



Sexual dimorphism in long-beaked common dolphins (*Delphinus capensis*) from KwaZulu-Natal, South Africa

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We examined external morphometric parameters in incidentally caught long-beaked common dolphins (*Delphinus capensis*) from the east coast of South Africa for evidence of sexual dimorphism. We evaluated sexual dimorphism and allometric growth in 26 external body measurements from 211 individuals and assessed size and shape dimorphism. Most characteristics analyzed showed a negative allometric relationship to total body length for both males and females. Twenty-one measurements showed significant differences between the sexes. Among these were the 3 girth measurements, the length of the dorsal fin base, the distance between the tip of the upper jaw to the midpoint of the umbilicus, and the distance between the tip of the upper jaw to the center of the anus. Fourteen of the 26 characteristics analyzed showed significant differences in body shape between the sexes. Our results indicated that moderate sexual dimorphism is present in long-beaked common dolphins from this region, with males being both significantly longer and more robust than females. Sexual dimorphism in this species may be related to their mating or foraging strategies.

Key words: allometry, *Delphinus capensis*, mating strategies, morphometrics, sexual dimorphism, South Africa

Differences in external features between the sexes of animals can include size, shape, presence of appendages (teeth, horns, and tusks), and coat or skin coloration (Heyning 1984; Jefferson 1990; Derocher et al. 2005; Jefferson et al. 2008; Ralls and Mesnick 2009), and this is usually referred to as sexual dimorphism. Among mammals, sexual dimorphism is pronounced in primates, elephants, pinnipeds, and ungulates (Ralls 1977), and usually becomes distinct when the animals near the age of sexual maturity (Jefferson et al. 2008).

Some species of cetaceans also show a degree of sexual dimorphism (Jefferson et al. 2008), which is expressed in differences in body size or shape between the sexes (Ralls 1977; Tolley et al. 1995; Jefferson et al. 2008; Ralls and Mesnick 2009). In cetaceans, males are often larger than females, with the most pronounced sexual dimorphism seen in sperm whales (*Physeter macrocephalus*), killer whales (*Orcinus orca*), narwhals (*Monodon monoceros*), beaked whales (Ziphiidae), and belugas (*Delphinapterus leucas*) (Heyning 1984; Jefferson et al. 2008; Ralls and Mesnick 2009; Thompson et al. 2014). Although sexual dimorphism is not obvious in many smaller

odontocetes, Hersh et al. (1990) and Tolley et al. (1995) reported that male common bottlenose dolphins (*Tursiops truncatus*) from the east coast of Florida and Sarasota were more robust and had larger appendages than females of the same species. Other examples of small odontocetes with sexual dimorphism are Dall's porpoise (*Phocoenoides dalli*—Amano and Miyazaki 1996) and the short-beaked common dolphin (*Delphinus delphis*—Heyning and Perrin 1994; Neumann et al. 2002; Murphy 2006). In cetaceans, reverse sexual size dimorphism also has been reported for baleen whales and porpoises (Ralls 1976; Read and Hohn 1995; Ralls and Mesnick 2009; Torre et al. 2014). Examples include the humpback whale (*Megaptera novaeangliae*—Connor et al. 2000; Pack et al. 2009) and Dall's porpoise (Jefferson 1990; Amano and Miyazaki 1993). Greater body size of female baleen whales is thought to enable them to better withstand the energetic demands associated with pregnancy or lactation during long-distance migration, and to produce larger calves (Connor et al. 2000; Pack et al. 2009; Ralls and Mesnick 2009). The larger body size enables the females to store more energy in the form of blubber (Connor et al. 2000;

Ralls and Mesnick 2009), therefore improving survival of their offspring (i.e., bigger females are better mothers—Ralls 1976).

The extent of sexual dimorphism within a species also can vary among geographical regions (Bell et al. 2002). Amano and Miyazaki (1996) suggested that sexual dimorphism in some species, such as Dall's porpoise, is correlated with environmental conditions. A related factor is food availability since low productivity of the habitat may lead to poor dimorphic development (Murphy and Rogan 2006). Amano and Miyazaki (1996) reported that populations of Dall's porpoise from the offshore area of the North Pacific showed little sexual dimorphism in body size and skull morphology due to the region being relatively unproductive.

Examination of allometry is one way to quantify the growth rate of a species. This method examines growth rates of different body parts (Huxley 1932; Klingenberg 1996; Murphy 2004; Mallette et al. 2015) and can thus present information on the degree of sexual dimorphism present within a species. Allometric relationships provide fundamental information on the life histories and social structure of populations, as well as knowledge about different ontogenetic stages (Klingenberg 1996; Clark and Odell 1999; Mallette et al. 2015). There are 3 types of allometry, namely static, ontogenetic, and evolutionary allometry (Klingenberg 1996). Static allometry (also referred to as size allometry) results from variation in size among individuals of the same population and age group (Klingenberg 1996). Ontogenetic (growth) allometry deals with covariation among morphometric characteristics during growth (Klingenberg 1996; McLellan et al. 2002; Mallette et al. 2015). Evolutionary allometry reflects covariations in different traits in different populations of the same species or closely related species (Klingenberg 1996). Ontogenetic allometry was evaluated in harbor porpoises (*Phocoena phocoena*) from the western North Atlantic, and females had higher growth rates compared to males (McLellan et al. 2002). Mallette et al. (2015) examined growth rates in *T. truncatus* and found that most of the skeletal characters and the brain attained maximum sizes before maturity. Allometry thus gives information on growth rates among species or between females and males of a species.

Even though studies have documented sexually dimorphic features in delphinids such as adult sperm whales, killer whales, and beaked whales, the differences between sexes in some delphinids are generally too slight to reliably distinguish them at sea (Neumann et al. 2002; Neumann and Orams 2005). However, adult males may be positively identified by the presence of a post-anal hump (Neumann et al. 2002). Some studies have shown the presence of sexual dimorphism in *Delphinus* spp. For example, females of *D. delphis* from both the eastern North Pacific (Heyning and Perrin 1994; Murphy 2006) and waters off the Irish coast (Murphy and Rogan 2006) were significantly shorter in total body length than males. Examining skeletal material, Heyning and Perrin (1994) further found that cranial variables were on average more than 10% larger and body lengths on average 5% longer in males than females. In contrast, no evidence of sexual dimorphism was found in the skulls of *D. delphis*

from southern Australia and Bell et al. (2002) suggested it was likely that sexual dimorphism in this species varies geographically.

