Age, growth, reproduction and sexual dimorphism of the striped dolphin, *Stenella coeruleoalba*, off the south-east coast of southern Africa

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"Man had always assumed that he was more intelligent than dolphins
because he had achieved so much…the wheel, New York, war and so on,
whilst all the dolphins had ever done was muck about in the water
having a good time. But conversely the dolphins believed themselves
to be more intelligent than man for precisely the same reasons"

Douglas Adams

Abstract

The striped dolphin, *Stenella coeruleoalba,* is an oceanic dolphin found worldwide in tropical to warm temperate waters. Globally populations are threatened through direct fishing, by-catch and pollution. Little is known about the life history of this species in South African waters and it is currently listed as ‘Data Deficient’ by the International Union for Conservation of Nature (IUCN). Critical to the conservation and management of this species is an understanding of basic life history parameters. For the present study, metadata and tissues from 101 stranded *S. coeruleoalba* along the south-east coast of southern Africa between 1969 and 2012 were analyzed to examine age and growth, male and female reproduction and sexual dimorphism. Age and growth were determined by counting the number of growth layer groups (GLG’s) present in their teeth. A von Bertalanffy growth curve gave the best fit to the data and indicated that physical maturity was reached around 21 years in males and 18 years in females. Additionally, asymptotic lengths were reached at 231cm and 224cm in males and females, respectively. The maximum ages obtained were 21 years for males and 20 years for females. Length at birth was estimated to be between 116cm and 119cm for males and between 112cm and 114cm for females.

The reproductive status of the adult dolphins was assessed by histological and macroscopic analyses of gonadal tissue. Sexual maturity was attained before physical maturity in both sexes. The males reached sexual maturity between 8 and 12 years of age and between 209 and 224cm in total body length. The maximum combined testis weight comprised about 0.24% of the total body weight and sexual maturity was reached between a combined testis weight of 16 and 41g, a mean testis length of 8 and 10cm, and a mean seminiferous tubule diameter of 44 and 70µm. Females attained sexual maturity between 7 and 8 years of age and between 213 and 216cm in total body length. The ovulation rate was 0.32 per year and the majority of ovulations occurred in the left ovary, with ovulations occurring in the right ovary only in individuals older than 10 years of age. The annual pregnancy rate was calculated to be 26%. Reproductive seasonality could not be established due to the small sample size and the absence of samples throughout the year. However, both conceptions and births appear to occur in both August and December/January. Additionally, testis weight and seminiferous tubule diameters appear to fluctuate throughout the year, which could suggest reproductive seasonality in this species.

Sexual size dimorphism in mature adults was evident for a number of external measurements, however, sexual shape dimorphism was not present in this species. Mature males had significantly longer and wider pectoral fins, dorsal fins and flukes than females ($p<0.05$ in all cases). It was suggested that the larger appendages are required for male on male combat during intraspecific competition for females. Additionally, larger appendages aid in thermoregulation, propulsion and maneuverability. Females had a significantly greater distance between the tip upper jaw and the genital aperture and anus, which was expected due to differences in anatomy between male and female genital openings. Overall, *S. coeruleoalba* did not exhibit distinct sexual dimorphism and together with the relatively small testes in relation to the total body weight (0.24%) it was proposed that this species demonstrates a less extreme form of polygyny. Additionaly, the results of this study are important to the understanding of the basic biology of the species.

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Chapter 1

General Introduction

1.1 Genus and species

1.1.1 Genus Stenella (Gray 1866)

The genus *Stenella* is classified in the order Cetacea, suborder Odontoceti, superfamily delphinoidae, family Delphinidae and subfamily Delphininae (Archer II and Perrin, 1999). Species that belong to the genus are small to medium sized dolphins that reach lengths of up to 2.5 meters (Ross, 1984; Kroese, 1993). Their body structure is slender to robust with a long and narrow beak and a well formed melon that tapers anteriorly (Ross, 1984; Kroese, 1993). The body colouration is pale ventrally and dark dorsally and the different species belonging to *Stenella* are distinguished from each other by distinctive pigmentation patterns (Ross, 1984; Fraser and Noble, 1970). *Stenella* spp. have between 33 and 60 teeth per jaw, which are small and pointed (Ross, 1984).

The taxonomy of this genus is still confused due to the insufficient number of specimens that can be used to delineate distinct populations (Ross, 1984). However, currently the genus contains five extant species, namely the striped dolphin (*Stenella coeruleoalba*), the clymene dolphin (*Stenella clymene*), the spinner dolphin (*Stenella longirostris*) (subspecies – Gray’s spinner dolphin (*S. l. longirostris*), eastern spinner dolphin (*S. l. orientalis*), central American spinner dolphin (*S. l. centroamericana*) and dwarf spinner dolphin (*S. l. roseiventris*)), the Atlantic spotted dolphin (*Stenella frontalis*) and the pantropical spotted dolphin (*Stenella attenuata*) (subspecies- offshore pantropical spotted dolphin (*S. a. attenuata*) and the coastal pantropical spotted dolphin (*S. a. graffmani*)) (Archer II and Perrin, 1999; Committee on Taxonomy, 2013). *Stenella coeruleoalba*, *S. longirostris* and *S. attenuata* are found in all three major ocean basins and *S. coeruleoalba* and *S. attenuata* have been recorded off the south-east coast of southern Africa (Best, 2007). *Stenella clymene* and *S. frontalis* are only distributed in the Atlantic Ocean and have been sighted on the west coast of central Africa (Best, 2007).

1.1.2 Stenella coeruleoalba (Meyen 1833)

The striped dolphin has been recognised since the 1970's in the Mediterranean Sea (Pilleri and Pilleri, 1982). It first received a scientific name in 1833 by the German zoologist F.J.F Meyen who named it *Delphinus coeruleoalbus*. The name was based on a specimen that had been harpooned off the south Atlantic coast of South America near the mouth of the River Plate (Ross, 1984; Perrin *et al.*, 1994). After this it was assigned a number of different names before receiving its current scientific name *Stenella coeruleoalba.* Fraser and Noble (1970) investigated the variation in the number of bands running along the striped dolphins body length, because it was thought that there were two species or subspecies, namely; *Stenella euphrosyne* and *Stenella coeruleoalba*. It was concluded that the variation was not taxonomically important and they were grouped as one species under the name *Stenella coeruleoalba*.

1.2 External characteristics

1.2.1 Colour pattern

The striped dolphin received its Latin name from its intricate colour pattern, which was derived from the latin word *caeruleus* meaning ‘sky-blue’ and *albus* meaning ‘white’ (Leatherwood and Reeves, 1983). The colour pattern of the striped dolphin is distinctive, although it can easily be confused with the Fraser’s dolphin (*Lagenodelphis hosei*) at sea, because they both have prominent lateral stripes (Best, 2007). Primary features include a dark grey/blue-black stripe running from the eye to the anus and from the eye to the flipper. In addition, *S. coeruloealba* possesses a white/light grey V-shaped ‘shoulder blaze’ that originates above the eye and runs laterally towards the base of the dorsal fin (Figures 1.1 and 1.2) (Leatherwood and Reeves, 1983; Ross; 1984; Archer II, 2009). In some individuals a further dark stripe branches from the eye to the anus stripe and runs towards the ventral field (Archer II, 2009). A faint secondary stripe may also be present along the ventral surface (Archer II, 2009). Because of this individual variability and possible geographic variability caution must be used when relying on these characteristics for species identification (Fraser and Noble, 1970; Perrin *et al.*, 1994).

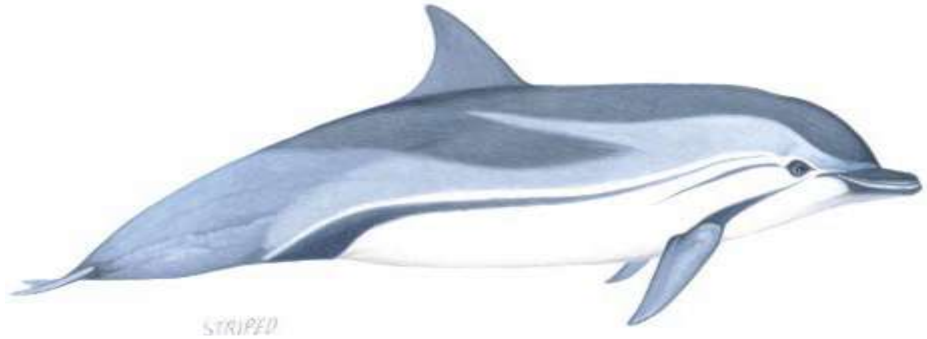

Figure 1.1 Illustration of the Striped dolphin (*Stenella coeruleoalba)* highlighting its unique patterning (Hobbs, 2002).

Figure 1.2 Striped dolphins (*Stenella coeruleoalba*) breaking the water (Hobbs, 2002).

1.2.2 Size

Adult *S. coeruloealba* can reach body lengths of about 180 to 250cm, with an average length between 220 and 230cm (Kroese, 1993; Perrin *et al*., 1994). Both the largest and the heaviest recorded male specimens were recorded from South Africa: the longest was 265cm long (Kroese, 1993; Best, 2007) and the heaviest recorded specimen was 156kg (measuring 240cm in length) (Perrin *et al.,* 1994). Mean maximum body length in southern African animals is 265cm for males and 240cm for females (Kroese, 1993; Best, 2007). In contrast, in the western Pacific Ocean, the maximum body length is 240cm for males and 220cm for females (Archer II and Perrin, 1999; Archer II, 2009). In the Mediterranean Sea, smaller maximum body lengths of 210cm in males and 208cm in females have been recorded (Di-Meglio *et al.*, 1996; Calzada *et al*., 1996). Asymptotic lengths indicate that males grow slightly larger than females (Leatherwood and Reeves, 1983; Kroese, 1993; Perrin *et al*., 1994; Best, 2007; Archer II, 2009).

1.3 Distribution

1.3.1 Range

Stenella coeruleoalba is an offshore dolphin that is distributed worldwide in both the Southern and Northern Hemispheres (Kroese, 1993). The species occurs in tropical to warm-temperate waters of the Atlantic, Pacific and Indian Oceans and the Mediterranean Sea (Ross 1984; Wilson *et al.*, 1987; Dizon *et al*., 1994; Perrin *et al.*, 1994; Best, 2007).

Not many studies have been conducted on the distribution of *S. coeruleoalba* in the Atlantic Ocean. However, in the south-west Atlantic, *S. coeruleoalba* was recorded in both tropical and warm-temperate waters, with the majority of the sightings occurring off the southern coast of Brazil and Argentina (Moreno *et al*., 2005). In the Pacific Ocean, the striped dolphin is distributed from the west coast of North America to the central tropical Pacific and extends its distribution into Japanese waters (Miyazaki *et al*., 1974). In the eastern tropical Pacific *S. coeruleoalba* distribution extends along the equator into the central Pacific Ocean (Au and Perryman, 1985). In the North West Pacific, *S. coeruleoalba* are commonly found near Japan, south of 42^{o}N (Kasuya, 1999). However, they are absent or found at low densities in the Sea of Japan, East China Sea and in the waters around Ryukyu Islands (Kasuya, 1999). In the Mediterranean Sea, high densities of *S. coeruleoalba* are found in the Alboran Sea towards the Straits of Gibraltar and in the waters east and north of Corsica, including the Ligurian Sea (Forcarda *et al*., 1994).

Along the African coast, *S. coeruleoalba* has been recorded from Gabon, Angola, South Africa, Mozambique and Kenya (Rosenbaum and Collins, 1981; Ross, 1984; Findlay *et al.*, 1992; Weir, 2007). Weir (2007) found that *S. coeruleoalba* had a high relative abundance off northern Angola and was resident year round. In South African waters, strandings have occurred along the east coast and around the Cape Peninsula as far west as Ysterfontein (33°22'S, 18°09'E) (Findlay *et al*., 1992; Peddemors, 1999). Ross (1984) recorded strandings from Mpelane, Natal (32°30'E) to False Bay, south-west Cape (17°30'E), 90% of which occurred east of Mossel Bay.

A number of discrete populations of *S. coeruleoalba* have been proposed: one/two off South Africa, one/two in the eastern tropical Pacific (ETP), and another in the western North Pacific (Leatherwood and Reeves, 1983, Kroese, 1993). Miyazaki *et al.* (1974) concluded that the continuity in distribution in the Pacific Ocean does not mean that both sides of the North Pacific encompass the range of a single population; it was proposed that there could be a number of discrete populations. It has also been proposed that within the eastern tropical Pacific (ETP), *S. coeruleoalba* is divided into a north and south geographic race (Perrin, 1975a; Perrin *et al*., 1985). However, Perryman and Lynn (1994) concluded that there was no significant difference between the proposed races and that they belong to one population. It is important to note that the population within the Mediterranean is genetically distinct from their conspecifics in the Atlantic Ocean due to the isolation between the populations (Bourret *et al*., 2007; Notarbartolo di Sciara *et al*., 2008). It is uncertain whether *S. coeruleoalba* off the African coast belong to the same population or if there are two distinct populations (Findlay *et al*., 1992; Best, 2007). Conry (2012) observed distinct cranial sexual dimorphism between east coast and west coast animals, indicating that these populations are separate.

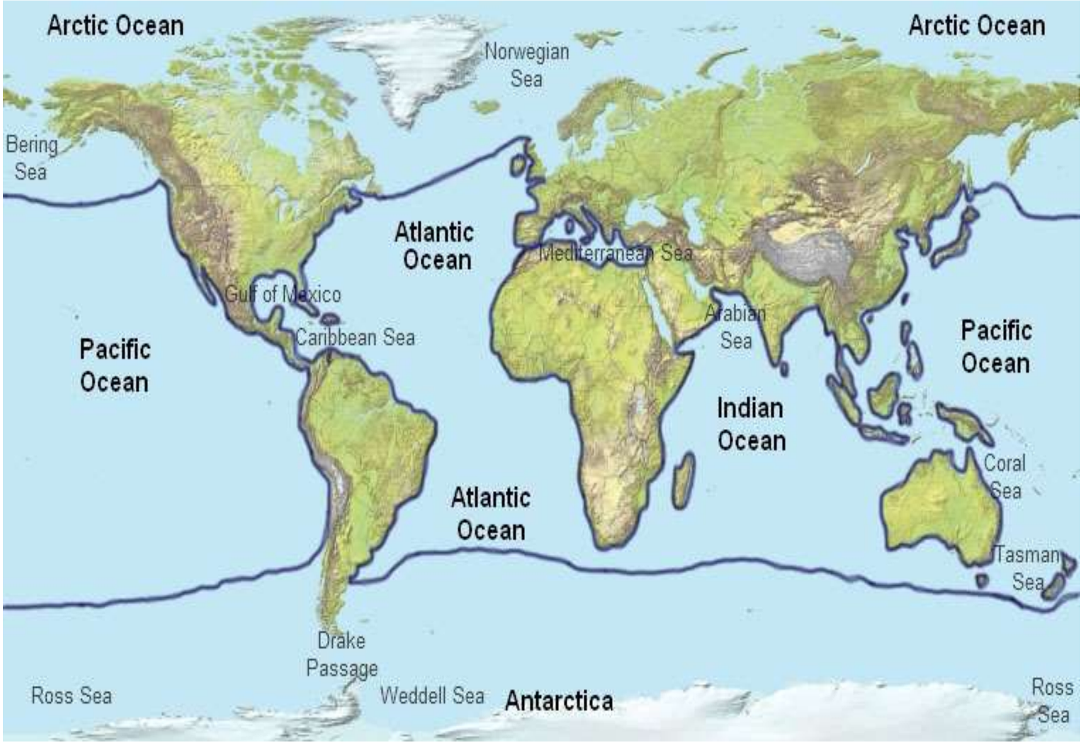

Figure 1.3 Worldwide distribution of *Stenella coeruleoalba* (the blue lines represent the boundary) (Hubbs *et al*., 1973; Wilson *et al*., 1987; Findlay *et al*., 1992; Dizon *et al*., 1994; Perrin *et al*., 1994; Ballance and Pitman, 1998).

1.3.2 Habitat

Stenella coeruleoalba prefers deep, oceanic waters beyond the continental shelf (Perrin *et al*., 1994; Archer II, 2009). For example, off South Africa, all sightings occurred in waters deeper than 500 metres (Findlay *et al*., 1992) and off Angola sightings occurred even deeper, with a mean depth of 1785 metres (Weir, 2007). In the Mediterranean Sea, *S. coeruleoalba* typically prefer open waters beyond the continental shelf and over the continental slope towards the offshore productive waters (Forcarda *et al*., 1994; Panigada *et al*., 2008). Moreno *et al*. (2005) investigated *S. coeruleoalba* distribution and habitat preferences in the south-west Atlantic, and found a different result. With the few sightings that were available *S. coeruleoalba* seemed to prefer shallow waters less than 200 meters. It is unlikely that *S. coeruleoalba* only have a coastal distribution, because oceanic prey was found in the stomach contents of a stranded striped dolphin on the south-east coast of Brazil, suggesting *S. coeruleoalba* occurs in deeper waters within the Atlantic Ocean as well (Rosas *et al*., 2002).

The distribution and habitat preference of *S. coeruleoalba* has been extensively investigated in the ETP (Wade and Gerrodette, 1993). In this region, it has been observed that *S. coeruleoalba* prefers areas where conditions such as temperature and salinity are variable. Their distribution coincides with water masses characterized by upwelling, a weak thermocline and salinities of between 34 and 35 (Au and Perryman, 1985). In the Mediterranean Sea, *S. coeruleoalba* attain their highest densities in the most productive areas of the Mediterranean Sea, such as the Alboran Sea towards the Straits of Gibraltar and waters east and north of Corsica, including the Ligurian Sea (Forcarda *et al*., 1994). In Japanese waters, *S. coeruleoalba* inhabits a warm oceanic body of water (above 18°C) that moves seasonally by latitude (Kasuya, 1999). In addition, both the coastal and oceanic waters are influenced by the warm Kuroshio Current and *S. coeruleoalba* reaches its highest densities along the Northern periphery of this current (Miyakazi *et al*., 1974; Ross; 1984).

1.3.3 Abundance

No estimates on abundance or numbers are available at present for the southern African population, although estimates are available for other populations in other ocean basins. Balance and Pitman (1998) compared the distribution and abundance of cetaceans between the western tropical Indian Ocean, the ETP and the Gulf of Mexico. Out of these three regions, *S. coeruleoalba* was by far the most abundant in the ETP (Balance and Pitman, 1998). Population estimates for *S. coeruleoalba* in the ETP, obtained by annual cruises from 1986-1991, were estimated to be 1 900 000 individuals (Wade and Gerodette, 1993).

Stenella coeruleoalba is the most numerically abundant dolphin in Japanese waters, but numbers have declined due to the Japanese drive and hand harpoon fisheries (Kasuya, 1985). Kasuya (1985) showed that the catch off the Izu coast could not sustain the catch levels of the fisheries and the population declined from 10 000 in the 1960's to 1000 in the 1970's. Miyashita (1993) estimated the abundance of *S. coeruleoalba* in the western North Pacific using sighting data. In the northern offshore area estimates were 497 725 individuals, in the southern offshore area estimates were 52 682 individuals and in the coastal area 19 631 individuals.

In the western Mediterranean Sea, *S. coeruleoalba* is the most abundant cetacean but estimates are only available since the 1990-1992 epizootic die-off, with an estimated population of 117 880 individuals (Forcada *et al.*, 1994). Point estimates for various regions of the Mediterranean are as follows- Balearic Sea 5 826 individuals, Gulf of Lions 30 774 individuals, Ligurian Sea 14 003 individuals, South Balearic Sea 18 810 individuals and Alboran Sea 17128 individuals (Aguilar, 2000). No estimates are available for the Tyrrhenian Sea and the eastern Mediterranean. However, *S. coeruleoalba* is frequently seen in these areas, but densities are lower than in the western region (Aguilar, 2000).

1.3.4 Seasonal distribution

Unlike large whales, small cetaceans do not undertake long seasonal migrations, but rather show smaller scale movements in response to the fluctuating environment or seasonal movements of their prey (Reilly, 1990). Off Southern Africa, sightings were only made during summer in December, January and February; however, this may have been the result of uneven sighting effort (Findlay *et al.*, 1992). Stranding records along the South African coast indicated that the species does occur throughout the year and throughout all seasons (Ross, 1984).

In the ETP, *S. coeruleoalba* demonstrates a small seasonal change in distribution between winter and summer, extending more offshore during summer (Reilly, 1990). The shift in distribution is small because this species has such a large geographic range (Fiedler and Reilly, 1987). The distribution extension during summer correlates with the northward movement of the Intertropical Convergence Zone (ITCZ) and the seasonal formation of the thermocline ridge (Reilly, 1990; Reilly and Fiedler, 1994). *Stenella coeruleoalba* aggregates along the shallow thermocline, possibly because this acts as a barrier to the rapid escape of squid and fish (Reilly, 1990).

A diurnal migration is seen in the Mediterranean Sea, where *S. coeruleoalba* migrates offshore in the morning and inshore in the evenings to exploit near-shore resources (Gannier, 1999). *Stenella coeruleoalba* also shows a seasonal pattern in the Mediterranean where the species relative abundance peaks from May (start of summer) to October when water temperatures increase and then decline with the start of winter (December) (Laran *et al*., 2002; Laran and Drouot-Dulau, 2007). It has been suggested that the Tyrrhenian Sea and the Central Spanish Mediterranean Sea could be possible migrating areas. In Japanese waters seasonal shifts in distribution were also observed. Their movements were related to the seasonal change in oceanographic conditions or the seasonal movement of the Northern periphery of the Kuroshio Current over coastal waters (Miyazaki *et al*., 1974).

1.4 Biology

1.4.1 Age and Growth

A number of studies on age and growth of *S. coeruleoalba* have been conducted on Japanese populations by Miyakazi (1977a) and Kasuya (1972, 1976, 1985). In these waters the mean body length at birth is estimated as 100.5cm (Miyakazi, 1977a). Body length at birth is estimated in South African waters as 93 – 98.5cm (Kroese, 1993) and in the Mediterranean as 92.5cm (Aguilar, 1991). The Mediterranean population appears to be the smallest of the *S. coeruleoalba* species in the world (Aguilar, 2000). These differences are due to geographic variation and genetic isolation between populations (Aguilar, 2000).

