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Delphinid brain development from neonate to adulthood with comparisons to other cetaceans and artiodactyls

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ABSTRACT

Why do neonatal and adult delphinids have much larger brains than artiodactyls when they have common ancestors? We explore relationships between neonatal brain size, gestation duration, maternal body mass, and body growth. Cetacean brains grow fast in the womb and longer gestation results in a larger brain. Allometry shows that the larger the mother's body mass, the larger the neonatal brain. After birth, delphinid bodies grow much faster than brains, and the index of encephalization decreases even as brains grow beyond maturity. Delphinids' larger brain growth during life at sea may be explained by at least three differences from artiodactyls' life on land. First, the sea offers high calorie prey to support growth of a large brain. Second, life in water offers relief from gravity, allowing for a large head to contain a large brain. Third, sound in water may pass through an immersed body. This allows sounds from the water to reach the fetus, driving early development of delphinoid auditory brain parts. As an example of this, the dolphin ear bone is very large at birth. Furthermore, the auditory nervous system appears mature well before birth. Compared with artiodactyls, these three differences likely result in a larger delphinid brain.

Key words: dolphin, porpoise, whale, cetacean, brain size, brain growth, neonate, gestation.

Around fifty million years ago, some ancestors of artiodactyls began to leave the land for a life in water (Gingerich *et al.* 2001, Berta *et al.* 2005) and became the animals we know as cetaceans (whales, dolphins, and porpoises). Now these animals belong to a larger order of mammals, the Cetartiodactyla (cetaceans and artiodactyls). In leaving the land, cetaceans were freed from some gravitational constraints that might limit their size. They also gained access to a rich, high calorie food supply that enabled many of them to grow very large. We have long known that cetaceans have large brains but data on growth of cetacean brains across the lifespan are extremely rare.

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Brain size of terrestrial mammals has long been studied. These data offer insights into the life history, metabolism, function, ecology, and evolution of these animals (Harvey and Krebs 1990, Barton and Capellini 2011, Boddy *et al.* 2012, Isler and van Schaik 2012). Although body growth curves have been presented for some cetaceans involved in commercial whaling or fishery bycatch (Laws 1959, Lockyer 2007 and references therein), very little data are available on growth of the brain in most cetacean species. Often, brain measures of individuals are presented without companion information on maturity. Although scarce, ontogenetic data on brain mass relative to body mass have been presented for some cetacean species (Perrin *et al.* 1977, Miyazaki *et al.* 1981, McLellan *et al.* 2002, Mallette *et al.* 2016). With the exception of these aforementioned studies, some species have been represented by inaccurately measured data in the literature.

For instance, an erroneous mass from an alcohol-dehydrated blue whale (*Balaenoptera musculus*) brain represented the species in the literature for over 100 yr (Ridgway and Van Alstyne 2017). Another problem arose from the use of endocasts as a proxy for brain mass (Jerison 1973; Marino *et al.* 2000, 2004; Montgomery *et al.* 2013). The cranial vault of cetaceans, especially in larger whales, contains large vascular networks and tentorium cerebelli that may take up to 65% of the cranial vault volume (see table 3 in Ridgway *et al.* 2017). Without taking this nonbrain tissue into consideration, using endocasts alone may lead to overestimation of brain size. Scarcity of cetacean brain mass data in the literature, particularly from the mysticetes, makes erroneous data that much more detrimental to the progress that is being made to understand cetacean brain-body relations.

Furthermore, much of the current data on cetacean brains come from both mature and immature animals, but with little data on neonatal brains. The need for data on the size of the brain at birth and its growth to maturity is often mentioned in the literature (Sacher and Staffeldt 1974, Marino 1997, Barton and Capellini 2011, Isler and van Schaik 2012). With an extensive data set collected over 50 yr, we seek to highlight important differences in the brains of cetaceans based on maturation.

Sacher and Staffeldt (1974) demonstrated a positive allometric relationship between gestation duration and adult brain mass in 91 species of homeothermic placental mammals. Weisbecker and Goswami (2010) also found evidence of this pattern in another study of precocial placental mammals and formulated the “Neonatal Maturity Hypothesis” based on the pattern. The literature is conflicted as to whether there is evidence of this pattern in cetaceans. Perrin *et al.* (1977) found support for this pattern in stenellids, but Marino (1997) found no such evidence. In the years since these publications, various authors have provided more precise data on cetacean gestation time (*e.g.*, Robeck *et al.* 2004, 2009; O’Brien and Robeck 2012) and on neonatal brain size (Ridgway and Hanson 2014). The current study provides a much larger data set of cetaceans, with specimens of various developmental stages, to address whether the Neonatal Maturity Hypothesis is supported for cetaceans.

In addition to faulty data and failing to account for differences due to maturity, cetaceans have been mistakenly generalized in some literature, suggesting that all adult cetaceans have large brains relative to their bodies. However, Ridgway *et al.* (2017) demonstrated great variation in cetacean brain size relative to their body size. In addition to variations in gross brain morphology, brain parts also vary by taxa. For example, delphinids have the largest cerebellums relative to body mass and to body length of all cetaceans.

This study presents allometric relationships between cetacean neonatal brain size and body growth for the first time. The data reported in this study come from

cetaceans with known body mass, body length, and maturity. Limited results have been previously published by Ridgway *et al.* (1966), Ridgway (1981, 1986, 1990), Tarpley and Ridgway (1994), Ridgway and Tarpley (1996), Marino *et al.* (2000), Hanson *et al.* (2013), Ridgway and Hanson (2014), and Ridgway *et al.* (2017). The goal of the present study was to elucidate delphinid brain relationships among the genera and species: (1) neonatal brain mass *vs.* mother's body mass, (2) index of encephalization for adult *vs.* neonate brains, and (3) brain growth trends across their lifespan. We also wanted to compare neonatal brain size against gestation duration to test the hypothesis that species with longer gestations produce larger brains. More broadly, we wanted to compare brain mass and growth of Delphinidae with the small amount of data available for other Cetacea and Artiodactyla.