Common dolphins are widely distributed, occurring in all tropical, subtropical, and temperate seas, both inshore and offshore (Neumann and Orams 2005; Samaai et al. 2005; Murphy and Rogan 2006). Their distribution is seasonal and is mostly influenced by the availability of prey (Cockcroft and Peddemors 1990; Neumann and Orams 2005; Perrin 2009). Off South Africa, long-beaked common dolphins are found off the Eastern Cape coastline in the austral summer and migrate north into KwaZulu-Natal waters during winter, following the seasonal range expansion of sardines (*Sardinops sagax*) from the Agulhas Bank into KwaZulu-Natal waters during May and June (Cockcroft and Peddemors 1990; O'Donoghue et al. 2010; Van der Lingen et al. 2010; Ambrose et al. 2013).

In recent molecular studies, Amaral et al. (2012a, 2012b) and Murphy et al. (2013) suggested uncertainty in taxonomic and phylogenetic relationships within the genus *Delphis*, particularly for the long-beaked common dolphin (*D. capensis*). The 2 *Delphinus* species are thought to occur allopatrically. While early published studies on common dolphins in the subregion referred to the species as *D. delphis* (Best 2007), these pre-date the taxonomic revision of this species. Jefferson and Van Waerebeek (2002) examined the cranial morphometrics of 153 common dolphin skulls from South Africa and concluded that all specimens belonged to *D. capensis*. Using cranial material, Samaai et al. (2005) suggested that most common dolphins off South Africa were *D. capensis*, but suggested that *D. delphis* may be found off the west coast. He also suggested that data on parasites and stomach contents showed that *D. capensis* had a more inshore habitat than *D. delphis* off South Africa. Through genetic studies, Natoli et al. (2006, 2008) confirmed the presence of *D. capensis* off the eastern coast of South Africa. Earlier published records can be assumed to refer primarily to *D. capensis* (Best 2007).

Data on the degree of sexual dimorphism are important for understanding the natural history and ecology of a species, but to date no study has examined sexual dimorphism in *D. capensis* off South Africa. Thus, the aim of the present study was to examine the presence of size and shape dimorphisms in long-beaked common dolphins using animals incidentally caught in shark nets off the KwaZulu-Natal coastline of South Africa.

MATERIALS AND METHODS

According to Best (2007), Natoli et al. (2006, 2008), and Samaai et al. (2005), common dolphin specimens from the KwaZulu-Natal coast were all assigned to *D. capensis* and the present study only used specimens from this area. All data were sourced from the Graham Ross Marine Mammal Collection at the Port Elizabeth Museum, Port Elizabeth, South Africa, and originate as bycatch animals recovered from shark nets off the KwaZulu-Natal coast, South Africa (Fig. 1; Appendix I), over a 38-year period (July 1974–August 2012). Because these animals were incidentally caught, they were assumed to be

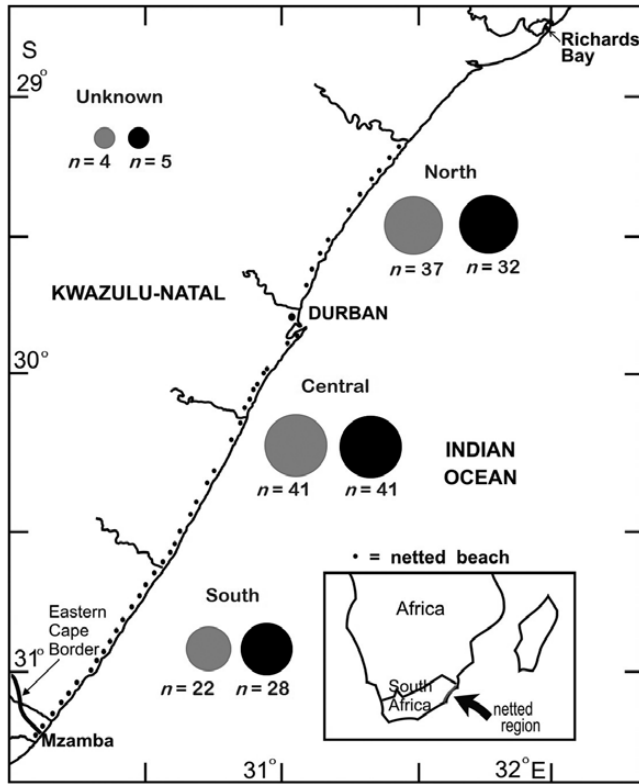


Fig. 1.—Map showing locations of shark net installations and the distribution of bycatch of *Delphinus capensis* along the KwaZulu-Natal coastline of South Africa. The sample sizes of specimens used in this study are indicated by the diameters of the circles for the different regions. Females = ●; males = ●; and n = sample sizes.

representative of the wild population (Lane et al. 2014). All data from carcasses that were noted as either very decayed, scavenged by sharks, or pregnant were removed from the data set. Because data sets may not have been complete for each individual, sample sizes varied for the various analyses as stated in the text. Total body length and 25 external measurements, including girth measurements, were analyzed (Table 1). Body length measurements (Fig. 2) were carried out following the guidelines of Norris (1961).

Allometry.—Both mature (76 females, 58 males) and immature (28 females, 49 males) specimens were included to examine allometric growth (totals = 104 females, 107 males). Measurements were converted to a logarithmic scale, and the growth equation $y = ax^b$ was created to determine allometric relationships, where y is the dependent variable, x is the total body length, b is the growth coefficient, and a is the intercept (Schmidt-Nielsen 1993).

The allometric equation $y = ax^b$ was derived by Huxley (1932) to describe relationships between body size and morphological characteristics of an organism. From this equation, y and x are organism measurements, whereas a and b are constants (Klingenberg 1996). The growth coefficient b indicates whether an allometric relationship is positive, negative, or isometric. Positive allometry is indicated when b is greater than 1, which means the body part is bigger in relation to the whole body than would be expected. Isometric allometry is when b

is equal to 1 and indicates that body parts are growing at the same rate as the whole body. Negative allometry is found when b is less than 1, which indicates that the body parts are smaller than would be expected in relation to the whole body. The slopes were tested to determine if they were significantly different from 1.0 and if they were significantly different between sexes by using t -tests, $t_s = (b - 1)/(SE_b)$, where b is the growth coefficient tested, SE_b is the standard error of the growth coefficient, and t_s is the sample t -value which is compared to $t_{0.05}$ (d.f.) (Read and Tolley 1997).