Teeth begin to erupt when the dolphin is approximately 110cm in length and start feeding on solid food at about 133cm (Miyakazi, 1977a). The mean weaning age is about 1.5 years of age, with some individuals continuing to suckle until 2 to 3 years of age (Miyakazi, 1977a). Both sexes of *S. coeruleoalba* reach an average body length of 166cm in the first year and 180cm at the end of the second (Miyakazi, 1977a; Perrin *et al*., 1994). Around the end of their third year, however, the male growth rates exceed that of the females (Perrin *et al*., 1994). Females cease to grow and reach an asymptotic length earlier than males at an age of 12 years, whereas males keep growing for another year until about 13 years (Miyakazi, 1977b; Aguilar, 2000).

In Japanese waters, asymptotic length is obtained at 236cm and 225.3cm for males and females, respectively (Miyakazi 1977a). Asymptotic lengths are attained earlier in the north east Atlantic Ocean at 216cm for males and 200cm for females (Di-Meglio *et al.*, 1996). In the Mediterranean Sea, where the dolphins are smaller, asymptotic lengths are 191.2cm and 194.7cm for males and females, respectively (Di-Meglio *et al.*, 1996; Calzada *et al*., 1996). Maximum ages of *S. coeruleoalba* in the Meditteranean Sea are 25 and 22 years of age for males and females, respectively (Di-Meglio *et al.,* 1996). These estimates are much lower than those obtained for *S. coeruleoalba* in Japanese waters of 50 years for males and 49 years for females (Kasuya, 1976).

1.4.2 Reproduction

The gestation period for *S. coeruleoalba* is estimated to be approximately 12 months (Kasuya, 1972; Ross, 1984; Aguilar, 2000). It has been suggested that breading is seasonal with births occurring in summer (January – February) and in winter (May- August) along the South African coast (Kroese, 1993). In Japan (Northern Pacific), two breeding seasons were also identified, one in November and December and another in May and June (Kasuya, 1972). In the Mediterranean Sea only a single peak of calvings is recorded annually, from late summer to autumn (peak in mid-October). This coincides with the warmest and most productive period in the western Mediterranean Sea, and occurs just before an increase in productivity (Aguilar, 2000). This is not unusual in mammals as lactation, which has the highest energetic demand, coincides with a peak in productivity (Bronson, 1989). Adult females show a calving interval of 3.2 years on average; however, this interval increases if more time is spent lactating or resting and the oldest females may even stop calving completely (Miyakazi, 1984). In the Mediterranean a longer interval of four years was found (Calzada *et al*., 1996).

Kroese (1993) found the onset of sexual maturity between 210 and 230cm for male and between 200 and 240cm for female *S. coeruleoalba* off the coast of South Africa. Similarly, in the western north Pacific, average age at maturity was found to be about nine years for both males and females (Kasuya, 1972; Miyakazi, 1977a). However, Kasuya (1985) suggested that the age of sexual maturity for females declined from 9.7 years in 1966 to 7.4 years in 1976. This decrease is thought to be in response to a decrease in density caused by overfishing (Kasuya, 1985). In Mediterranean waters, females reach sexual maturity around 12 years of age at a length of 187cm (Calzada *et al*., 1996) and males around 11.3 years of age at a length of 190cm (Aguilar, 2000).

1.4.3 Feeding ecology

Stenella coeruleoalba is an opportunistic feeder that exploits a wide variety of crustatceans, fish and squid including oceanic, pelagic and bathypelagic schooling species (Blanco *et al*., 1995; Aguilar, 2000, Ringelstein *et al*., 2006). Data collection from different regions of the world suggests that myctophid fish and cephalopods constitute the dominant prey item for *S. coeruleoalba*, although the contribution of the two prey items demonstrates a high degree of spatial variability. For example, off the south-eastern coast of South Africa, Ross (1984) examined 21 striped dolphin stomachs and found that their diet consisted of fish which constituted the largest proportion (80%) of the diet and cephalopods (20%). Myctophids were the most abundant group of fish, making up 66.5% of all prey species recorded (Ross, 1984). Similarly, stomach content analyses have shown that Mediterranean striped dolphins feed predominantly on bony fishes. However cephalopods seem to form an equally important part of their diet within the region (Wurtz and Marrale, 1993; Blanco *et al*., 1995; Aguilar, 2000). Even though fish constituted a small percentage, hake (*Merluccius* sp.) was the most predominant fish species (8.7%) consumed off the west coast of South Africa (Sekiguchi *et* *al*., 1992). Sekiguchi *et al*. (1992) found that chokka squid (*Loligo vulgaris reynaudii*) made up the most important part of the diet of *S. coeruleoalba* (74.4%), not fish. The diet of *S. coeruleoalba* in the north-east Atlantic Ocean was similar to the South African coast, consisting of fish and cephalopods as well as crustaceans (Ringelstein et al., 2006). By number these groups constituted 62.1%, 32.4% and 5.3%, respectively (Ringelstein *et al*., 2006). Relatively few studies have been conducted on the feeding ecology of the Japanese *S. coeruleoalba*. Miyazaki *et al*. (1973) analysed the stomach contents of 27 dolphins from two schools. Myctophidae represented 64% of the diet and two species of squid, the Japanese Flying Squid (*Tadarodes pacificus*) and the Luminous Flying Squid (*Symplectoteuthis luminosa*) were the most dominant (Miyazaki *et al*., 1973). The regional diversity of this dolphin reveals its foraging plasticity and ability to adapt to different habitats (Perrin *et al*., 2008).

Blanco *et al*. (1995) found that a high proportion of the cephalopods in the diet had luminous organs and many showed diurnal migrations. In South Africa, more than 80% had luminous organs (Ross, 1984). The digestion condition of the stomach contents suggested that most of the foraging took place at dusk or in the early hours of the evening when deep sea organisms migrate to the surface waters (Ringelstein *et al*., 2006). Additionally, a clear diurnal pattern of diving was also observed using satellite transmitting tags in the North Pacific Ocean (Minamikawa *et al*., 2003). The average diving depth during the day was 22.6 metres and during the night it was 126.7 metres, with a maximum depth of 705 metres (Minamikawa *et al*., 2003).

1.4.4 School structure

Off the south-east coast of South Africa school sizes for *S. coeruleoalba* were estimated to be between four and several hundred animals, with over half the schools containing more than 100 individuals (Ross, 1984). Findlay *et al*. (1992) calculated the mean group size to be 74.5 individuals per group. In Angolan waters, the school sizes were much smaller, with a mean group size of 59.3 individuals (Weir, 2007). Along the Japanese coast larger schools were found, with a mean size of 415 dolphins and a maximum of 2 327 dolphins (Miyazaki, 1977b). However, very few of the encountered schools reached sizes of over 1000 dolphins and most were less than 500 dolphins (85.8%) (Miyazaki, 1977b; Miyazaki and Nishiwaki, 1978). A seasonal change and diurnal change in school size was observed in Japanese waters (Miyazaki and Nishiwaki, 1978). Along the Japanese coast whole schools are captured at a time by fisheries, and provide information on school sizes. On the west coast of Japan, large schools of more than 1000 individuals are caught from April to May and from December to January, while smaller schools of less than 300 individuals are caught all year round (Miyazaki and Nishiwaki, 1978). On the east coast of Japan, larger schools were captured during November and January, when the main fishing season takes place (Miyazaki and Nishiwaki, 1978). Larger schools were also found throughout the region in the early mornings between 05:00 and 09:00am, suggesting that schools merge when feeding at night and then split up during the day (Miyazaki and Nishiwaki, 1978).

In the Mediterranean Sea, group sizes ranged from 1 to 300 dolphins (Forcarda *et al*., 1994). Before the mass die-off of *S. coeruleoalba* in 1990 (epizootic) caused by a morbillivirus, the mean school size was 25.3 animals (Forcarda *et al*., 1994). However, during the epizootic the mean size dropped to 7.0 individuals per group and groups larger than 50 were rarely reported (Forcada *et al*., 1994). Thereafter school sizes recovered with a mean size of 13.2

dolphins per group (Forcada *et al*., 1994). The decrease in mean school size is thought to be the result of the death of individuals or larger schools splitting up in to smaller ones (Forcada *et al*., 1994).

Stenella coeruleoalba has been found in mixed species groups associated with the short beaked common dolphin (*Delphinus delphis*) and the Risso's dolphin (*Grampus griseus*) in the Mediterranean Sea (Frantiz and Herzing, 2002). Similarly, *S. coeruleoalba* and the short beaked common dolphin (*D. delphis)* were found in mixed species groups in the western English Channel and Bay of Biscay (Hobbs, 2002). In the ETP, *S. coeruleolba* and *D. delphis* have very similar distributions and prefer waters with more variable conditions compared to the spotted (*S. attenuata*) and spinner (*S. longirostris*) dolphin (Au and Perryman, 1985).

1.5 Population Threats

1.5.1 Directed fisheries

The largest directed catches occur in the waters of Japan, by means of drive and hand harpoon fisheries in several locations in the region. Dolphin drive fisheries have been operated since the late 14th century in about 52 Japanese villages (Kasuya, 1999). Current drive fisheries are limited to the Izu Peninsula and in Wakayama Prefecture and hand harpoon fisheries are limited to Chiba and Wakayama Prefecture (Kasyua, 1999). Dolphin catches within this fishery have declined since 1950's due to the decline in the population caused by overfishing (Kasuya, 1999; Reeves *et al*., 2010). There is a strong demand for dolphin meat in Japan and this makes it difficult to set effective conservation measures (Reeves *et al*., 2010). Kasuya (1985) investigated the effect of exploitation on reproductive parameters and found that exploitation caused a decrease in the age at sexual maturity and a decrease in calving interval. Other directed fisheries include small French and Spanish harpoon fisheries in the Mediterranean Sea (Collet, 1983). These fisheries also take *S. coeruleoalba* for human consumption, but in smaller numbers compared to the Japanese fisheries (Collet, 1983).

1.5.2 Bycatch

Incidental catches of *S. coeruleoalba* are of great concern and need to be managed as they can cause a threat to population densities (Perrin *et al*., 1994). Incidental catches occur in gill nets, drift nets, purse seines, and other gear in the Mediterranean, ETP, north-eastern Atlantic, north Pacific, and in the north-eastern Indian Ocean (Perrin *et al*., 1994). In most parts of the Mediterranean Sea fishing intensity is high and diverse in terms of fishing gear used. Therefore the conflict between fishing activities and the striped dolphin is very high with the potential for large bycatch (Aguilar, 2000). The pelagic driftnet fishery for tuna and swordfish has the potential for the largest by-catch, with three major countries, namely Italy, Spain, and Morocco, exploiting these species (Aguilar, 2000). Italian drift fishermen target albacore tuna (*Thunnus alalunga*) and swordfish (*Xiphias gladius*) (Nortarbartolo di Sciara, 1990; Di Natale and Notarbartolo di Sciara, 1994). This fleet is based in more than a hundred ports and are estimated to have a bycatch of at least 10 cetaceans per boat per season and 7000 drown in fishing gear every year in Italian waters (Nortarbartolo di Sciara, 1990). The Spanish driftnet fishery is directed towards swordfish (*X. gladius*) and they are restricted to a small area around the Straits of Gibraltar (Di Natale and Notarbartolo di Sciara, 1994, Silvani *et al*., 1999). The estimated total bycatch of *S. coeruleoalba* was 183 individuals in 1993 and 145 individuals in 1994 (Silvani *et al*., 1999). In the Indian Ocean there has been an increase in the driftnet fishery off Madagascar, which may impact *S. coeruleoalba* stock, because it over-laps with its range (Kroese, 1993). In addition, although rare, *S. coeruleoalba* have also been captured in the KwaZul-Natal shark nets (n=3) along the South African coast (Cockcroft, 1990). Many more incidental catches probably occur in tropical to warm temperate waters around the world.

1.5.3 Pollution

The Mediterranean is an enclosed sea that is surrounded by highly industrialised countries. Chemical pollutants are often found in high concentrations in this ecosystem, many of which can have deleterious impacts on cetaceans and other living organisms (Aguilar, 2000). In 1990 a morbillivirus (species not ascertained) began to affect the striped dolphins in the Mediterranean Sea, killing hundreds of dolphins that subsequently washed up along the western Mediterranean coast (Aguilar and Raga, 1993; Forcada *et al*., 1994). Domingo *et al*. (1992) provided definitive evidence that a morbillivirus similar to phocine distemper virus was the primary cause of the die-off of the striped dolphin. However, the affected dolphins showed a number of physiological alterations that could not be explained by the morbillivirus. The diseased dolphins were further examined and it was discovered that they had high organochlorine concentrations, especially polychlorinated biphenyls (PCB’s), which were also found at high concentrations in the water column of the Mediterranean Sea (Aguilar and Raga, 1993). PCB’s are active depressors of the immune system and increase susceptibility to other infections (Aguilar and Raga, 1993).

Organochlorine concentrations present in stranded dolphins along the east coast of South Africa have been investigated for 14 cetacean species, including *S. coeruleoalba* (Cockcroft *et al*., 1991). Organochlorine contamination was generally low in comparison to the Northern

Hemisphere and the coastal dolphins appeared to have higher concentrations compared to the oceanic dolphins (Cockcroft, 1999). Cetaceans that inhabit inshore waters had higher mean blubber concentrations of PBCs than cetaceans that inhabit more offshore regions, such as *S. coeruleoalba* (Cockcroft *et al*., 1991; Cockcroft, 1999). None of the organochlorine pollutant concentrations were high enough to warrant concern (Cockcroft *et al*., 1991). However, it has been suggested that coastal contamination maybe a concern for inshore species, such as the humpback dolphin (*Sousa chinensis*) (Karczmarski, 2000). Organochlorines are associated with a number of physiological disruptions, affecting growth, reproduction, and the immune system (Aguilar, 2000). Therefore high levels of organochlorines or other contaminants can have deleterious consequences to *S. coeruleoalba* populations worldwide.

1.5.4 Conservation status

Along the southern African coast there are no estimates of population size for *S. coeruleoalba* and human induced mortality within the subregion appears to be minimal at present. As a consequence *S. coeruleoalba* is categorised as Lower Risk: Conservation dependent by the International Union for the Conservation of Nature (IUCN) and is of “least concern” in the South African Red Data Book. In Japanese waters, where populations have decreased due to overfishing, catch limits have been put in place to try and conserve this species in the region (Kasuya, 1999).

1.6 Objectives

Very little is known about the general biology of *S. coeruleoalba* off southern Africa, with only two studies conducted in the past three decades (Ross, 1984; Kroese, 1993). In both instances, studies were conducted on stranded animals. Since these two studies many more specimens of *S. coeruleoalba* have stranded, providing more information for analysis and warranting a new investigation. Therefore this study aims to provide a better understanding of age, growth, reproduction and sexual dimorphism of *S. coeruleoalba* in southern Africa. It is important to have an understanding of life history parameters for the management and conservation of the South African population, particularly with the increasing drift net activities off Madagascar and the overfishing of many fish populations off southern Africa (Kroese, 1993). Therefore the aims of the present study are to determine the following parameters:

1. Age and growth parameters
2. Reproductive parameters
3. The presence of sexual dimorphism within the population

Chapter 2

Study Site and Sample

2.1 Study site

For the present study animals stranded along the South African coastline, from Mossel Bay (34°10’48.88” S; 22°08’01.48” E) on the west coast to Sodwana Bay (27°33’23.25”S; 32°40’02.29”E) on the KwaZulu-Natal coast were examined. The oceanography of this area is dominated by the greater Agulhas Current system, which is the largest western boundary current in the Southern hemisphere (Ansorge and Lutjeharms, 2007). This current draws most of its water from the south-west Indian Ocean sub-gyre and is established somewhere between 25°S and 30°S (Shannon, 1989; de Ruijter *et al.,* 1999). The Agulhas Current is an oligotrophic narrow (<100km wide), warm and an intense current extending to the ocean floor (Ansorge and Lutjeharms, 2007). The current flows southwards along the narrow (8-10 km wide) shelf edge and then starts to move offshore as the shelf starts to broaden at about East London/Port Alfred eventually forming the Agulhas Bank (~240km across) (Lutjeharms and Ansorge, 2001; de Ruijter *et al.*, 1999; Shannon, 1989; Ross, 1984). Once the current has reached the southern tip of the Agulhas Bank, it turns back on its self to form the Agulhas Retroflection, which flows into the South Indian Ocean as the Agulhas Return Current (Lutjeharms and van Ballegooyen, 1988; Lutjeharms and Ansorge, 2001) (Figure 2.1).

On the west coast, stretching from Cape Town up to Angola is the cool, northward flowing Benguela Current (Ansorge and Lutjeharms, 2007). In contrast to the Agulhas Current, the Benguela Current is cold, shallow, nutrient rich and highly productive (Ansorge and Lutjeharms, 2007).The region where the two currents merge is very unstable, and the large temperature difference between the Agulhas and Benguela Currents creates a barrier between East and West in the region where the two currents meet (fluctuates seasonally between Cape Agulhas and Cape point, Cape Town) (Shannon, 1989).

The temperature regime of the study area is characterized by a decrease in temperature from north to south along the east coast (van der Elst, 1981). Maximum temperatures are recorded between January and March (ranging from 27^{o}C in the North to 15^{o}C in the South) while minimum temperatures occur between July and September (ranging from 22^{o}C in the North to 13^{o}C in the South) (van der Elst, 1981; Shannon, 1989). The salinity of the Agulhas Current surface water ranges between 35.2 and 35.3 with higher salinities found at greater depths (Shannon, 1989).

2.2 Sample

For the purpose of this study, samples and records from the Port Elizabeth Museum, Graham Ross Marine Mammal collection, collected between 1969 and 2012 were used. Each specimen has a Port Elizabeth Museum (PEM) number and information for each specimen is given in Appendix A. In total, 128 specimens of *Stenella coeruleoalba* were in the collection of which 127 were strandings and one was a net catch along the KwaZulu-Natal coastline. The geographic distributions of the strandings are shown in Figure 2.2. The lines highlight seven hotspots where the animals were collected.

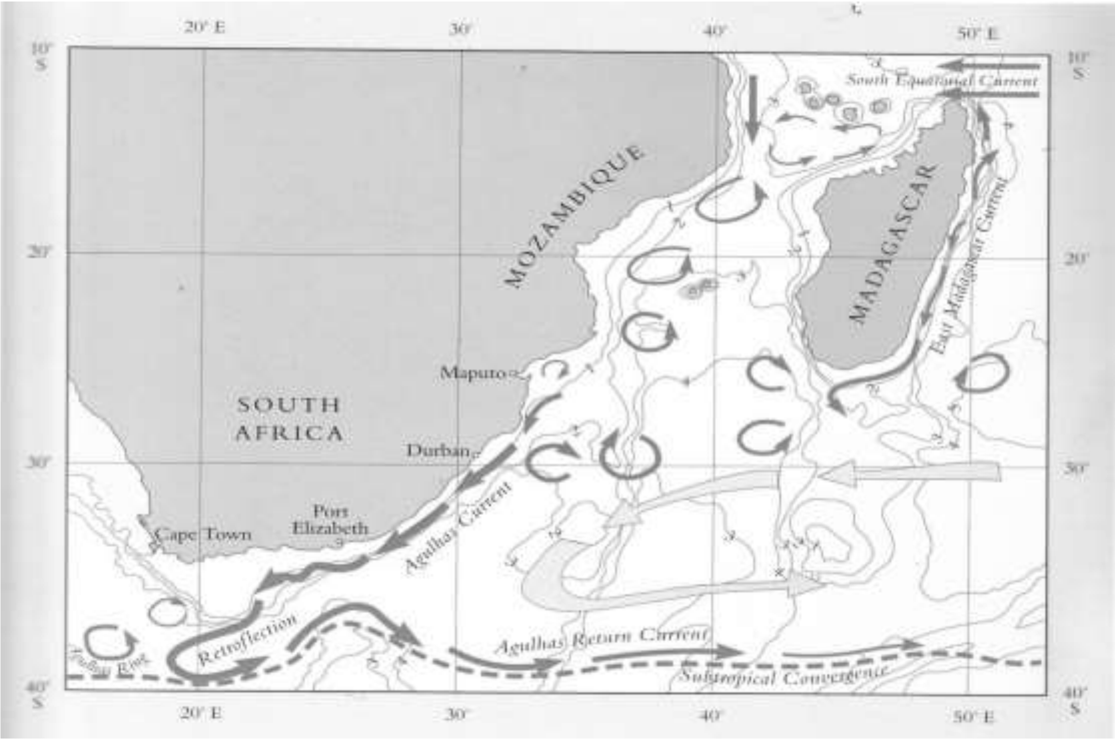

Figure 2.1 Diagram of Southern Africa, showing the oceanographic features of the study area. Highlighting the movement of the Agulhas Current (map from Ansorge and Lutjeharms, 2007).

Out of the total 128 specimens available, 18 were data deficient and the sex of nine individuals was unknown, therefore these could not be used for any analyses. Thus data from a total of 101 specimens were used for this study. Of the 101 specimens, 61 were male and 40 were female.

The total body length (TBL) of each animal was measured in centimetres in a straight line from the tip of the upper jaw to the bottom of the notch of the tail flukes using a tape measure (Norris, 1961). In the samples analysed the TBL of male *S. coeruleoalba* ranged from 99cm to 265cm, while those of the females ranged from 93cm to 240cm. The size-frequency analysis for *S. coeruleoalba* showed a normal distribution, skewed to the right (Figure 2.3).

The majority of the males TBL ranged between 200 and 259cm, whereas most of the females fell within the size range of 200 and 239cm. No females were collected in the length class between 160cm and 179cm.

