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Author:

[Cozzi, Bruno](#), Department of Comparative Biomedicine and Food Science, University of Padova
[Mazzariol, Sandro](#), Department of Comparative Biomedicine and Food Science, University of Padova

[Podestà, Michela](#), Museum of Natural History of Milan

[Zotti, Alessandro](#), Department of Animal Medicine, Production and Health, University of Padova

[Huggenberger, Stefan](#), , Department II of Anatomy (Neuroanatomy), University of Cologne

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Abstract:

The sperm whale *Physeter macrocephalus* (Linnaeus, 1758) is the largest toothed whales and possesses the highest absolute values for brain weight on the planet (together with the killer whale *Orcinus orca*). Former calculations of the encephalization quotient (EQ), which is used to compare brain size of different mammalian species, showed that the sperm whale brain is smaller than expected for its body mass. However, the data reported in the literature and formerly used to calculate the sperm whale EQ suffered from a potential bias due to the tendency to measure mostly larger males of this extreme sexually dimorphic species. Accordingly, we found that the brains of female sperm whales are close to the absolute weight range of the males, but, given



the much lower body mass of females, their EQ results more than double of what reported before for the whole species, and is thus nearly into the primate range (female EQ = 1.28, male EQ = 0.56). This sexual dimorphism is unique among mammals. Female sperm whales live in large families in which social interactions and inter-individual communication are essential, while adult males live solitarily. Thus the particular sex-specific behavior of SWs may have led to a maternally-driven social evolution, and eventually contributed to achieve female EQ values (but not male EQs) among the highest ever calculated for mammals with respect to their large body mass.

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An Unparalleled Sexual Dimorphism of Sperm Whale Encephalization

**Bruno Cozzi¹, Sandro Mazzariol¹, Michela Podestà², Alessandro Zotti³,
and Stefan Huggenberger⁴**

¹*University of Padova, Italy*

²*Museum of Natural History of Milan, Italy*

³*University of Padova, Italy*

⁴*University of Cologne, Germany*

The sperm whale *Physeter macrocephalus* (Linnaeus, 1758) is the largest toothed whales and possesses the highest absolute values for brain weight on the planet (together with the killer whale *Orcinus orca*). Former calculations of the encephalization quotient (EQ), which is used to compare brain size of different mammalian species, showed that the sperm whale brain is smaller than expected for its body mass. However, the data reported in the literature and formerly used to calculate the sperm whale EQ suffered from a potential bias due to the tendency to measure mostly larger males of this extreme sexually dimorphic species. Accordingly, we found that the brains of female sperm whales are close to the absolute weight range of the males, but, given the much lower body mass of females, their EQ results more than double of what reported before for the whole species, and is thus nearly into the primate range (female EQ = 1.28, male EQ = 0.56). This sexual dimorphism is unique among mammals. Female sperm whales live in large families in which social interactions and inter-individual communication are essential, while adult males live solitarily. Thus the particular sex-specific behavior of SWs may have led to a maternally-driven social evolution, and eventually contributed to achieve female EQ values (but not male EQs) among the highest ever calculated for mammals with respect to their large body mass.

The encephalization quotient (EQ; Jerison, 1973) is one of the most diffuse equations used to compare the brains of different mammalian species (Boddy et al., 2012; Roth, 2015) and predicts whether a certain species has a brain larger (EQ > 1), equal (EQ = 1), or smaller (EQ < 1) than expected for its body mass. The mammalian species that have EQ > 1 include apes and some small sized dolphins. Elephants and killer whales are the only large mammals (weighing far more than 1 ton) with an EQ > 1. It is common knowledge that sperm whales (SW; *Physeter macrocephalus*) and killer whales (KW; *Orcinus orca*) possess the heaviest brains on the planet (SW: 9.20 g, KW: 9.30 g; Figure 1; Kojima, 1951; Shindo, 1975) but the enormous body mass of SW prompts a relatively low EQ value (EQ < 1; Manger, 2006). Other large bodied mammals like Perissodactyla (horses and rhinos) and most Cetartiodactyla (including hippos, giraffes and several even-toed mammals) fall in the group of the below-the-expected EQ (EQ < 1). It has been hypothesized that brain expansion in mammals is evolutionary associated, among other parameters, to sociality (Dunbar, 1998; Marino et al., 2007; Shultz & Dunbar, 2010). The EQ is not per se a sign of intelligence (Dicke & Roth, 2016); however, a lower than 1 value suggests certain limitations to cognitive capabilities (e.g., self-recognition, use of tools) or to the ability to build complex social interactions with fellows of the same and other species (reviewed by Gregg, 2013).