Sexual dimorphism.—For the analysis of sexual dimorphism, data on the external measurements of 76 mature female and 58 mature male *D. capensis* were examined. Only measurements from cranially mature animals were included in this analysis. Cranial maturity was determined by fusion of most or all cranial sutures, following Jefferson and Van Waerebeek (2002). An analysis of variance (ANOVA) was used to analyze variations in size between male and female *D. capensis*. An analysis of covariance (ANCOVA) was then performed on each allometric relationship to determine whether there were significant differences between males and females, allowing inference of the presence of shape dimorphism within the species. Statistical analyses were conducted using STATISTICA 7.0 at $\alpha = 0.05$ level of significance.

RESULTS

Allometry.—Overall, most characteristics (17/25) showed similar growth patterns between females and males (Table 2). Considering the intercepts of the growth regression, all features for males were generally larger than for females. The T-tDF and NAB showed a significantly greater allometric increase in females than in males (Table 2). T-AG, T-Ea, E-B, flipper (AF and WF), and tail flukes (WFL and ND) showed a significantly greater allometric increase in males compared to females (Table 2; Figs. 3 and 4). The total body length was a good predictor of the selected external body measurements analyzed, whereby most R^2 values were ≥ 0.7 (Table 2; Figs. 3 and 4). Exceptions were when R^2 was < 0.7 between TBL and T-AG, T-Ea, E-Ea, E-AG, E-B, T-B, GAX, AF, WF, LDF, WFL, and ND in females (Table 2). In males, low R^2 values were recorded between TBL and T-AM, E-AG, AF, ND (Table 2). These low R^2 values could be due to the small sample size for specimens of immature females ($n = 8$) for a few measurements or indicate poor strength of the correlation between certain body measurements and the total body length.

Linear body measurements.—Most of the linear measurements of the head (6/8 in females and 4/8 in males; Table 2), such as T-AM, T-AG, T-Ea, and E-B, exhibited negative allometry ($b < 1$). T-E in both sexes, and T-B in males, exhibited positive allometry and isometric growth, respectively. Females also showed isometry for T-DF, T-MGS, and T-A (Table 2). T-F, T-tDF, and T-MU exhibited positive allometry in females ($b > 1$; Table 2). In contrast, males showed positive allometry in T-F, isometric growth in T-MU, and negative allometry in T-tDF. As with females, males also showed positive allometry in T-F and isometric growth in T-MGS and T-A (Table 2).

Table 1.—External body measurements of *Delphinus capensis* caught as bycatch along the KwaZulu-Natal coast, South Africa. All measurements were taken in a straight line parallel to the long axis of the body, except if marked with *, in which case they were the shortest distances between the 2 points as measured along the curve of the body.

Characteristics	Abbreviation
Tip of the upper jaw to deepest part of notch	TBL
Tip of the upper jaw to center of eye	T-E
Tip of the upper jaw to apex of melon	T-AM
Tip of the upper jaw to angle of gape	T-AG
Tip of the upper jaw ear	T-Ea
Center of eye to ear*	E-Ea
Center of eye to angle of gape*	E-AG
Center of eye to blowhole*	E-B
Tip of the upper jaw to center of blowhole	T-B
Tip of the upper jaw to anterior insert of flipper	T-F
Tip of the upper jaw to anterior insert of dorsal fin	T-DF
Tip of the upper jaw to tip of dorsal fin	T-tDF
Tip of the upper jaw to midpoint of umbilicus	T-MU
Tip of the upper jaw to midpoint of genital slit	T-MGS
Tip of the upper jaw to center of anus	T-A
Girth at axilla*	GAX
Girth at maximum*	GM
Girth at anus*	GA
Flipper: anterior insert to tip*	ATF
Flipper: axilla to tip*	AF
Flipper: maximum width	WF
Dorsal fin: height*	HDF
Dorsal fin: length of base	LDF
Tail flukes: tip to tip width*	WFL
Tail flukes: notch anterior border*	NAB
Tail flukes: depth of notch	ND

Appendage measurements.—In females, flipper measurements (i.e., AF and WF), as well as all dorsal fin measurements (i.e., HDF and LDF) and tail fluke measurements (i.e., WFL and ND), showed negative allometry (Table 2). Isometric growth was observed in 2 measurements (i.e., ATF and NAB) in females. In males, all the appendage measurements (measurements 19–26; Table 2) except ATF and WF exhibited negative allometry. ATF and WF were isometric in males, but were isometric and negative, respectively, in females (Table 2).

Girth measurements.—Except for isometric growth observed in the GA in females, all other girth measurements exhibited negative allometry in both males and females (Table 2).

Sexual dimorphism.—The total body length of mature females ranged from 203.5 to 240 cm, whereas that of mature males ranged from 214 to 255 cm (Fig. 5). Size dimorphism was evident in *D. capensis* from this study when variations of external measurements were tested between females and males using ANOVA. TBL and 21 other external measurements showed size dimorphism, with males being significantly longer and more robust in almost all the external measurements (Table 3).

DISCUSSION

Knowledge about the degree of sexual dimorphism in cetaceans may give insights into the life history strategy of a

species. Sexual dimorphism also provides information with regard to the mating system, breeding behavior, and social structure, as well as the habitat preference and the foraging habits of cetaceans (Tolley et al. 1995; Murphy and Rogan 2006). In this study, we found male *D. capensis* to be significantly longer and more robust than females in 6 linear body measurements and 3 girth measurements. Murphy and Rogan (2006) also found that male *D. delphis* from the Irish Sea were significantly longer and more robust than females in most of the characteristics measured. Overall, our results depict a pattern of sexual dimorphism similar to that reported in other studies of delphinids (Ralls and Mesnick 2009). The shape of the dorsal fin of *P. dalli* from the northwestern North Pacific differed between males and females, and males had an exaggerated post-anal hump, whereas this was absent in females (Jefferson 1990). In addition, male *P. dalli* were longer and heavier than females (Jefferson 1990). Males also were longer and more robust than females in the coastal spotted dolphin (*Stenella attenuata graffmani*) from Bahía de Banderas, Mexico (Sanvicente-Añorve et al. 2004). Some cetacean species, such as pilot whales (*Globicephala* spp.), *Cephalorhynchus* spp., and *Lagenorhynchus* spp., have pronounced sexual dimorphism in dorsal fin shape or size. Sexual dimorphism was reported in killer whales and pilot whales, where adult males had larger dorsal fins than females (Clark and Odell 1999; Ralls and Mesnick 2009).

