

Organ weights of three dolphin species (*Sousa chinensis*, *Tursiops aduncus* and *Delphinus capensis*) from South Africa: implications for ecological adaptation?

S. PLÖN*, K.H. ALBRECHT†, G. CLIFF# AND P. W. FRONEMAN^

Contact e-mail: stephanie@bayworld.co.za

ABSTRACT

Data from bycaught, but otherwise presumed healthy individuals can contribute important biological data on species of cetaceans that are otherwise lacking. This study utilises data collected from systematic necropsies performed between October 1970 and May 2010 on 142 Indo-Pacific humpback dolphins (*Sousa chinensis*), 607 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), and 640 long-beaked common dolphins (*Delphinus capensis*) incidentally caught and drowned in the shark nets off KwaZulu-Natal, South Africa. The aim of this analysis was to: (1) determine average absolute and relative organ weights for the three taxa as baseline values for later pathological examinations; and (2) examine potential correlations with the physiology and ecology in the three genera. Body length-weight relationships were described for the three species, indicating that *S. chinensis* is more robust than *T. aduncus*, with *D. capensis* being the smallest species out of the three taxa. Organ weights, as a percentage of total body weight were examined for the three delphinids. Organs examined included heart, lungs and trachea, liver, kidneys, spleen, and testes. Relative heart, liver and kidney weights were significantly larger in the small-bodied, fast-swimming *D. capensis*, than in the slower, more coastal *S. chinensis* and *T. aduncus*, possibly reflecting differences in activity patterns between the three species. Relative lung and trachea weights were not significantly different in the three species. Combined testes weight, as a percentage of total body weight, in combination with information on group size and sexual dimorphism suggested a monogamous or extreme polygynous (harem) mating system in *S. chinensis*, frequent copulations in *T. aduncus*, and sperm competition in *D. capensis*. The results of the present study suggest that the relative sizes of the major organs in the three genera are a reflection of the differing life histories and ecologies of the species examined.

KEYWORDS: INCIDENTAL CATCHES; AFRICA; INDO-PACIFIC HUMPBACK DOLPHIN; INDO-PACIFIC BOTTLENOSE DOLPHIN; LONG-BEAKED COMMON DOLPHIN

INTRODUCTION

Allometric relationships between organ weights and body weights have been the topic of numerous studies of mammalian taxa (Calder, 1983; Davis, 1962; Jürgens *et al.*, 1981; Lindstedt and Calder, 1981; Piscitelli *et al.*, 2010; Stahl, 1965; 1967; Western, 1979). Data from the Order Cetacea, however, are generally lacking. Information on organ weights in wild cetaceans is valuable for a number of reasons: to further the understanding of the physiology and overall biology of these animals, to provide comparative data with other species (both marine and terrestrial), and to establish baseline data that may be used to evaluate pathological change. Allometry is an important tool in comparative anatomy and physiology; the weight of an organ must, however, be examined in relation to the absolute size of the body to determine whether its weight is above or below the average value normally observed (Prothero, 1982; Slijper, 1958).

A number of previous studies have examined organ weights in odontocetes (for example Cowan, 1966; Cowan and Tajima, 2006; Gahr and Pilleri, 1969; Innes *et al.*, 1986; Kastelein and van Battum, 1990; McLellan *et al.*, 2002; Miyazaki *et al.*, 1981; Perrin and Roberts, 1972; Pilleri and Gahr, 1969; Piscitelli *et al.*, 2010; Turner *et al.*, 2006) and pinnipeds (Bryden and Erickson, 1976; Oftedal *et al.*, 1989;

Stewardson *et al.*, 1999). However, studies that examine organ weights in relation to body weights in an ecological context are rare for cetaceans (McLellan *et al.*, 2002; Miyazaki *et al.*, 1981; Perrin and Roberts, 1972; Ridgway and Kohin, 1995). There is therefore a lack of consideration as to the physiological and ecological pressures that may have shaped the observed patterns. This may in part be due to the logistical constraints in obtaining total body weight measurements from cetaceans. Body length measurements are taken as part of standard necropsy protocols of cetaceans (Norris, 1961), but body length is not always sufficient to accurately calculate body weight in these animals (Kastelein and van Battum, 1990). Although Slijper (1958) remarked that organ weights for a number of large baleen whale species were available as a byproduct of the economic importance of these animals at that time, enormous logistical challenges and time constraints are involved in weighing baleen whale carcasses, either whole or piecemeal (Lockyer, 1976; Lockyer and Waters, 1986; Omura, 1950). Thus due to logistical reasons, body weight measurements often pose a problem, even in smaller odontocetes (Cowan, 1966).

Baseline data on the normal variability in organ size in relation to body weight as well as histology are necessary to better interpret pathological changes in these genera (Cowan and Tajima, 2006; Turner *et al.*, 2006). Such data from

*South African Institute for Aquatic Biodiversity (SAIAB) and South African Environmental Observation Network (SAEON), c/o PE Museum/Bayworld, PO Box 13147, Humewood, Port Elizabeth, 6013, South Africa.

†Hochschule Bremen – University of Applied Sciences, Biomimetics, Neustadtswall 30, 28199 Bremen, Germany.

#KwaZulu-Natal Sharks Board, 1a Herrwood Drive, Private Bag 2, Umhlanga, 4320, South Africa.

^Department of Zoology and Entomology, Rhodes University, PO Box 90, Grahamstown, 6140, South Africa.

stranded animals are sometimes compromised because the animals can be desiccated or emaciated, and as a result may not yield a normal organ weight/body weight ratio (Cowan and Tajima, 2006). As the animals used in the present study were incidentally caught in shark nets off the South African coastline and subsequently died, it was assumed that they were in a normal condition and therefore may be considered representative of a wild population.

Indicators such as testes weight to body weight ratio, sexual dimorphism and group size have been used to provide information on the mating systems of terrestrial mammals (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986; Rose *et al.*, 1997). This approach has been applied in cetaceans as a basis to formulate hypotheses about the mating system of a species (e.g. Aguilar and Monzon, 1992; Brownell and Ralls, 1986; Cockcroft, 1993; Slooten, 1991; Van Waerebeek and Read, 1994). In odontocetes, small testes in relation to body weight, together with a large degree of sexual dimorphism and small group sizes, are thought to be indicative of a monogamous or extreme polygynous mating system, such as a harem or roving male strategy. Conversely, large relative testis weights, the absence of sexual dimorphism, and large group sizes are attributed to frequent copulations and sperm competition (Cockcroft, 1993; Connor *et al.*, 2000; Plön and Bernard, 2007; Van Waerebeek and Read, 1994).

Shark net installations along the KwaZulu-Natal coastline of South Africa have been in place since 1952 and today cover 23km in total along a 320km stretch of coast (Fig. 1) (Cliff and Dudley, 1992; Cliff, pers. comn). The nets are checked and maintained about 20 times per month by the KwaZulu-Natal Sharks Board (KZNSB). As part of a long-term agreement, data and samples from dolphins incidentally caught in these nets are being accessioned to the Graham Ross Marine Mammal collection at the Port Elizabeth Museum (PEM) in the Eastern Cape province of South Africa. These data and samples provide invaluable information on the natural history and ecology of the individual species caught, as well as information on diseases and any potential adverse effects of environmental conditions on the dolphins. The three main species incidentally caught in the nets are the long-beaked common dolphin *Delphinus capensis*, the Indo-Pacific bottlenose dolphin *Tursiops aduncus*, and, to a lesser extent, the Indo-Pacific humpback dolphin, *Sousa chinensis* (Best, 2007).

As the data from the present study are examined in view of the different mating styles shown by the three dolphin species considered, a brief overview is given here on different ecological aspects of the individual species, such as body size, group size and distribution.

S. chinensis is thought to exhibit sexual dimorphism – males are larger, with a maximum length of up to 279cm, compared to females, which have been recorded of reaching up to 249cm (Best, 2007; Ross and Best, 1989). The average group size is less than 10 animals for the species off South Africa (Karczmarski *et al.*, 1999; Ross, 1984; Ross *et al.*, 1994). These dolphins are coastal and are usually not observed in water depths over 25m or more than 400m offshore (Karczmarski *et al.*, 2000) and are found most often in the surf zone (less than 15m deep) (Friedmann and Daly, 2004; Ross *et al.*, 1994).

Despite bottlenose dolphins being cosmopolitan and widely studied, their taxonomy is unresolved (Fury and Harrison, 2008; Hale *et al.*, 2000; Rice, 1998). *T. aduncus* was first described from South Africa (Ross, 1977), and later confirmed genetically (Natoli *et al.*, 2004). It occupies inshore areas along the coastline compared to *T. truncatus*, which is found further offshore (Rice, 1998; Ross, 1977; 1984). Although it is not always possible retrospectively to discern which form/species some of the past records apply to, it has been assumed that all coastal records belong to the *aduncus* form (Best, 2007). Average adult lengths are 243cm in males and 238cm in females, and the form is smaller than *T. truncatus* (Best, 2007; Ross, 1984). Group sizes for this species range from 40 to 100 animals (Cockcroft *et al.*, 1992; Saayman *et al.*, 1973). *T. aduncus* mostly occupies the coastal regions in waters less than 50m deep, and is found all along the South African coastline between False Bay and Mozambique (Best, 2007) in a wide range of habitats, including lagoons and estuaries (Findlay *et al.*, 1992).