MATERIALS AND METHODS

The species included in our data set are listed by taxonomic family in Table S1. Our sample of adult, subadult, and neonatal cetaceans represented both odontocetes (10 families, 29 genera, 42 species) and mysticetes (3 families, 5 genera, 9 species). For each species, Table S1 also displays the number of specimens from each of the three age groups. Data on body length permitted maturity estimation (Perrin *et al.* 1984), allowing us to categorize animal maturity with respect to body length. Neonates were classified as animals that were 60 d or younger. Animals were classified as adults if they exceeded mature body length (see Table S1), and animals were classified as subadults if they did not exceed mature length but were older than 60 d.

Brain masses presented in this study were measured directly by the authors, extracted from the literature, or shared by colleagues. The origin of each data point is noted in Table S1. Data sources are listed as "author," "other," and "lit." The authors in this study directly measured the "author" data points. A recent open access paper covering only adult cetacean brains presents more detailed information on methods for brain measures (Ridgway *et al.* 2017). "Lit" data points were extracted from the literature, and "other" data points were previously unpublished and came from personal correspondence, stranding events, *etc.* Observed gestation durations came from the literature (Hayssen *et al.* 1993, Robeck *et al.* 2004, O'Brien and Robeck 2012). All data points came from individual animals. Neonatal data presented here are mainly from brains extracted after fishery bycatch and brains extracted from animals that died of natural causes in human care or stranded on beaches.

Cetacean brains appear to contain slightly more white matter (DeGraaf 1967), and white matter is heavier than gray matter (Gompertz 1902). Thus, specific gravity of cetacean brains is slightly higher than the 1.036 generally stated for the human brain (Gompertz 1902). Specific gravity was determined in a subset of cetacean brains by immersion in water (specific gravity 1.0). The amount of water displaced is equal to brain volume. The mass of the brain in air minus the immersed mass is divided by the mass in air to yield the specific gravity of our cetacean brains, which was 1.04. Most brains were not weighed while immersed, thus brain volume was calculated by dividing brain mass by 1.04, the mean specific gravity calculated for cetacean brains. For our regressions, we have used both brain mass and brain volume.

All linear regressions and resulting linear equations were generated in XLSTAT (2016.3, Statistical Innovations Inc., Boston, MA). Before completing the regression analyses, brain mass, body mass, and gestation duration were log-transformed (with base 10) to derive a linear equation that describes an allometric (biological scaling)

relationship between two of the variables. In addition to testing the allometric relationship between gestation duration and mother's body mass with brain size, regressions were also used to present allometric relationships between brain size and maturity. We used the formula of Jerison (1973) to compare the index of encephalization (EQ) across maturity in six odontocete species: $EQ_i = \frac{E_i}{0.12P_i^{2/3}}$ (EQ_i = index of encephalization for species i ; E_i = brain mass in g for species i ; P_i = body mass in g for species i). Jerison's EQ is a number that represents how much larger or smaller a brain is relative to the expected brain size based on body size.

RESULTS

Factors Affecting Neonatal Brain Size

Our data show that, across four species of delphinids, neonatal brain mass scales to the 0.51 power of maternal body mass (Fig. 1); maternal body mass spanned a wide range for these four species, from 60 kg in *C. commersonii* to over 3,000 kg in *O. orca*. We also used our data to compare adult and neonatal EQ. The extent to which neonatal and adult animals of 15 cetacean species differ in EQ is displayed in Table 1. We also compared neonatal brain volumes with gestation durations by species. There is a linear relationship and strong positive correlation between neonatal delphinids' brain volumes and gestation duration (in days) (Fig. 2). Gestation duration scales to the 0.23 power of brain volume.

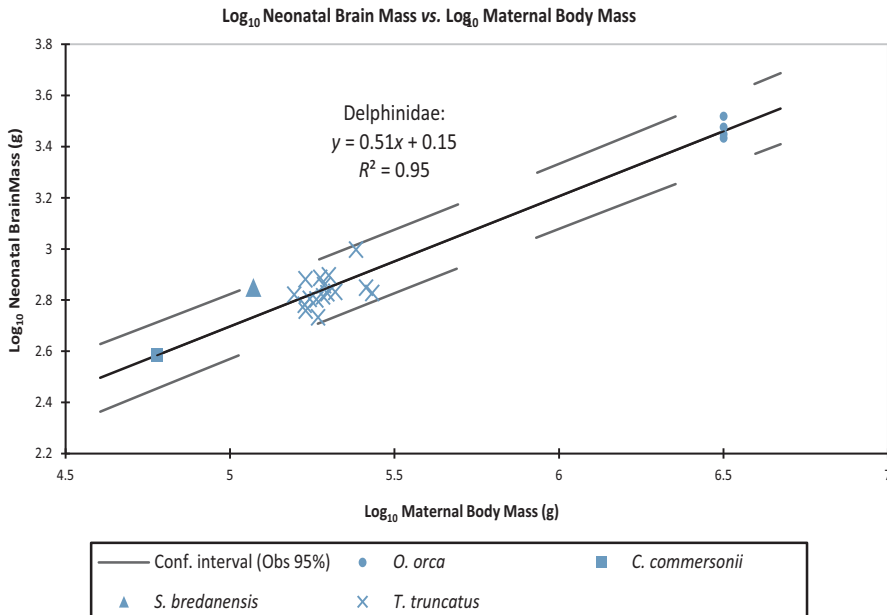


Figure 1. There is a strong, positive correlation between maternal body mass and neonatal brain mass in these four delphinid species; neonatal brain mass scales to the 0.51 power of maternal body mass.