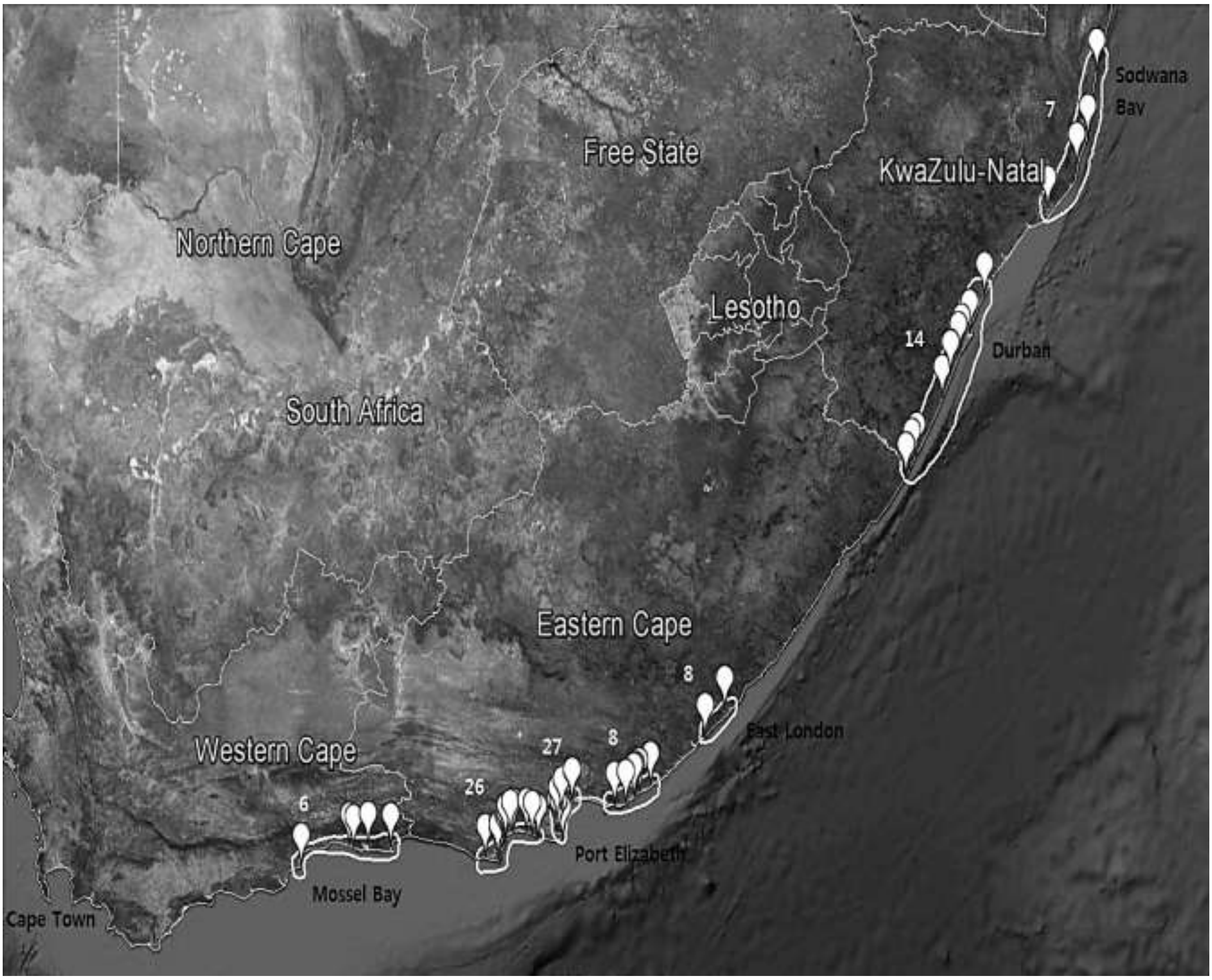

Figure 2.2 Stranding locations of *S. coeruleoalba*, highlighting seven hotspots and the number of specimens collected in each hotspot between 1969 and 2012 (n=96; 32 specimens had an unknown location).

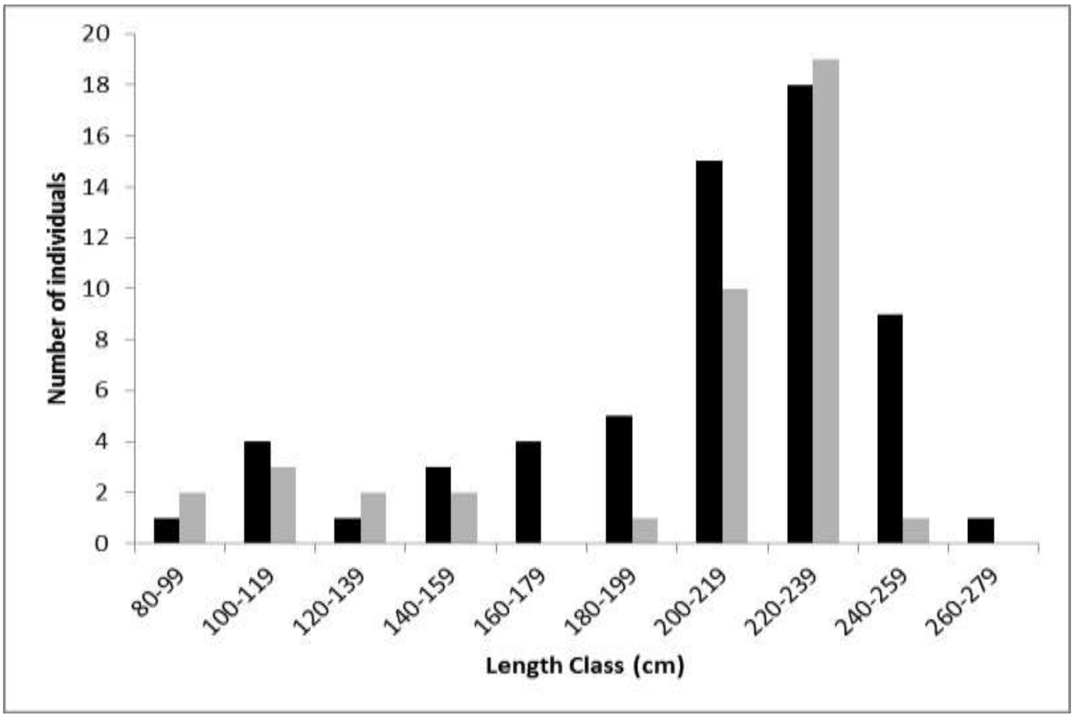

Figure 2.3 Size-frequency of male (n=61) and female (n=40) *S. coeruleoalba* available for the study (one male and one females had an unknown total body length). The black bars indicate males and the grey bars females.

The length at which sexual maturity of *S. coeruleoalba* is attained was determined from the published literature (Ross, 1984) (Figure 2.4). Males were considered as sexually mature above the length of 218cm and females above the length of 210cm. In the sample of 61 males, 29 were sexually mature and 32 sexually immature. Of the total 40 females, 27 were sexually mature and 13 were sexually immature.

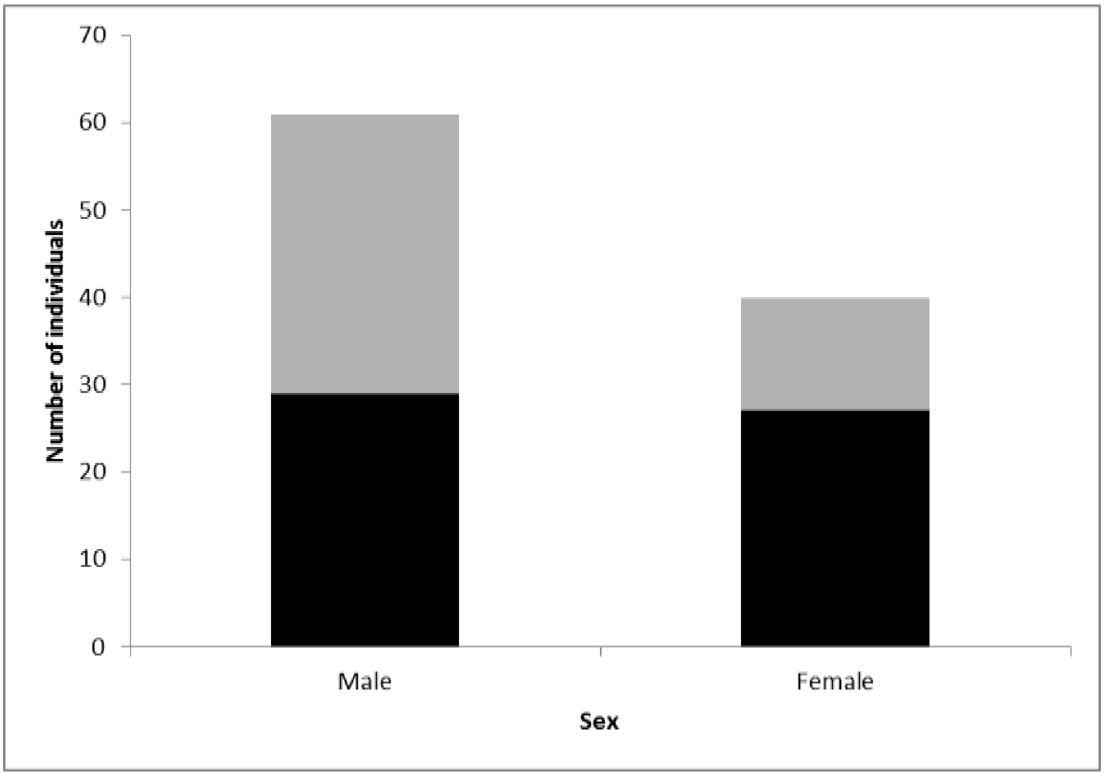

Figure 2.4 The number of male (n=61) and female (n=40) individuals in the sample that were sexually mature or immature based on total body length. The black bars indicate sexually mature and the grey bars sexually immature individuals.

Due to the absence of metadata for some specimens, the number of individuals considered for each section varied. The number of individuals used for each section is listed in Table 2.1.

Table 2.1 The number of male and female specimens used in each section/chapter.

	Number of males	**Number of females**	**Total sample size**
Growth and age determination Chapter 3	32	25	57
Reproduction Chapter 4	21	27	48
Sexual dimorphism Chapter 5	27	22	49

2.2.1 Growth and age determination

The size-frequency analysis of male and female specimens used for the age determination (n=57) showed a normal distribution (Figure 2.5). The majority of the males had a TBL of between 200 and 259cm, while the females varied in size between 200 and 239cm TBL. The smallest male and female specimens measured 99cm and 112cm, respectively, while the largest male and female specimens measured 250cm and 240cm, respectively. No female specimens in the length classes between 80 and 99cm, 120 and 139cm and 160 and 179cm had teeth available for age determination.

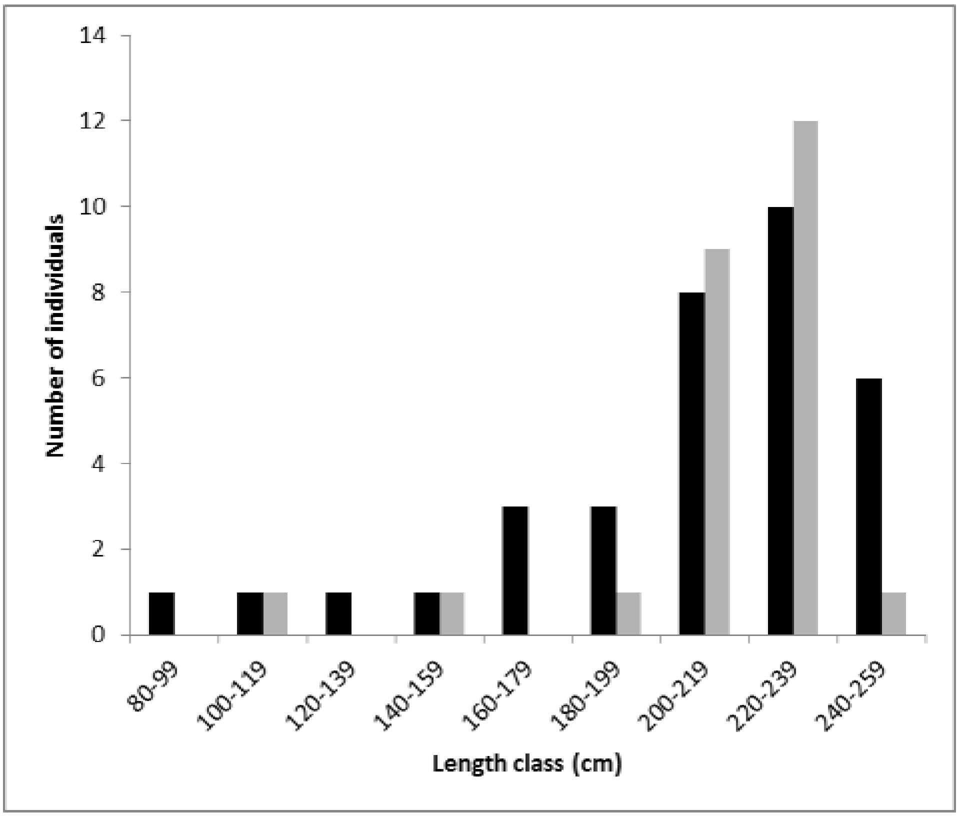

Figure 2.5 Size-frequency of male (n=34) and female (n=25) *S. coeruleoalba* used for age determination. The black bars indicate males and the grey bar females.

2.2.2 Reproductive analysis

Tissue samples to assess the reproductive status of *S. coeruleoalba* were available for 49 individuals. The tissue sample for the reproductive analysis comprised of females with a TBL between 145cm and 240cm and males between 99cm and 250cm. In the size-frequency analysis a number of length classes had no specimens (Figure 2.6). Based on published literature all of the missing length classes for both males and females were sexually immature individuals (Ross, 1984). The majority of males and females were found in the length classes between 200cm and 239cm TBL.

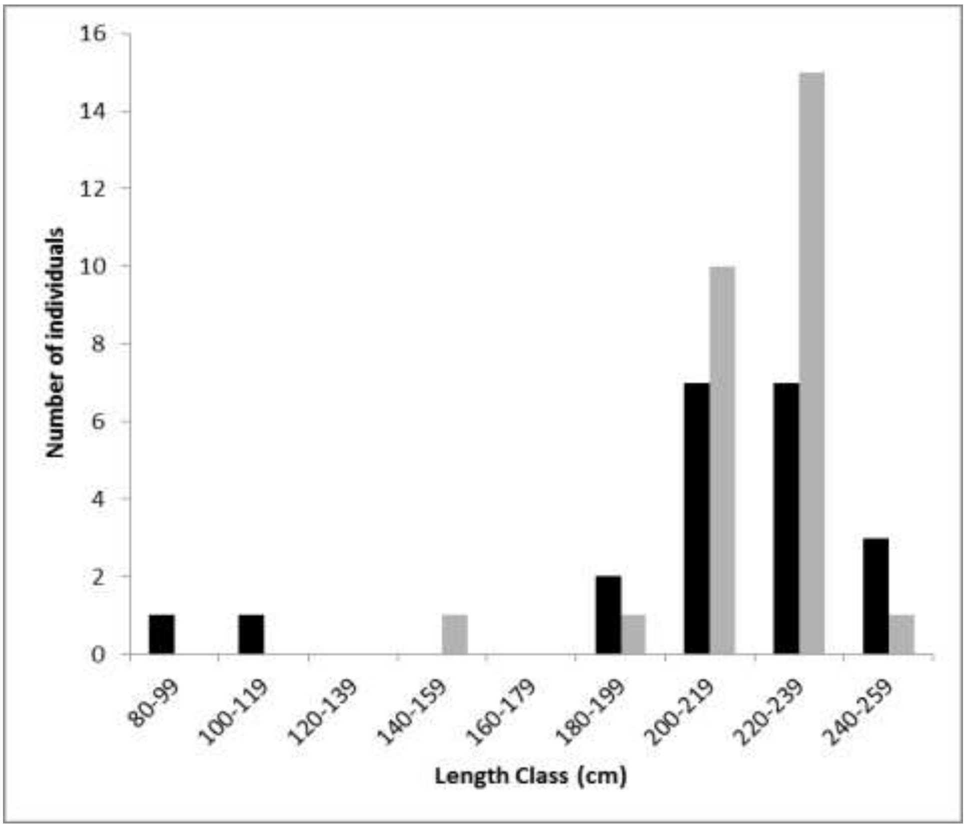

Figure 2.6 Size frequency of male (n=21) and female (n=27) *S. coeruleoalba* used for the reproductive analysis. The black bars indicate males and the grey bars females.

2.2.3 Sexual Dimorphism

For the determination of sexual dimorphism, only mature individuals were analysed. Based on this study, males and females with a total body length greater than 224cm and 215cm, respectively, were used in the analyses. Figure 2.7 illustrates the length frequency of the sample. The majority of the males fell in the length class between 240 and 244cm, while the majority of the females fell in the length class between 220 and 224cm.

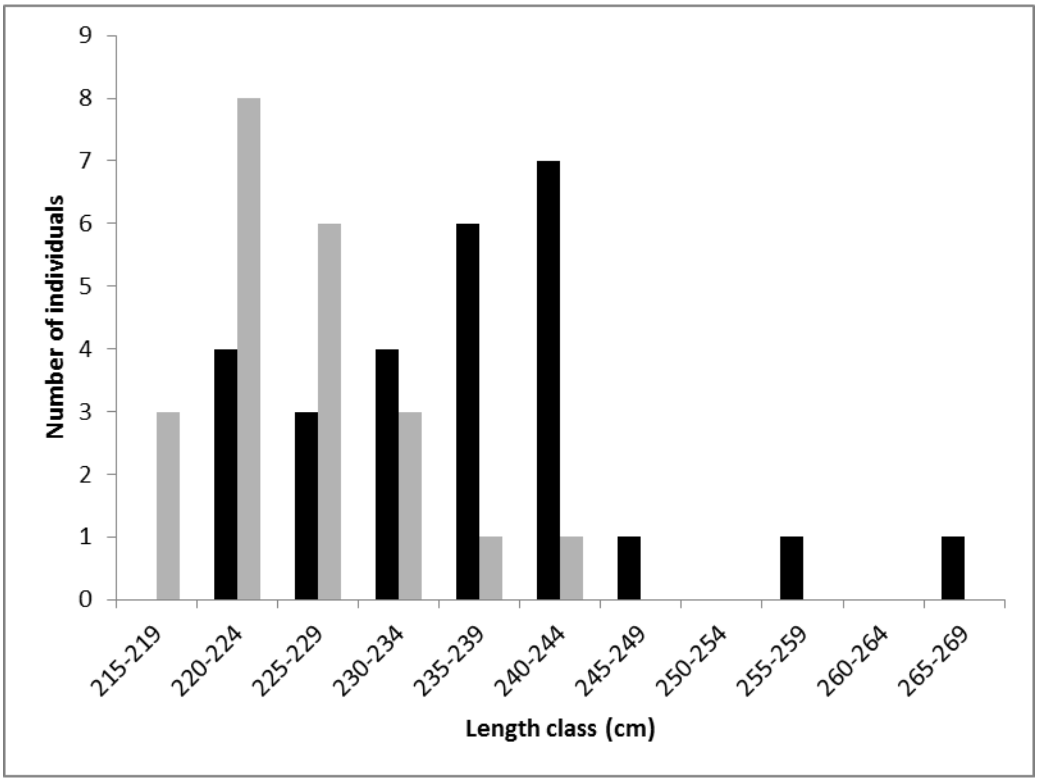

Figure 2.7 Size-frequency of sexually mature male (n=27) and female (n=22) *S. coeruleoalba* used for the sexual dimorphism analysis. The black bars indicate male and the grey bars females.

Chapter 3

Age and growth of *Stenella coeruleoalba*

3.1 Introduction

Age estimation is used to obtain a value of age in animals where the real age is not known (Hohn, 2002). It is estimated by counts of the growth layers deposited in hard tissues of the body such as teeth or bone (Klevezal and Kleinenberg, 1969; Hohn, 2002). The layers that are deposited in these tissues are broadly similar to the growth rings found in trees (Hohn, 2002). Primarily, teeth are used to estimate age in marine mammals, such as odontocetes, pinnipeds, sea otters and polar bears (Hohn, 2002). Since the 19th century zoologists have described growth layers in odontocete teeth without actually understanding their importance (Scheffer and Myrick, 1980). Scheffer (1950) and Laws (1952) were the first to recognise the value of these layers in aging otariids and phocids, respectively. In the case of cetaceans, Nishiwaki and Yagi (1953) were the first to use dental layers for aging. By the late 1960's the use of teeth for age determination had been applied to most species of toothed sea mammals (Scheffer and Myrick, 1980).

3.1.1 Tooth morphology and histology

Teeth are one of the hardest and long lasting structures in an animals' body. They are easy to preserve and store for later processing and are readily available from dead individuals (Langvatn, 1995; Hohn, 2002). Odontocetes have conical, homodont dentition that maybe curved in one or more planes (Myrick, 1991). Homodont dentition means that all the teeth have the same morphology and are not differentiated (Hohn, 2002). Furthermore, odontocetes have monophydont teeth, meaning that they have one set of teeth throughout their life (Peyer, 1968). Odontocete teeth usually do not undergo remodelling and grow continuously throughout the life of the individual (Hohn, 2002). These characteristics allow a complete growth record from time of birth to time of death laid down in the teeth.

Teeth are specialised bony structures comprised of minerals on a matrix of collagen fibres (Langvatn, 1995). They are made up of a crown and a root. The crown protrudes above the gum and the root is embedded in the gum and jaw (Klevezal and Kleinenberg, 1969) (Figure 3.1). Structurally, the tooth is made up of enamel, dentine, a central pulp cavity and cementum (Klevezal and Kleinenberg, 1969) (Figure 3.1).

Enamel

Enamel is the hardest tissue in the body and forms an external covering for dentine (Perrin and Myrick, 1980; Langvatn, 1995) (Figure 3.1). Enamel is deposited prenatally (before birth) and does not have any purpose in age determination for animals (Myrick, 1980).

Dentine

Dentine is a calcified tissue that comprises most of the tooth (root and crown) (Perrin and Myrick, 1980). It is covered on the crown by enamel and on the root by cementum (Perrin and Myrick, 1980) (Figure 3.1). For the purposes of aging dentine, dentine in the tooth is divided into two types, namely, prenatal and postnatal dentine (Figure 3.1). Prenatal dentine is poorly layered orthodentine that is deposited before birth on the outside of the neonatal line (Perrin and Myrick, 1980) (Figure 3.1). While, postnatal dentine is well layered and is deposited after birth on the inside of the neonatal line (Perrin and Myrick, 1980) (Figure 3.1).