Although both *D. delphis* and *D. capensis* have been reported from the South African subregion (Best, 2007), prior genetic (Natoli *et al.*, 2006) and morphometric (Samaai *et al.*, 2005) analyses of specimens caught in the shark nets off KwaZulu-Natal have identified the specimens as *D. capensis* and thus all animals included in the present sample are assumed to belong to that species. *D. capensis* off South Africa show a maximum adult body length of 254cm in males and 222cm in females (Heyning and Perrin, 1994; Ross, 1984; Ross and Best, 1989). This species is found in groups of 100s to 1,000s of individuals, with an average group size of 302, but appear to have social units of around 30 animals (Cockcroft and Peddemors, 1990; Evans, 1994). Along the South African coastline *D. capensis* occupies waters of less than 500m in depth (Findlay *et al.*, 1992; Rice, 1998). Annual migrations in winter along the east coast are common, following the annual ‘Sardine Run’, which begins in the Eastern Cape and travels up to the north coast of KwaZulu-Natal (Findlay *et al.* 1992). However, sightings of *D. capensis* in KwaZulu-Natal waters have been made in both summer and winter (Findlay *et al.*, 1992).

The aim of the present study was to: (1) provide baseline data on absolute and relative organ weights of three dolphin species incidentally caught in the shark nets along the KwaZulu-Natal coastline of southern Africa; and to (2) explore potential correlations between the relative weight the individual organs contribute to the total body weight and the ecology of the three species examined.

MATERIALS AND METHODS

Sample

For the present study, data for 142 *S. chinensis*, 607 *T. aduncus*, and 640 *D. capensis* were analysed. All data were available from the Graham Ross Marine Mammal Collection at the Port Elizabeth Museum, Port Elizabeth, South Africa, and originate from animals incidentally caught and drowned in the shark nets off KwaZulu-Natal (Fig. 1). No stranded specimens were included in the analyses. All data from carcasses that were noted as either rotten, shark bitten, or pregnant were removed from the dataset. The data analysed included total body weight and length as well as weights for the heart, lung and trachea, liver, kidneys, spleen and testes.

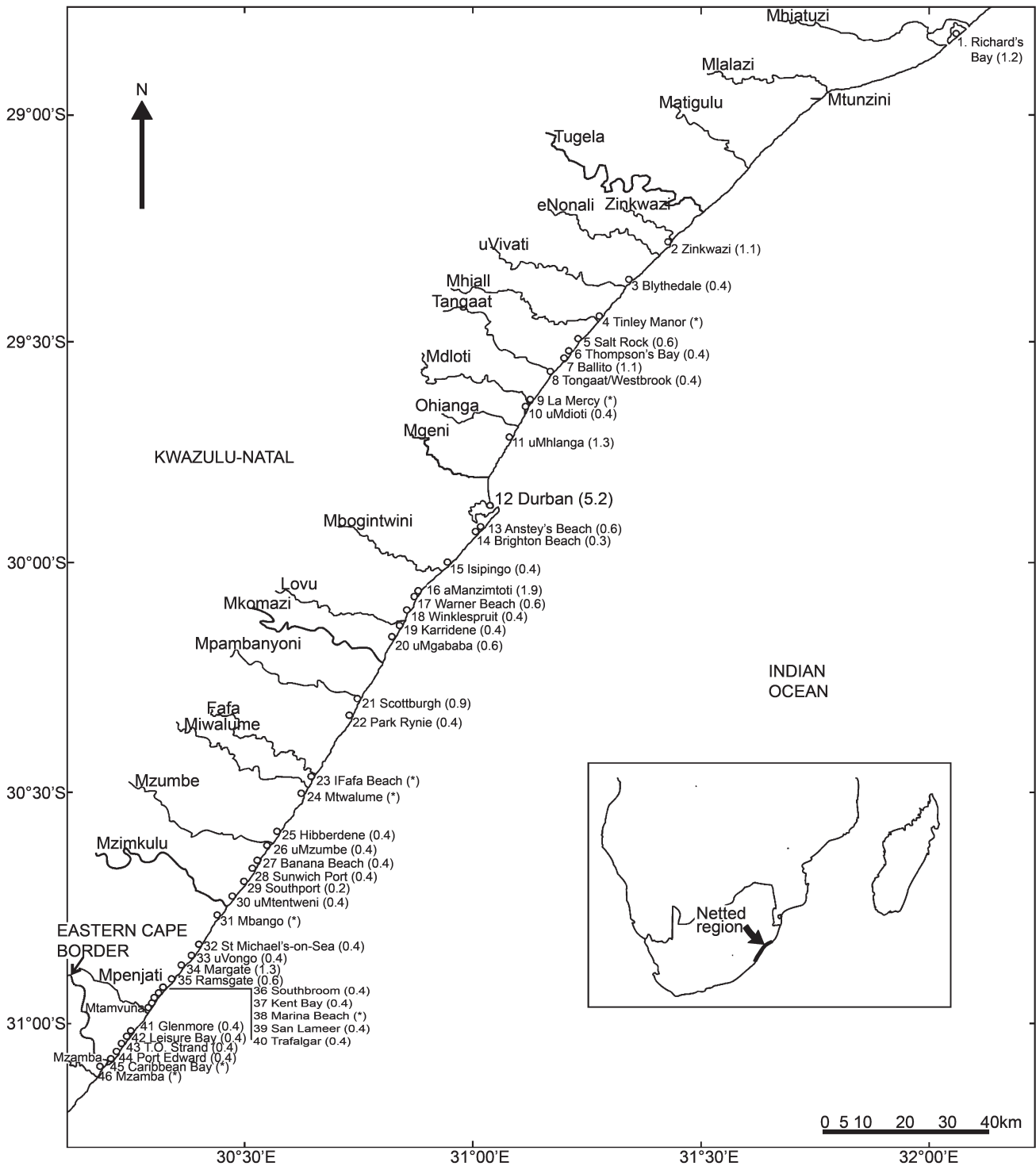


Fig. 1. Shark net installations along the KwaZulu-Natal coastline. Numbers in parentheses show the length of netting in km as of November 2006. Source: KZNSB.

As datasets may not have been complete for each individual, sample sizes vary for the individual organ weights as stated in the text. The time period over which these data were collected for the individual species was as follows: *S. chinensis*: 28 November 1979–29 April 2010, *T. aduncus*: October 1970–11 May 2010, and *D. capensis*: 14 Aug 1974–16 Nov 2009.

Standard body length and weight measurements of the dolphin carcasses were determined as the carcasses arrived at KZNSB. Body length measurements were carried out following the guidelines of Norris (1961). Thereafter the

carcasses were frozen until further analyses were conducted. The carcasses were defrosted prior to systematic necropsies. The heart, lung and trachea were removed together from the thoracic cavity and the heart was separated out by severing the dorsal aorta and all major blood vessels at the entrance to the heart. It was then drained of blood and blood clots were washed out prior to weighing. The lung and trachea (including the larynx) were weighed together, and, in some instances, the lungs were dissected free at the level of the principal bronchus and weighed individually. Organs up to 3kg were weighed to the nearest gram on a digital balance (Nagata). Organs over

3kg were weighed using a hand-suspended Salter balance. The reproductive status of the animals was noted upon necropsy based on macroscopic examinations of the reproductive organs (i.e. presence/absence of sperm in the epididymis, presence of corpora on the ovaries). The epididymides were removed from the testes before a combined testis weight was obtained for each individual.

Total body length-weight relationships were established for all three dolphin species and described by allometric equations of the form $y = ax^b$, where a = y -intercept, b = slope, x = total body weight (kg), and y = total organ weight (g). Relative organ weights were calculated for each individual and expressed as a percentage of body weight. To compare the relative organ weights between the three genera, the percentage data were arc-sine transformed (Zar, 1999) before an ANOVA and *post-hoc* Tukey test were carried out. To examine potential differences between males and females for each of the three species, individual organ weights and body weights were log-transformed and allometric equations generated for either sex for each of the three species. Slopes and y -intercepts were compared using an ANCOVA multiple regression analysis with a predetermined alpha (α) set at 0.05. All statistical analyses were conducted using *STATISTICA* v. 9 (StatSoft Inc.).

To evaluate the contribution the testes made to the overall body weight, the combined testes weights of only mature males of the three dolphin species were analysed. While no previous data on maturity of male *S. chinensis* were available, an increase of combined testes weight was observed at about 223cm body length and 200g combined testes weight in the sample. Thus subsequently only data for animals over 223cm in body length and/or over 200g combined testes weight were used to determine combined testes weight as a percentage of total body weight ($n = 23$).

For *T. aduncus* only males over 225cm in body length and/or over 300g combined testes weight were analysed ($n = 90$) (following Cockcroft and Ross, 1990a), and for *D. capensis* only males over 220cm body length and/or over 200g combined testes weight were analysed ($n = 172$) (following Mendolia, 1989).

RESULTS

Body length-weight relationships

Individual plots of body weight versus length for males, females and sexes combined for all three species are shown in Figs 2, 3 and 4, respectively. Allometric equations for these relationships are provided in Table 1.

Out of 92 male and 50 female *S. chinensis* examined, the shortest animals measured 145cm and 150cm and weighed 43kg and 46kg, respectively. The longest specimens of *S. chinensis* in the present study were a 276cm long male, weighing 280kg and a 251cm long female, weighing 188kg (Fig. 2).

Of 299 male and 308 female *T. aduncus* examined, the shortest animals were a 100cm long male, weighing 9.75kg and a 120cm long female, weighing 19kg (Fig. 3). The heaviest male specimen was 246cm long and weighed 248kg, although the longest male measured 262cm, but only weighed 226kg (Fig. 3). The longest female *T. aduncus* measured 256cm and weighed 190kg (Fig. 3).

For *D. capensis* length and weight data for 328 males and 312 females were available. The shortest male measured 114cm and weighed 18kg, while the shortest female was 107cm long, weighing 21kg (Fig. 4). The longest male was 265cm long and weighed 192kg (Fig. 4). A 252cm long female, weighing 80kg may be considered unrepresentative for animals from this population; thus the longest female measured 240cm and weighed 148kg (Fig. 4).