Linear body measurements.—Both female and male *D. capensis* exhibited isometric allometry in most of the linear body measurements and this implied that most of the characteristics were growing at the same rate as the total body length. The remaining measurements, which were all the cranial measurements, exhibited negative allometry, indicating that these measurements of the body became relatively shorter as the total body length increased. Read and Tolley (1997) suggested that negative allometry in the cranial portion of this species may reflect the significance of early development of the cranial features. Thus, cranial characteristics will achieve their final size before the skeleton stops growing. Sanvicente-Añorve et al. (2004) reported that male coastal spotted dolphins in Bahía de Banderas, Mexican Pacific coast, exhibited negative allometry in most of their body measurements. Negative allometry in the cranial measurements of *D. capensis* in the current study could be an indication of well-developed cranial features required for efficient respiration and sonar emissions early in the lives of these animals. These results were in contrast with findings for *D. delphis* from the northeastern Atlantic (Murphy 2004), which showed positive allometry in the cranial measurements of both female and male short-beaked common dolphins. Amano and Miyazaki (1993) noted negative allometry in Dall's porpoise in the northwestern North Pacific and Read and Tolley (1997) reported negative allometry in cranial measurements in the harbor porpoise from the Bay of Fundy. The differences in the development of some characteristics that result in differences in allometry in different species may be an indication of environmental factors such as temperature and food availability, which vary in geographic localities.

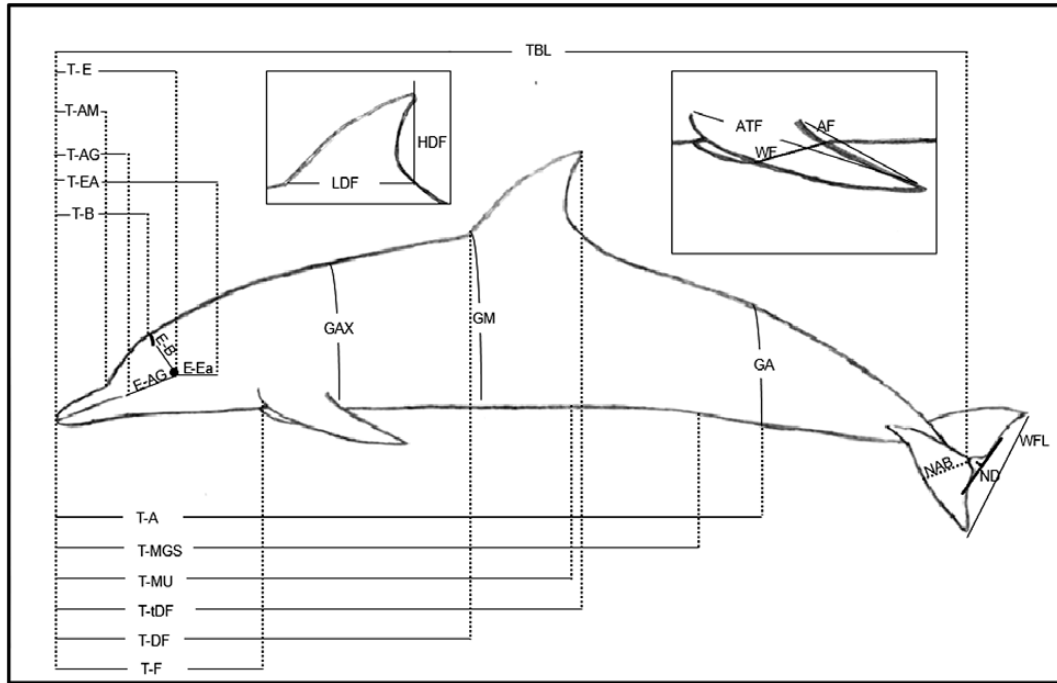


Fig. 2.—Standard external measurements of *Delphinus capensis* used in this study (adapted from Norris 1961). For descriptions of measurements refer to Table 1.

Table 2.—Allometric analyses of 25 external body measurements using the model $y = ax^b$ for males and females of *Delphinus capensis* collected as bycatch along the KwaZulu-Natal coast, South Africa. n = sample size; $SE(b)$ = standard error of b ; $b = 1?$ indicates test for isometric growth; $F = M?$ indicates test for differences in slope b between females and males at $P < 0.05$, with significant differences indicated as $F < M$ or $F > M$.

Characteristics	Females	$SE(b)$	R^2	n	$b = 1?$	Males	$SE(b)$	R^2	n	$b = 1?$	$F = M?$
T-E	$y = 0.624x^{1.108}$	0.104	0.687	54	> 1	$y = 0.557x^{1.152}$	0.058	0.876	58	> 1	$F = M$
T-AM	$y = 1.457x^{0.715}$	0.073	0.669	50	< 1	$y = 1.626x^{0.566}$	0.083	0.473	54	< 1	$F = M$
T-AG	$y = 1.520x^{0.546}$	0.113	0.322	51	< 1	$y = 0.998x^{0.902}$	0.079	0.722	52	< 1	$F < M$
T-Ea	$y = 1.762x^{0.351}$	0.125	0.187	36	< 1	$y = 0.654x^{1.044}$	0.103	0.741	38	$= 1$	$F < M$
E-Ea	$y = 1.882x^{0.588}$	0.171	0.271	34	< 1	$y = 1.972x^{0.458}$	0.129	0.312	30	< 1	$F = M$
E-AG	$y = 1.848x^{0.612}$	0.155	0.279	42	< 1	$y = 1.661x^{0.837}$	0.148	0.472	38	< 1	$F = M$
E-B	$y = 1.694x^{0.499}$	0.193	0.149	40	< 1	$y = 0.625x^{1.351}$	0.137	0.747	35	> 1	$F < M$
T-B	$y = 0.996x^{0.851}$	0.112	0.545	50	$= 1$	$y = 0.662x^{1.066}$	0.055	0.886	51	$= 1$	$F = M$
T-F	$y = 0.374x^{1.160}$	0.103	0.718	52	> 1	$y = 0.267x^{1.218}$	0.05	0.916	57	> 1	$F = M$
T-DF	$y = 0.257x^{1.044}$	0.059	0.865	51	$= 1$	$y = 0.201x^{1.076}$	0.024	0.974	56	> 1	$F = M$
T-IDF	$y = 0.124x^{1.046}$	0.066	0.845	48	> 1	$y = 0.641x^{0.800}$	0.062	0.772	51	< 1	$F > M$
T-MU	$y = 0.097x^{1.112}$	0.082	0.833	39	> 1	$y = 0.242x^{1.039}$	0.03	0.966	44	$= 1$	$F = M$
T-MGS	$y = 0.158x^{0.998}$	0.054	0.876	50	$= 1$	$y = 0.293x^{0.946}$	0.037	0.924	57	$= 1$	$F = M$
T-A	$y = 0.142x^{0.997}$	0.061	0.862	45	$= 1$	$y = 0.212x^{0.965}$	0.015	0.987	56	$= 1$	$F = M$
GAX	$y = 0.922x^{0.670}$	0.114	0.356	68	< 1	$y = 0.785x^{0.765}$	0.06	0.709	68	< 1	$F = M$
GM	$y = 0.565x^{0.838}$	0.055	0.838	49	< 1	$y = 0.860x^{0.713}$	0.053	0.732	68	< 1	$F = M$
GA	$y = 0.685x^{0.909}$	0.0777	0.732	52	$= 1$	$y = 0.943x^{0.757}$	0.036	0.879	63	< 1	$F = M$
ATF	$y = 1.004x^{0.869}$	0.083	0.647	61	$= 1$	$y = 0.691x^{1.082}$	0.037	0.927	68	$= 1$	$F < M$
AF	$y = 1.377x^{0.693}$	0.084	0.542	60	< 1	$y = 1.571x^{0.542}$	0.08	0.414	67	< 1	$F = M$
WF	$y = 1.757x^{0.544}$	0.077	0.459	61	< 1	$y = 1.286x^{1.005}$	0.039	0.909	67	$= 1$	$F < M$
HDF	$y = 1.384x^{0.717}$	0.066	0.71	50	< 1	$y = 1.374x^{0.717}$	0.045	0.815	59	< 1	$F = M$
LDF	$y = 1.418x^{0.600}$	0.087	0.484	52	< 1	$y = 1.256x^{0.701}$	0.047	0.796	59	< 1	$F = M$
WFL	$y = 1.310x^{0.615}$	0.071	0.551	63	< 1	$y = 1.026x^{0.784}$	0.026	0.927	72	< 1	$F < M$
NAB	$y = 1.326x^{0.889}$	0.061	0.778	63	$= 1$	$y = 1.663x^{0.574}$	0.068	0.506	72	< 1	$F > M$
ND	$y = 2.181x^{0.345}$	0.063	0.33	62	< 1	$y = 2.104x^{0.548}$	0.074	0.449	69	< 1	$F < M$