Table 1. Comparison of adult and neonate index of encephalization (EQ) for 15 cetacean (1 mysticete, 14 odontocete) species. EQs were derived from brain and body masses in Table S1.

Family	Species	Adult EQ	Neonate EQ
Balaenopteridae	<i>B. physalus</i>	0.495	2.297
Delphinidae	<i>C. commersonii</i>	5.149	7.234
	<i>D. delphis</i>	3.962	7.801
	<i>G. griseus</i>	4.055	5.807
	<i>L. acutus</i>	3.805	6.632
	<i>L. obliquidens</i>	4.635	8.315
	<i>O. orca</i>	2.425	8.317
	<i>S. bredanensis</i>	5.633	8.065
	<i>T. truncatus</i>	3.972	8.328
Physeteridae	<i>P. macrocephalus</i>	0.681	4.402
Kogiidae	<i>K. breviceps</i>	1.703	4.767
Pontoporiidae	<i>P. blainvilliei</i>	1.930	2.571
Monodontidae	<i>D. leucas</i>	2.643	5.764
Phocoenidae	<i>P. phocoena</i>	2.837	4.406
	<i>P. dalli</i>	2.909	3.275

Brain Growth from Neonate to Adult

We compared brain mass and maturity of six different odontocete species (four from family Delphinidae, one from Kogiidae, and one from Phocoenidae) for which we had data for various-sized animals from neonates to fully mature adults, with the exception of data from *S. coeruleoalba* that ranged from young subadult to adult age. (Fig. 3). *S. longirostris*, *K. breviceps*, *O. orca*, *T. truncatus*, *S. coeruleoalba*, and *P. dalli* all appear to have brain growth beyond sexual maturity. We also investigated EQ as a function of maturity across six odontocetes, for which we had robust data (Fig. 4), and found that EQ appears to decrease with increasing body length in *O. orca*, *T. truncatus*, *S. coeruleoalba*, *P. macrocephalus*, *P. dalli*, and *K. breviceps*.

Comparison with Terrestrial Relatives

We compared mature body and brain mass between seven terrestrial cetartiodactyls (and an African elephant) with eight delphinids of similar body size. These comparisons are presented in Table 2. The cetacean adults have brains that are approximately 1.5 to almost 10 times larger compared to their terrestrial counterparts of similar body mass. The neonatal comparisons are also quite extreme; as neonatal cetacean brains are about two to three times larger than their terrestrial counterparts.

DISCUSSION

Factors Affecting Neonatal Brain Size

Sacher and Staffeldt (1974) derived a formula relating neonatal brain mass to gestation duration in terrestrial mammals: $\log G = 0.274 \log E_n + 0.144 \log A_e + 0.173 \log N + 1.853$ (G = gestation time in days; E_n = neonatal brain mass in grams; A_e = ratio of neonatal to adult brain mass; N = litter size, 1 in cetaceans). Perrin *et al.* (1977) employed this relationship to predict gestation time in delphinids of the

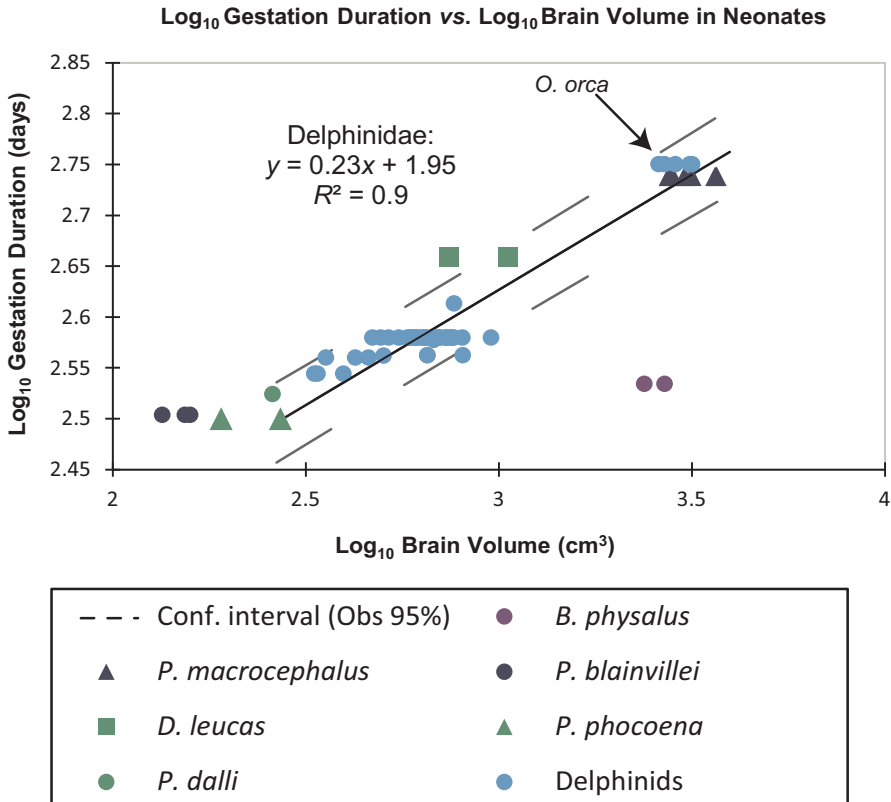


Figure 2. Linear relationship between neonate brain volume and gestation duration (in days). The regression includes only delphinids. Other species were plotted but not included in the regression. The species *O. orca* is indicated by a black arrow. There is a strong, positive correlation between neonatal delphinid brain volume and gestation duration; gestation duration scales to the 0.23 power of neonatal brain volume.

genus *Stenella*. We still do not have data on conception dates and parturition dates (observed gestation times) on that genus for comparison with the prediction from brain mass. Few neonatal cetacean brain masses or volumes have been published in the literature (Perrin *et al.* 1977, see fig. 4B in Mallette *et al.* 2016). It appears that our neonatal brain mass data for *T. truncatus* and for *Stenella* spp. are very similar to the values measured by Mallette *et al.* (2016) and Perrin *et al.* (1977).