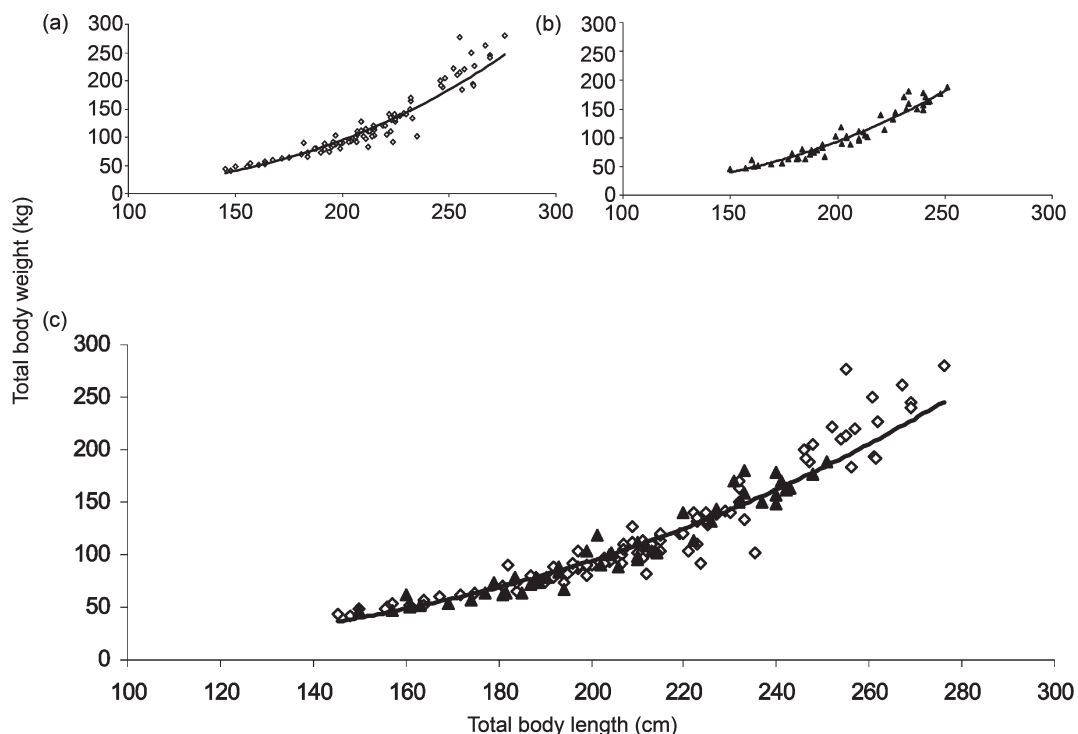


Fig. 2. Body length-weight relationships for (a) male *S. chinensis*, (b) female *S. chinensis*, and (c) both sexes of *S. chinensis* (diamond = males; triangle = females).

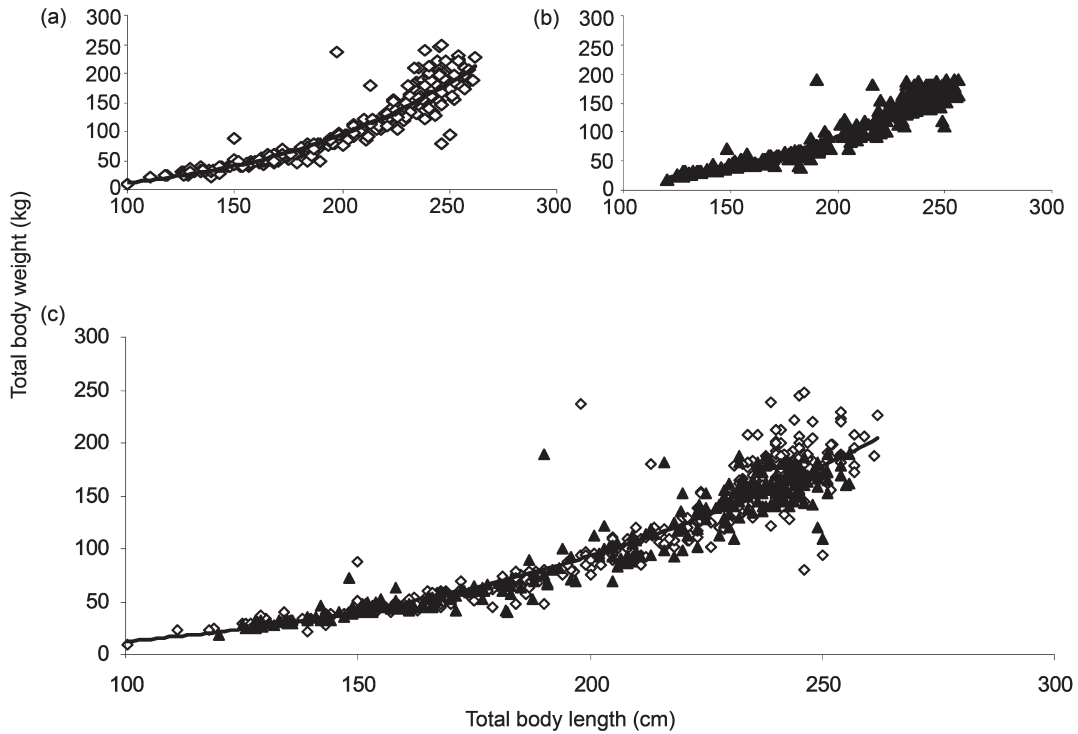


Fig. 3. Body length-weight relationship for (a) male *T. aduncus*, (b) female *T. aduncus*, and (c) both sexes of *T. aduncus* (diamond = males; triangle = females).

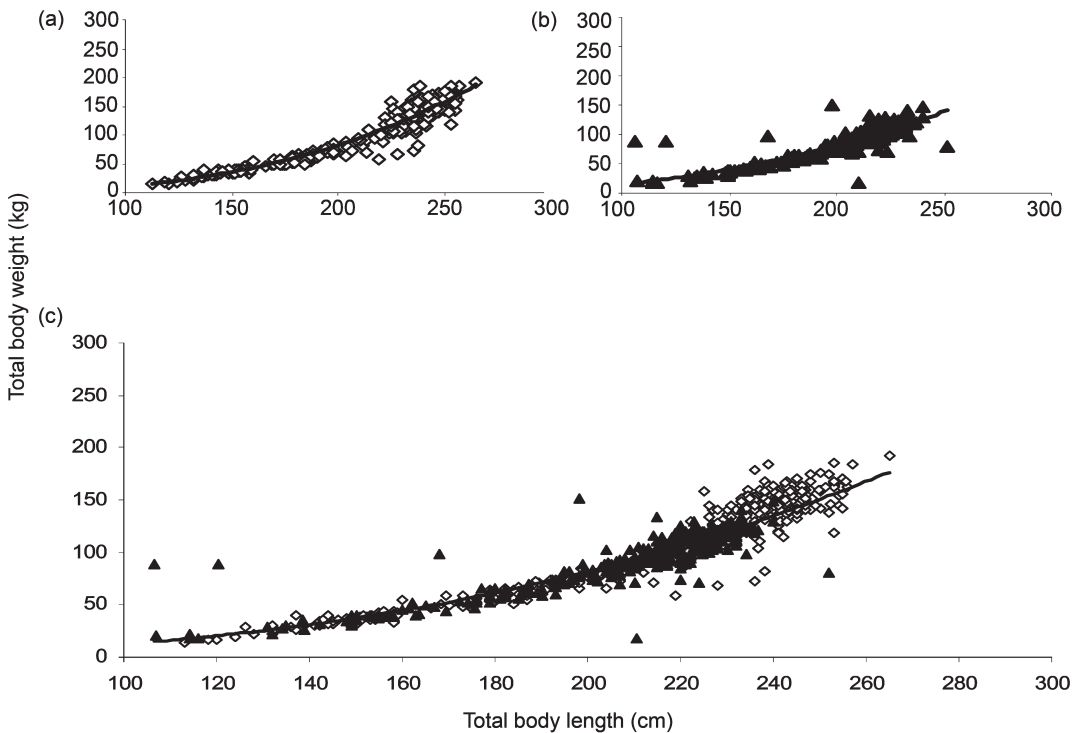


Fig. 4. Body length-weight relationship for (a) male *D. capensis*, (b) female *D. capensis*, and (c) both sexes of *D. capensis* (diamond = males; triangle = females).

These length-weight relationships indicate the differences in body size between the three species (Figs 2, 3 and 4), with the largest *S. chinensis* male being substantially larger (14cm longer and 32kg heavier) than the largest *T. aduncus* male. In females of the two species, however, there was little difference in body size, the largest *S. chinensis* female being 5cm shorter than the largest *T. aduncus* female and weighing 2kg less. Similarly, the difference in body length between

the longest male *T. aduncus* and the longest *D. capensis* male was negligible (262cm vs. 265cm, respectively), but the heaviest *T. aduncus* male was 56kg heavier than the heaviest *D. capensis* male. In females this difference between the species was 16cm and 42kg. The observed difference between *T. aduncus* and *D. capensis* was substantially larger than between *S. chinensis* and *T. aduncus*, indicating that *D. capensis* is considerably smaller than the other two species,

Table 1

Allometric equations for length-weight relationships for all three species of delphinids.

Species	Sex	N	Equation	R ²
<i>Sousa chinensis</i>	M	92	$y = 0.00001x^{2.9692}$	0.9335
	F	50	$y = 0.00001x^{2.9765}$	0.9434
	M & F	142	$y = 0.00001x^{2.9762}$	0.9372
<i>Tursiops aduncus</i>	M	299	$y = 0.00001x^{2.9605}$	0.932
	F	308	$y = 0.00003x^{2.8429}$	0.9468
	M & F	607	$y = 0.00002x^{2.9011}$	0.9379
<i>Delphinus capensis</i>	M	328	$y = 0.00002x^{2.9229}$	0.9538
	F	312	$y = 0.0002x^{2.4169}$	0.7918
	M & F	640	$y = 0.00004x^{2.7408}$	0.8938

with *S. chinensis* being the most robust out of the three species.