Shape dimorphism in *D. capensis* in the present study was evident in several measurements: T-B, T-DF, T-F, E-B, T-A, and T-MGS. Further sexual dimorphism in T-E, T-AM, T-B, T-DF, T-F, and E-B in this species indicated differences in skull shape,

with males having larger skulls. Larger skulls in most delphinids were reported in male bottlenose whales (*Hyperoodon* spp.), beaked whales (*Mesoplodon* spp.), sperm whales, and, to a smaller degree, bottlenose dolphins (Cranford 1999; Ralls

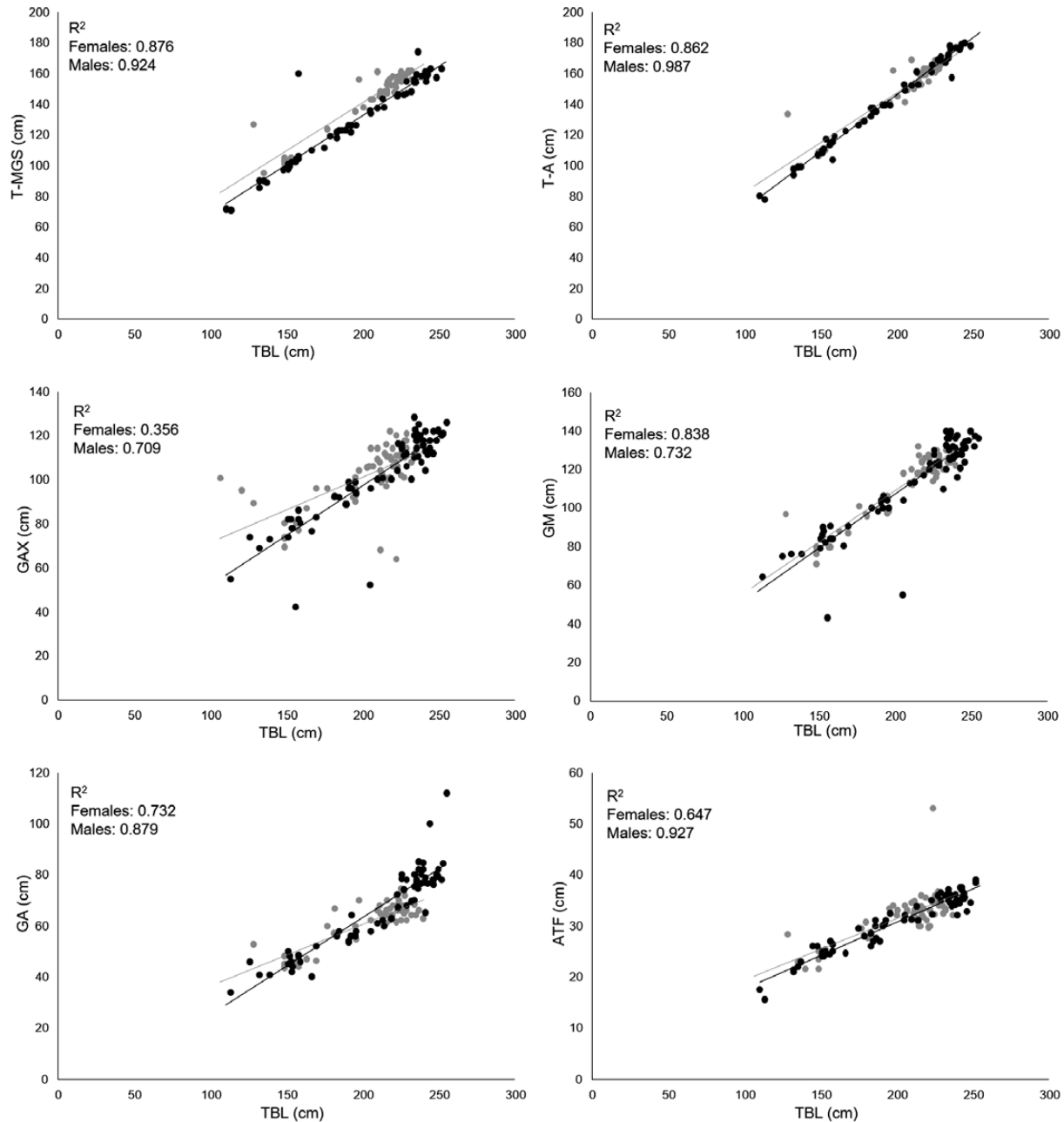


Fig. 3.— R^2 values and linear regression of selected body measurements against total body length (TBL) in female and male *Delphinus capensis* collected as bycatch along the KwaZulu-Natal coast, South Africa. Gray circles (•) and line = females; black circles (•) and line = males.

and Mesnick 2009). Larger and more densely ossified skulls of male bottlenose whales are used in defensive encounters as they have been observed head butting, while the massive nasal complex in male sperm whales is probably used for sound generation (Cranford 1999; Ralls and Mesnick 2009). Differences in the head region between sexes would be significant if males use the head in male–male aggressive encounters. Sexual dimorphism in the T-MGS and T-A is expected as in most male cetaceans the genital slit is further forward than in females (Tolley et al. 1995; Murphy 2004; Murphy and Rogan 2006).