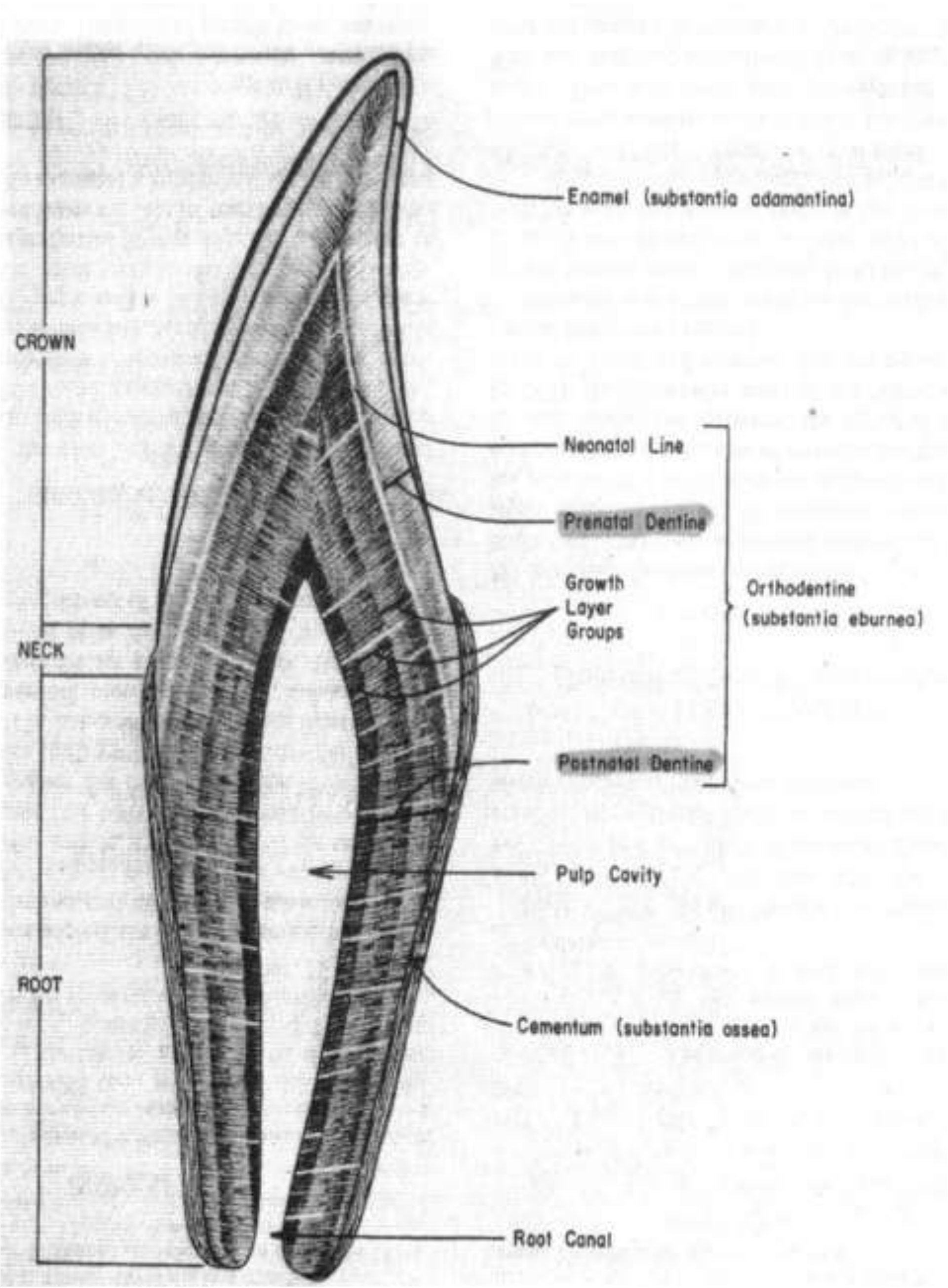

Figure 3.1 Morphology of a dolphin tooth (Perrin and Myrick, 1980).

Neonatal line

The neonatal line is a well-developed growth layer of orthodentine that separates prenatal and postnatal dentine (Perrin and Myrick, 1980). The formation of this layer is thought to be caused by a sudden change in nutrition at birth (Perrin and Myrick, 1980).

Pulp cavity

The pulp cavity is located at the centre of the tooth (Figure 3.1) and it is surrounded by postnatal dentine (Perrin and Myrick, 1980). In life, the pulp cavity is composed of connective tissue and fibres, as well as blood vessels and nerves (Langvatn, 1995). Odontoblasts are also present in the pulp cavity and are found on the bordering part of the cavity (Langvatn, 1995). These cells are responsible for the formation of new dentine at the wall of the pulp cavity (Klevezal and Kleinenberg, 1969). Eventually, the pulp cavity becomes completely filled with dentine and dentine deposition ceases (Klevezal and Kleinenburg, 1969; Kroese, 1993). After the occlusion (closure) of the pulp cavity globular masses of secondary dentine may occur in the region of the pulp cavity called pulp stones, and these make age determination difficult (Perrin and Myrick, 1980). Additionally, pulp stones can, and often do occur prior to dentine occlusion (Perrin and Myrick, 1980).

Cementum

Cementum covers the outside of the root and functions as the ‘attachment bone’ of the tooth (Perrin and Myrick, 1980; Langvatn, 1995) (Figure 3.1). It is deposited postnatally by cementocytes and forms layers with lamellae running parallel to the root (Perrin and Myrick, 1980; Myrick *et al*., 1983; Langvatn, 1995). Deposition is said to be unrestricted, and represents the animals' entire life (Myrick *et al.*, 1983; Langvatn, 1995).

3.1.2 Growth layers

When odontocete teeth erupt they are made up of enamel and a thin layer of prenatal dentine surrounding a large pulp cavity (Klevezal and Kleinenburg, 1969; Myrick *et al*., 1983). As the animal grows, postnatal dentine is deposited by the odontoblasts inwards from the neonatal line into the pulp cavity (Myrick *et al*., 1983). The postnatally deposited dentine forms layers within the tooth which are used for age determination. When pulp cavity occlusion occurs dentine may not be suitable to estimate the age of the individual (Myrick *et al*., 1983). Unlike dentine deposition, cement deposition is unrestricted, therefore cemental layers can be used to estimate maximum ages of older animals where dentinal estimates are not possible due to occluded pulp cavities and pulp stones (Myrick *et al*., 1983).

Age determination has been conducted by counting the growth layers present in the dentine and cementum of teeth in many delphinids, including the striped dolphin (*Stenella coeruleoalba)* (Kasuya, 1972; Kasuya, 1976; Kroese, 1993), the spinner dolphin (*Stenella longirostris)* (Myrick *et al*., 1983), pantropical spotted dolphin (*Stenella attenuata)* (Myrick *et al*., 1983), Atlantic spotted dolphin (*Stenella frontalis)*(Siciliano *et al*., 2007), common bottlenose dolphin (*Tursiops truncatus*) (Hohn *et al*., 1989; Cockcroft and Ross, 1990; Siciliano *et al*., 2007), dusky dolphins (*Lagenorhynchus obscurus*) (Best, 1976) and short-beaked common dolphin (*Delphinus delphis*) (Gurevich *et al*., 1980; Murphy, 2004). An annual layer in dentine and cement is comprised of two bands, differing in optical density and staining intensity in decalcified sections (Klevezal and Kleinenberg, 1969). These differences are a result of varying calcium content (Klevezal and Kleinenberg, 1969). In a longitudinal tooth section broad opaque and narrow translucent bands running along the length of the tooth are observed in both the dentine and cement (Klevezal and Kleinenberg, 1969). If sections are stained with haematoxylin, the broad opaque band stains weakly, while the narrow translucent band stains strongly (Klevezal and Kleinenberg, 1969).

One opaque and one translucent band make up a growth layer group (GLG), which is defined as "a repeating or semi-repeating pattern of adjacent groups of incremental growth layers within the dentine, cementum, or bone, which is defined as a countable unit'' (Perrin and Myrick, 1980). The contrast between the bands in a GLG varies between mammals. Within these individual bands are thin accessory bands. These accessory bands may be mistaken as a complete growth layer (Klevezal and Kleinenberg, 1969). In odontocetes, accessory lines are numerous and appear within all GLG's (Klevezal and Kleinenberg, 1969).

The differing calcium content between the bands can be explained by differing growth rates over a period of time (Klevezal and Kleinenberg, 1969). One band represents slow growth, and is therefore more calcified, while the other band represents fast growth and is less calcified (Klevezal and Kleinenberg, 1969). The narrow, translucent band in the dentine is formed during winter, when growth is slow, and the broad, opaque band is formed during summer, when growth is faster (Klevezal and Kleinenberg, 1969). Therefore, based on a number of odontocetes such as the sperm whale (*Physeter catodon)*, common bottlenose dolphin (*T. truncatus)* and short-beaked common dolphin (*D. delphis*), the formation of GLG's is a result of seasonal changes in growth rates (Klevezal and Kleinenberg, 1969).

3.1.3 Age determination

Age determination is important in assessing life history parameters of a population such as age and length at physical maturity and growth rates (Myrick *et al*., 1983). The dynamics of a population cannot be understood without knowledge of age composition, age at sexual maturity, age at first reproduction and longevity (Myrick *et al*., 1983). In addition, age determination has become a popular approach for population and/or stock assessment and management for many marine mammals (Scheffer and Myrick, 1980).

In order to use GLG's for age determination the rate of GLG deposition must be confirmed. Accurate age determination has presented many difficulties for researchers, as there are only a few known-age animals to standardise results (Hohn, 2002). Myrick *et al.* (1984) described three approaches that have been used to determine deposition rates. The first is tetracycline labelling in living organisms, the second, is multiple extractions of teeth over time and the third, is the examination of teeth from known-age individuals. These will be described in detail below.

The application of the antibiotic tetracycline, forms a fine mark in growing teeth and bone (Hohn, 1990). A number of prior studies have used tetracycline labelling of teeth on captive common bottlenose dolphins (*T. truncatus*) (Myrick and Cornell, 1990), Hawaiian spinner dolphins (*S. longirostris*) (Myrick *et al*., 1984), dusky dolphins (*L. obscurus*) (Best, 1976) and short-beaked common dolphins (*D. delphis*) (Gurevich *et al*., 1980). The results indicated that dentinal GLG deposition appears to be annual, and that one GLG represents one year of growth (Best, 1976; Gurevich *et al*., 1980; Myrick *et al*., 1984; Myrick and Cornell, 1990). Using a similar approach, Kroese (1993) found that the number of GLG's present (two and a bit) in a captive striped dolphin (*S. coeruleoalba*) did not correspond to the actual time elapsed between tetracycline labelling and death (three years 18 days). He attributed this difference to the ill health of the dolphin prior to its death and concluded that illness can delay or alter dentine deposition (Kroese, 1993).

Multiple extractions of teeth from the same individual over a period of time is another way to determine if deposition is annual. Using this method, an annual deposition rate of dentine was confirmed for free ranging common bottlenose dolphins (*T. truncatus*) (Hohn *et al*., 1989).

Known age dolphins are those that have been kept in captivity for most, if not all of their lives (Hohn, 1990). These dolphins can be used to validate annual deposition of growth layers (Hohn, 1990). Hohn *et al.* (1989) examined 26 known-age or approximately known age individuals. Teeth were examined without knowledge of the age and estimated ages were the same or very close to the known age of each individual (Hohn *et al*., 1989). In another study on common bottlenose dolphins, an annual deposition rate was confirmed from 13 captive dolphins in Florida (Sergeant *et al*., 1973).

The use of GLG’s in age determination in delphinids is generally accepted, even if growth layer calibration has not been performed on all species. This is because the appearance and structure of GLG’s are very similar between many delphinids (Hohn *et al*., 1989). Therefore, annual GLG deposition from species such as the common bottlenose dolphin can be applied to other delphinid species where growth layer calibration is not available, and age estimates can be made (Hohn *et al*., 1989).

3.1.4 Age determination in Stenella species

A number of age determination studies have been conducted on *Stenella* species, namely in the Mediterranean Sea (Di-Meglio *et al*., 1996; Letizia *et al*., 1997), Indian Ocean (Ross, 1984; Kroese, 1993), Pacific Ocean (Nishiwaki and Yagi, 1953; Kasuya, 1976; Miyazaki, 1977a; Chivers, 2002) and NE Atlantic Ocean (Di-Meglio *et al*., 1996; Siciliano *et al*., 2007). One study conducted by Myrick *et al*. (1984) on Hawaiian spinner dolphins (*S. longirostris*) aimed to calibrate dental layers based on tetracycline marking. The study was conducted on seven captive dolphins and an annual deposition rate was confirmed (Myrick *et al*., 1984). The other studies applied annual GLG deposition based on the similarities in appearance and structure with other delphinids where dental calibration had been done.

The ‘layered pattern’ in *S. coeruleoalba* teeth was first observed in 1953 by Nishiwaki and Yagi. Alternating opaque and translucent layers are present in the dentine and the cementum of their teeth (Kasuya, 1976; Miyazaki, 1977a, Ross, 1984; Kroese, 1993). A number of studies concluded that the deposition of GLG’s was annual in *S. coeruleoalba,* and one growth layer represented one year of growth (Kasuya, 1976; Miyazaki, 1977a, Ross, 1984; Kroese, 1993). Ross (1984) previously examined the teeth of 14 stranded *S. coeruleoalba* off the coasts of South Africa and aged them using dentinal counts only. The maximum age he obtained was 15 years for a male individual (Ross, 1984).

3.1.5 Aim of the present chapter

The aim of this chapter was to obtain age estimates for male and female *S. coeruleoalba* along the southeast coast of South Africa and to generate growth curves based on length-at-age and weight-at-age data. This allows parameters such as length at birth, weight at birth, length, weight and age at physical maturity, and longevity to be determined. These parameters are necessary for understanding the biology of this species and for their conservation (Myrick *et al*., 1983; Hohn, 2002). Many dolphins are caught in anti-shark nets and as by-catch in fisheries every year. In terms of conservation, the continued survival of these species depends on adequate management based on knowledge of their life history (Cockcroft and Ross, 1990).

3.2 Materials and Methods

3.2.1 The Sample

As reported in Chapter 2, teeth from a total of 57 (32 male and 25 female) specimens were available for age determination. The size-frequency analysis of the sample is shown in Chapter 2 (Figure 2.5). It was not known where exactly the teeth were removed from in each specimen. Most of the teeth were preserved dry, with a few of them preserved in 50% iso-propyl alcohol. One tooth was chosen from each specimen for age determination, selecting one that shows the least curving (i.e. curved only in one plane) and with little or no dentinal abrasions and wear. However, in some instances these factors could not be avoided as all the teeth available were worn.

3.2.2 Preparation of longitudinal sections of teeth

In order to obtain longitudinal sections of teeth for age determination, preparation included decalcifying, sectioning, staining and mounting the sections onto glass slides. These methods are described in detail by Myrick *et al*. (1983) for teeth from *S. attenuata* and *S. longirostris*. Individual whole teeth were immersed in 45ml of RDO (a commercially produced decalcifying agent, Apex Engineering Products Corporation); until it was flexible and slightly translucent. Decalcifying times ranged from two to 95 hours depending on tooth size. Once the teeth were rubbery in texture, they were rinsed in tap water for three hours to remove excess RDO. The tooth was then mounted on a specimen block with O.C.T. compound as a cryomatrix and sectioned longitudinally from the apex to the base using a Shandon mini cryostat microtome (kept at -25^{o}C). A number of 25 -40 µm thick sections (Dellabianca *et al.,* 2012; Santos *et al.,* 2003) were taken from the central portion of the tooth, placed into a petri dish and rinsed in tap water to remove any residual RDO, preventing it from interfering in the staining process.

3.2.3 Staining and Mounting

The longitudinal sections were immersed in Mayer's haematoxylin (Myrick *et al*., 1983) for 20 minutes for staining. Thereafter the sections were checked under an Olympus SZ dissecting microscope with transmitted light; at 10x magnification. If the sections were not dark enough they were re-stained for approximately 15 minutes or until they were dark enough. Excess stain was removed by placing the sections into a petri dish with tap water. The sections were then 'blued' in 0.5% solution of Ammonia for five minutes to enhance the contrast between the layers (Myrick *et al*., 1983). Subsequently they were rinsed in tap water again. To retain the colour of the stain the sections were placed into a 1:1 solution of glycerin and distilled water for five to ten minutes. They were then transferred into 100% glycerin and examined under a dissecting microscope using transmitted light.

Only those sections that were mid-longitudinal with a sharply pointed apex were selected for age determination. As sections that were cut off-centre may result in the loss of fine layers that are deposited closest to the pulp cavity in older animals (Hohn, 2002). The best thin sections were dried with a paper towel and placed on a slide next to each other. The wrinkles were smoothed out using a glass rod and mounted with DPX mounting medium and then labelled.

3.2.4 Age Determination

Allowing a few hours for drying, the slides were examined under an Olympus SZ dissecting microscope with transmitted light. The teeth were first examined at 10x magnification to identify the layered pattern and if necessary were magnified up to 15x magnification for an age estimate. The best section on the slide was selected and the age was estimated by counting the growth layer groups (GLG's). A GLG consists of a thin, lightly stained boundary layer followed by a thick, darkly stained layer (Myrick *et al.*, 1983). When these two layers are present the GLG is considered complete. If a GLG was incomplete, it was compared to the last fully formed layer to estimate the completion of the last, not fully formed layer as a percentage thereof. The completion of the last layer was estimated to the nearest 0.5 GLG i.e. if it was more than half it was considered a fully formed layer (100%), but if it was less than a half-formed layer it was not considered as a new layer (0%).

Age estimates were carried out 'blind' with no reference to biological data such as body length and sex, to avoid any biases. The teeth were read three times and if these estimates were within 15% of each other an average was obtained. This value was compared with another independent reader (Z. Nolte, Rhodes University), who read each tooth once. If the two estimates from the two independent readers were within 15% of each other the average was used, but if there was more than 15% difference, the estimates were discussed by both readers until a consensus was reached.

3.2.5 Age estimates from dentinal versus cemental counts

Dentinal growth layers were counted and recorded in individuals where occlusion of the pulp cavity had not yet occurred. If the pulp cavity was fully occluded, dentinal, as well as cemental growth layers were counted and recorded. To examine whether cemental growth layers could provide a good estimate of age in these individuals (Kasuya, 1976), a scatterplot of dental and cement GLG counts was generated in Microsoft Excel 2010. A line of linear regression was fitted to the data. This was done to determine whether there is a correlation between dentinal and cemental counts, and, ultimately, determine if cemental counts will be useful in individuals with an occluded pulp cavity. Cemental layers were examined under an Olympus BX50 compound microscope at 200x magnification.

3.2.6 Growth curve

To plot a growth curve for *S. coeruloealba*, the age estimate for each specimen was plotted against total body length (TBL) and mass. Microsoft Excel 2010 was then used to plot a von Bertalanffy growth curve and a Gompertz growth curve for male and female dolphins separately and male and female dolphins combined. Both models were used for comparative purposes with previously published work on this and other delphinids. The model with the best fit was determined by examining the r^2 value. The equations are as follows:

Von Bertalanffy growth function:

$$L^{t} = L\infty\ (1\text{-}e^{-k\ (t\text{-}to)})$$

Where:

L = length,

k = growth rate constant,

L∞ = asymptotic length,

to = length at birth,

e = exponential,

t = estimated age

Gompertz growth function:

$$Y(t) = ae^{be\wedge\ ct}$$

Where:

a=upper asymptotic length,

b = length at birth,

c = sets growth rate,

e = exponential,

t = estimated age

3.3 Results

3.3.1 Tooth histology

Figure 3.2 shows the longitudinal sections through two *S. coeruleoalba* teeth viewed under a dissecting microscope operated at 10x magnification using transmitted light. The dentinal matrix appeared light blue with alternating darkly stained and lightly stained layers, which formed a sharp point at the midline. The neonatal line was clearly visible and it was easy to distinguish between prenatal and postnatal dentine. However, accessory lines within the postnatal dentine were numerous. The first GLG was generally the widest, with the widths of the layers decreasing towards the pulp cavity (Figure 3.2). Some pulp cavities were close to occlusion and it was difficult to read the last few GLG's, therefore these counts may be underestimated.

3.3.2 Relationship between dentinal and cemental GLG's

The relationship between dentinal counts and cemental counts for 44 individuals is shown in Figure 3.3. The correlation coefficient was high indicating a good correlation ($r^2 = 0.926$) between dentinal and cemental age estimates. This indicates cemental layers can be used for age estimation in cases where the pulp cavity is closed. Dentinal and cemental age estimates were well correlated up to an age of about 11 years (Figure 3.3). This suggests that occlusion of the pulp cavity can occur from 11 years of age and the smallest individual with an occluded pulp cavity measured 227cm in total body length.