Table 3 expands upon the findings of Perrin *et al.* (1977), displaying gestation duration and neonatal and adult brain mass for 17 cetacean species from our data set. For most of the family Delphinidae, we observe a close fit of our data to the Sacher and Staffeldt (1974) formula. The *Phocoena* and *Phocoenoides* data include only three neonates and those from *Delphinus* also represent just three neonates. More data from these species are required to determine if they may better fit the formula. The killer whale has the longest gestation period among the delphinids (and also among all cetaceans), and its observed gestation period and brain mass also fit well with the predicted duration of the Sacher and Staffeldt formula. Our data from delphinids, such

as *T. truncatus* and *O. orca*, demonstrate a very good fit to the formula of Sacher and Staffeldt (1974), as their observed (actual) gestation durations are close to those predicted by the formula (Table 3). Based on known conception dates, mean gestation for *T. truncatus* is 376 d (O'Brien and Robeck 2012), and mean gestation for *O. orca* is 553 d (Robeck *et al.* 2004). The Sacher and Staffeldt formula predicts 377 d for *T. truncatus* and 566 d for *O. orca*.

Unlike delphinid gestation duration, observed mysticete gestation duration does not fit the formula (Table 3). Gestation has been tracked on a large number of mysticetes during whaling activities of the 19th and early 20th centuries. It is likely that gestation estimates from mysticete whales are reasonably accurate. Mysticete whales have relatively short periods of gestation compared to the larger odontocetes, *Physeter* and *Orcinus*, considering their body size and brain size (Table 3). In addition, mysticete whales have much shorter periods of lactation compared to some of the odontocetes (Brodie 1969). Mysticetes are filter feeders, engulfing large amounts of densely spaced prey items (Williams 2006). In contrast, the larger delphinids hunt for individual, more elusive prey. To learn a hunting strategy for individual prey items most likely requires a longer period of learning, and thus a longer period of nursing (Brodie 1969).

Marino (1997) found no relation between EQ and gestation time among 15 odontocetes. However, with more precise data on cetacean gestation duration (*e.g.*, Robeck *et al.* 2004, 2009; O'Brien and Robeck 2012) and our data on neonatal brain mass, we found a significant positive relationship between brain mass and gestation duration across some odontocete species (*O. orca*, *S. bredanensis*, *C. commersoni*, *L. obliquidens*, *T. truncatus*, and *P. macrocephalus*). Therefore, our data support the Neonatal Maturity Hypothesis (Weisbecker and Goswami 2010) for delphinids.

In two delphinid species, *O. orca* and *T. truncatus*, it is obvious that brain growth rate is much higher *in utero* compared to postnatal brain growth rate. For example, brains of *O. orca* require 10 yr or more to double their neonatal brain mass; *T. truncatus* brains may require 8–10 yr to reach full size (Fig. 3). Cranium diameter is likely to be a good predictor of brain growth *in utero*. Each year, numerous pregnant *T. truncatus* are examined with ultrasound. This method has been used to measure the biparietal diameter of the *T. truncatus* fetus at various points of development during gestation (Lacave *et al.* 2004). For this cetacean, it should be possible to develop an accurate profile of brain growth *in utero*.

Figure 5 displays a well-developed neonatal killer whale brain compared to an adult killer whale brain on the same scale. It is interesting to compare the long killer whale gestation with the much shorter gestation of the fin whale (*B. physalus*) (Fig. 2). It appears that the fin whale neonate grows a brain that is only slightly smaller than the killer whale neonate in a much shorter period of time. More data on neonatal brain size in mysticete whales is needed. In our data set, brain mass values for neonatal fin whales are comparable to brain mass values for adult bowhead whales (*B. mysticetus*). Fin whales mature at 5–8 yr (Laws 1959), while bowhead whales do not mature until 12–20 yr of age (Atkinson and Yoshioka 2007); bowhead whales are suggested to have very long life spans, perhaps over 100 yr (George *et al.* 1999, Charvet and Finlay 2012). Bowhead whales also have longer gestation durations compared to fin whales (*ca.* 14.5 mo *vs.* 11–12 mo) (Reese *et al.* 2001). *B. mysticetus* and other right whales have, relative to body size, the smallest brains of all cetaceans (Ridgway *et al.* 2017). More data on neonatal brain size in mysticetes may help us to determine