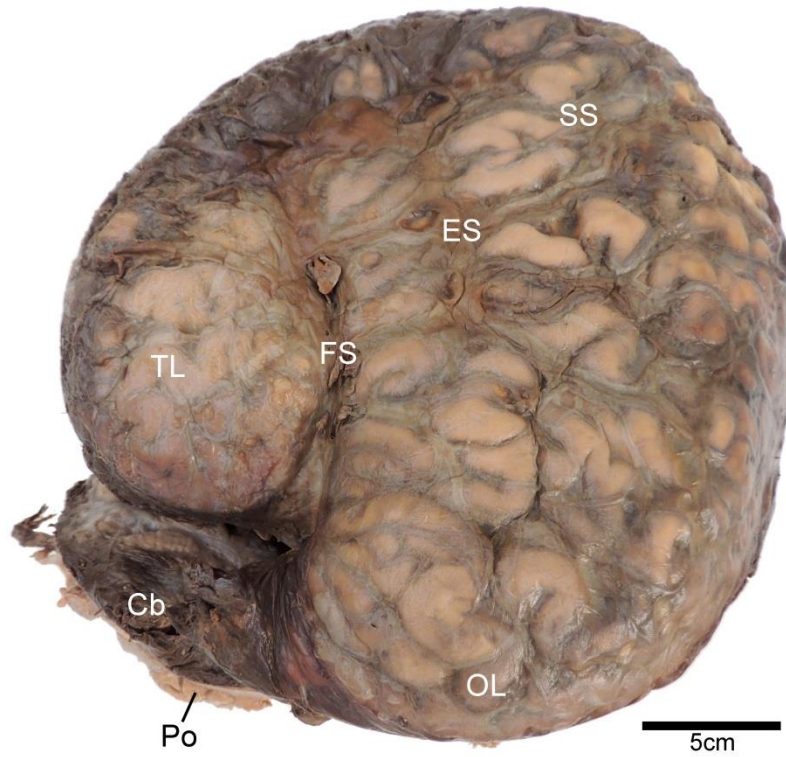


Figure 1. Right lateral view of the brain of an adult female sperm whale (ID # 335, Mediterranean marine mammal tissue bank, Padova) with pia mater and blood vessels attached. Cb: cerebellum, ES: ectosylvian sulcus, FS: Sylvian cleft, OL: orbital lobe, Po: Pons, SS: suprasylvian sulcus, TL: temporal lobe.

Here we re-examined the data of SWs available in the literature, added fresh information, and re-calculated the EQ. In comparison, we also added data on KW.

Method

Data on all the cetaceans brains were obtained by the literature or by directly measuring SW brain weights in our laboratories. Provenience of the brains and specimens is listed in Tables 1 and 2.

To calculate the EQ we used the classical formula $EQ = E_i / 0.12 \times P^{2/3}$; E_i = mean brain weight, P = mean body weight (Jerison, 1973). We are aware of the existence of alternatives to the classical formula, proposed to slightly correct the value of the slope (Kruska, 2005) but decided to use the most accepted formula, since its general significance remains.