Appendage measurements.—In this study, most appendage measurements showed negative allometry in both females and males of *D. capensis*. This may be attributed to the significance

of the early development of these features (Read and Tolley 1997; Mallette et al. 2015), because they may be important for calves to swim effectively immediately after birth (Noren et al. 2006; Torre et al. 2014). The significance of dorsal fins reaching the final size before the dolphin reaches its final body size may be related to thermoregulatory constraints. Rommel et al. (1992, 1993) showed that the dorsal fin and flukes in bottlenose dolphins have a superficial venous system, which acts as a countercurrent heat exchanger associated with the testes in males and the uterus and fetus in females. Amano and Miyazaki (1993) suggested that the development of tail flukes and muscles to generate thrust is necessary for the fast swimming speed and diving behavior in Dall's porpoise. Dolphins

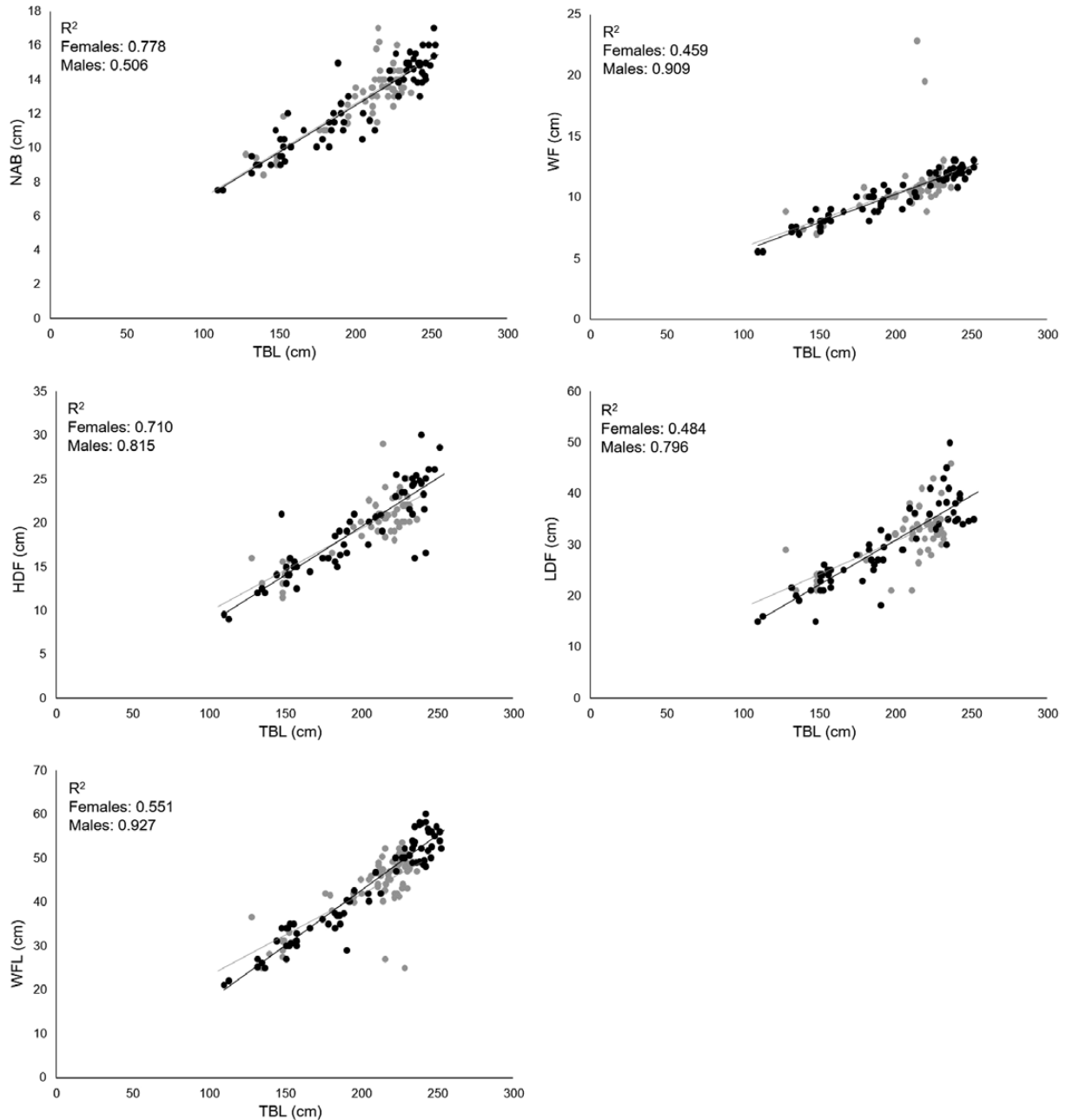


Fig. 4.— R^2 values and linear regression of selected body measurements against total body length (TBL) in female and male *Delphinus capensis* caught as bycatch along the KwaZulu-Natal coast, South Africa. Gray circles (•) and line = females; black circles (•) and line = males.

generate thrust with tail flukes (Noren et al. 2006) and their growth and development of posterior muscles in *D. capensis* as the animal grows would also play a vital role in swimming speed. This would explain the presence of a broader dorsal fin base and larger flukes in males, because these traits would be required to assist in greater maneuverability and propulsion when swimming and pursuing females for mating, as well as help with thermoregulation (Tolley et al. 1995). Tolley et al. (1995) reported that it would furthermore assist in aggressive encounters with other males, perhaps during intraspecific competition for females. MacLeod (1998) and Connor et al. (2000) suggested that cetaceans, particularly dolphins, often use flukes to strike each other during aggressive encounters. Therefore,

if larger appendages could facilitate propulsion and maneuverability in males, a significant difference between the sexes would also be expected in dorsal fin and fluke measurements.