Organ weights as a percentage of body weight

The trend in absolute organ weights between the three species of dolphins was such that the largest absolute weights were usually present in *T. aduncus*, followed by *D. capensis*, with *S. chinensis* having the smallest absolute organ weights (Table 2). One exception were the absolute liver weights, which were slightly higher in *D. capensis* than *T. aduncus* (Table 2).

This general trend was reversed in the spleen, which was largest in *S. chinensis* (mean = 94.04g ± 38.52), followed by *D. capensis* (mean = 80.39g ± 55.95), with *T. aduncus* having the smallest spleen in terms of absolute size out of the three species (mean = 66.68g ± 33.28) (Table 2).

If, however, the organ weights are considered relative to body weight of the three delphinid species, a different pattern emerges. The relative heart weights showed the reverse trend observed in absolute body size between the three species as the heart was larger in relation to the overall body weight in *D. capensis* (mean = 0.62% ± 0.11), than it was in *T. aduncus* (mean = 0.6% ± 0.14) or *S. chinensis* (mean = 0.52% ± 0.08). This trend was supported by results from an ANOVA and *post-hoc* Tukey test, which showed that the relative heart weights of *S. chinensis*, *T. aduncus* and *D. capensis* were significantly different from each other (*F*-value = 70830.01, *p*<0.001).

The same trend of largest relative organ weights in the smallest species was true for the relative weights of liver and kidneys: both made up the larger percentage of body weight in *D. capensis* (mean = 2.47% ± 0.58 and 0.85% ± 0.19, respectively) than in *T. aduncus* (mean = 2.03% ± 0.47 and 0.8% ± 0.19, respectively) and *S. chinensis* (mean = 1.93% ± 0.39 and 0.67% ± 0.12, respectively). This result was supported by the ANOVA analysis and Tukey test, which showed that the relative liver weights of *D. capensis* were significantly larger than those of *T. aduncus* and *S. chinensis* (*F*-value = 32427.98, *p*<0.001); no significant difference in organ weights was found between the latter two species. Kidney weights proved to be significantly different for all three species, with *D. capensis* having the largest kidneys and *S. chinensis* the smallest ones (*F*-value = 42225.54, *p*<0.05).

Relative weights for the lungs and trachea combined were larger in *T. aduncus* (mean = 4.33% ± 0.88) than they were

Table 2

Absolute and relative organ weights from three dolphin species incidentally caught in the shark nets off the KwaZulu-Natal coast of South Africa.

Species:	<i>Sousa chinensis</i>	<i>n</i>	<i>Tursiops aduncus</i>	<i>n</i>	<i>Delphinus capensis</i>	<i>n</i>
Heart						
Minimum weight (g)/(%)	240/0.36	131	118/0.23	350	84/0.09	308
Maximum weight (g)/(%)	1,250/0.88		1,550/1.91		1,367/1.11	
Mean weight (g) (±SD)/	591.11 (±219.91)/		637.83 (± 311.98)/		635.45 (±256.91)/	
Mean % of body weight (±SD)	0.52 (±0.08)		0.6 (±0.14)		0.62 (±0.11)	
Lungs and trachea						
Minimum weight (g)/(%)	1,550/2.39	131	962/1.43	333	720/1.33	296
Maximum weight (g)/(%)	8,675/6.11		11,050/9.05		8,430/7.27	
Mean weight (g) (±SD)/	4,420.59 (±1808.52)/		4,789.92 (±2,514.66)/		4,227.27 (±1,809.32)/	
Mean % of body weight (±SD)	3.88 (±0.57)		4.33 (±0.88)		4.1 (±0.81)	
Lungs						
Minimum weight (g)/(%)	1,900/2.97	9	1,350/0.78	24	3,050/2.61	7
Maximum weight (g)/(%)	4,700/3.96		8,300/6.14		5,161/4.29	
Mean weight (g) (±SD)/	3,396.11 (±1047.86)/		3,276.49 (±2,037.36)/		4,243 (±745.1)/	
Mean % of body weight (±SD)	3.25 (±0.33)		3.8 (±0.98)		3.7(±0.62)	
Liver						
Minimum weight (g)/(%)	718/0.77	92	109.9/0.16	323	53/0.19	307
Maximum weight (g)/(%)	6,100/3.2		5,500/3.87		6,512/4.52	
Mean weight (g) (±SD)/	2,290.23 (±1049.47)/		2,356.31 (±1,357.69)/		2,605.25 (±1,224.24)/	
Mean % of body weight (±SD)	1.93 (±0.39)		2.03 (±0.47)		2.47 (±0.58)	
Kidneys						
Minimum weight (g)/(%)	263/0.45	92	160/0.32	312	115/0.34	289
Maximum weight (g)/(%)	2,080/0.96		2,970/2.09		3,250/2.32	
Mean weight (g) (±SD)/	790.64 (±363.93)/		918.97 (±530.96)/		910.3 (±425.23)/	
Mean % of body weight (±SD)	0.67 (±0.12)		0.8 (±0.19)		0.85 (±0.19)	
Spleen						
Minimum weight (g)/(%)	43/0.02	61	11/0.01	181	8/0.01	192
Maximum weight (g)/(%)	211/0.2		192.4/0.2		460/0.33	
Mean weight (g) (±SD)/	94.04 (±38.52)/		66.68 (±33.28)/		80.39 (±55.95)/	
Mean % of body weight (±SD)	0.09 (±0.04)		0.07 (±0.04)		0.08 (±0.05)	

in either *D. capensis* (mean = 4.1% ± 0.81) or *S. chinensis* (mean = 3.88% ± 0.57). If just lung weights were considered, the same trend was observed (*T. aduncus*: mean = 3.8 ± 0.98; *D. capensis*: mean = 3.7% ± 0.62; *S. chinensis*: mean = 3.25% ± 0.33). However, sample sizes for lung weights were very small and may therefore not be representative for the species. The ANOVA results using combined lung and trachea weights showed no significant differences between the three species (*F*-value = 26364.09, *p*>0.05).

Examining the relative spleen weights between the three species the trend seemed reversed, with *S. chinensis* showing the largest relative weights (mean = 0.09% ± 0.04), followed by *D. capensis* (mean = 0.08% ± 0.05) and *T. aduncus* having the smallest spleen (mean = 0.07% ± 0.04). The ANOVA results confirmed that (*F*-value = 5077.023, *p*<0.001).

A summary of the allometric relationships of the various organs with body size in all three delphinids is supplied in Table 3. All organs showed a strong correlation with body size, with the exception of the spleen in all three species (Table 3).

The ANCOVA analysis indicated no significant differences between males and females of *S. chinensis* for the lungs and trachea, liver, kidney and spleen (*p*>0.05 in all cases), but showed that males had significantly larger hearts than females (*p*<0.05) (Fig. 5). No significant differences between males and females were found in *T. aduncus* (*p*>0.05) or *D. capensis* (*p*> 0.05) in all cases (Figs 6 and 7).

Table 3

Allometric equations for organ-weights versus body weight relationships for all three species of delphinids.

Organ	Sex	<i>n</i>	Equation	R ²
<i>Sousa chinensis</i>				
Heart	M	86	$y = 1.8367x^{0.5686}$	0.9002
	F	46	$y = 0.4492x^{1.4913}$	0.9368
Lungs and trachea	M	83	$y = 2.5751x^{0.4779}$	0.883
	F	46	$y = 2.467x^{0.5456}$	0.9338
Liver	M	64	$y = 2.1638x^{0.5981}$	0.8127
	F	28	$y = 2.1432x^{0.6171}$	0.7476
Kidneys	M	62	$y = 1.7207x^{0.7065}$	0.8411
	F	30	$y = 1.6918x^{0.7467}$	0.9088
Spleen	M	42	$y = 1.5096x^{0.3705}$	0.1325
	F	21	$y = 1.6881x^{0.1362}$	0.0278
<i>Tursiops aduncus</i>				
Heart	M	170	$y = 1.8426x^{0.5864}$	0.866
	F	180	$y = 1.7845x^{0.6356}$	0.9102
Lungs and trachea	M	158	$y = 2.5975x^{0.483}$	0.9106
	F	165	$y = 2.5444x^{0.5183}$	0.8978
Liver	M	164	$y = 2.1345x^{0.6202}$	0.7691
	F	159	$y = 2.0885x^{0.6626}$	0.7394
Kidneys	M	151	$y = 1.8233x^{0.661}$	0.8865
	F	161	$y = 1.7612x^{0.7226}$	0.9058
Spleen	M	80	$y = 1.1405x^{0.666}$	0.4399
	F	101	$y = 1.2889x^{0.4458}$	0.2646
<i>Delphinus capensis</i>				
Heart	M	165	$y = 1.7813x^{0.6476}$	0.9148
	F	143	$y = 1.8187x^{0.6136}$	0.7475
Lungs and trachea	M	158	$y = 2.5163x^{0.5165}$	0.9047
	F	136	$y = 2.5367x^{0.5105}$	0.7787
Liver	M	167	$y = 2.1752x^{0.6322}$	0.9134
	F	140	$y = 1.9798x^{0.7858}$	0.7267
Kidneys	M	155	$y = 1.7478x^{0.7303}$	0.9093
	F	134	$y = 1.7045x^{0.7918}$	0.8654
Spleen	M	106	$y = 1.2789x^{0.538}$	0.1789
	F	87	$y = 1.2652x^{0.4842}$	0.1185

Testis weight as a percentage of body weight

The smallest combined testis weight in relation to total body weight was observed in *S. chinensis*, where it constituted on average 0.43% of the total body weight (Table 4). The testes were somewhat larger in *T. aduncus*, where the combined testes weight made up on average 0.64% of the total body weight in mature males. The largest combined testis weight was seen in *D. capensis*, where it constituted on average 2.01% of the total body weight (Table 4). An ANOVA showed significant differences between the three species (*F*-value = 158.406, *p*<0.001).