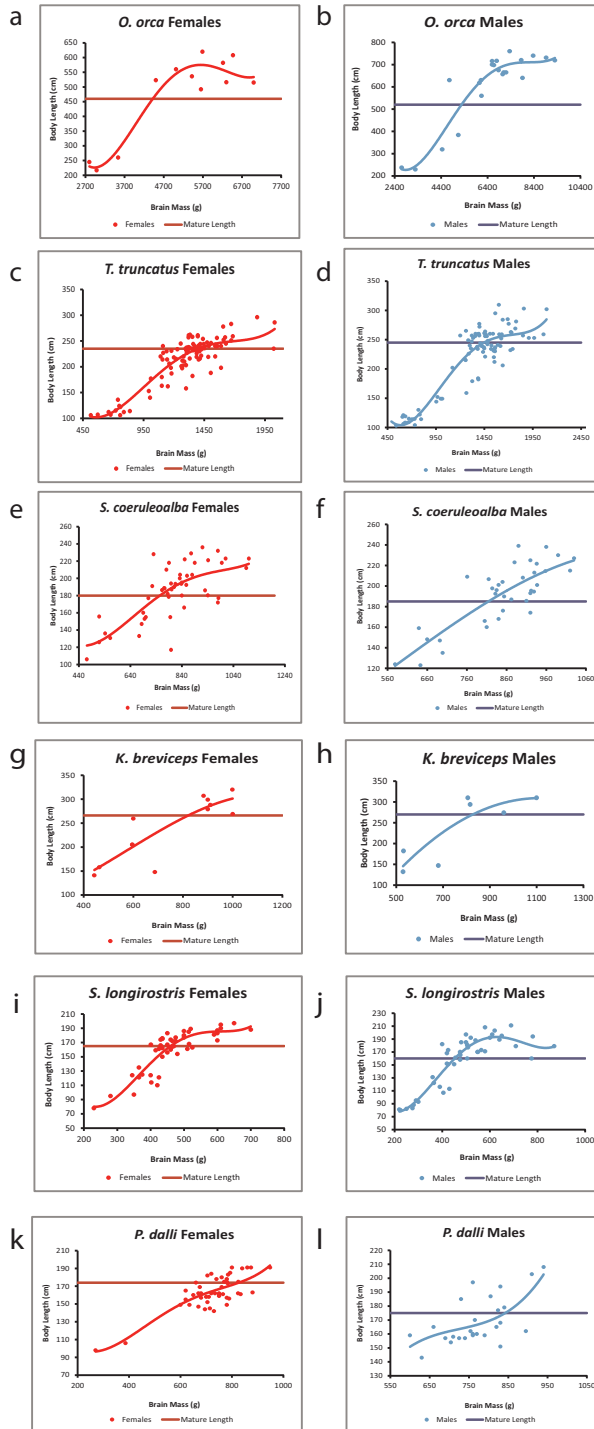


Figure 3. Brain mass relative to maturity (assessed by body length) in six different species. The horizontal line in each species plot represents the length at maturity. Female killer whales (a) (*O. orca*) reach sexual maturity at about 460 cm body length and as young as 8 yr of age (Dahlheim and Heyning 1999), while male killer whales (b) reach sexual maturity at about 520 cm length when they are around 15 yr of age (Dahlheim and Heyning 1999). Female Common bottlenose dolphins (c) (*T. truncatus*) reach sexual maturity at a length of 235 cm and at an average age of 8–9 yr (Wells and Scott 1999), and males (d) reach sexual maturity at a length of about 245 cm and an approximate age of 10 yr (Wells and Scott 1999). Female striped dolphins (e) (*S. coeruleoalba*) reach sexual maturity at 180 cm and about 7 yr of age (Perrin *et al.* 1994); males (f) reach sexual maturity at about 185 cm and about 11 yr of age (Perrin *et al.* 1994). Female pygmy sperm whales (g) (*K. breviceps*) reach sexual maturity at about 266 cm body length (Caldwell and Caldwell 1989), and males (h) reach sexual maturity at about 270 cm length (Caldwell and Caldwell 1989). Female spinner dolphins (i) (*S. longirostris*) reach sexual maturity at a length of 165 cm and at an average age of 4–7 yr (Perrin and Gilpatrick 1994) while males of this species (j) attain sexual maturity at a length of about 160 cm and an approximate age of 7–10 yr (Perrin and Gilpatrick 1994). Lastly, female Dall's porpoises (k) (*P. dalli*) reach sexual maturity at 174 cm and about 5 yr of age (Houck and Jefferson 1999), and males (l) reach sexual maturity at about 175 cm and about 5 yr of age (Houck and Jefferson 1999).

if other balaenopterids are born with especially large brains near the size of adult balaenid brains or if the fin whale is an exception.

Brain Growth from Neonate to Adult

An extensive study of over 20,000 fresh human brains, ranging from newborn to over 85 yr of age, revealed that the largest increase in brain mass (for both sexes) occurred during the first 3 yr of life (Dekaban *et al.* 1978). Brain mass increases more than twofold in the first year of life for humans. The neonatal human brain is about 20%–30% of the adult volume (Passingham 1975, Dekaban *et al.* 1978, Dobbing and Sands 1979) compared to about 40% or even 50% or more in many cetaceans (Table 3). Chimpanzee neonates also have brains of about 40% of the adult volume (DeSilva and Lesnik 2006).

We compared brain mass and maturity of four species of delphinids, one phocoenid, and one member of the family Kogiidae (*K. breviceps*) for which we had data from neonates to fully mature animals (Fig. 3). There is considerable evidence among terrestrial mammals that larger brains take longer to grow both in the womb and after birth (Boddy *et al.* 2012). This is also the case for cetaceans we studied. Killer whales, with the largest of the delphinid brains and the longest gestation period of all cetaceans, appear to have continued brain growth past sexual maturity (Fig. 3). Thus, the periods of brain growth in these animals could be as long as 20 yr. Long periods of postnatal growth might support development of social relationships for animals living in stable groups. Connor (2007) presented a case for the involvement of complex social relationships in development of large brains.