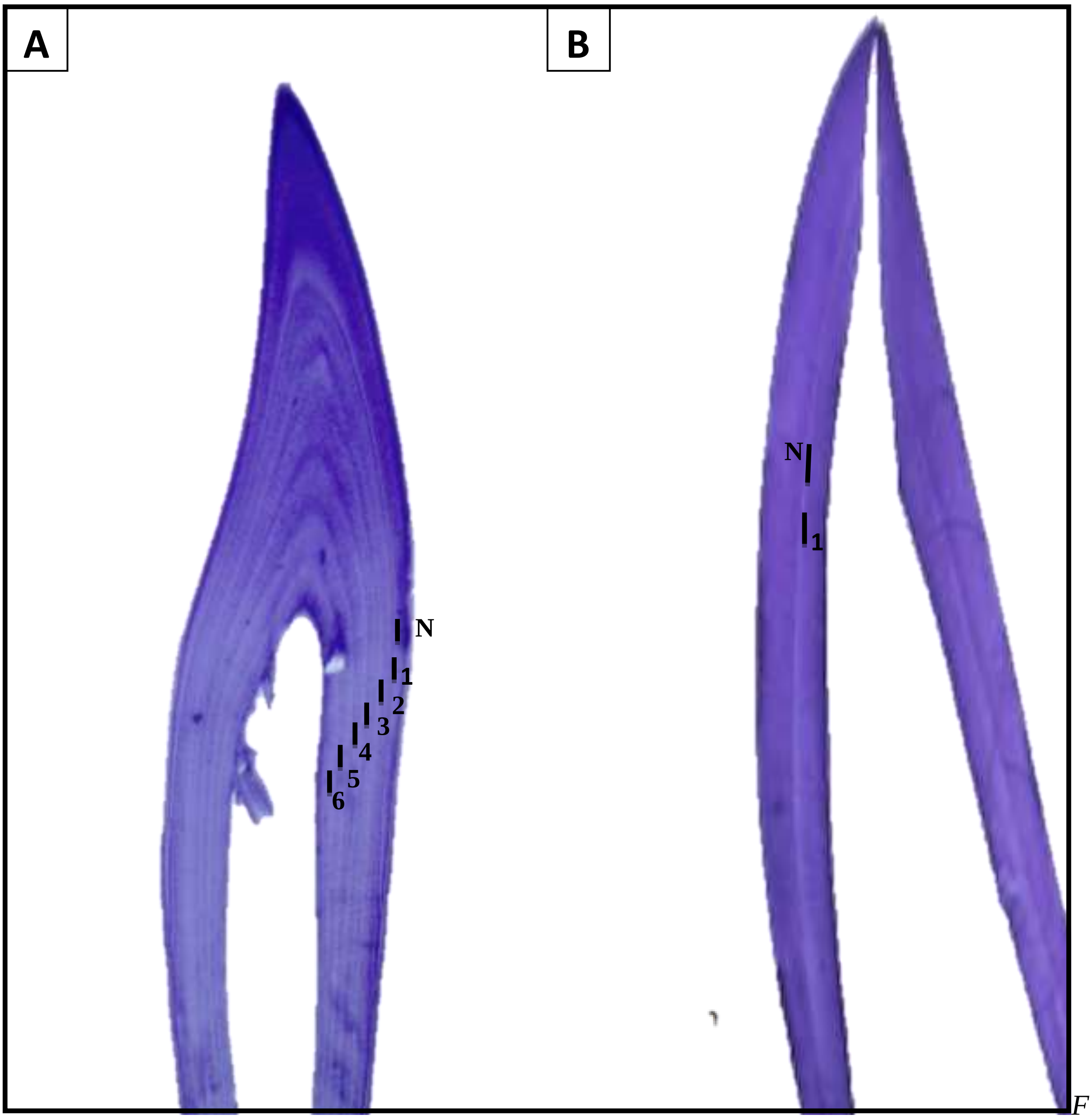

Figure 3.2 Longitudinal sections of teeth from two *S. coeruleoalba* specimens (A- PEM N0781, B- PEM N1776), viewed under a dissecting microscope with transmitted light (x10 magnification). The bars on the photograph indicate the neonatal lines (N) as well as the number of GLG's (A- six GLG's, B- one GLG).

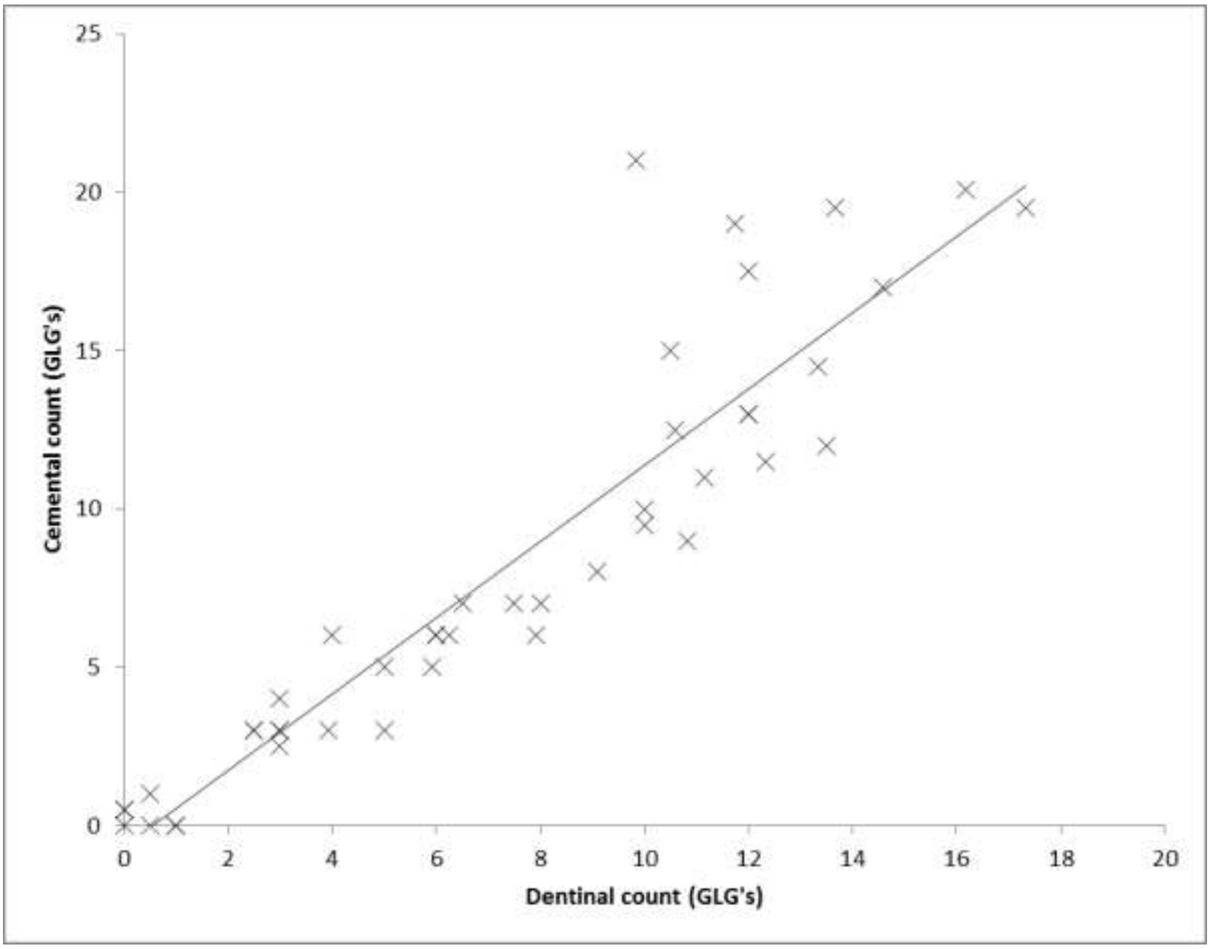

Figure 3.3 The relationship between dentinal and cemental GLG’s in the teeth of *S. coeruleoalba* stranded off the south-east coast of South Africa. A linear regression is fitted to the data (r^2 = 0.926).

3.3.3 Length and age

Both the von Bertalanffy growth model and the Gompertz growth model were fitted to body length versus age estimate data for both males and females. Both growth models had the best fit to the female data (von Bertalanffy r^2 = 0.893; Gompertz r^2 = 0.891) (Table 3.1). However, overall the von Bertalanffy growth model had a better fit for both male and female data and the data for sexes combined (von Bertalanffy - males r^2 = 0.840; females r^2 = 0.893; combined sexes r^2 = 0.852, Gompertz – males r^2 = 0.837; females r^2 = 0.891; combined sexes r^2 = 0.846) (Table 3.1).

Table 3.1 Comparison of r^2 values generated by the Von Bertalanffy growth function and the Gompertz growth function.

Growth model	**males**	**females**	**Combined males and females**
Von Bertalanffy growth function	0.840	0.893	0.852
Gompertz growth function	0.832	0.891	0.846

Von Bertalanffy growth function

A von Bertalanffy growth curve was fitted to length-at-age data for males and females separately and for males and females combined (Figure 3.4). A summary of the parameters are listed in Table 3.2. The r^2 values generated for the sexes separately and combined were close to one, indicating a good fit to the data (Males: r^2 = 0.840; Females: r^2 = 0.893; Combined: r^2 = 0.852).

Length increase is rapid for the first few years in both male and female *S. coeruleoalba*, thereafter the increase slows down and reaches a plateau (Figure 3.4). Length increase is rapid until about five years of age and until about 210cm in length for males and until about four years of age and 200cm in length for females.

Table 3.2 Parameters derived from a Von Bertalanffy and Gompertz growth equation for male and female *S. coeruleoalba*.

	Parameter	**Males (Length (cm))**	**Females (Length (cm))**	**Combined males and females (Length (cm))**
Von Bertalanffy growth function	L_1	99	112	99
	L_2	244	228	244
	L_∞	230.76	224.36	227.20
	to	116.20	112.19	114.85
	K	0.344	0.372	0.364
	n	32	25	57
	r^2	0.840	0.893	0.852
Gompertz growth Function	L_1	99	112	99
	L_2	244	228	244
	a	229.87	223.61	226.39
	b	119.09	113.79	117.37
	c	0.408	0.442	0.431
	n	32	25	57
	r^2	0.832	0.891	0.846

L_1 = Smallest length in the sample

L_2 = Largest length in the sample

L_∞ = Asymtotic length

to = Length at birth

k = Growth constant

a = Asymtotic length

b = Length at birth

c = Growth constant

n = Sample size

Individuals were considered physically mature if they had a TBL equal to or greater than the asymptotic value generated by the von Bertalanffy equation. The curve estimated asymptotic lengths to be 230.76cm for males and 224.36cm for females. The males appear to reach physical maturity at about 21 years of age, while the females reach physical maturity earlier at about 18 years of age.

Length at birth was estimated to be 116.20cm for males and 112.19cm for females by the equation. Both these values are most likely overestimated, as a result of having only a few younger individuals present in the sample (between 80- 200 cm TBL - n (males) = 10; n (females) = 3).

When males and females were combined growth was rapid up to about 4 years of age and 200cm TBL (Figure 3.4). Thereafter the curve began to flatten out and reached an asymptotic length of 227.20cm at about 20 years old and the curve estimated length at birth to be 114.85cm.

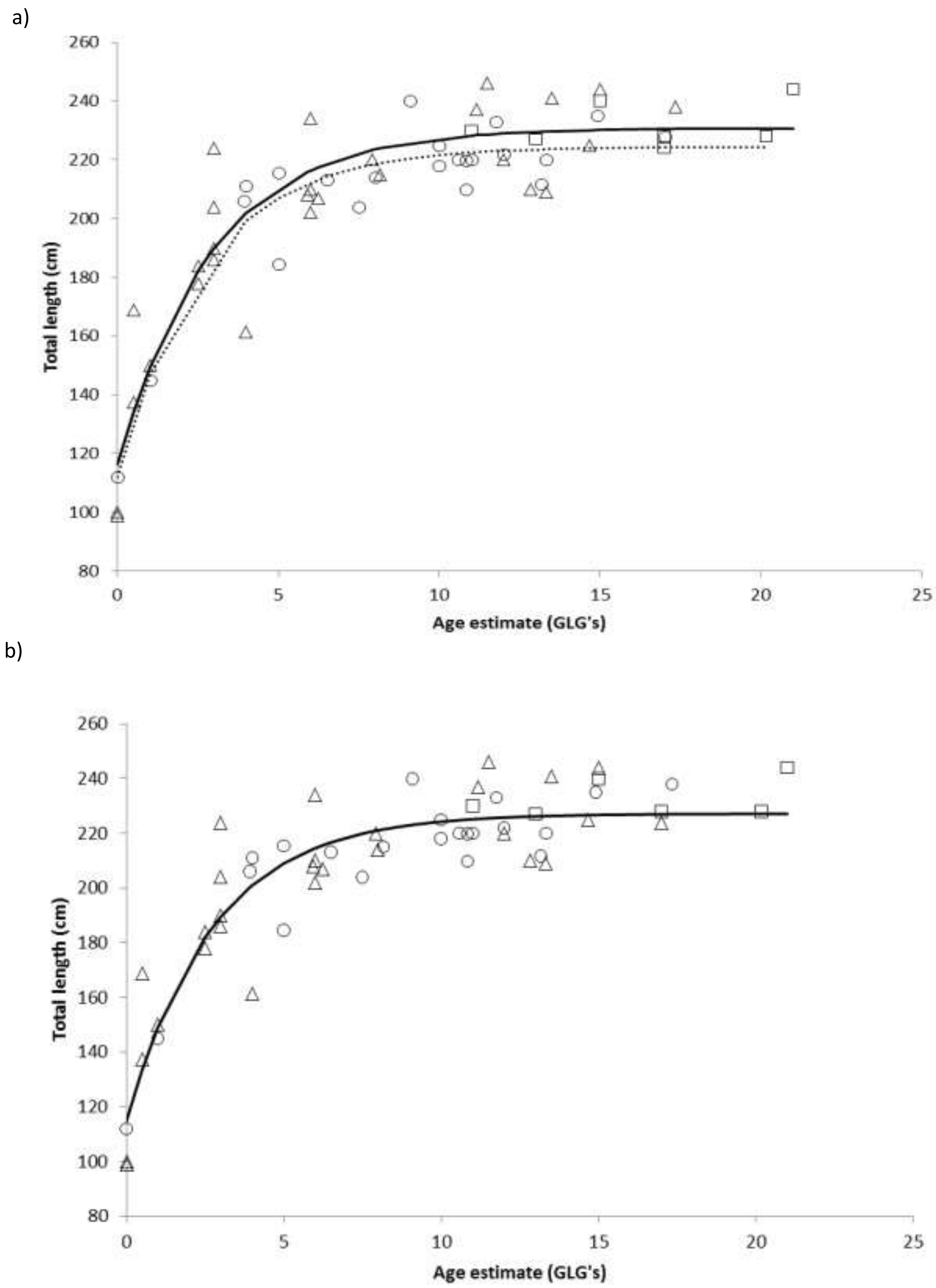

Figure 3.4 Von Bertalanffy growth curve fitted to length-at-age data of *S. coeruleoabla* for males and females separately (a) and males and females combined (b). The triangles represent males, the circles represent females and the squares represent specimens where cemental counts were used, (r^2 = 0.845 (males), r^2 = 0.893 (females), r^2 = 0.853 (combined)).

Gompertz growth function

The parameters of the Gompertz growth curve conducted on male and female *S. coeruleoalba* are indicated in Table 3.2. The Gompertz curve estimated asymptotic length to be reached at 229.87cm and 223.61cm for males and females, respectively (Table 3.2). Based on these estimates, males reach physical maturity at about 21 years of age and females at about 20 years of age. Length at birth for male *S. coeruleoalba* was estimated to be 119.09cm, while for females it was estimated to be 113.79cm. These estimates are much higher than those generated by the von Bertalanffy growth function. When males and females were combined asymptotic length was reached at 226.39cm at about 20 years old and length at birth was predicted to be 117.37cm.

Of the total number of teeth examined, only 35% of the male and 20% of the females had < 5 GLG's. The longest male in the sample measured 244 cm and the longest female 228cm. Based on cemental counts, the oldest male in the sample was estimated to be 21 years of age and the oldest female estimated to be 20.2 years old.

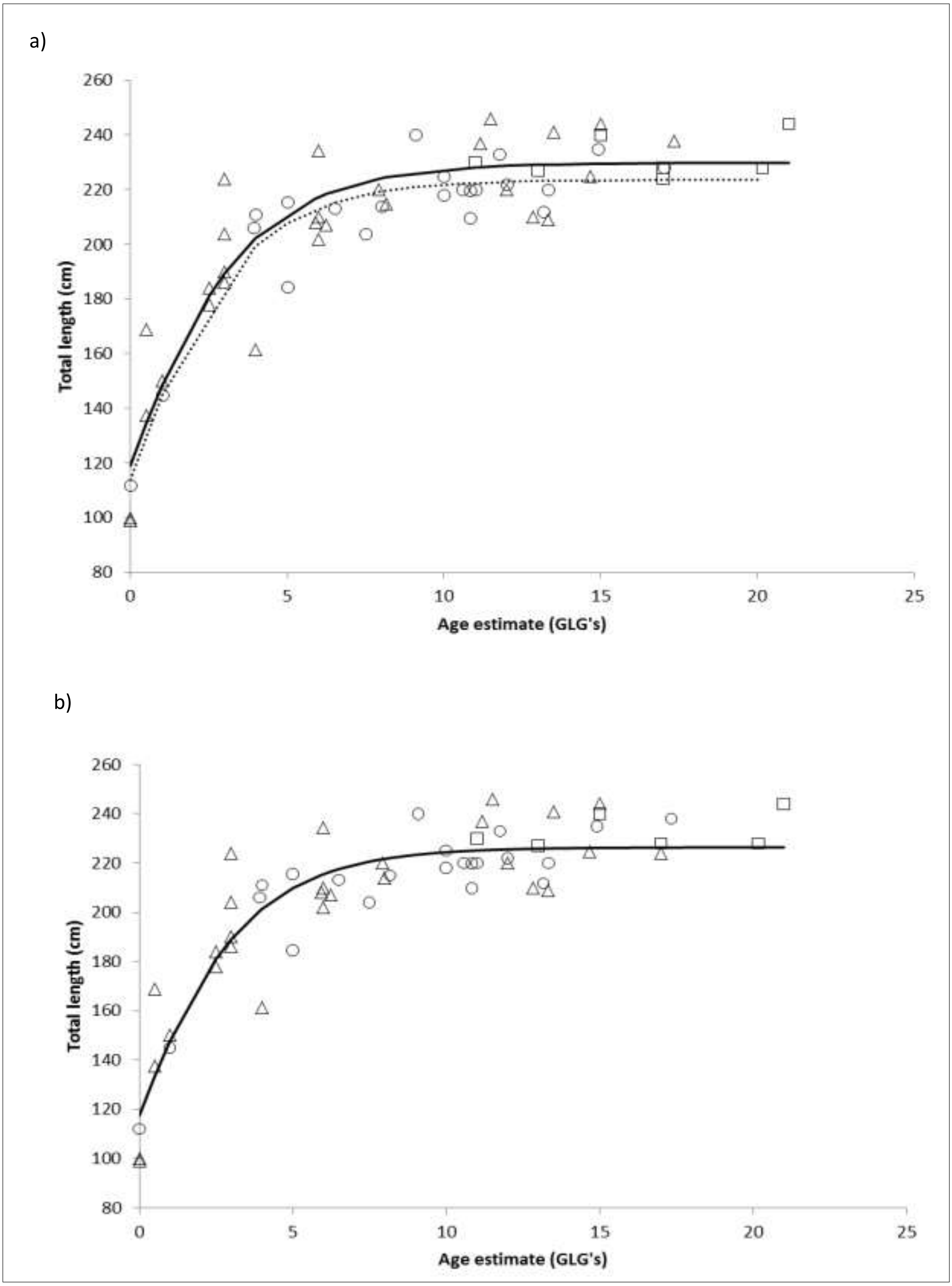

Figure 3.5 Gompertz growth curve fitted to length-at-age data of *S. coeruleoalba* for males and females separate (a) and for males and females combined (b). The triangles represent males, the circles represent females and the squares represent specimens where cemental counts were used, (r^2 = 0.847 (combined), r^2 = 0.837 (males), r^2 = 0.891 (females)).

3.3.4 Weight and age

The von Bertalanffy growth model and the Gompertz growth model were fitted to body weight versus age estimate data. The von Bertalanffy growth equation gave the best fit, based on the r^2 values (Table 3.3). However, the Gompertz growth model fitted the female data best (Table 3.3).

Table 3.3 Comparison of r^2 values generated by the von Bertalanffy growth function and the Gompertz growth function.

Growth model	**males**	**females**	**Combined males and females**
Von Bertalanffy growth function	0.832	0.833	0.849
Gompertz growth function	0.815	0.837	0.830

Von Bertalanffy growth function

A summary of the parameters generated from the von Bertalanffy growth model are listed in Table 3.4. Growth curves were fitted to males and females separately and to males and females combined (Figure 3.6).

The asymptotic weights for *S. coeruleoalba* were estimated to be 127.98kg and 124.21kg for males and females, respectively. These weights are reached at ages greater than 21 and 20 years of age for males and females, respectively. The growth curve estimated weight at birth to be 19.82kg for males, and 11.28kg for females. Initial weight increase is not as rapid as it is for length. However, weight increase is rapid in the first six and seven years for males and females, respectively, after which weight increase slows. The males are heavier than the females in the first four years, thereafter the females overtake the males but both sexes reach a plateau at similar weights of 128kg (male) and 124kg (female) (Figure 3.6). Both growth curves only just begin to reach a plateau at about 21 years for males, and 20 years for females.

When males and females were combined the growth function estimated asymptotic weight to be 125.20kg, which is reached at an age greater than 21 years old. Weight at birth was predicted to be 16.56kg and weight increase is rapid in the first four years to about 75kg in mass, thereafter weight increase slows and plateaus near the end of the curve.

Gompertz growth function

A Gompertz growth curve was fitted to weight-at-age data and the parameters are shown in Table 3.4. The curve estimated asymptotic weight to be 118.41kg for males and 121.07kg for females. Similarly to the von Bertalanffy growth function, these weights are reached at ages greater than 21 and 20 years of age for males and females, respectively. Weight at birth was predicted by the model to be 23.19kg for males and 16.61kg for females. The males are initially heavier than the females and at about five years of age the females overtake the males and reach a greater asymptotic mass (Figure 3.7). For the first five years weight increase is rapid for males and females up to a weight of about 83kg, thereafter weight increase slows and plateaus.

When the sexes were combined the rate of weight increase is rapid in the first five years up to about 84kg in mass. The growth curve reaches an asymptotic weight of 119.97kg at an age of about 21 years. Weight at birth was estimated by the model to be 21.44kg.

Table 3.4 Parameters derived from a Von Bertalanffy and Gompertz growth equation for male and female *S. coeruleoalba*.