DISCUSSION

Relative organ weights as a reflection of a species' ecology

The data on body size, group size, and distribution range indicate that *S. chinensis* is a robust delphinid that occurs in small groups and has a coastal distribution with a relatively small range (Best, 2007; Karczmarski *et al.*, 2000). Data on travel speeds for the species in South Africa have been reported to be 4.8km hr⁻¹ (Saayman and Tayler, 1979); personal observations support the notion that the species cannot be considered a fast swimmer. In contrast, *T. aduncus* is moderately smaller in body size, occurs in larger groups and has wider distribution range than *S. chinensis*, with faster travel speeds, ranging from 2.8km/hr⁻¹ to 9.9km hr⁻¹ reported for South African waters (Best, 2007; Cockcroft *et al.*, 1990; Saayman *et al.*, 1972). *D. capensis* is the smallest of the three dolphins considered, but occurs in large schools and is a fast-swimming, oceanic species with a large distribution range (Best, 2007); swimming bursts of 20.5–32km hr⁻¹ have been reported for the species (Rohr *et al.*, 2002). The trend in absolute organ weights observed during this investigation with smaller species, such as *D. capensis* having larger organs than the largest species, *S. chinensis*, appears counter-intuitive. Calculation of the relative organ weights in relation to body weight indicated a different trend, which can be explained by the different physiologies and ecologies of the three genera.

The significantly larger relative heart, liver, and kidneys in *D. capensis*, compared to the other two species, may reflect the higher metabolism or 'work rate' in this active, fast-swimming, oceanic species. Heart weight in cetaceans has been the subject of some investigation. Ridgway and Kohin (1995) presented relative heart weights for three genera of small odontocetes and concluded that differences in heart weight are due to differences in physiological and ecological demands. The largest relative heart weights were found in the fast-swimming, offshore species (Dall's porpoise, *Phocoenoides dalli*). The heart weight was intermediate in the slower swimming species (Pacific white-sided dolphin *Lagenorhynchus obliquidens*), and smallest in the most inshore, slowest moving species (common bottlenose dolphin *T. truncatus*) (Ridgway and Kohin, 1995). A similar trend was observed during this study with the fast swimming, offshore, *D. capensis* having the largest heart in relation to body weight. Slijper (1958) reported heart weights for a number of cetacean species and suggested that activity and swimming speed may play a role in the relative size of the heart in relation to the body weight. Bryden (1972)

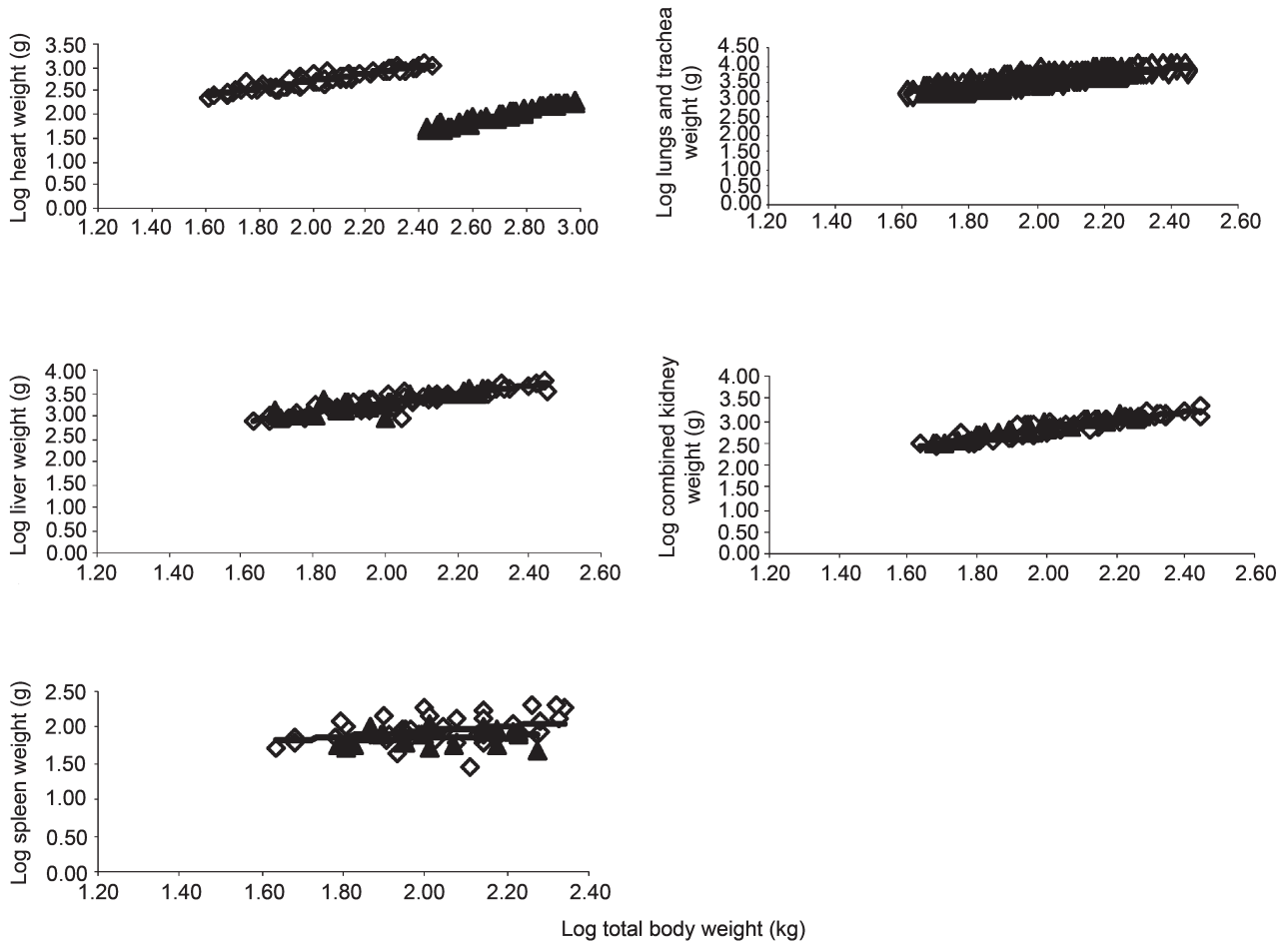


Fig. 5. Log respective organ weight (g) versus log total body weight (kg) for adult male (diamond) and female (triangle) *S. chinensis*.

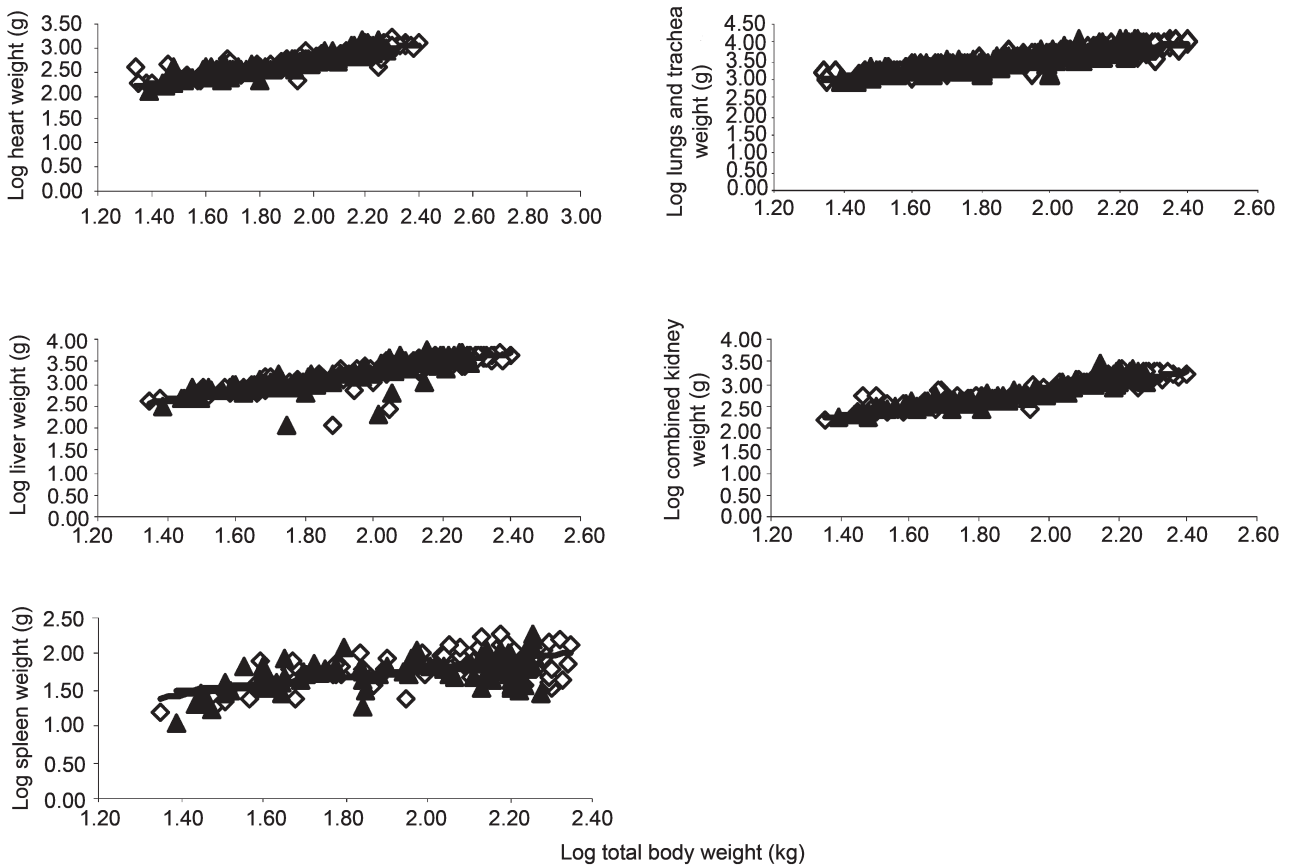


Fig. 6. Log respective organ weight (g) versus log total body weight (kg) for adult male (diamond) and female (triangle) *T. aduncus*.

