technique for measuring the length of whales from boats at sea. *Rep. Int. Whal. Comm. No. 40*. pp. 581–588.
- Gordon, J.C.D. 1991. Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalization. *J. Zool. (Lond.)*, **224**: 301–314.
- Jaquet, N., Dawson, S., and Douglas, L. 2001. Vocal behavior of male sperm whales: Why do they click? *J. Acoust. Soc. Am.* **109**: 2254–2259. doi:10.1121/1.1360718. PMID: 11386576.
- Kahn, B., Whitehead, H., and Dillon, M. 1993. Indication of density-dependent effects from comparisons of sperm whale populations. *Mar. Ecol. Prog. Ser.* **93**: 1–7.
- Lettevall, E., Richter, C., Jaquet, N., Slooten, E., Dawson, S., Whitehead, H., Christal, J., and McCall Howard, P. 2002. Social structure and residency in aggregations of male sperm whales. *Can. J. Zool.* **80**: 1189–1196. doi:10.1139/z02-102.
- Madsen, P.T., Payne, R., Kristiansen, N.U., Wahlberg, M., Kerr, I., and Møhl, B. 2002. Sperm whale sound production studied with ultrasound time/depth-recording tags. *J. Exp. Biol.* **205**: 1899–1906. PMID: 12077166.
- MathWorks Inc. 2001. *MATLAB®*. Version 6.1.450, release 12.1, with Signal Processing Toolbox [computer program]. The MathWorks Inc., Natick, Mass.
- McComb, K., Moss, C., Durant, S.M., Baker, L., and Sayialel, S. 2001. Matriarchs as repositories of social knowledge in African elephants. *Science (Washington, D.C.)*, **292**: 491–494. PMID: 11313492.
- Møhl, B., Larsen, E., and Amundin, M. 1981. Sperm whale size determination: outlines of an acoustic approach. *FAO Fish. Ser.* **5**: 327–332.
- Moss, C.J., and Poole, J.H. 1983. Relationships and social structure of African elephants. In *Primate social relationships: an integrated approach*. Edited by R. Hinde. Blackwell Scientific, London. pp. 315–325.
- Pavan, G., Hayward, T.J., Borsani, J.F., Priano, M., Manghi, M., Fosfati, C., and Gordon, J. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985–1996. *J. Acoust. Soc. Am.* **107**: 3487–3495. doi:10.1121/1.429419. PMID: 10875393.
- Pitman, R.L., Ballance, L.T., Mesnick, S.L., and Chivers, S. 2001. Killer whale predation on sperm whales: observations and implications. *Mar. Mamm. Sci.* **17**: 494–507.
- Poole, J.H. 1994. Sex differences in the behaviour of African elephants. In *The differences between the sexes*. Edited by R.V. Short and E. Balaban. Cambridge University Press, New York. pp. 331–346.
- Rendell, L., and Whitehead, H. 2003. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. Lond. B. Biol. Sci.* **270**: 225–231. doi:10.1098/rspb.2002-2239.
- Rendell, L., and Whitehead, H. 2004. Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurement. *Anim. Behav.* **67**: 865–874. doi:10.1016/j.anbehav.2003.04.018.
- Rhineland, M.Q., and Dawson, S.M. 2004. Measuring sperm whales from their clicks: stability of interpulse intervals and validation that they indicate whale length. *J. Acoust. Soc. Am.* **115**: 1826–1831. doi:10.1121/1.1689346. PMID: 15101660.
- Rice, D.W. 1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758. In *Handbook of marine mammals*. Vol. 4. Edited by S.H. Ridgway and R. Harrison. Academic Press, London. pp. 177–233.
- Waters, S., and Whitehead, H. 1990. Population and growth parameters of Galápagos sperm whales estimated from length distributions. *Rep. Int. Whal. Comm. No. 40*. pp. 225–235.
- Watkins, W.A., and Schevill, W.E. 1977. Sperm whale codas. *J. Acoust. Soc. Am.* **62**: 1485–1490. doi:10.1121/1.381678.
- Weilgart, L., and Whitehead, H. 1993. Coda vocalizations in sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. *Can. J. Zool.* **71**: 744–752.
- Weilgart, L., Whitehead, H., and Payne, K. 1996. A colossal convergence. *Am. Sci.* **84**: 278–287.
- Whitehead, H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* **38**: 237–244. doi:10.1007/s002650050238.
- Whitehead, H. 2003. *Sperm whale societies; social evolution in the ocean*. University of Chicago Press, Chicago.
- Whitehead, H., and Waters, S. 1990. Social organization and population structure of sperm whales off the Galápagos Islands, Ecuador (1985 and 1987). *Rep. Int. Whal. Comm. Spec. Issue No. 12*. pp. 249–257.
- Whitehead, H., and Weilgart, L. 1991. Patterns of visually observable behavior and vocalizations in groups of female sperm whales. *Behaviour*, **118**: 275–296.
- Whitehead, H., and Weilgart, L. 2000. The sperm whale: social females and roving males. In *Cetacean societies: field studies of whales and dolphins* Edited by J. Mann, R.C. Connor, P.L.

Tyack, and H. Whitehead. The University of Chicago Press, Chicago. pp. 154–172.

Zimmer, W.M.X., Madsen, P.T., Telson, V., Johnson, M.P., and Tyack, P.L. 2005. Off-axis effects on the multipulse structure of

sperm whale usual clicks with implications for sound production. *J. Acoust. Soc. Am.* **118**: 3337–3345. doi:10.1121/1.2082707. PMID: 16334703.