	Parameter	Males (weight (kg))	Females (weight (kg))	Combined males and females (weight (kg))
Von Bertalanffy Growth function	W_1	8.6	13	8.6
	W_2	157	134	157
	$W\infty$	127.98	124.21	125.20
	to	19.82	11.28	16.56
	K	0.17	0.22	0.19
	n	22	18	40
	r^2	0.832	0.833	0.839
Gompertz Growth Function	W_1	8.6	13	8.6
	W_2	157	134	157
	a	118.41	121.07	119.97
	b	23.19	16.61	21.44
	c	0.31	0.33	0.31
	n	22	18	40
	r^2	0.815	0.837	0.830

W_1 = Smallest weight in the sample

W_2 = Largest weight in the sample

$W\infty$ = Asymtotic weight

to = Weight at birth

k = Growth constant

a = Asymtotic weight

b = Weight at birth

c = Growth constant

n = Sample size

r^2 = Goodness of fit

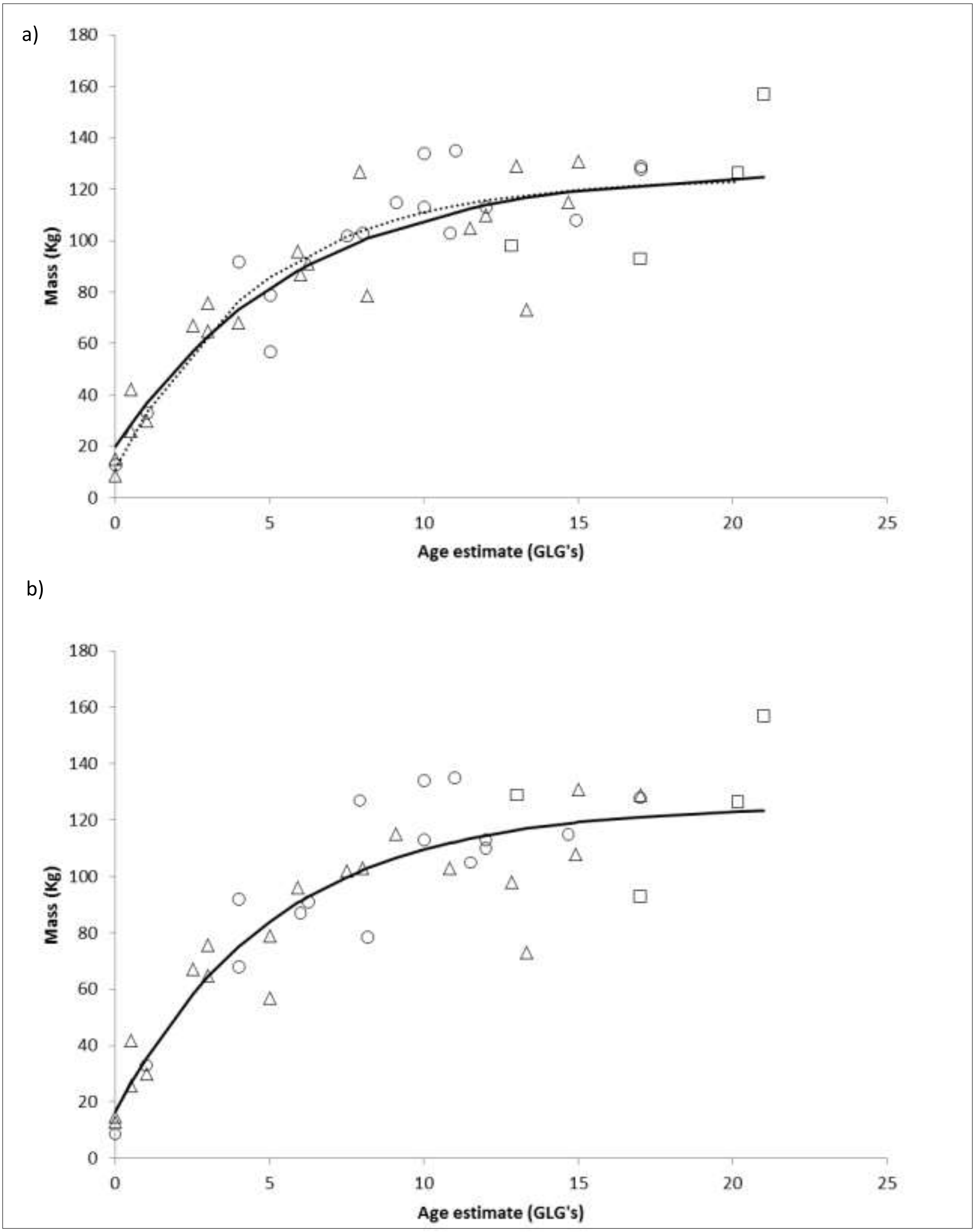

Figure 3.6 Von Bertalanffy growth curve fitted to weight-at-age data of *S. coeruleoabla* for males and females separately (a) and males and females combined (b). The triangles represent males, the circles represent females and the squares represent specimens where cemental counts were used, (r^2 = 0.840(combined), r^2 = 0.835 (males), r^2 = 0.833(females)).

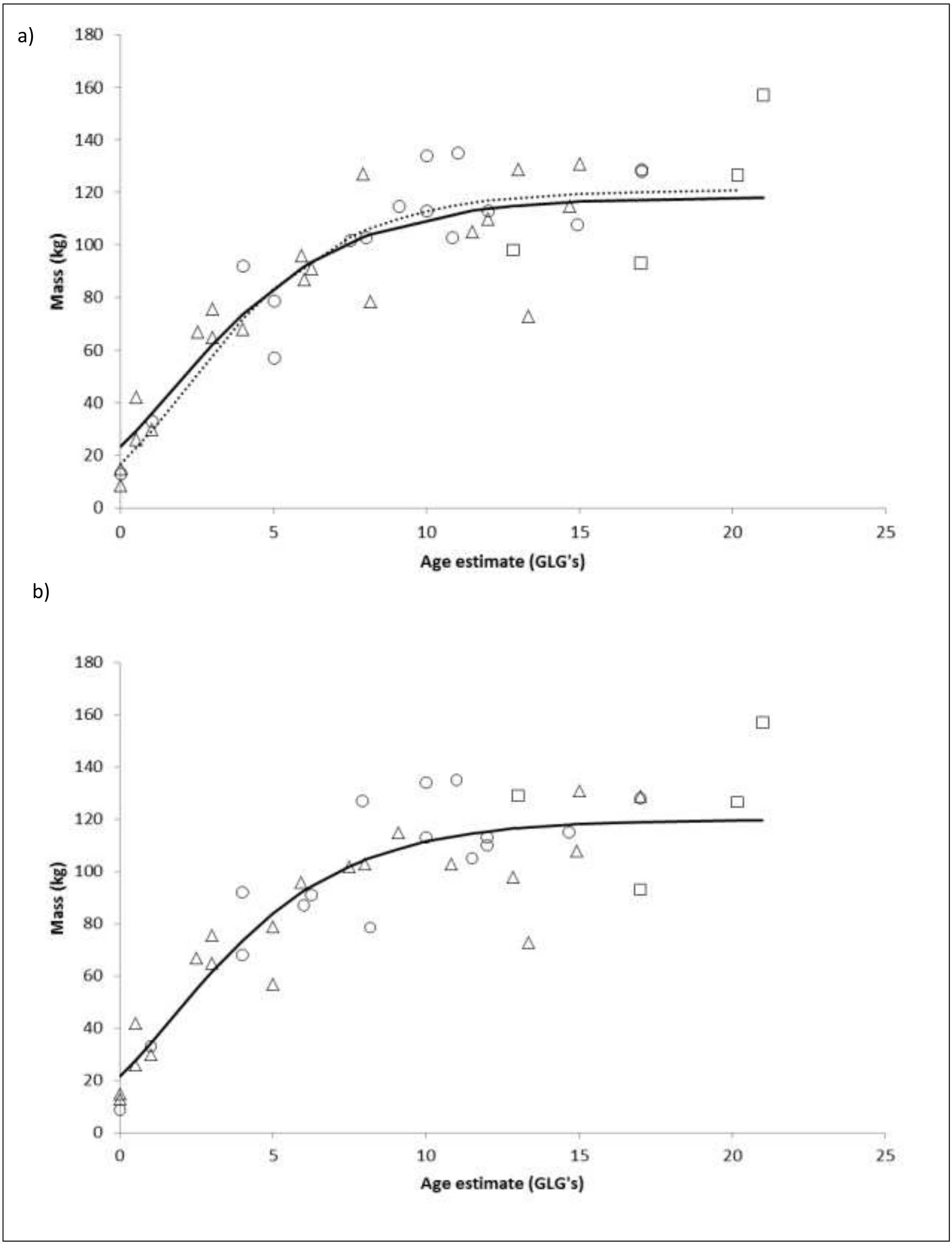

Figure 3.7 Gompertz growth curve fitted to weight-at-age data of *S. coeruleoalba* for males and females separately (a) and for males and females combined (b). The triangles represent males, the circles represent females and the squares represent specimens where cemental counts were used, (r^2 = 0.832(combined), r^2 = 0.820(males), r^2 = 0.837(females)).

3.4 Discussion

3.4.1 Tooth histology

The general histology of the longitudinal sections of *S. coeruleoalba* teeth obtained during the current study supports previous findings in the published literature (Kasuya, 1972; Kasuya, 1976). The postnatal dentine comprised of alternating opaque and translucent bands, and the growth layers present in the dentine and cementum could be distinguished into GLG's. Accessory lines were numerous within the dentine making age estimation challenging. During this study I had the opportunity to age humpback dolphins (*Sousa chinensis*) and compare their teeth with *S. coeruleoalba* teeth. The teeth of humpback dolphins (*S. chinensis*) are very different to *S. coeruleoalba* teeth, in that they are larger in size, have less accessory lines and the growth layers are more evenly spaced. Overall, age estimation is less challenging in humpback dolphins (*S. chinensis*).

3.4.2 Relationship between dentinal and cemental GLG's

There was a good correlation between dentinal and cemental GLG counts ($r^2 = 0.926$), indicating that cemental age estimates were reliable in individuals where the pulp cavity was occluded. Unexpectedly, in some individuals the cemental counts were lower than the dentinal counts. The reason for this could be that the cemental layers were damaged when the gum tissue was removed from the tooth as some of the teeth were preserved with gum tissue still attached to the tooth. The dentinal and cemental counts are closely correlated up to about 11 years, thereafter the cemental counts are higher. This suggests that pulp cavity occlusion occurs from 11 years of age. Kroese (1993) found a close correlation between dentinal and cemental counts up to 14 years age for the same population.

3.4.3 Length and age

There were more males than females in the sample and most animals were estimated to be between five and 15 years of age (Figure 3.8). There were only a few individuals older than 15 years of age in the sample (n= 2 for males; n = 4 for females) (Figure 3.8) and there were only a few females younger than two years old (n=2). The reasons for this are unknown, however, calving may take place off-shore or the unhealthy, younger dolphins are more easily preyed upon and strand less frequently (Kroese, 1993).

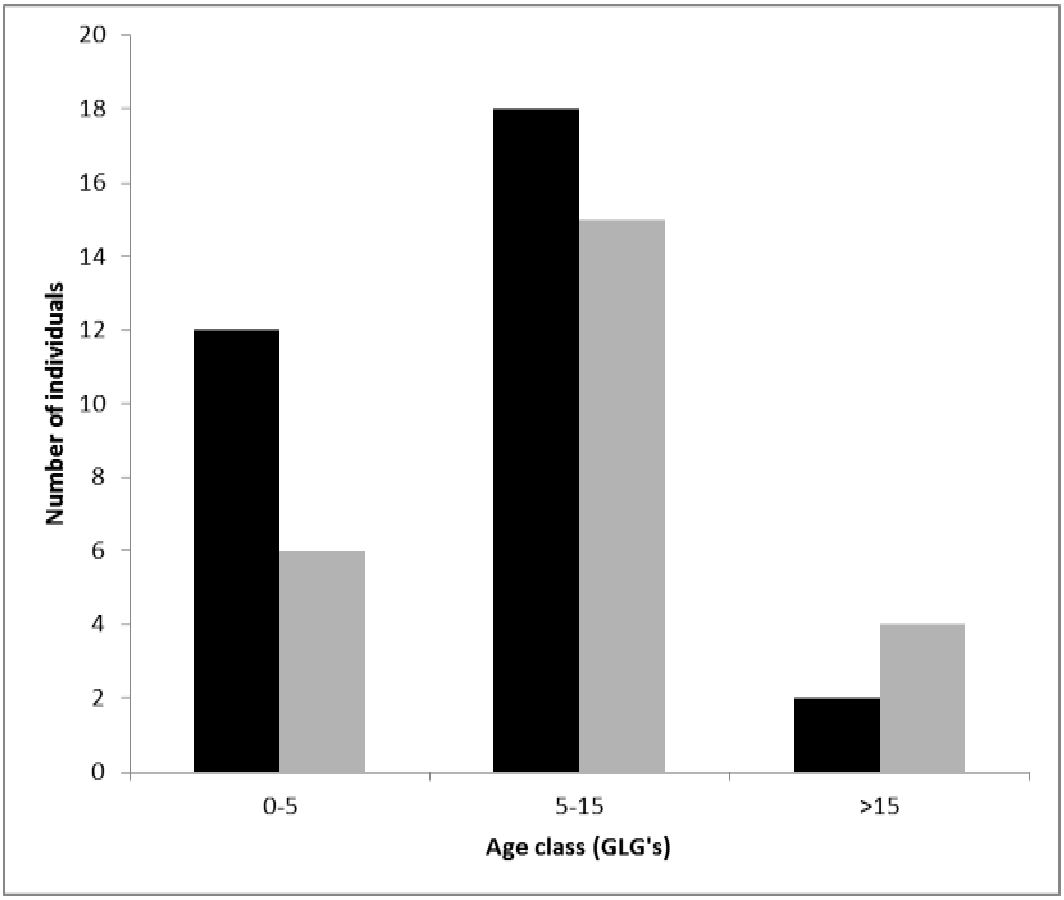

Figure 3.8 Number of individuals in the sample for age determination broken down by age classes. The black bars represent the males and the grey bars represent the females. Black bars represent males and grey bars represent females.

Growth rate

The growth curves generated for both sexes of *S. coeruloealba* show a rapid increase in length with age in the first five years and four years for males and females, respectively. This is somewhat different to a previous study on striped dolphin growth in South Africa, where growth was rapid in the first five and six years for males and females, respectively (Kroese, 1993). In contrast, Kasuya (1972) studied striped dolphin growth in Japanese waters and found that length increase is most rapid up to two years for both males and females. The large initial increase in body length after birth reflects the rapid development of the calf which is needed to reach thermoregulatory equilibrium and social and motor independence from its mother (Cockcroft and Ross, 1990).

The growth curves indicate that growth in males and females is similar in the first five years of their life. Thereafter the males have a faster growth rate and reach a higher mean body length. In the present study, males measured between 148cm and 149cm, and females between 144cm and 147cm by the end of their first year. These results are similar to a previous study on striped dolphins in southern Africa where males measured about 150cm and females about 145cm by the end of the first year (Kroese, 1993). In the Japanese population, males and females reached a higher body length of 166cm by the end of their first year (Miyazaki, 1977a). This links in with the fast initial growth rate of *S. coeruleoalba* discussed above. Additionally, the larger body length attained by the Japanese population in the first year suggests that this population has a higher growth rate, which could be linked to productivity.

Based on the present and published data, females of *S. coeruleoalba* generally have a higher growth rate constant (k) than the males. In both models, the estimated growth rate constant (k) of the females exceeds that of the males (Table 3.1). This is in agreement with a number of previous studies on striped dolphin populations in South Africa (Kroese, 1993), and in the NE Atlantic Ocean (Di-Meglio *et al.*, 1996). This is also true for other delphinids, such as the short-beaked common dolphin (*D. delphis*) (Murphy and Rogan, 2006) (Table 3.5 and 3.6). One exception was a study conducted on the striped dolphin population in the Mediterranean Sea where the male growth rate constant exceeded that of the females (Di-Meglio *et al*., 1996) (Table 3.6).

The growth rate constants estimated during the present study were less than those obtained for striped dolphins in the NE Atlantic Ocean and Mediterranean Sea (Di-Meglio *et al*., 1996). The sample sizes in those studies, however, were smaller than the present study, 52 and 44 animals, respectively, which may account for the difference. However, another explanation could be due to geographic variation in environmental conditions between the Indian Ocean, Mediterranean Sea and NE Atlantic Ocean. An environments productivity and indirectly sea temperature, has been found to influence dolphin growth (Di-Meglio *et al.*, 1996).

Length at birth

The von Bertalanffy and the Gompertz growth functions predicted length at birth for male *S. coeruleoalba* to be about 116 and 119cm, respectively. These estimates are about 5 cm larger than those estimated for the females, 112cm and 114cm, respectively. The smallest individual in the whole sample measured 93cm, indicating that *S. coeruleoalba* are born at lengths shorter than predicted in these models. In the previous study on the South African population, lower values for length at birth of 107.7cm and 91.2cm were obtained for males and females, respectively (Kroese, 1993). An explanation for the difference between the present study and Kroese's (1993) study is that Kroese (1993) examined *S. coeruleoalba* specimens from both the west coast and east coast of South Africa. Recently, a significant difference in dorsal and ventral cranial shape between the west and east coast populations has been found (Conry, 2012). Overall, the west coast dolphins have a larger cranium (Conry, 2012). This could account for the difference in length at birth for *S. coeruleoalba* between the studies. Additionally, Miyazaki (1977b) obtained a value of 100cm for mean length at birth for male and female Japanese striped dolphins. The higher values obtained during this study are probably an artefact of having only a few small individuals available.

Asymptotic length

The asymptotic lengths estimated by the von Bertalanffy growth curve were 231cm for males and 224cm for females. These values were similar to those generated by the Gompertz growth function, which were 230cm and 224cm for males and females, respectively. These values are less than those obtained by Kroese (1993), who previously found that males reached an asymptotic length of 246cm and females a length of 230cm in the South Africa. As mentioned above, Kroese's (1993) study contained both west coast and east coast specimens, and west coast animals have a significantly larger cranium, which could suggest that these dolphins are larger in total body size and account for the difference in asymptotic length between the present study and Kroese's (1993) study. Di-Meglio *et al*. (1996) studied the NE Atlantic and Mediterranean populations. They found lower asymptotic lengths of

216cm and 200cm for males and females, respectively, in the NE Atlantic population, and lengths of 191cm and 195cm for males and females, respectively, in the Mediterranean population. The differences in asymptotic length between the populations may be due to varying environmental conditions, particularly temperature and or food availability, both of which can influence body size and growth (Ross and Cockcroft, 1990).

The estimated asymptotic length of male (von Bertalanffy growth function (VBGF) – 231cm; Gompertz growth function (GGF) – 230cm) *S. coerueleoalba* off the south east coast of southern Africa was between 6 and 7cm larger than the females asymptotic length (VBGF – 224; GGF – 224). Similarly, in the Japanese population male asymptotic length was 8cm larger than that of the females (Kasuya, 1972). Kroese (1993) found a much larger difference between male and female asymptotic lengths for the South African population where males were 16cm larger than the females. The reason for the difference is that Kroese (1993) had both west and east coast animals in his sample, which have been found to be significantly different populations based on cranial size (Conry, 2012).

When animals reach asymptotic length, they are physically mature (Kroese, 1993). This means that the dolphins stop growing and do not increase in body length anymore. In the present study, males reach physical maturity at 21 years of age, while females attained physical maturity at about 18 years of age. These results are comparable to those of Kroese's (1993) on the South African population where the males reached asymptotic length at 25 years of age and the females at 20 years of age. Similar findings are reported for the Japanese stock, where the males reach asymptotic lengths at 21 years and females at 17 years of age (Kasuya, 1976). The reason females reach physical maturity earlier could be due to reproduction, which is an energy costly process and they may need to direct all their energy towards this rather than to growth.

Maximum length and age

In the sample for age determination, the maximum recorded length for male and female *S. coeruleoalba* was 244cm and 228cm, respectively. However, in the sample as a whole the largest specimen measured 265cm in total body length and was a male. Unfortunately, this specimen did not have teeth available for age estimation. In an earlier study on the South African population, a maximum recorded length of 250 cm was reported in a male (Ross, 1984). This individual was estimated to be 12+ years (Ross, 1984). In a study on the Japanese population a maximum length of 255cm was recorded for a male who was estimated to be 21 years of age (Kasuya, 1972).

The maximum age estimates obtained during the present study were 21 years for males and 20.2 years for females. Similarly, for Mediterranean Sea population maximum age estimates of 25 and 22 years were obtained for males and females, respectively using dentinal and cemental GLG’s (Di-Meglio *et al.*, 1996). Di-Meglio *et al*. (1996) also examined the NE Atlantic *S. coeruleoalba* population and found the maximum ages to be 29 and 23 years old for males and females, respectively. Similar findings were reported for the Japanese population using dentinal layers, where the oldest male was 25 years and the oldest female 26 years (Kasuya, 1972). In a later study on the Japanese population, using dentinal and cemental layers, the estimates were much higher, at 50 years and 49 years for males and females, respectively (Kasuya, 1976). Similarly, for the South African population, Kroese

(1993) had much higher estimates of 47 years and 42 years for males and females, respectively. However by only counting dentinal layers Ross (1984) obtained maximum ages of 15 and 12+ for males and females, respectively, for the same population. The greatest source of error in age determination is the misinterpretation of GLG's (Hohn *et al*., 1989). However, the age estimates obtained in this study were confirmed by two independent readers (Zianca Nolte and Stephanie Plön). Additionally, Ross (1984) aged 14 *S. coeruleoalba* specimens off the coast of South Africa using dental counts, five of which were re-examined during this study. The age estimates were similar between the two studies, except in one case where Ross (1984) used dentinal GLG's and in the present study cemental GLG's were used due to an occluded pulp cavity (Table 3.5).

Table 3.5 Comparison of dentinal age estimates between the present study and Ross's (1984) study

PEM Number	Length (cm)	Sex	Ross's (1984) estimate (GLG's)	Present studies estimate (GLG's)
N0114	178	♂	1.5	2.5
N0228	206	♀	3	3.92
N0264	228	♀	12+	16 (20.17*)
N0289	244	♂	12+	15
N0439	234.3	♂	5.5	6

*Cemental GLG count

The difference between maximum recorded lengths and asymptotic lengths between males and females may suggest sexual dimorphism between the sexes. However, no significant differences in cranial size and shape were found between the sexes in the same population (Conry, 2012).