Weight of the bodies were either available from the literature or calculated using specific formulas reported in the literature. For details see Tables 1 and 2. Statistical differences were tested by the Mann-Whitney U-Test using the Merlin Statistics Software 2.5 (Millar, 2015).

Table 1
 Data Available in the Literature on the Brain of Sperm Whales

Species	Body weight (kg) from reference	Body weight (kg) calculated after (Lockyer, 1976)	Body weight (kg) calculated after (Best, 2009)	Body weight (kg) calculated after (Gingerich, 2016) *	Body length (m)	Brain weight (g)	EQ	References and notes
<i>Physeter macrocephalus</i> females		15,171	13,640	10,646	10.90	5,500	0.76	(Berzin, 1972; Povinelli et al., 2014), EQ calculated with body weight calculated after (Best, 2009)
		13,339	11,993	9,342	10.40	6,500	0.98	
	8,840	8,840	7,948	6,150	8.95	6,700	1.33	
	5,115	5,115	4,599	3,527	7.33	7,200	2.06	
	17,000	NA	NA	NA	NA	5,428	0.65	
M	6,978	10,616	9,545	7,416	9.40	6,475	1.28	
<i>Physeter macrocephalus</i> males	42,500	46,186	41,525	32,997	16.36	6,400	0.41	(Kojima, 1951), body weight calculated by (Gihl & Pilleri, 1969)
	41,000	41,646	37,443	29,703	15.76	7,000	0.46	
	41,000	39,492	35,506	28,143	15.46	7,000	0.46	
	34,000	35,386	31,815	25,172	14.85	7,000	0.52	
	34,000	35,386	31,815	25,172	14.85	7,000	0.52	
	34,000	35,386	31,815	25,172	14.85	7,300	0.55	
	35,000	37,403	33,628	26,631	15.15	7,700	0.57	
	42,500	46,186	41,525	32,997	16.36	8,000	0.52	
	41,000	39,492	35,506	28,143	15.46	8,000	0.53	
	35,000	37,403	33,628	26,631	15.15	8,000	0.59	
	34,000	35,386	31,815	25,172	14.85	8,000	0.60	
	34,000	35,386	31,815	25,172	14.85	8,200	0.61	
	39,000	25,138	22,601	17,784	13.11	8,338	0.57	
	28,000	29,767	26,763	21,117	13.94	8,600	0.73	
	42,500	46,186	41,525	32,997	16.36	8,700	0.56	
	41,000	39,492	35,506	28,143	15.46	9,000	0.59	
	34,000	35,386	31,815	25,172	14.85	9,200	0.69	
	36,700	35,990	32,358	25,609	14.94	9,200	0.66	
M	37,178	37,594	33,800	26,774	15.14	7,924	0.56	(Ridgway & Hanson, 2014), original data in (Jacobs & Jensen, 1964)

Note. * The body weight calculation after Gingerich (2016) is based on a formula deriving from extant cetaceans and not explicitly from sperm whales. NA = not available.

Table 2

Data Available in the Literature on the Brain of Killer Whales

Species	Body weight (kg) from reference	Body weight (kg) calculated after (Lockyer, 1976)	Body weight (kg) calculated after (Best, 2009)	Body weight (kg) calculated after (Gingerich, 2016) *	Body length (m)	Brain weight (g)	EQ	References and notes
<i>Orcinus orca</i> females	1,862		1,963	1,378	5.23	4,500	2.36	(Lilly, 1967)
	2,090		2,128	1,476	5.36	5,420	2.63	(Ridgway & Hanson, 2014), original data in (Ridgway & Brownson, 1984)
	2,409		2,786	1,856	5.82	6,215	2.74	
	2,090		2,128	1,476	5.36	5,667	2.75	(Tarpley & Ridgway, 1994)
	2,077		1,878	1,327	5.16	6,229	3.04	
<i>M</i>	2,106		2,177	1,503	5.39	5,606	2.71	
<i>Orcinus orca</i> males	3,273		3,392	2,193	6.18	6,052	2.18	(Ridgway & Hanson, 2014), original data in (Ridgway & Brownson, 1984)
	1,877		2,456	1,667	5.60	6,138	3.20	(Ridgway & Hanson, 2014), original data in (Ridgway & Tarpley, 1996)
	5,568		4,529	2,804	6.75	6,875	1.73	
	3,455		4,313	2,690	6.65	7,100	2.46	
	6,750		5,570	3,343	7.19	9,300	2.06	(Ridgway & Hanson, 2014), original data in (Shindo, 1975)
	<i>M</i>	4,185		4,052	2,539	6.47	7,093	2.33