Our fresh brain mass values show that EQ in *T. truncatus* is around 8 at birth and decreases as length increases to maturity around an EQ of 4 (Fig. 5). In *O. orca*, EQ is similar to *T. truncatus* at birth but decreases as body length increases to maturity around an EQ of 2. In *K. breviceps*, the pygmy sperm whale, EQ decreases from about 5 to about 1.5, while in its giant relative *P. macrocephalus*, the sperm whale, EQ

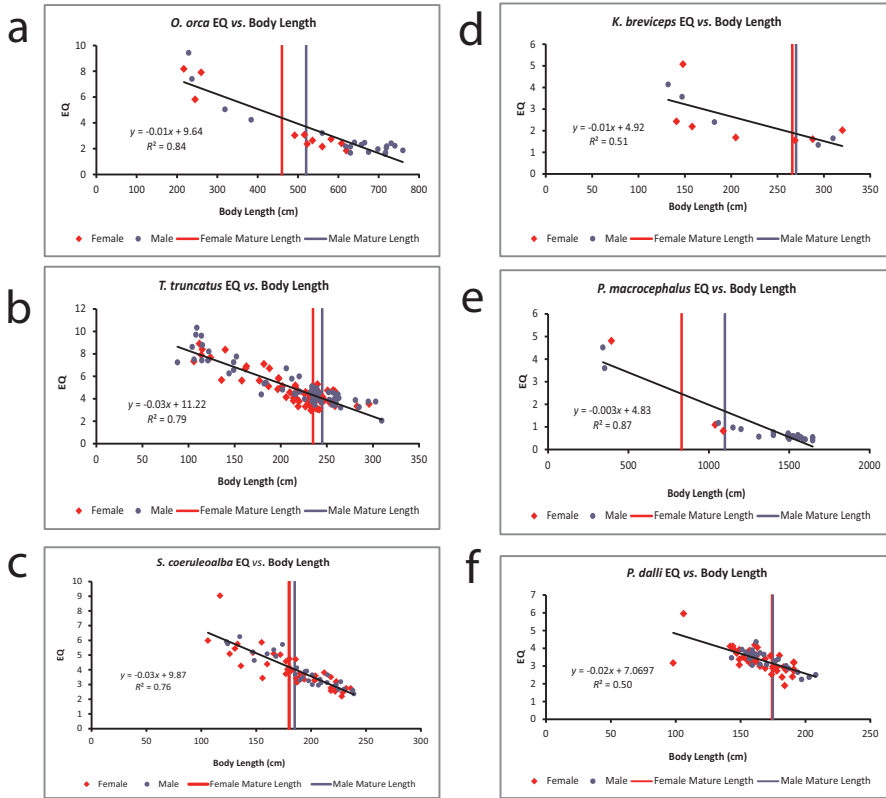


Figure 4. Encephalization quotient (EQ) and body lengths. Body lengths are used as a general indicator for maturity of these animals. Three delphinids (*Orcinus orca*, *Tursiops truncatus*, and *Stenella coeruleoalba*) are compared with EQ and body length against two members of Physeteroidea (*Kogia breviceps* and *Physeter macrocephalus*) and one member of Phocoenidae (*Phocoenoides dalli*). In each case, EQ declines as the animal grows toward a mature body length and perhaps beyond. EQ was measured directly from brain masses, except for a few of the larger *O. orca* for which brain mass was calculated from endocranial volume. Body mass varies considerably in mature animals. As a result, EQ in mature *T. truncatus* varies from around 3 to 5 and in *O. orca* from about 1.5 to 3. One outlier EQ value of 2 from a male *T. truncatus* was from an overweight animal.

decreases from around 4.5 to about 0.5 (Fig. 4). It appears that EQ changes rather dramatically over the course of development in these cetacean species.

Comparison to Terrestrial Relatives

As seen in Table 2, the adult delphinids have brains up to ten times as large as terrestrial cetartiodactyls of similar body size. Delphinid neonates have brains that are about two to three times the size of terrestrial cetartiodactyl neonates of similar body mass. Thus, even with similar sized bodies and, in some cases, shorter gestation

Table 2. Comparison of seven terrestrial cetartiodactyls (and the African elephant) with eight aquatic cetartiodactyls on brain and body mass for neonates and adults. ABoM = adult body mass; ABrM = adult brain mass; NBoM = neonatal body mass; NBoM = neonatal brain mass. All brain and body mass data for the aquatic species come from Table S1.

Terrestrial species	Common name	ABoM (kg)	ABrM (g)	NBoM (kg)	NBrM (g)	Aquatic species	Common name	AboM (kg)	ABrM (g)	NboM (kg)	NBrM (g)
<i>D. donax phillypsi</i>	Blesbok antelope	60 ^a	155 ^a	—	—	<i>D. delphis</i>	Common dolphin	68	715	11	430
<i>S. scrofa</i>	Wild boar	149 ^b	133 ^b	—	—	<i>L. acutus</i>	Atlantic white-sided dolphin	156	1,285	28	733
<i>T. strepsiceros</i>	Greater kudu	218 ^a	307 ^a	—	—	<i>T. truncatus</i>	Bottlenose dolphin	190	1,550	18	685
<i>G. camelopardalis</i>	Giraffe	470 ^c	537 ^c	150 ^c	428 ^c	<i>G. griseus</i>	Risso's dolphin	301	2,132	85	796
<i>C. bactrianus</i>	Bactrian camel	594 ^d	518 ^d	—	—	<i>G. macrorhynchus</i>	Short-finned pilot whale	654	2,679	—	—
<i>B. taurus</i>	Cow	598 ^e	492 ^e	25 ^e	199 ^e	<i>D. leucas</i>	Beluga	560	2,087	50	938
<i>H. amphibius</i>	Hippopotamus	1,351 ^f	720 ^f	40 ^e	195 ^e	<i>G. melas</i>	Long-finned pilot whale	1,369	3,499	—	—
<i>L. africana</i>	African elephant	5,000 ^a	4,619 ^a	—	1,724 ^h	<i>O. orca</i>	Killer whale	3,723	6,642	171	3,006

^aHerculano-Houzel (2015).