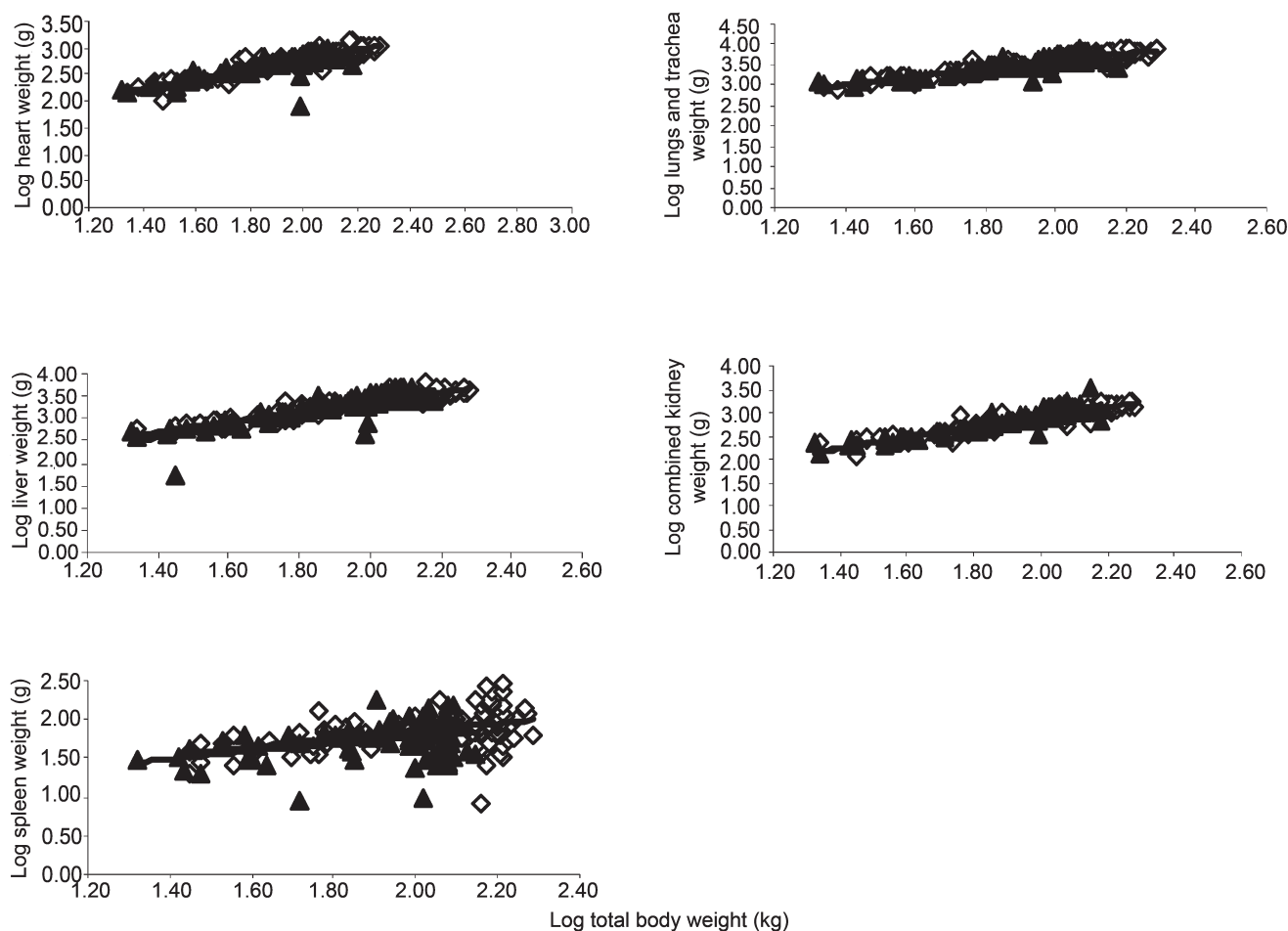


Fig. 7. Log respective organ weight (g) versus log total body weight (kg) for adult male (diamond) and female (triangle) *D. capensis*.

concluded that the relative heart size within different groups of mammals is probably as closely related to activity, speed and other physiological factors as it is to body weight (Bryden, 1972). Greater relative heart weights in pinnipeds have also been explained using increased activity, for example in Ross seals (*Ommatophoca rossi*) as compared to crabeater seals (*Lobodon carcinophagus*; Bryden and Erickson, 1976), and Cape fur seals (*Arctocephalus pusillus*) in comparison to Antarctic fur seals (*A. gazella*) (Stewardson *et al.*, 1999), with the two former species having to dive deeper and feeding on faster prey than the latter.

Relative liver weights previously reported for cetaceans reflect an inverse relationship between body size and relative liver weight, which was also apparent during the present study. Slijper (1958) reported an average weight of liver of 3.22% of body weight for the harbour porpoise *Phocoena phocoena*, 2.20% of body weight for a number of dolphin

species, and 1.20% of body weight for the sperm whale *Physeter macrocephalus*. Perrin and Roberts (1972) reported an average liver weight equivalent to 2.53% body weight for the spotted dolphin (*Stenella graffmani* = *attenuata*) and 1.90% of body weight for the spinner dolphin *S. longirostris*. Prothero (1982) examining liver weights over a large range of mammalian taxa, both aquatic and terrestrial, concluded that there were no differences in relative liver weights between aquatic and terrestrial mammals or between males and females, although he observed that the proportion of the liver tissue contributed to the overall body weight decreases with increasing body weight.

Slijper (1962) commented that the relative weight of the kidneys in small cetaceans in general is exceptionally large, reporting relative weights 0.84% of total body weight for several porpoises, 1.10% of body weight for *T. truncatus*, and 0.93% for *L. obliquidens*. *S. attenuata* show average relative kidney weights of 0.98% and *S. longirostris* of 0.65% (Perrin and Roberts, 1972). An inverse relationship between relative kidney weight to body weight as seen in three species examined in the present study has not been reported previously.

Although a trend in relative heart, liver and kidney weights was observed between the three species examined, surprisingly no significant difference was found in the relative lung and trachea weights. Previous studies on lung mass in cetaceans suggest that the lungs of delphinids and phocoenids are larger than those of similar sized terrestrial

Table 4

Combined testis weight as a percentage of total body weight for mature male animals.

Species	<i>Sousa chinensis</i>	<i>Tursiops aduncus</i>	<i>Delphinus capensis</i>
<i>n</i>	26	90	172
Minimum weight (%)	0.16	0.20	0.07
Maximum weight (%)	0.7	1.12	4.19
Mean % weight (±SD)	0.43 (±0.12)	0.64 (±0.20)	2.01 (±0.88)

mammals (Bryden, 1972; Kooyman, 1973; Kooyman and Sinnett, 1979; Piscitelli *et al.*, 2010), while the relative lung mass of deeper diving odontocetes (kogiids, physeterids, and ziphiids) is similar to that of similar sized terrestrial mammals (Piscitelli *et al.*, 2010). Dive depths for the three species off South Africa examined here are non-existent, but available data on stomach content analyses indicate that *S. chinensis* feeds in shallow, inshore, often estuarine habitats (Barros and Cockcroft, 1991; 1999), while *T. aduncus* feeds mainly on coastal reef fishes (Cockcroft and Ross, 1990b) and *D. capensis* on epipelagic shoaling fish (Young and Cockcroft, 1994). As all three delphinids examined can be considered relatively shallow divers, which are 'fast' breathing (meaning high ventilation rate, short ventilation/dive times, and high lung volume exchanged per breath) (Kooyman, 1973; Piscitelli *et al.*, 2010), and thus no differences in lung weight would be expected between the three species. In comparison, the lungs of *S. attenuata* and *S. longirostris* are very similar in size, making up 3.2% of the body weight and 3.3%, respectively (Perrin and Roberts, 1972). In *P. phocoena* the lungs make up 3.5%, in *T. truncatus* 2.87% and 3.59% in *L. obliquidens* (Slijper, 1958).

The significantly smaller spleen found in *T. aduncus* in the present study, compared to that of *D. capensis* and *S. chinensis*, is intriguing, particularly in conjunction with the weak allometric relationship of this organ with body weight found for all three species examined. As the function of the spleen is the creation, storage and filtration of red blood cells as well as involvement in active immune response, no obvious explanation is to date at hand for this observation. Bryden (1972) remarked that the spleen in cetaceans is very small (0.02%) in comparison with that of most terrestrial mammals, where it constitutes around 0.3% of the body weight. Relative spleen weights reported for other odontocetes support this, with average values *S. attenuata* and *S. longirostris* being 0.06% and 0.04%, respectively (Perrin and Roberts, 1972). Interestingly, sexual dimorphism in spleen weights has also been reported for *S. longirostris*. For *P. phocoena* and *T. truncatus*, the spleen constitutes 0.02% and 0.09% of the total body weight (Slijper, 1958). Thus the relative weights of 0.09%, 0.07% and 0.08% of total body weight found for *S. chinensis*, *T. aduncus* and *D. capensis*, respectively, during this investigation are in accordance with relative spleen weights for small cetaceans published previously.