Girth measurements.—All girth measurements, except for the anal girth (which exhibited isometry), exhibited negative allometry in both females and males. The early development of this body part could indicate the importance of increased muscle mass early for more strength and better swimming (Read and Tolley 1997; Clark and Odell 1999). The results of our study were in contrast with results obtained for short-beaked common dolphins from the Irish Sea (Murphy and Rogan 2006), where all girth measurements (GAX, GM, and GA) in both females and males exhibited isometric growth. These studies

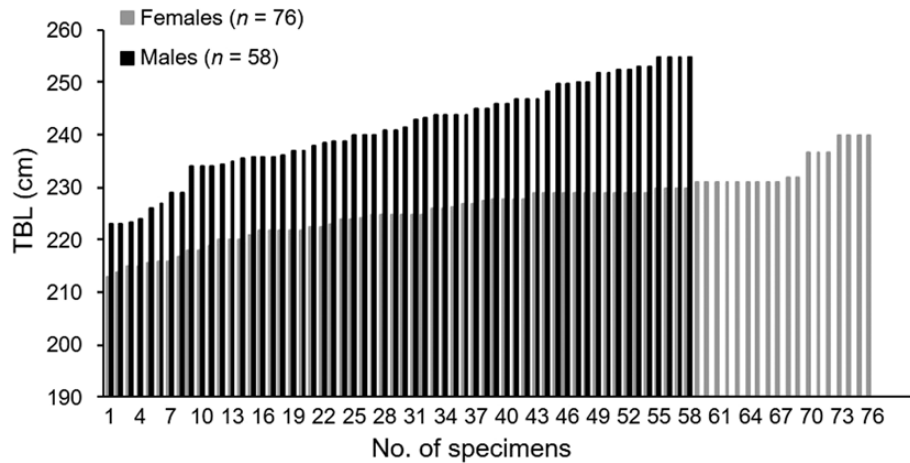


Fig. 5.—Distributions of total body lengths (TBL) of female and male *Delphinus capensis* collected as bycatch along the KwaZulu-Natal coast, South Africa.

Table 3.—Descriptive statistics for external body measurements (in cm) of mature male and female *Delphinus capensis* collected as bycatch along the KwaZulu-Natal coast, South Africa. Analysis of variance (ANOVA) was used to compare body size and analysis of covariance (ANCOVA) was used to compare body shape. n = sample size, α = 0.05. Significant P -values indicated by an asterisk.

Characteristics	Females					Males					Size	Shape
	Mean	SD	Max.	Min.	n	Mean	SD	Max.	Min.	n	P ANOVA	P ANCOVA
TBL	221.14	8.13	240.00	203.50	76	238.29	8.75	255.00	214.00	58	< 0.000*	
T-E	34.84	2.14	40.00	30.50	41	36.21	2.05	40.00	32.00	22	0.017*	0.015*
T-AM	16.74	1.66	20.00	13.00	37	16.22	1.70	19.20	11.00	21	0.266	0.019*
T-AG	29.55	3.46	39.50	17.00	41	31.34	1.86	35.00	27.50	21	0.010*	0.149
T-Ea	39.20	4.67	45.00	16.50	31	42.41	3.45	52.00	37.00	18	0.009*	0.051
E-Ea	5.64	0.56	7.00	4.20	30	5.99	0.42	7.00	5.10	15	0.023*	0.367
E-AG	5.88	0.81	9.00	4.50	34	6.26	1.09	10.00	5.00	18	0.208	0.250
E-B	17.33	2.03	21.00	11.50	32	18.90	1.12	21.00	17.00	17	0.001*	0.284
T-B	37.06	2.97	42.00	26.00	40	38.62	1.87	42.20	36.00	21	0.015*	0.010*
T-F	48.84	2.52	56.00	44.00	40	51.94	2.78	59.00	46.00	22	< 0.000*	0.001*
T-DF	99.27	3.89	106.00	90.00	39	103.06	5.11	111.00	91.00	22	0.005*	0.000*
T-tDF	131.10	5.64	145.00	121.50	37	138.39	7.73	157.00	120.00	22	0.000*	0.002*
T-MU	103.68	4.47	115.00	95.00	28	111.08	7.82	125.00	90.00	17	0.002*	0.000*
T-MGS	153.07	5.84	162.00	143.00	40	155.37	7.77	174.40	138.00	23	0.225	0.000*
T-A	160.63	6.74	170.00	141.00	32	171.70	7.66	182.00	153.00	21	< 0.000*	0.000*
GAX	110.20	6.08	122.00	97.00	46	115.41	7.04	128.00	100.00	37	0.001*	0.467
GM	124.00	10.04	175.00	112.20	35	129.33	7.49	140.00	110.00	39	0.013*	0.421
GA	65.96	3.07	74.60	61.00	41	77.80	9.22	112.00	60.00	36	< 0.000*	0.001*
ATF	33.27	1.83	36.80	29.80	47	35.34	1.80	39.00	31.00	30	< 0.000*	0.200
AF	11.24	2.28	22.80	8.80	47	11.97	0.66	13.00	10.00	30	0.046	0.005*
WF	23.63	2.27	26.80	12.00	47	25.91	1.65	28.50	22.00	30	< 0.000*	0.099
HDF	21.32	2.10	29.00	18.00	39	24.23	2.47	30.00	19.00	20	< 0.000*	0.037*
LDF	33.57	4.32	45.80	21.00	40	37.47	4.74	50.00	30.00	21	0.003*	0.009*
WFL	45.51	5.25	53.40	25.00	47	52.82	3.55	60.00	47.00	35	< 0.000*	0.047*
NAB	13.76	1.03	17.00	11.50	47	14.71	0.89	17.00	13.00	35	< 0.000*	0.144
ND	2.55	0.59	5.00	1.20	46	2.80	0.52	4.00	1.90	34	0.043*	0.416

reported that isometric growth reflected the need for posterior muscle development as the dolphin reaches maturity (Tolley et al. 1995; Murphy and Rogan 2006). Larger girths in male killer whales, common bottlenose dolphins, and short-beaked common dolphins may be attributed to increased muscle mass, which would result in increased strength for better swimming speed (Tolley et al. 1995; Clark and Odell 1999; Murphy and Rogan 2006).