^bMinervini *et al.* (2016).

^cGraic *et al.* (2017).

^dXie *et al.* (2011).

^eBallarin *et al.* (2016).

^fSilva and Downing (1995).

^gSacher and Staffeldt (1974).

^hShoshani *et al.* (2006).

Table 3. Gestation and brain size. The predicted gestation period was derived by applying the Sacher and Staffeldt formula and using our brain mass data. Sheep (*O. aries*), cows (*B. taurus*), giraffes (*G. camelopardalis*), and hippopotamuses (*H. amphibius*) were included in the table to compare cetaceans to other members of the Cetartiodactyla taxonomic order. Humans (*H. sapiens*) were also included for comparison. Cetaceans appear to have similar neonatal/adult brain mass ratios compared to other animals of the Cetartiodactyla order. Sources for the published gestation durations and cetacean brain masses can be found in Table S1.

Taxonomic family Genus species	Neonatal brain mass (g)	Adult brain mass (g)	Neonate/ adult (%)	Published gestation (days)	Predicted gestation (days)
Delphinidae					
<i>C. commersonii</i>	370	783	47.3	334	324
<i>D. delphis</i>	430	715	60.2	363	359
<i>G. griseus</i>	796	2,132	37.3	410	386
<i>L. acutus</i>	733	1,285	57	365	401
<i>L. obliquidens</i>	523	1,198	43.6	356	352
<i>O. orca</i>	3,006	6,642	45.3	553	566
<i>S. attenuata</i>	353	711	49.6	—	304 ^a
<i>S. longirostris</i>	247	541	45.6	—	286 ^a
<i>S. bredanensis</i>	706	1,454	48.6	378	388
<i>T. truncatus</i>	685	1,550	44.2	376	377
Monodontidae					
<i>D. leucas</i>	938	2,087	44.9	456	414
Phocoenidae					
<i>P. phocoena</i>	242	506	47.7	316	266
<i>P. dalli</i>	270	803	33.6	334	282
Physeteridae					
<i>P. macrocephalus</i>	3,308	7,693	43	547	582
Pontoporiidae					
<i>P. blainvillei</i>	154.9	223.9	69.2	319	271
Ziphiidae					
<i>M. europaeus</i>	971	1,680	57.8	—	—
Balaenopteridae					
<i>B. physalus</i>	2,640	6,718	39.3	342	537
Bovidae					
<i>B. taurus</i>	199 ^b	456 ^b	43.6	278 ^c	270
<i>O. aries</i>	69	130 ^d	53	150 ^e	208
Giraffidae					
<i>G. camelopardalis</i>	428 ^f	537 ^f	79.7	459 ^c	363
Hippopotamidae					
<i>H. amphibius</i>	195 ^b	590 ^b	33.1	240 ^e	258
Hominidae					
<i>H. sapiens</i>	380 ^g	1,400 ^b	27	280 ^e	324

^aPerrin *et al.* (1977).

^bSacher and Staffeldt (1974).

^cKiltie (1982).

^dMinervini *et al.* (2016).

^eHayssen *et al.* (1993).

^fGraïc *et al.* (2017).

^gBlinkov and Glezer (1968).



Figure 5. One example each of a male neonate brain of *O. orca* compared with a brain of a male adult. The ratio of cerebellum mass to the mass of the whole brain is similar in the neonate and adult. The mass of the neonate brain is 3,292 g, while the adult brain mass is 7,100 g.

periods, neonatal and adult cetaceans have much larger brains than their terrestrial counterparts (see Table 2).

For example, the neonatal elephant brain may be over 1,600 g (Pagel and Harvey 1988). Shoshani *et al.* (2006) gave one value of 1,724 g for a neonatal elephant brain. Our neonatal killer whales had brains almost twice as large as the neonatal elephant. The elephant gestation, at around 656 d (Wittemyer *et al.* 2007), is even longer than that of the killer whale, at 553 d. The neonatal killer whale brain grows to a mass that is almost twice as large as the neonatal elephant's brain within a much shorter period of gestation.

Underwater Acoustics: Hearing and Sonar

Members of the family Delphinidae have the largest relative total brain size among cetaceans. They also have the largest relative cerebellum size (Ridgway *et al.* 2017). Like other cetaceans, delphinids live their entire lives in the water where sound travels over four times as fast as in air at the same temperature. This simple fact impacts every aspect of cetacean existence, including brain development. According to Langworthy's (1932) study of the *T. truncatus* brain, numerous tracts of acoustic fibers reach the cerebral cortex, allowing the cortex to reach an advanced stage of development on the basis of these acoustic impulses.

Bats also use sonar. Since they do not have large brains some have suggested that the bat's brain size is an argument against the involvement of acoustic capability in the explanation for the large brain size of delphinids (*e.g.*, Manger 2006, Marino 2007). However, there are many differences in using sonar (echolocation) between bats in air and cetaceans in water. Worthy and Hickie (1986) summarized the findings of Wood and Evans (1980) and suggested various differences between bat and delphinid echolocation. These included differences in sonar sound bandwidth (tonal sounds *vs.* broadband clicks). Delphinids need to detect targets such as fish and squid

that are very similar in density to their water environment. The intervals between delphinid sonar click emissions are very short. Short intervals for reception of echoes from closely spaced but separate objects require rapid processing by the brain. Other comparisons have been made based on brain size and neural responses (Ridgway 1986, Huggenberger 2008).