Testis weight and mating system

Cockcroft (1993) hypothesised previously that the combined testis size of these three delphinids in relation to group size and sexual dimorphism within the individual species may give indications as to the mating system. He reported an average relative testes weight of 0.7% for *S. chinensis*, 1% for *T. aduncus*, and 4.2% for *D. capensis* (Cockcroft, 1993). Although the trend of smallest values for average relative testis weight in *S. chinensis* (present study: 0.4%), followed by somewhat larger testes in *T. aduncus* (0.6% of total by weight), with the biggest testes found in *D. capensis* (2%) is also seen in the present study, the values are somewhat lower than those reported by Cockcroft (1993). However, interestingly the maximum values seen in the present study concur with the average values presented by Cockcroft

(1993). Plön and Bernard (2007), in reviewing available data for combined testis sizes in relation to proposed mating systems for cetaceans, concluded that relatively small testes in relation to body weight indicate a monogamous or extreme polygynous mating system. Conversely, relatively large testes are indicative of frequent copulations and sperm competition. In this sense the data from the present study indicate that the small relative testis weight in association with sexual dimorphism and small group sizes seen in *S. chinensis* is representative of a mating system in which a single male has access to a number of females. The somewhat larger testes, reduced sexual dimorphism, and larger group size in *T. aduncus* is indicative of more frequent copulations by males (Connor *et al.*, 2000; Plön and Bernard, 2007). The relatively large testes seen in *D. capensis*, with no sexual dimorphism and large group sizes prevalent in this species are representative of sperm competition (Cockcroft, 1993; Connor *et al.*, 2000; Plön and Bernard, 2007).

SUMMARY

In summary, the results of the present study suggest that the relative size of the major organs in the three genera examined here are a reflection of the differing life histories and ecologies of the species. Absolute organ weight has been shown to have little biological meaning and organ weights need to be considered in relation to body weight. While the above organ weights are in accordance with similar studies carried out previously on other cetacean genera, recent findings on *P. phocoena* suggest that on average 27% of the total body weight in adult animals is made up of blubber (McLellan *et al.*, 2002). The contribution of blubber to the total weight is even higher in juvenile animals (Lockyer, 1993; McLellan *et al.*, 2002; Miyazaki *et al.*, 1981). Unfortunately, contributions of blubber weight to the total body weight could not be taken into account during this study as these measurements were not available for the majority of the carcasses. Thus it is unclear whether this would skew the data in any way, particularly as the contribution of blubber weight to the total body weight appears to vary between species as well between seasons (Lockyer, 1993). However, future studies should aim to account for contributions of blubber weight to total body weight to elucidate these issues.

The baseline data on organ weights in the three genera established in the present study will form the basis of more detailed pathological and health examinations of the carcasses in the future and hopefully contribute to identification of what presents 'normal' organ weights in the three species. These will then be available for comparison with data from strandings or heavily diseased animals.

ACKNOWLEDGEMENTS

The authors would like to acknowledge Graham Ross, who had the foresight to establish the marine mammal collection at the Port Elizabeth Museum and examine and accession the unfortunate specimens that drown in the shark nets to this collection for availability for future research. In addition, we are indebted to everyone who has worked on and contributed to this collection, in particular Vic Cockcroft, Vic Peddemors, Wendy Kant, Gillian Watson, and Greg

Hofmeyr. Furthermore, we thank Philipp Zungu and other KZNSB laboratory staff for their assistance. We would also like to thank Ann Pabst and Peter Best, whose comments greatly improved an earlier version of the manuscript.

REFERENCES

- Aguilar, A. and Monzon, F. 1992. Interspecific variation of testis size in cetaceans: a clue to reproductive behaviour? *Eur. Res. Cet.* 6: 162–64.
- Barros, N.B. and Cockcroft, V.G. 1991. Prey of humpback dolphins (*Sousa plumbea*) stranded in the eastern cape Province, South Africa. *Aquat. Mamm.* 17(3): 134–36.
- Barros, N.B. and Cockcroft, V.G. 1999. Prey resource partitioning between Indo-Pacific hump-backed (*Sousa chinensis*) and bottlenose dolphins (*Tursiops truncatus*) off South Africa – competitive exclusion or mutual tolerance? 12th Biennial Conference on the Biology of Marine Mammals, Maui, Hawaii. [Abstract only].
- Best, P.B. 2007. *Whales and Dolphins of the Southern African Subregion*. Cambridge University Press, Cape Town.
- Brownell, R.L. and Ralls, K. 1986. Potential for sperm competition in baleen whales. *Rep. int. Whal. Commn (special issue)* 8: 97–112.
- Bryden, M.M. 1972. Growth and development of marine mammals. pp.1–79. In: Harrison, R.J. (eds). *Functional Anatomy of Marine Mammals*. Academic Press, New York and London.
- Bryden, M.M. and Erickson, A.W. 1976. Body size and composition of Crabeater seals (*Lobodon carcinophagus*) with observations on tissue and organ size in Ross seals (*Ommatophoca rossi*). *J. Zool., London.* 179: 235–47.
- Calder, W.A. 1983. Ecological scaling: mammals and birds. *Ann. Rev. Ecol. Syst.* 14: 213–30.
- Cliff, G. and Dudley, S.F.J. 1992. Protection against shark attack in South-Africa, 1952–90. *Aust. J. Mar. Freshwater Res.* 43(1): 263–72.
- Cockcroft, V.G. 1993. Size: the only male reproductive strategy? 10th Biennial Conference on the Biology of Marine Mammals, Galveston, Texas, USA, 11–15 November. [Abstract only].
- Cockcroft, V.G. and Peddemors, V.M. 1990. Seasonal distribution and density of common dolphins off the south east coast of southern Africa. *S. Afr. J. Mar. Sci* 9: 371–77.
- Cockcroft, V.G. and Ross, G.J.B. 1990a. Age, growth and reproduction of bottlenose dolphins from the east coast of southern Africa. *Fish. Bull.* 88(2): 289–302.
- Cockcroft, V.G. and Ross, G.J.B. 1990b. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. pp.295–308. In: Leatherwood, S. and Reeves, R.R. (eds). *The Bottlenose Dolphin*. Academic Press, San Diego, California. 653pp.
- Cockcroft, V.G., Ross, G.J.B. and Peddemors, V.M. 1990. Bottlenose dolphin *Tursiops truncatus* distribution in Natal's coastal waters. *S. Afr. J. Mar. Sci* 9: 1–10.
- Cockcroft, V.G., Ross, G.J.B., Peddemors, V.M. and Borchers, D. 1992. Estimates of density and undercounting of bottlenose dolphins off northern Natal, South Africa. *S. Afr. J. Wildl. Res.* 22: 102–09.
- Connor, R.C., Read, A.J. and Wrangham, R. 2000. Male reproductive strategies and social bonds. pp.247–69. In: Mann, J., Connor, R.C., Tyack, P.L. and Whitehead, H. (eds). *Cetacean Societies: Field Studies of Dolphins and Whales*. University of Chicago Press, Chicago. 433pp.
- Cowan, D.F. 1966. Observations on the pilot whale *Globicephala melaena*: organ weight and growth. *Anat. Rec.* 155: 623–28.
- Cowan, D.F. and Tajima, Y. 2006. The thyroid gland in bottlenose dolphins (*Tursiops truncatus*) from the Texas coast of the Gulf of Mexico: normal structure and pathological changes. *J. Comp. Path.* 135: 217–25.
- Davis, D.D. 1962. Allometric relationship in lions vs. domestic cats. *Evolution* 16: 505–14.
- Evans, W.E. 1994. Common dolphin, white-bellied porpoise – *Delphinus delphis* Linnaeus, 1758. pp.191–224. In: Ridgway, S.H. and Harrison, R. (eds). *The First Book of Dolphins*. Academic Press, London and San Diego. 416pp.
- Findlay, K.P., Best, P.B., Ross, G.J.B. and Cockcroft, V.G. 1992. The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. *S. Afr. J. Mar. Sci* 12: 237–70.
- Friedmann, Y. and Daly, B. 2004. *Red data book of the mammals of South Africa: a conservation assessment*. CBSG Southern Africa, Conservation Breeding Specialist Group (SSC/IUCN), Endangered Wildlife Trust, South Africa.
- Fury, C.A. and Harrison, P.L. 2008. Abundance site fidelity and range patterns of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in two Australian subtropical estuaries. *Mar. Freshw. Res.* 59: 1015–27.
- Gihl, M. and Pilleri, G. 1969. On the anatomy and biometry of *Stenella styx* Gray and *Delphinus delphis* L. (Cetacea, Delphinidae) of the western Mediterranean. pp.219. In: Pilleri, G. (eds). *Invest. Cetacea*. Brain Anatomy Institute, Berne, Switzerland.
- Hale, P.T., Barreto, A.S. and Ross, G.J.B. 2000. Comparative morphology and distribution of the *aduncus* and *truncatus* forms of bottlenose dolphin *Tursiops* in the Indian and Western Pacific Oceans. *Aquat. Mamm.* 26(2): 101–10.
- Harcourt, A.H., Harvey, P.H., Larson, S.G. and Short, R.V. 1981. Testis weight and breeding systems in primates. *Nature* 293: 55–57.
- Heyning, J.E. and Perrin, W.F. 1994. Evidence for two species of common dolphins (Genus *Delphinus*) from the eastern North Pacific. *Contrib. Sci. [Los Angeles]* 442: 1–35.
- Innes, S., Lavigne, D.M., Earle, W.M. and Kovacs, K.M. 1986. Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Mar. Mammal Sci.* 2(3): 227–29.
- Jürgens, K.D., Bartels, H. and Bartels, R. 1981. Blood oxygen transport and organ weights of small bats and small non-flying mammals. *Respir. Physiol.* 45: 243–60.
- Karczmarski, L., Cockcroft, V.G. and McLachlan, A. 1999. Group size and seasonal pattern of occurrence of humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. *S. Afr. J. Mar. Sci* 21: 89–97.
- Karczmarski, L., Cockcroft, V.G. and McLachlan, A. 2000. Habitat use and preferences of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. *Mar. Mammal Sci.* 16(1): 65–79.
- Kastelein, R.A. and van Battum, R. 1990. The relationship between body weight and morphological measurements in harbour porpoises (*Phocoena phocoena*) from the North Sea. *Aquat. Mamm.* 16: 48–52.
- Kenagy, G.J. and Trombulak, S.C. 1986. Size and function of mammalian testes in relation to body size. *J. Mammal.* 67: 1–22.
- Kooyman, G.L. 1973. Respiratory adaptation in marine mammals. *Am. Zool.* 13: 457–68.
- Kooyman, G.L. and Sinnott, E.E. 1979. Mechanical properties of the harbour porpoise lung, *Phocoena phocoena*. *Respir. Physiol.* 36: 287–300.
- Lindstedt, S.L. and Calder, W.A. 1981. Body size, physiological time, and longevity of homeothermic animals. *Quart. Rev. Biol.* 56: 1–16.
- Lockyer, C. 1976. Body weights of some species of large whales. *J. Cons. Int. Explor. Mer* 36(3): 259–73.
- Lockyer, C. 1993. Seasonal changes in body fat condition of Northeast Atlantic pilot whales, and their biological significance. *Rep. int. Whal. Commn (special issue)* 14: 325–50.
- Lockyer, C. and Waters, T. 1986. Weights and anatomical measurements of northeastern Atlantic fin (*Balaenoptera physalus*, Linnaeus) and sei (*B. borealis*, Lesson) whales. *Mar. Mammal Sci.* 2(3): 169–85.
- McLellan, W.A., Koopman, H.N., Rommel, S.A., Read, A.J., Potter, C.W., Nicolas, J.R., Westgate, A.J. and Pabst, D.A. 2002. Ontogenetic allometry and body composition of harbour porpoises (*Phocoena phocoena* L.) from the western North Atlantic. *J. Zool. (Lond.)* 257: 457–71.
- Mendolia, C. 1989. Reproductive biology of common dolphins (*Delphinus delphis*, Linnaeus) off the south east coast of southern Africa. MSc thesis, University of Port Elizabeth. 75pp.
- Miyazaki, N., Fujise, Y. and Fujiyama, T. 1981. Body and organ weight of striped and spotted dolphins off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 33: 27–67.
- Natoli, A., Cañadas, A., Peddemors, V.M., Aguilar, A., Vaquero, C., Fernández-Piqueras, P. and Hoelzel, A.R. 2006. Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). *J. Evol. Biol.* 19: 943–54.
- Natoli, A., Peddemors, V.M. and Hoelzel, A.R. 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. *J. Evol. Biol.* 17: 363–75.
- Norris, K. 1961. Standardized methods for measuring and recording data on the smaller cetaceans. *J. Mammal.* 42(4): 471–76.
- Oftedal, O.T., Bowen, W.D., Widdowson, E.M. and Boness, D.J. 1989. Effects of suckling and the postsuckling fast on weights of the body and external organs of harp and hooded seal pups. *Biol. Neonate* 56: 283–300.
- Omura, H. 1950. On the body weight of sperm and sei whales located in the adjacent waters of Japan. *Sci. Rep. Whales Res. Inst., Tokyo* 4: 1–13.
- Perrin, W.F. and Roberts, E.L. 1972. Organ weights of non-captive porpoise (*Stenella* spp.). *Bull. Southern California Acad. Sci.* 71(1): 19–32.
- Pilleri, G. and Gihl, M. 1969. Zur Anatomie und Pathologie von *Inia geoffrensis* de Blainville 1817 (Cetacea, Susuidae) aus dem Beni, Bolivien. *Invest. on Cetacea* 1: 94–106.
- Piscitelli, M.A., McLellan, W.A., Rommel, A., Blum, J.E., Barco, S.G. and Pabst, D.A. 2010. Lung size and thoracic morphology in shallow- and deep-diving cetaceans. *J. Morphol.* 271: 654–73.
- Plön, S. and Bernard, R.T.F. 2007. Testis, spermatogenesis, and testicular cycles. pp.215–44. In: Miller, L. (eds). *Reproductive Biology and Phylogeny of Cetacea – Whales, Dolphins and Porpoises*. Science Publishers, Enfield, New Hampshire.
- Prothero, J.W. 1982. Organ scaling in mammals: the liver. *Comp. Biochem. Physiol.* 71A: 567–77.