In addition, GA was sexually dimorphic in this study, with males having a significantly larger anal girth compared to

females. In most delphinid species, males possess post-anal humps, resulting in significantly larger anal girths than females (Connor et al. 2000; Murphy 2004). The presence of the post-anal hump was also observed in mature males of the long-beaked common dolphin in the present study (Fig. 6) and is thought to be a secondary sexual feature of mature males (Neumann and Orams 2005; Ralls and Mesnick 2009). Neumann and Orams (2005) illustrated that a post-anal hump was present in males of the short-beaked common dolphin of Mercury Bay, New Zealand. The post-anal hump may constitute a display signal



Fig. 6.—Photographs of *Delphinus capensis*. Mature female (top) showing absence of post-anal hump. Mature male (bottom) showing presence of post-anal hump. Photographs by G. Hofmeyr, Port Elizabeth Museum.

to potential mates or may be a visual sign in establishing dominance hierarchies among other males (Neumann et al. 2002; Murphy and Rogan 2006). The presence of a post-anal hump has been observed in other delphinids, such as male Hawaiian spinner dolphins (*Stenella longirostris*), where a male poses to emphasize its hump during aggressive encounters with other males and during aerial spins (Connor et al. 2000).

Neumann et al. (2002) and Murphy et al. (2005) reported that post-anal hump size is positively correlated with testis size in *D. delphis* and due to this, Murphy et al. (2013) suggested the post-anal hump in these dolphins serves in female choice, allowing identification of the males that have the largest testes or perhaps can produce the largest quantity of sperm. The statistical difference in body size and shape between males and females, the degree of sexual dimorphism, and testis size may be used as indicators of the mating system of a species (Neumann et al. 2002; Perrin and Mesnick 2003; Murphy et al. 2005; Plön and Bernard 2007). In mammals, the absence of apparent sexual dimorphism and presence of relatively large testes are indicative of a polygynandrous mating system (females and males both have more than 1 partner—Jefferson 1990; Mesnick and Ralls 2002; Murphy et al. 2005; Plön and Bernard 2007). In some delphinid species, such as *D. delphis*, *S. longirostris*, *P. dalli*, and *Lagenorhynchus obscurus*, moderate sexual dimorphism exists, with males having relatively large testes, suggesting that these species exhibit sperm competition (Jefferson 1990; Connor et al. 2000; Perrin and Mesnick 2003; Murphy et al. 2005). Male common dolphins occurring off South Africa mate with more than 1 female during the breeding season, and Mendolia (1989) suggested that the development of larger testes in males aids in sperm competition. Plön et al. (2012) reported that male *D. capensis* off KwaZulu-Natal had the largest combined testes weight and suggested that

the combined characteristics of large group sizes in long-beaked common dolphins, the fact that sexual dimorphism is not apparent, and that males possess relatively large testes are indicative of sperm competition. This suggests that *D. capensis* females may mate with multiple males, resulting in the development of large testes, which aids in sperm competition.

In conclusion, this study showed that sexual dimorphism in both body size and shape is evident in the long-beaked common dolphins off KwaZulu-Natal, South Africa, with males being longer and more robust than females. However, this study did not explore skeletal characteristics, such as cranial features, to see whether sexual dimorphism is also present in these characters. Future studies should investigate skeletal or cranial measurements for evidence of sexual dimorphism in *D. capensis*. Comparison of the degree of sexual dimorphism in *D. capensis* from KwaZulu-Natal with that found in other *D. capensis* populations globally in conjunction with investigations on the productivity of the KwaZulu-Natal coastline compared to other localities in the world would help elucidate if the degree of sexual dimorphism is influenced by the availability of food (Bell et al. 2002). The similarities and differences in sexual dimorphism and allometry among species of cetaceans indicate an important area for further work toward understanding their foraging, breeding behaviors, and social structure.

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APPENDIX I

PORT ELIZABETH MUSEUM ACCESSION NUMBER AND SEX (M OR F) OF SPECIMENS USED IN THIS STUDY

N0006 M, N0215 F, N0216 F, N0217 M, N0218 F, N0219 F, N0220 M, N0249 M, N0254 F, N0255 F, N0256 F, N0396 F, N0397 F, N0409 F, N0411 M, N0417 M, N0418 M, N0498 F, N0500 F, N0502 F, N0503 F, N0505 F, N0507 F, N0509 F, N0510 F, N0511 M, N0512 M, N0513 F, N0514 F, N0515 F, N0516 F, N0517 F, N0518 F, N0545 M, N0546 F, N0548 M, N0549 F, N0730 M, N0731 M, N0732 M, N0733 F, N0734 F, N0735 M, N0741 F, N0743 F, N0744 M, N0745 F, N0746 M, N0747 M, N0748 M, N0750 F, N0753 F, N0754 M, N0755 M, N0756 F, N0757 F, N0764 M, N0790 F, N0791 M, N0793 F, N0867 F, N0900 M, N0901 F, N0902 F, N0903 M, N0904 F, N0905 M, N0906 F, N0933 F, N0972 M, N0999 F, N1050 M, N1059 M, N1087 F, N1088 F, N1089 F, N1090 F, N1091 M, N1092 M, N1094 M, N1096 F, N1098 F, N1120 M, N1150 M, N1153 F, N1163 M, N1164 M, N1165 M, N1166 F, N1167 F, N1168 F, N1169 M, N1170 M, N1187 M, N1189 M, N1195 M, N1206 F, N1207 M, N1208 M, N1209 F, N1210 M, N1320 M, N1373 F, N1392 M, N1393 F, N1394 F, N1424 M, N1425 M, N1436 M, N1437 F, N1438 M, N1439 F, N1853 M, N2070 F, N2072 F, N2074 M, N2079 F, N2080 M, N2092 M, N2094 M, N2095 M, N2096 F, N2097 M, N2098 F, N2100 F, N2101 F, N2102 M, N2103 M, N2104 M, N2105 F, N2106 F, N2108 F, N2178 M, N2223 F, N2229 F, N2231 M, N2232 M, N2233 M, N2234 M, N2266 M, N2268 M, N2270 F, N2276 M, N2277 M, N2278 M, N2286 M, N2292 M, N2295 F, N2300 M, N2301 M, N2302 F, N2314 M, N2315 M, N2316 M, N2318 M, N2319 F, N2320 M, N2321 F, N2322 M, N2323 F, N2329 F, N2339 M, N2342 F, N2343 F, N2345 M, N2871 F, N3057 F, N3058 M, N3059 M, N3065 F, N3066 M, N3067 F, N3069 F, N3070 F, N3073 F, N3074 M, N3075 F, N3079 M, N3082 M, N3083 M, N3084 F, N3121 F, N3126 F, N3129 M, N3131 F, N3132 M, N3133 M, N3160 F, N3161 M, N3162 M, N3170 M, N3171 M, N3315 M, N3320 F, N3321 F, N3333 M, N3339 M, N3347 M, N3437 F, N3472 F, N3473 F, N3481 M, N3579 M, N3580 M, N4353 F, N4354 M, N4646 F, N4647 M, N4682 F, N4682 F, N4684 M.