Perhaps an even greater difference between bat and dolphin brain expansion has to do with the acoustic environment during development. The cetacean body, except for the lungs and other air-containing spaces, is a close impedance match to water (Au 1996). It is highly likely that sound from the environment passes into the pregnant cetacean's body through the amniotic fluid to the developing cetacean. This may drive the early development of the auditory system. The dolphin brain's auditory fibers are already myelinated in the womb long before the cetacean is born (Hosokawa *et al.* 1969, Solntseva 1999, Montie *et al.* 2007). Early myelination of the auditory system suggests that the cetacean fetus can hear. If a sound source is coupled to the mother's body, the human fetus can hear at a gestational age of about 29 wk (Moore *et al.* 1995). At this time, the auditory nervous system is at least partially myelinated. It is likely that the dolphin fetus can hear sounds from the ocean environment as its mother swims.

Audiograms of the developing cetacean fetus have not yet been done. Many ultrasound examinations of developing dolphins are done each year so, using methods analogous to those used by Moore *et al.* (1995), fetal audiograms should be possible. Coupling of sounds from the water may allow the fetus to hear its mother and nearby animals within the group. The developing cetacean inside the womb may hear a wide range of sounds long before it is born (Mello and Amundin 2005). This could be an advantage for cetaceans that live in groups compared to solitary species. Fetal sound reception very possibly drives the extreme development of the cetacean auditory nervous system, empowering cetaceans to maximize their use of sound within the marine environment. Thus, fetal hearing tests might link delphinids' early auditory ability and the development of a large brain.

Metabolism, Energetics, and Life Span

Our data show that neonatal brain mass scales to between 0.5 and 0.6 power of maternal body mass (Fig. 1). Similarly, delphinid cortex surface area scales to about the 0.6 power of body mass (Ridgway *et al.* 2017). In contrast, Martin (1981) found that neonatal brain mass in terrestrial mammals scales to the 0.75 power of maternal body mass. The terrestrial's low calorie food compared to the delphinid mother's high calorie food is a major difference between the groups. Large amounts of high calorie food facilitate development of large brained delphinid offspring and may help to support brain growth during a long period of nursing.

Hofman (1993) hypothesized that encephalization and metabolism may direct the evolutionary course of lifespan, growth and reproduction. Hofman's hypothesis is supported by the elephant's high encephalization, long life span, and its relatively low metabolic rate. Elephants consume large amounts of plant material, but their food is relatively low in caloric value. Christiansen (2004) states "both the basal and the field metabolic rates of extant elephants are lower than predicted for a hypothetical mammal, in accordance with their body size and subsistence on low-quality foods." In contrast, the killer whale, the largest delphinid, does not appear to support Hofman's (1993) hypothesis. Killer whales and elephants are both highly encephalized, but killer whales consume many more calories each day (Noren 2011, Williams

et al. 2017). Neonatal cetacean brains, such as those of sperm and killer whales, grow to twice the size of the neonatal elephant brain within a shorter period of gestation.

Measurements of oxygen and glucose consumption revealed that delphinids have a higher metabolic rate compared to most terrestrial mammals, and measures of the aerobic costs of swimming and diving demonstrate the delphinids' high energy lifestyle (Ridgway 1990, Williams *et al.* 2001, Ridgway *et al.* 2006, Noren 2011, Williams *et al.* 2017). The metabolic rate of adult bottlenose dolphins and killer whales is much higher than the value predicted by Kleiber's law, which states that an animal's metabolic rate scales to the 0.75 power of its body mass (Noren 2011, Williams *et al.* 2017). A delphinid's high energy aquatic lifestyle and its abilities to swim fast and chase elusive prey underwater are enabled by a high-calorie diet that is digested by long alimentary tracts (Williams *et al.* 2001). We suggest that the rich, high calorie food supply of cetaceans has enabled them to support the metabolic demands of a large brain.

Conclusion

We found that delphinid brains grow to between 1.5 and 10 times as large as similar sized terrestrial cetartiodactyls. Delphinids' larger brain growth during life at sea may be explained by at least three differences from terrestrial cetartiodactyls' life on land. First, the sea offers high calorie prey to support growth of a large brain. Second, life in water offers relief from gravity, allowing for a large head to contain a large brain. Third, sound in water may pass through an immersed body. This allows sounds from the water to reach the fetus, driving early development of delphinoid auditory brains to enable development of an effective sonar system.

The data presented herein expand upon the data that are currently available in the literature on cetacean brain size and growth across maturity and body size. In our data set, we included measures of brain mass, brain volume, body mass, gestation duration, body length, and EQ. We found a positive and direct correlation between gestation duration and brain volume for neonates of Delphinidae, the taxonomic family from which the majority of our data came. Neonatal brain mass is also positively and directly correlated with maternal body mass in delphinids. Upon investigating the trajectory of brain growth from birth to maturity, we found that EQ decreases as body length increases and brain mass appears to grow beyond sexual maturity in most of the odontocete species we examined. There is a slower rate of brain growth from neonatal to adult length for larger delphinids, such as *Orcinus orca*, than for smaller delphinids and members of the family Phocoenidae. The expanded data set of the present study offers a platform for future investigations on cetacean brain development across the lifespan.

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SUPPORTING INFORMATION

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Table S1. Data set of all cetaceans used in our analyses. Sexes, ages (adult, subadult, or neonate), body lengths, brain and body masses, gestation durations, taxonomic classifications, and origin of data are given for individuals of 52 cetacean species (9 mysticete, 43 odontocete). Counts of specimens per species from each of three age groups (adult, subadult, and neonate) and from each of three sources of data origin (author, literature, and other) are given under the “Brain data-species counts” tab. A separate table comparing encephalization indices for neonate and adult female cetaceans (and humans) is included under the “Neonate-Adult Brain-Body mass” tab.