Note. * The body weight calculation after Gingerich (2016) is based on a formula deriving from extant cetaceans and not explicitly from killer whales.

Results

Here we re-evaluated the data available in literature for SWs of both sexes (Tables 1 and 2). Interestingly, the EQ of female SWs more than doubles the EQ of males (1.28 vs. 0.56; Figure 2), and the difference is thus highly significant ($p = 0.002$; Table 3). Data for female SWs are scarce probably because selective preference for measurements of the longer (or heavier) individuals was possibly a consequence of the hunt for the wider targets or the highest oil yield. In particular the spermaceti organ, containing the formerly commercially valuable spermaceti oil, is absolutely and relatively much larger in male SWs. With this in mind, careful scrutiny of the literature indicated that in fact most recorded data on SWs (including brain and body weight) came from individuals either identified as males, or from SWs not identified by gender, but with body length in the male-only range.

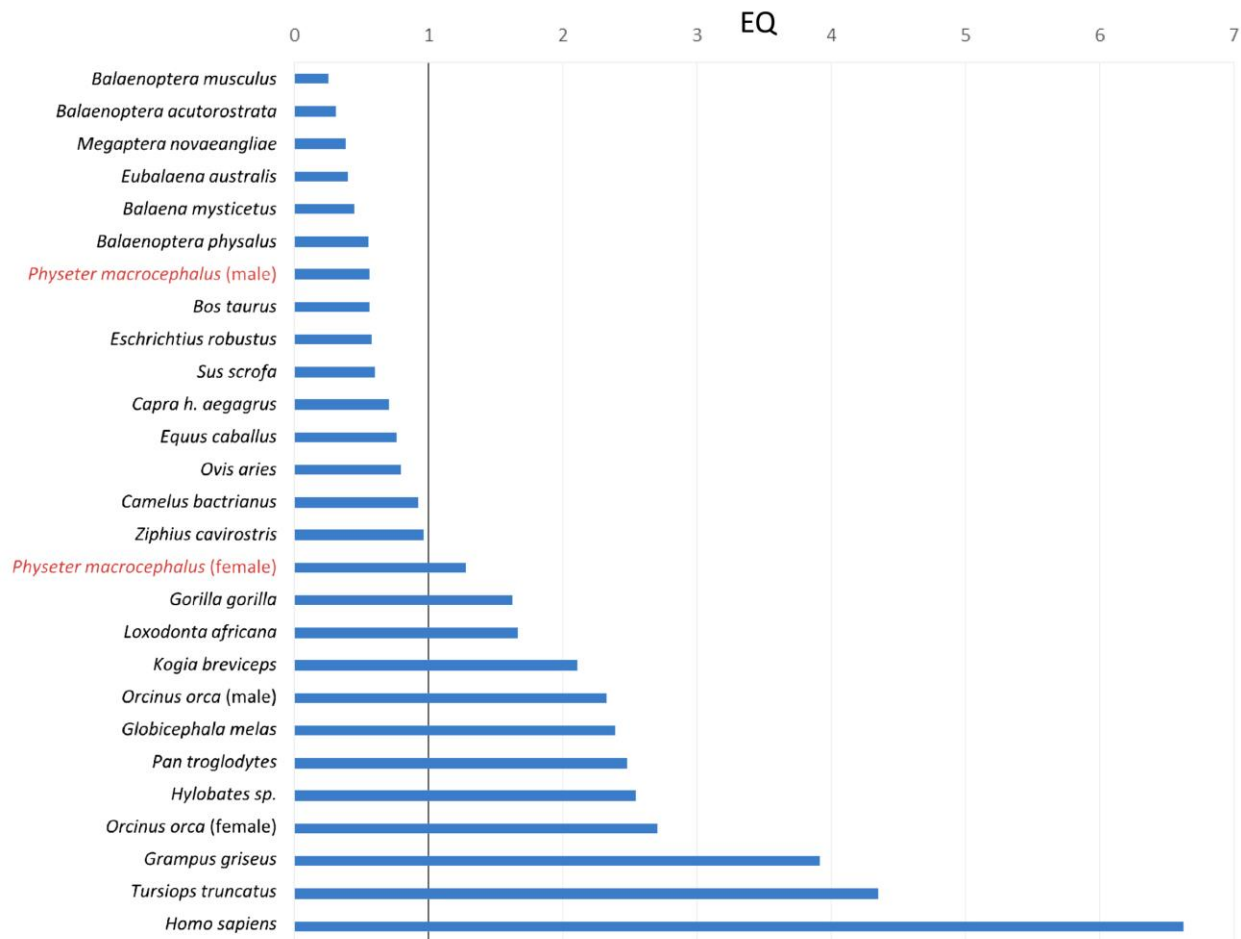


Figure 1. **Encephalization quotient of selected mammalian species.** Note that the EQ of the female sperm whale (SW) is higher than expected (EQ > 1) but the EQ of male SW is less than half of it. Data taken from references given in the Tables 1 and 2.

Table 3

Mann-Whitney U-Statistics. Test Variable: EQ; Grouping Variable: Sex

<i>Physeter macrocephalus</i>	Mann-Whitney U	0
	Wilcoxon W	171
	Z	-3.066
	<i>p</i> (2-tailed)	0.002
<i>Orcinus orca</i>	Mann-Whitney U	6
	Wilcoxon W	21
	Z	-1.358
	<i>p</i> (2-tailed)	0.175

Interestingly, also the KW, another relatively large and sexually dimorphic toothed whale, shows indications of a sexual difference in the EQ. Female KWs have an EQ of 2.71, higher than the EQ of 2.33 of males (not significant; Figure 2; Tables 2 and 3). However, detailed comparisons between the brain of SWs and that of KWs are limited by the striking differences in the respective cerebellar mass and organization (Ridgway & Hanson, 2014).