3.4.4 Weight and age

Growth rate

In both growth models, for males and females combined, mass increased rapidly in the first five years (von Bertalanffy growth function (VBGF)) and four years (Gompertz growth function (GGF)), thereafter the rate slows down and reaches a plateau. Kroese (1993) in an earlier study on the South African population predicted the same, and mass increase was most rapid up to five years of age. However, the growth rate constant (k) generated by VBGF was slower than in the present study (Kroese = 0.030; present study = 0.20). The growth rate constant predicted by the GGF (0.32) was closer to those obtained in the NE Atlantic and Mediterranean populations which were 0.390 and 0.257, respectively (Di-Meglio *et al*., 1996).

When males and females were analysed separately, the males had a lower growth rate constant (k) than the females in both models. These results are in agreement with the Mediterranean and the NE Atlantic populations where female growth rate constants were higher than the males (Di-Meglio *et al*., 1996). In both growth curves a plateau is not quite reached, the reason for this is being that there are only six individuals older than 15 years of age in the sample. Female growth rate eventually overtakes male growth rate at about four years of age (GGF) and five years of age (VBGF). In the Mediterranean population female growth rate also overtook the males, but at a larger age of six years, and the females reached a mean body mass slightly larger than the males (Di-Meglio *et al*., 1996). This is in agreement with the present study, where the females had a greater asymptotic weight.

Weight at birth

Weight at birth for males and females combined was estimated at 16.6kg by the VBGF and 21.4kg by the GGF. These masses are much higher than those predicted for the population a number of years earlier, which was predicted to be 0.6kg (Kroese, 1993). When males and females were analysed separately, weight at birth for males was estimated at 19.8kg (VBGF) and 23.2kg (GGF), and for females at 11.3kg (VBGF) and 16.6kg (GGF). These masses may be overestimated due to the lack of individuals younger than two years of age (n = 5 for males; n = 2 for females).

Maximum weight and age

In the present study, the maximum recorded mass for males and females was 157kg and 129kg, respectively. These values are in agreement with those previously reported in South Africa, which were 157kg and 130kg, respectively (Kroese, 1993). In the Mediterranean population and the NE Atlantic population the maximum mass was much smaller at about 97kg and 125kg, respectively (Di-Meglio *et al.*, 1996). These differences in maximum weight are most likely due to geographical differences in food availability and temperature which affect body size and growth (Di-Meglio *et al.*, 1996).

Asymptotic weight

When the sexes were separated, asymptotic weights were estimated to be 127.98kg (VBGF) and 118.41kg (GGF) for males, and 124.21kg (VBGF) and 121.07kg (GGF) for females. These values are much higher than those predicted for the NE Atlantic population, which were 104.2kg and 90.5kg for males and females, respectively (Di-Meglio *et al.*, 1996). The

Mediterranean population was much smaller, with asymptotic weights of 78.1kg and 78.9kg for males and females, respectively (Di-Meglio *et al*., 1996). When the sexes were combined, asymptotic weights were predicted to be 125.20kg (VBGF) and 119.97kg (GGF) in the present study. These predicted masses are much less than those estimated in an earlier study on the South African population where asymptotic weight was estimated to be 177.3kg (Kroese, 1993). The difference could be due to the presence of both east coast and west coast animals in Kroese's (1993) sample. The NE Atlantic and Mediterranean populations were estimated to have lower asymptotic weights of 100.3kg and 78.9kg, respectively. Again, these differences are likely due to geographic variations in food availability and temperature between the regions, which affect growth rates (Di-Meglio *et al*., 1996). The differences in asymptotic weight also suggest that *S. coeruleoalba* off the south east coast of South Africa have a larger overall body size in comparison to the NE Atlantic and Mediterranean populations. It appears that the Mediterranean Sea population has the smallest overall body size.

3.4.5 Comparison with other delphinids

In order to compare the data obtained from the growth curves for *S. coeruleoalba*, the parameters of the Gompertz and the von Bertalanffy models were compared for other delphinids in the published literature (Table 3.6 and Table 3.7). It is worth noting that the majority of these studies employed the Gompertz growth model.

Table 3.6 Growth parameter values from the von Bertalanffy growth model fitted to length-at-age and weight-at-age data for different delphinid species.

Species and Area	**Male**			**Female**			**References**
	L∞	**to**	**K**	**L∞**	**to**	**K**	
Striped dolphin *Stenella coeruleoalba* (NW Indian Ocean)	230.76	116.2	0.344	224.36	112.2	0.372	Present study
Striped dolphin *Stenella coeruleoalba* (NW Indian Ocean)	245.90		0.078	229.82	93.0	0.15	Kroese, 1993
Striped dolphin *Stenella coeruleoalba* (NW Pacific Ocean)	-	-	-	222.4	99.8	0.26	Kasuya, 1976
	W∞	**to**	**K**	**W∞**	**to**	**K**	
Striped dolphin Stenella coeruleoalba (NW Indian Ocean)	125.20	16.6	0.19	Males and females combined			Present study
Striped dolphin Stenella coeruleoalba (NW Indian Ocean)	177.67	5.5	0.03	Males and females combined			Kroese, 1993

Generally, as the asymptotic length (L∞/a) increases in both models, the growth rate constant (k/c) decreases. The von Bertalanffy parameters in the present study were very different to the previous study conducted by Kroese (1993) for the South African population. His asymptotic values were larger and his growth rate constants were smaller. This difference could be because Kroese (1993) included both west coast and east coast animals, which we now know are very different (Conry, 2012). The present values for the females were similar to those attained by Kasuya (1976) for female dolphins. The weight-at-age data in the present study is also very different to Kroese's (1993) data. His asymptotic weight is much higher and his growth constant smaller.

Table 3.7 Growth parameter values from the Gompertz growth model fitted to length-at-age and weight-at-age data for different delphinid species.

Species	**Male**			**Female**			**References**
	a	**b**	**c**	**a**	**b**	**c**	
Striped dolphin *Stenella coeruleoalba* (NW Indian Ocean)	229.87	119.1	0.408	223.61	113.8	0.442	Present study
Striped dolphin *Stenella coeruleoalba* (NE Atlantic Ocean)	216.07	-	0.51	200.10	-	0.64	Di-Meglio *et al.*, 1996
Striped dolphin *Stenella coeruleoalba* (Mediterranean Sea)	191.20	-	0.65	194.75	-	0.38	Di-Meglio *et al.*, 1996
Short-beaked common dolphin *Delphinus delphis* (Atlantic Ocean)	211.6	108.8	0.41	197.4	104.1	0.54	Murphy and Rogan, 2006
Striped dolphin *Stenella coeruleoalba* (NW Indian Ocean)	227.205	117.4	0.420	Combined males and females			Present study
Short-beaked common dolphin *Delphinus delphis* (S Atlantic Ocean)	215.9	111.7	0.62	Combined males and females			Siciliano *et al.*, 2007
Atlantic spotted dolphin *Stenella frontalis* (S Atlantic Ocean)	224.4	128.7	0.15	Combined males and females			Siciliano *et al.*, 2007
	W∞	**to**	**K**	**W∞**	**to**	**K**	
Striped dolphin *Stenella coeruleoalba* (NW Indian Ocean)	118.41	23.2	0.31	121.07	16.6	0.33	Present study
Striped dolphin *Stenella coeruleoalba* (NE Atlantic Ocean)	104.24	-	0.407	90.49	-	0.422	Di-Meglio *et al.*, 1996
Striped dolphin *Stenella coeruleoalba* (Mediterranean Sea)	78.05	-	0.252	78.95	-	0.267	Di-Meglio *et al.*, 1996

The Gompertz parameters in the present study were different to the results obtained by Di-Meglio *et al*. (1996), who studied the striped dolphin along the French coast, in the NE Atlantic Ocean and Mediterranean Sea. The asymptotic lengths were much smaller compared to the present study, which would be due to geographical differences between populations. However, the growth rate in the present study was similar to those obtained for the short-beaked common dolphin (*D. delphis*) in the Atlantic Ocean, although the dolphins have smaller asymptotic lengths (Murphy and Rogan, 2006). Data obtained for the common and the Atlantic spotted dolphins (*S. frontalis*) in the South Atlantic Ocean were different (Siciliano *et al*., 2007). The asymptotic lengths were slightly smaller compared to the present result.

Asymptotic weight in the present study was larger than those obtained for striped dolphins in the Atlantic and Mediterranean Sea (Di-Meglio *et al*., 1996). However, the growth rates were similar between the present population and the Atlantic and Mediterranean populations.

In conclusion, age and growth varies geographically between *S. coeruleoalba* populations, which suggest that environmental conditions such as food availability and temperature have a large influence on age and growth within the species. Additionally, age and growth varies substantially between species in the same genus as well as similar sized delphinids, such as the short-beaked common dolphin, *D. delphis*. Age and growth will further be discussed in relation to other life history parameters in the final chapter.

Chapter 4

Reproductive biology and seasonality of *Stenella coeruleoalba*

4.1 Introduction

Reproductive parameters are important in the conservation and management of a species. Ideally, animals should be observed in their natural environment, but unfortunately this method of study is time consuming, expensive and not always possible. Consequently, to investigate reproductive parameters, other methods such as natural history assessment have to be conducted. Both stranded (Mendolia, 1989; Kroese, 1993; Calzada *et al.*, 1996) and by-caught (Kasuya, 1972; Kasuya, 1976; Miyazaki, 1977a; Miyazaki, 1984; Kasuya, 1985, Danil and Chivers, 2007) delphinids in South Africa and abroad have been used to study reproductive parameters. Reproductive parameters can be used to estimate the level of impact from fisheries (directed and incidental catches) and habitat degradation (Perrin and Henderson, 1984; Read and Gaskin, 1990). Parameters such as age at attainment of sexual maturity, calving interval and annual pregnancy rate have been used to determine the effect of over-exploitation on the Japanese striped dolphin (*Stenella coeruleoalba*) and spotted dolphin (*Stenella attenuata*) populations (Kasuya, 1985).

4.1.1 Spermatogenesis

Spermatogenesis involves the complex process of cell differentiation (Akin *et al.*, 1993). Hohn *et al*. (1985) defined three stages of sexual maturity, namely, immature, pubertal and mature. In the immature stage, seminiferous tubules are small and circular with only spermatogonia present (first stage of spermatogenesis) (Akin *et al*., 1993). Through mitosis, the spermatogonia eventually divide to form diploid primary spermatocytes (Akin *et al*., 1993). When this occurs, the animal has entered the pubertal stage, which is characterised by larger slightly elongated seminiferous tubules with both spermatogonia and spermatocytes present (Akin *et al*., 1993). The diploid primary spermatocytes further divide through meiosis to form haploid secondary spermatocytes, which almost immediately enter its second meiotic division to form spermatids (Akin *et al*., 1993). Finally, the spermatids undergo spermiogenesis and are transformed into mature spermatozoa (Akin *et al.,* 1993). When this occurs, the animal is characterized as mature, where seminiferous tubules are numerous, large and elongated with all stages of spermatogenesis present (Akin *et al.,* 1993). Within the seminiferous tubule, spermatogonia are located against the wall of the tubule, while the spermatozoa are located within the lumen. All other developmental stages are located between the two (Akin *et al.*, 1993).

4.1.2 Ovarian cycle

The ovarian cycle begins with the development of a follicle in the ovary. The follicle either develops and releases an oocyte or undergoes degeneration (atresia) (Akin *et al*., 1993). Follicle maturation includes the growth of the oocyte, an increase in the number of granulosa cells and the division of the cell wall into two layers (Akin *et al*., 1993). This gradual transition ultimately gives rise to the Graafian follicle (Akin *et al*., 1993). The oocyte then undergoes meiosis and forms what is called the secondary oocyte which is released at ovulation (Akin *et al.,* 1993). After ovulation, the follicle is transformed into a *corpus luteum,* which functions as an endocrine gland (Perrin and Donovan, 1984). If pregnancy occurs the *corpus luteum* persists as a secretory organ called a *corpus luteum* of pregnancy, which secrets the hormones necessary for the pregnancy (Perrin and Donovan, 1984). After pregnancy, the *corpus luteum* of pregnancy regresses and becomes a *corpus albicans* (Perrin and Donovan, 1984). However, if pregnancy does not occur, the *corpus luteum* is called a *corpus luteum* of ovulation and regression follows immediately to form a *corpus albicans* (Perrin and Donovan, 1984; Akin *et al*., 1993). Structurally, a *corpus luteum* appears as a protruding circular structure on the surface of the ovary and is composed of yellow coloured ganulosa cells arranged in convoluted layers (Akin *et al.*, 1993). Some *corpora lutea* contain a gelatinous central cavity while others are filled with connective tissue (Akin *et al.*, 1993).

Not all ovarian follicles produce an oocyte and undergo ovulation (Perrin and Donovan, 1984). In some cases, the Graafian follicle undergoes follicular atresia to form a *corpus atreticum* (Akin *et al*., 1993). Follicular atresia gives rise to secondary interstitial tissue or to an accessory *corpus luteum* which is hormonally active and forms an important part of the ovarian cycle (Perrin and Donovan, 1984).

4.1.3 Attainment of sexual maturity

It is important to have knowledge of the age and length at sexual maturity of odontocetes to understand the dynamics of a population (Kroese, 1993). Age and length at attainment sexual maturity (ASM) varies between species and between populations of the same species (Bryden and Harrison, 1986). There are a number of factors that influence age and length at ASM, including, environmental conditions, exploitation, diet and body mass (Bryden and Harrison, 1986; Wootton, 1987). Estimates of age and size at ASM and information on the reproductive cycle are important for understanding the reproductive strategy and ecology of a species. This information can be used in comparative biological studies (both inter- and intra-specific) and in the management of populations that are subject to mortality by man (Hohn *et al*., 1985). Therefore, this type of information can play an important role in stock assessment or in determining the degree of exploitation on a population (Perrin and Henderson, 1984; Read and Gaskin, 1990). In Japanese waters, the striped dolphin (*S. coeruleoalba*) is caught annually in drive fisheries. As a result, there has been a gradual decrease in the age and length at attainment of sexual maturity as well as the calving interval for the population, due to the high levels of exploitation (Kasuya, 1985). Therefore, having long term information about age and length at ASM is vital for determining if the population density of a species is changing, either due to over-exploitation or food availability. Additionally, information on length at sexual maturity for a species is especially useful in the field or for those animals that do not have an age estimate available (Perrin and Reilly, 1984).

Males

Sexual maturity in males is determined by the presence of spermatozoa or spermatids in the centre of the seminiferous tubule, the diameter of seminiferous tubules, testis weight and the presence of spermatozoa in the epididymis (Perrin and Reilly, 1984). The assumption made when using the presence of spermatozoa in the epididymis and seminiferous tubule is that sperm is produced consistently and constantly (Perrin and Reilly, 1984). This may not be true as it has been shown that male harbour porpoises (*Phocoena phocoena*) can enter a resting stage, during which the testes decrease in size and spermatozoa gradually disappear from the seminiferous tubules and epididymis (Neimanis *et al*., 2000).

A number of studies have been conducted on the reproductive biology of *Stenella* species. In studies on male spotted dolphins (*S. attenuata*) off the Pacific coast of Japan, age at sexual maturity was found to be 10.3 (Kasuya *et al.*, 1974) and 11.8 years of age (Kasuya, 1976).

Higher estimates were obtained for male spotted dolphins (*S. attenuata*) in the eastern tropical Pacific, were sexual maturity was reached between 13 and 16 years of age (Hohn *et al*., 1985). In a study on the striped dolphin (*S. coeruleoalba*) population off the south-east coast of South Africa (Kroese 1993), the age at which males reached sexual maturity was estimated to be between 10 and 12 years old. This estimate is higher than that obtained for the striped dolphin population off the Pacific coast of Japan, where males were estimated to reach sexual maturity at about 9 years of age (Kasuya, 1972; Kasuya, 1976; Miazaki, 1977b).

Male spotted dolphins (*S. attenuata*) in the eastern tropical Pacific, were found to reach sexual maturity at a mean body length of 186.4cm (Hohn *et al*., 1985), while, male spinner dolphins (*Stenella longirostris*) in the eastern tropical Pacific were found to attain maturity at an even shorter length of between 174cm and 176cm (Perrin *et al*., 1977). The mean length at which testes were found to be mature in striped dolphins (*S. coeruleoalba*) off the south-east coast of southern Africa was higher than the spotted and spinner dolphins, at 220cm (Kroese, 1993).

Females

Females are considered sexually mature when they have ovulated at least once, which is determined by the presence of at least one *corpus luteum* or *corpus albicans* in the ovaries (Perrin and Reilly, 1984). It is assumed that the scars of ovulation remain visible throughout the life of the animal and that the presence of these scars is a result of ovulation (Perrin and Reilly, 1984). Hirose *et al*. (1970) confirmed that *corpora albicantia* persist thought out the life of *S. coeruleoalba*.

Female spotted dolphins (*S. attenuata*) in the eastern tropical Pacific were estimated to reach sexual maturity at an average age of 11.4 years (Myrick et al., 1986). However, female spotted dolphins (*S. attenuata*) off the Pacific coast of Japan, were found to reach sexual maturity earlier at about 8.2 (Kasuya, *et al*., 1974) and 9 years of age (Kasuya, 1976). Similarity, female striped dolphin (*S. coeruleoalba*) populations off South Africa and off the Pacific coast of Japan, were found to reach maturity at about 8.9 (Kroese, 1993) and 9 years of age (Kasuya, 1972; Kasuya, 1976; Miyazaki, 1977a), respectively.

The length at ASM for female striped dolphins (*S. coeruleoalba*) along the south-east coast of southern Africa was estimated to be between 200cm and 240cm (Kroese, 1993). This large range is not very accurate, and it was concluded from this study that length was not a good predictor of sexual maturity (Kroese, 1993).

4.1.4 Seasonality

Many mammals show a seasonal variation in their reproduction, where mating or birth takes place at certain times of the year (Bronson, 1989). Whether a mammal reproduces seasonally or continuously is largely dependent on the environment (Bronson, 1989). Ultimate factors are those that are important in the long term and these include food availability, rainfall, temperature and competition between species (Bronson, 1989). The timing of reproduction is determined by environmental factors and food availability (Bronson, 1989). Some mammals have a highly specific diet and as a result tend to be more seasonal than those mammals that have a more general diet (Bronson, 1989). Mammals with highly specialised diets will suffer from seasonal changes in food availability; therefore they will only have enough energy for a reproductive event when food availability is plentiful. In general, breeding is often linked to annual migration patterns, for example, the long-beaked common dolphin (*Delphinus capensis*) off South Africa, inhabits the coastal waters of the Eastern Cape during summer and migrates to KwaZulu-Natal during winter in response to the sardine run (Ross, 1984; Reddy, 1996). Reddy (1996) found that these dolphins demonstrate seasonal reproduction. It was suggested that births in summer are timed so females have access to squid in the Eastern Cape and in winter calves have access to an abundance of fish during the sardine run in Natal (Reddy, 1996).

Based on dental layers, Kasuya (1972) reported two breeding seasons for the striped dolphin (*S. coeruleoalba*) population off the Pacific coast of Japan; these were in November and December and another in May and June. Later, three breeding seasons were reported for the same population, one from February to May, another from July to September and the last one in December (Miyazaki, 1977a). This study involved detailed examinations of the testes, ovaries and dental layers (Miyazaki, 1977a). A study conducted on male and female striped dolphins (*S. coeruleoalba*) off the south-east coast of South Africa had insufficient data (n= 7 males; n= 15 females) to determine whether breeding was seasonal or aseasonal (Reddy, 1996).

4.1.5 Aim of the present chapter

In the present study, the age and length at which sexual maturity is attained will be assessed for male and female *S. coeruleoalba* using macroscopic and histological examination of the testes and ovaries, respectively. Additionally, reproductive seasonality will be determined. A number of female reproductive parameters will be calculated, including ovulation rate, pregnancy rate and the components that make up the calving interval (gestation period, lactation period and resting period).

4.2 Materials and methods

4.2.1 Sample

Reproductive organs were available from 48 stranded *S. ceoruleoalba* specimens. Of the 48 reproductive organs available, 21 were from males and 27 from females. The size-frequency of the specimens from which the tissue were obtained is illustrated in Chapter 2 (Figure 2.6). The monthly sample sizes of both male and female *S. coeruleoalba* and the presence of foetuses collected over a period of 37 years (1975 – 2012) is presented in Table 4.1.

Table 4.1 Monthly sample sizes for male (n=21), females (n=27) and foetuses (n=11) of *S. coeruleoalba*.

Month of the year	J	F	M	A	M	J	J	A	S	O	N	D
Number of males	2	3	0	2	3	1	2	2	1	1	1	2
Number of females	1	1	5	1	1	4	2	1	3	1	3	4
Foetuses	0	1	2	`1	1	1	1	0	1	1	0	2

4.2.2 Male reproductive activity

Histological examination

A histological examination was undertaken on the 21 testes available to determine their sexual status. Only a few testis weights and measurements were available in the museum records, therefore before histological preparation, the length of each testis was recorded. On collection the Port Elizabeth museum staff fixed the testes in 10% formalin and then transferred them into 70% ethanol for storage in the museum. In some cases only a section of the testes was preserved to ensure sufficient penetration of formalin in the larger gonads. However, this was not true for all large gonads, as some were preserved whole. For this study, a 1cm^3 section was taken from the middle of every available preserved testis for histological examination. The tissue blocks were dehydrated in a series of alcohols (30% to 100%), immersed in xylene, and finally transferred into molten paraffin wax (Sigma - Paraplast plus) over night to ensure proper infiltration. The blocks were embedded in paraffin wax to be cut into thin sections (5-7µm) using a Leica microtome. The sections were mounted on slides and stained with haematoxylin and eosin. Slides were examined under an Olympus BX50 compound microscope at 200x and 400x magnification to determine maturity.