- Rice, D.W. 1998. *Marine Mammals of the World. Systematics and Distribution*. Special Publication No. 4, The Society for Marine Mammalogy, Allen Press Inc., Lawrence, Kansas. v–ix+231pp.
- Ridgway, S.H. and Kohin, S. 1995. The relationship between heart mass and body mass for three cetacean genera: narrow allometry demonstrates interspecific differences. *Mar. Mammal Sci.* 11(1): 72–79. In Notes.
- Rohr, J.J., Fish, F.E. and Gilpatrick, J.W., Jr. 2002. Maximum swim speeds of captive and free-ranging delphinids: critical analysis of extraordinary performance. *Mar. Mammal Sci.* 18(1): 1–19.
- Rose, R.W., Nevison, C.M. and Dixon, A.F. 1997. Testes weight, body weight and mating systems in marsupials and monotremes. *J. Zool. (Lond.)* 243: 523–31.
- Ross, G.J.B. 1977. The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. *Ann. Cape Prov. Mus. (nat.Hist.)* 11(9): 135–94.
- Ross, G.J.B. 1984. The smaller cetaceans of the southeast coast of southern Africa. *Ann. Cape Prov. Mus. (nat. Hist.)* 15(2): 173–410.
- Ross, G.J.B. and Best, P.B. 1989. Smaller whales and dolphins. pp.303–14. In: Payne, A.I.L. and Crawford, R.J.M. (eds). *Oceans of Life of Southern Africa*. Vlaeberg Publishers, Cape Town.
- Ross, G.J.B., Heinsohn, G.E. and Cockcroft, V.G. 1994. Humpback dolphins – *Sousa chinensis* (Osbeck, 1765), *Sousa plumbea* (G. Cuvier, 1829) and *Sousa teuszii* (Kükenthal, 1892). pp.23–42. In: Ridgway, S.H. and Harrison, R. (eds). *Handbook of Marine Mammals. Volume 5. The First Book of Dolphins*. Academic Press, London and San Diego. 416pp.
- Saayman, G.S., Bower, D. and Tayler, C.K. 1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. *Koedoe* 15: 1–24.
- Saayman, G.S., Tayker, C.K. and Bower, D. 1973. Diurnal activity cycles in captive and free-ranging Indian Ocean bottlenose dolphins (*Tursiops aduncus* Ehrenberg). *Behaviour* 44: 212–33.
- Saayman, G.S. and Tayler, C.K. 1979. The socioecology of humpback dolphins (*Sousa* sp.). pp.165–226. In: Winn, H.E. and Olla, B.L. (eds). *Behavior of Marine Animals – Cetaceans*. Plenum Press, New York and London. xix+438pp.
- Samaai, T., Best, P.B. and Gibbons, M.J. 2005. The taxonomic status of common dolphins *Delphinus* spp. in South African waters. *African Journal of Marine Science* 27(2): 449–58.
- Slijper, E.J. 1958. Organ weights and symmetry problems in porpoises and seals. *Arch. Neerl. Zool.* 13(1): 97–113.
- Slijper, E.J. 1962. *Whales*. 1st English ed. Hutchinson and Co., London. 475pp. [Translation of the Dutch book *Walvissen* published in 1958].
- Slooten, E. 1991. Age, growth and reproduction in Hector's dolphins. *Can. J. Zool.* 69: 1689–700.
- Stahl, W.R. 1965. Organ weights in primates and other mammals. *Science* 150: 1039–42.
- Stahl, W.R. 1967. Scaling of respiratory variables in mammals. *J. Appl. Physiol.* 22: 453–60.
- Stewardson, C.L., Hemsley, S., Meyer, M.A., Canfield, P.J. and Maindonald, J.H. 1999. Gross and microscopic visceral anatomy of the male Cape fur seal, *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae), with reference to organ size and growth. *J. Anat.* 195: 235–55.
- Turner, J.P., Clark, L.S., Haubold, E.M., Worthy, G.A.J. and Cowan, D.F. 2006. Organ weights and growth profiles in bottlenose dolphins (*Tursiops truncatus*) from the Northwestern Gulf of Mexico. *Aquat. Mamm.* 32(1): 46–57.
- Van Waerebeek, K. and Read, A.J. 1994. Reproduction of dusky dolphins, *Lagenorhynchus obscurus*, from coastal Peru. *J. Mammal.* 75(4): 1054–62.
- Western, D. 1979. Size, life history and ecology in mammals. *Afr. J. Ecol.* 17: 185–204.
- Young, D.D. and Cockcroft, V.G. 1994. Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: Opportunism or specialization? *J. Zool. (Lond.)* 234: 41–53.
- Zar, J.H. 1999. *Biostatistical Analysis*. 4th ed. Prentice Hall, Upper Saddle River, New Jersey, USA. 663pp.

Date received: January 2011.

Date accepted: October 2011.