Data on other dolphin species of great body and brain mass, such as the pilot whales (*Globicephala melas*; *G. macrorhynchus*), as well as references to brain and body measures of beaked whales, are scarce or limited to single specimens.

Discussion

We recently noted (Cozzi, Povinelli, Ballarin, & Granato, 2014) that most of the articles using the EQ (or similar equations based on brain and body weight) as a comparative tool in mammalian neuroanatomy rely on single measures, often extrapolated from old-to-very-old sources in the gray literature. Use of limited bibliographic sources may lead to the disappearance of interesting facts, including significant interspecies variation. Data on the great baleen and toothed whales (Gahr & Pilleri, 1969; Jansen, 1952) may suffer from the limitation imposed to brain sampling operations by the sheer body mass. Thus, the vast majority of data presently cited refers to specimens collected during whaling campaigns of the past, when captured baleen and sperm whales were dismembered on the ship deck by specialized personnel. Baleen whales have a slight sexual dimorphism in body mass (females are slightly larger than males) and therefore males cannot be told from females based only on the length of the specimens. However, SW is a highly dimorphic species. Females are definitely smaller (they reach approximately 10-11 m at full maturity) than males (that may reach 16 or even 18 m). Going back to the original sources for SW (Berzin, 1972; Kojima, 1951; Mangold-Wirz, 1966; Quiring, 1943; Ridgway & Brownson, 1984; Ries & Langworthy, 1937) we also noted that often the sex was not specified, although the length of the specimens identified them as males.

Females SWs spend their life in temperate waters nursing their young ones and aggregating in stable social units. Males, once they reach puberty, form smaller male-only aggregations that roam separately from the female groups, and then dissolve to leave mature bulls alone for the rest of their lives (except for the mating periods). Males travel far into high latitude cold waters to spend a great part of their times and return to warmer areas for the mating season (reviewed in Whitehead, 2003). This kind of lifestyle—solitarily living adult males, females with strong social bounds in their families and clans—is a unique feature of SWs among marine mammals.

Our recent data, compared with former figures from literature, suggest that the female SWs (but not male) evolved a brain larger than expected for their body mass ($EQ > 1$), with values near the ranges of primates, dolphins, and elephants (Figure 2). This fact is even more surprising since the usual coupling of brain and body mass is restricted in large whales due to sheer absolute size (Boddy et al., 2012). A similar trend is present also in KWs, in which females have EQs larger than males although the difference is not significant. So far, it is not possible to test this trend for other marine mammals with strong sexual dimorphism in body size, such as the California sea lion (*Zalophus californianus*), because data of brain mass together with sex are extremely scarce. Although sex differences in mammalian brain mass or even organization and structure are well known and have been thoroughly discussed (McCarthy, 2016), such disparity in the EQ remains unparalleled in mammals. Numerous and different factors may promote relative

and absolute increase in brain size in mammals (DePasquale, Neuberger, Hirrlinger, & Braithwaite, 2016; Dicke & Roth, 2016; Herculano-Houzel, 2015; Manger, 2006; Steinhausen et al., 2016), including sociality (Matějů et al., 2016). To the best of our knowledge there is no study applying to SW that may confirm or exclude the existence of a difference between the two sexes in the number of neurons, their dimensions, or their microcircuits as in some other mammals (Dicke & Roth, 2016; Elston, 2007; Herculano-Houzel, 2015). On the other hand, the intersexual difference of the EQ may be due to several factors inducing a selective pressure towards higher differentiation of secondary sexual characters, not necessarily linked to any neural function of sort. We emphasize that the social life of sperm whales, which is unique among the great whales (see above), is quite distinct in the two sexes. Female (but not adult male) SWs live in groups in which social interactions and inter-individual communication are essential. The sexual dimorphism of size is very pronounced, and may very well be reflected in the absolute dimensions of some internal organs. Nevertheless, the brains of female SWs are larger in relation to body size than male brains (mean quotient of brain weight and body weight of female SW is $7.5 \cdot 10^{-4}$, of male SW $2.2 \cdot 10^{-4}$; Table 1). Thus, the number of neurons would be similar in the two sexes, but with a smaller peripheral territory to control in females. One may wonder if the higher degree of social interactions that characterize the life of female SW has any direct or indirect relationship to the evolution of a brain as large as that of males in a body mass sensibly smaller. There is no indication for the evolution of the unique sexual dimorphism in SW body size and EQs from the fossil record, because the sex of documented fossils remains unknown. However, it is striking that body size was an important driver in recent SW evolution, since all relatives of the sperm whale clade (Physeteroidae), fossil or recent, were considerably smaller (Boersma & Pyenson, 2015).

We are currently not aware if—as for KW—the life of female SWs is prolonged far beyond the termination of their reproductive capabilities (Foster et al., 2012). This feature displayed by very few species beyond ours would have important consequences for the organization of the social units and the transmission of knowledge to the newborns and young. Nevertheless, the culturally determined behavior, which is typical of SWs (Gero, Bøttcher, Whitehead, & Madsen, 2016), and the particular matrilineal sociality, may be key factors in the evolution of high EQ (> 1) values for female SWs, while male EQs remained in the range of the baleen whales (well < 1 , see Figure 2).

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