Attainment of sexual maturity (ASM)

The testes were classed into three stages of maturity - immature, pubertal (early spermatogenesis) and mature (late spermatogenesis) (Hohn *et al*., 1985). Immaturity was characterised by small seminiferous tubules that were densely packed with interstitial tissue (Hohn *et al*., 1985). The tubules contained no lumen and only Sertoli cells and spermatogonia were present (Hohn *et al*., 1985). For pubertal animals, seminiferous tubule diameter was relatively small and they contained spermatogonia, spermatocytes and sometimes spermatids, but no spermatozoa (Hohn *et al*., 1985). Mature animals had enlarged seminiferous tubules with a large lumen and little interstitial tissue surrounding them. The tubules contained all the developmental stages of spermatogenesis: spermatogonia, spermatocytes, spermatids and spermatozoa (Hohn *et al*., 1985).

Based on histological examination, tissue preservation was poor, particularly in the larger testes. The poor condition of the tissue made it difficult to determine whether the animal was immature or pubertal (early spermatogenesis). Only about 50% of the samples were preserved adequately enough to determine the three stages of spermatogenesis. As a consequence, to take a conservative approach, individuals were classified as either mature (in late spermatogenesis) or immature (which included immature and pubertal animals) based on the presence or absence of spermatids and spermatozoa, respectively.

Mean seminiferous tubule diameter

The diameters of 20 seminiferous tubules were measured in each testis using photographs taken with an Olympus BX50 microscope fitted with a camera at a magnification of X10. The computer program, Olympus Analysis docu, was then employed to measure the diameter of the seminiferous tubules. Due to the advanced state of decomposition, tubule diameter could not be determined for three specimens.

4.2.3 Female reproductive activity

Macroscopic examination of the ovaries

Ovaries were available for macroscopic examination from 27 females. On collection by the museum staff, the ovaries and in some cases the whole uterine tract were fixed in 10% formalin and then transferred into 70% ethanol for storage. No ovary weights were available on the data sheets, therefore each ovary was weighed to the nearest gram. The ovaries were sectioned by hand at intervals of about 1mm in thickness and examined macroscopically for the presence of a *corpus luteum* (CL), *corpus albicans* (CA) or *corpus atreticum*. For each individual, the number of CA's and CL's in the ovaries was used to provide an index of the number of ovulations.

The number of corpora per ovary, as well as the weight of each ovary was recorded, and, where possible, the left and right ovary was identified. A paired t-test was then conducted on the number of corpora counted and the total weight of the ovary to see if there was a significant difference at the 5% level between the left and right ovaries.

The reproductive condition of the females (i.e. lactating/pregnant) was established at the time of the dissection by the collection staff, and, where possible, foetus length, weight and sex were recorded. For this study, the females where classified in to four reproductive states – immature, resting mature (not pregnant or lactating), mature and pregnant, and mature and lactating. This was done by using the metadata available in the museum records and the reproductive status of the ovaries determined during this study.

Attainment of sexual maturity (ASM)

Females were considered sexually mature if the ovaries contained at least one *corpus luteum* or *corpus albicans*. The number of corpora per ovary as well as their dimensions (length, width and height) (measured using a vernier callipers) were recorded.

Ivashin (1984) identifided *corpora atretica* in fin whales (*Balaenoptera physalus*), gray whales (*Eschrichtius robustus*) and sperm whales (*Physeter macrocephalus*). They were identified as small, yellow/orange filled cavities (Ivashin, 1984). Since *corpora atretica* result from a non-ovulatory event (Perrin and Donovan, 1984), they were not included in the corpora count above. However, it is important to note the presence of them and their appearance in different species, as they play an important role in the ovarian cycle by producing hormones (Perrin and Donovan, 1984).

Reproductive parameters

The various reproductive parameters, such as pregnancy rate, calving interval, resting period and ovulation rate were calculated for female *S. coeruleoalba* following Perrin and Reilly (1984). The annual pregnancy rate (APR) was determined by dividing the proportion of pregnant females in the sample by the length of gestation, expressed in years (Perrin and Reilly, 1984). The gestation period is the least variable component of the reproductive cycle within a species (Perrin and Reilly, 1984), therefore it was assumed to be 1 year (12 months) in the present study according to Kasuya (1972) and Miyazaki (1977b) who studied the Japanese striped dolphin population. Therefore, the calculation of APR was as follows:

$$APR = P/T_G$$

Where:

P = proportion of sample pregnant

T_G = Length of gestation

The calving interval (CI) is an estimate of the time between parturition in mature females. This interval was determined by calculating the inverse of the APR estimate (Perrin and Reilly, 1984).

$$CI = 1/APR$$

The lactation period (T_L) could not be calculated in the present study due to the lack of available data.

The resting period (T_R) was calculated as the proportion of resting females divided by the proportion of pregnant females in the sample (Perrin and Reilly, 1984). Resting females included those that were not pregnant or lactating. The resting period is calculated as follows:

$$T_R = T_G * R/P$$

Where:

T_R = resting period

T_G = length of gestation

R = proportion of sample resting

P= proportion of sample pregnant

The estimation of the ovulation rate was based on the assumption that CA's persist indefinitely (Perrin and Reilly, 1984). The ovulation rate was determined by fitting a linear regression to the ovarian corpora count against age. The slope of the regression line is equivalent to the rate at which corpora are formed (Perrin and Reilly, 1984).

4.3 Results

4.3.1 Male reproductive activity

Histological examination

The weights of the testes in *S. coeruleoalba* ranged from 8g to 178g on the right side and from 8g to 200g on the left side. A dependent paired t-test showed no significant difference in weight between left and right testes ($n=8$; $p = 0.492$). It was thus concluded that either testis could be examined to determine the sexual maturity of a specimen. Of the 21 males assessed for reproductive activity, 10 were categorised as immature, 10 as mature and one as inactive.

Immature testes were characterized by small, tightly packed seminiferous tubules with no lumen. The seminiferous epithelium was comprised of one layer of Sertoli cells and spermatogonia (Figure 4.1). Immature seminiferous tubule diameters ranged from 23.76µm to 69.61µm with an average diameter of 43.30µm (±15.4µm) (Table 4.2.).

Mature testes were characterized by enlarged seminiferous tubules with an open lumen and little interstitial tissue. The seminiferous epithelium comprised of three or more cell layers of spermatogonia, spermatocytes, spermatids and sometimes spermatozoa (Figure 4.2.). Mature seminiferous tubule diameters ranged from 43.54 to 110.58µm, with an average diameter of 74.66µm (±23.25µm) (Table 4.2.).

One individual was previously assessed by Reddy (1996) (N0289). This individual was reassessed and in agreement with Reddy (1996) was classed as inactive. Figure 4.3 illustrates how the tissue appeared. This individual measured 244 cm in length, had an estimated age of 15 years and weighed 131kg. The mean testis length was 10.5cm and the mean seminiferous tubule diameter was 54.54µm.

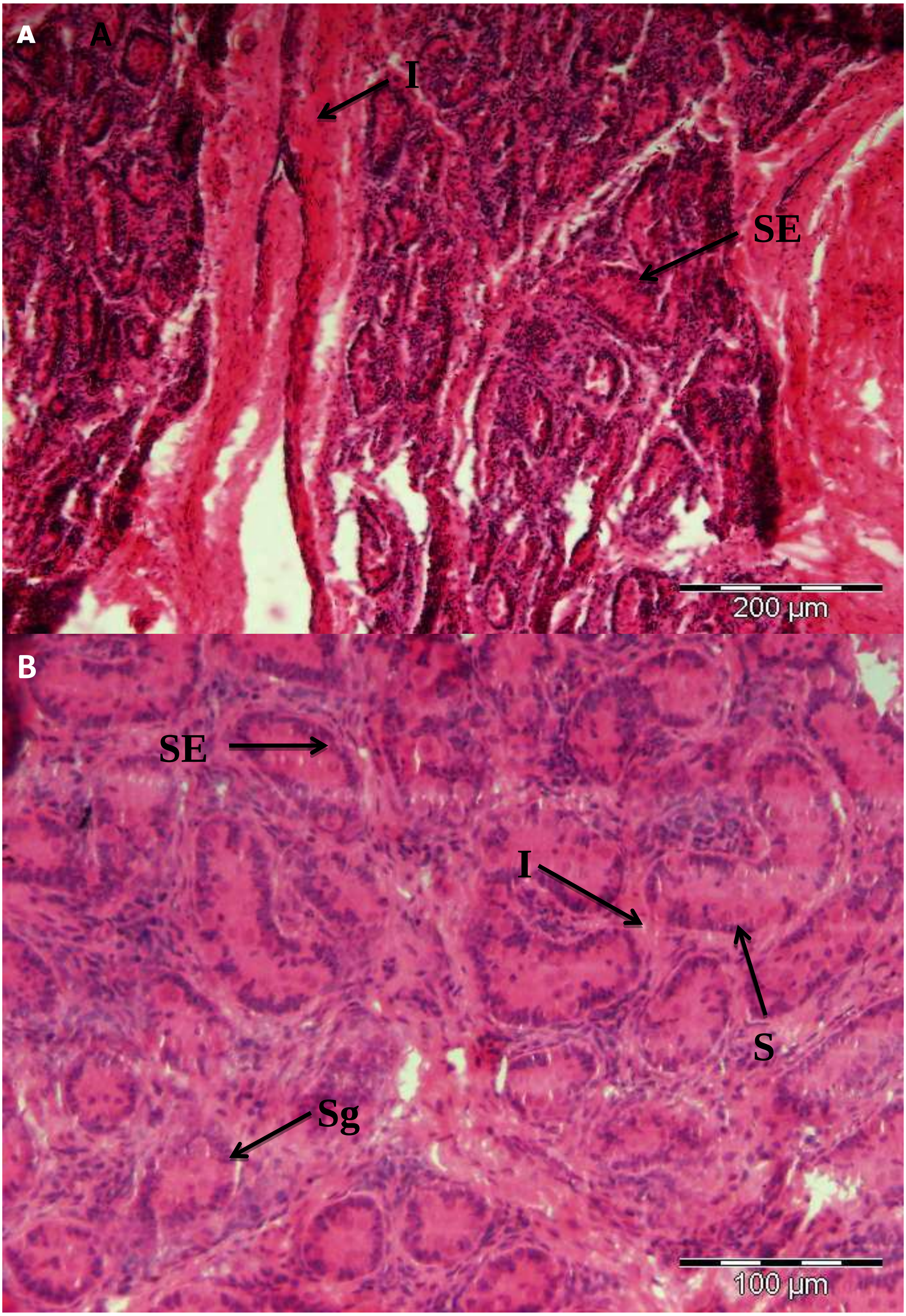

Figure 4.1 Photographic images of histological slides from immature testes (A – N1471 and B - N2838). I – interstitial tissue; SE – seminiferous epithelium; Sg – spermatogonia; S – Sertoli cell.

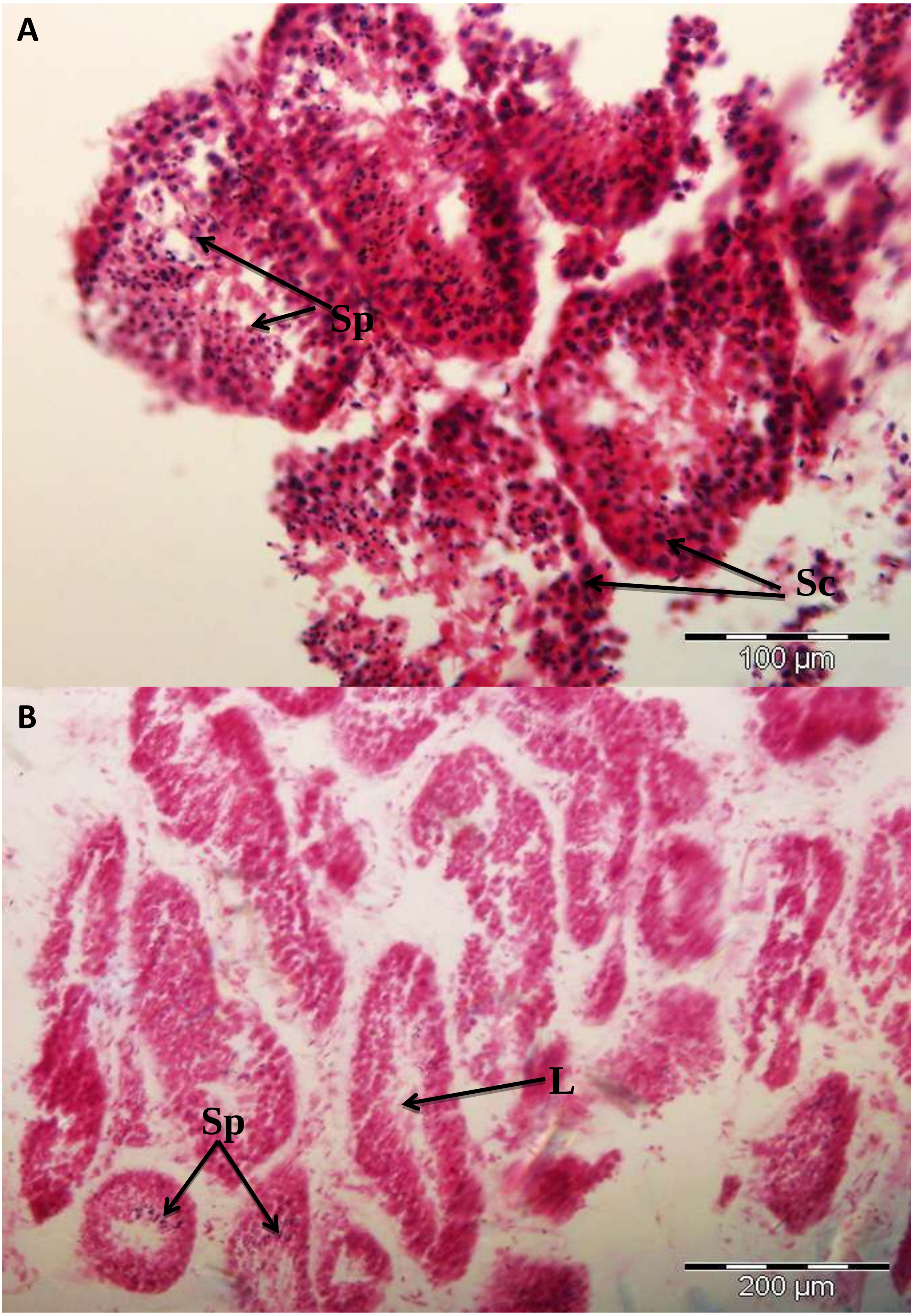

Figure 4.2 Photographic images of histological slides from mature testes (A - N3566 and B - N1119). Sp – spermatids, Sc – spermatocytes, L – lumen.

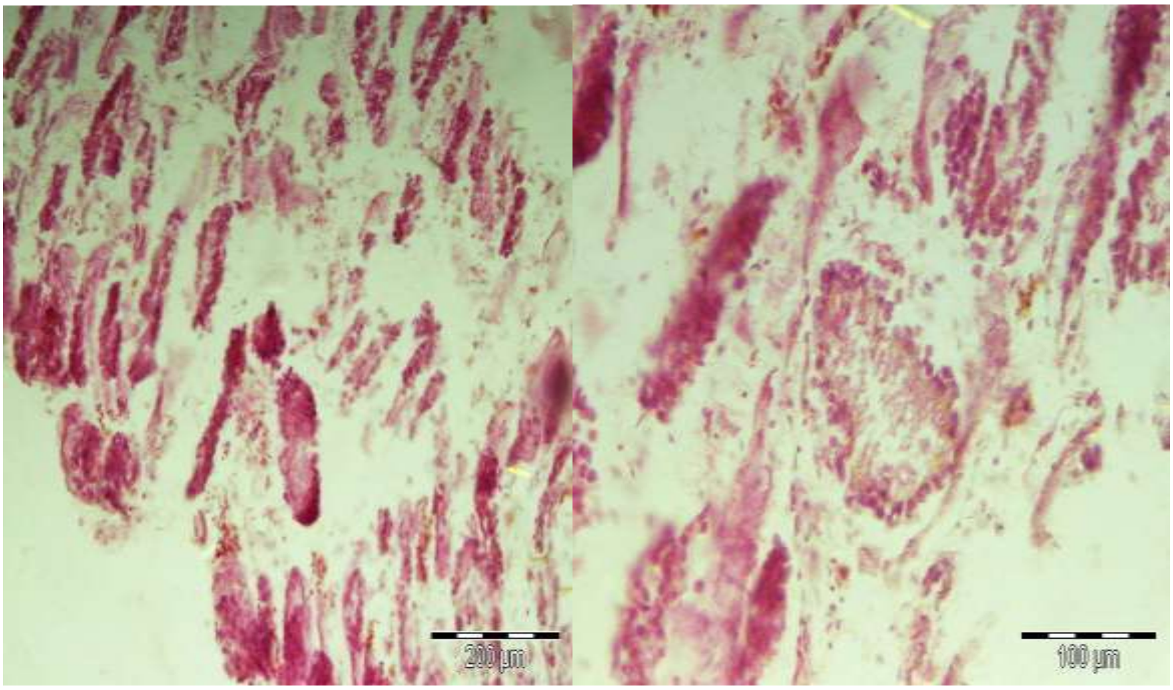

Figure 4.3 Photographic images of the histological slides from an inactive individual (N0289).

Although preservation of the tissue was generally poor, for three specimens (N0781, N1782 and N2462) early spermatogenesis was identifiable (data not shown). Figure 4.4 shows those individuals that were in early spermatogenesis. The seminiferous tubules are still small in diameter but the seminiferous epithelium has thickened and contains spermatogonia as well as spermatocytes, but no spermatozoa. These three individuals ranged from 207 to 224cm in body length, 91 to 95 kg in body weight and from three to 6.25 years of age. Their mean seminiferous tubule diameters ranged from 43.13 to 69.61 µm and mean testis length was available for two of the individuals, both measuring 6.7cm in length.

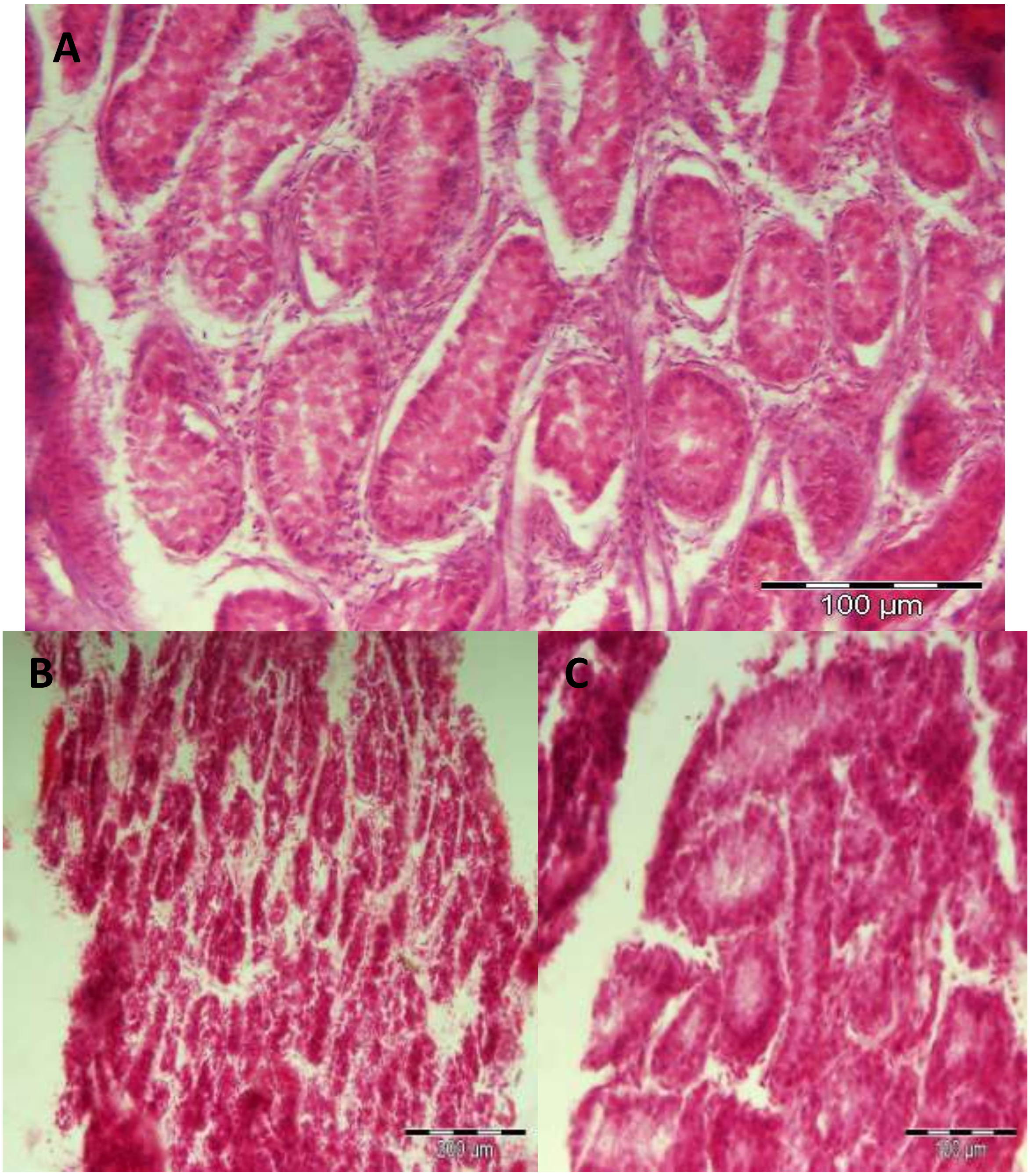

Figure 4.4 Photographic images of the histological slides from pubertal individuals (individuals in early spermatogenesis) (A - N1782, B - N0781, C - N2462).

Attainment of sexual maturity (ASM)

In general, immature individuals had small, thin, elongated testes, while mature individuals had large, thick, elongated testes. The combined testis weight of only one immature individual was available, which was 16g. The length of immature testes ranged from 2.10 to 8.40cm with an average length of 6.53cm (±2.12cm). The combined weight of mature testes ranged from 41.40 to 376g, with an average weight of 144.03g (±122.99g). Similarly, the average length of a mature testis was 12.16cm (±1.41cm; range 10 to 14.4cm in length) (Table 4.2.).

Table 4.2 Measurements of testis weight (g), testis length (cm) and seminiferous tubule diameter (µm) for immature and mature male *S. coeruleoalba*.

Maturity stage	Mean (±SD)	Range	Sample size
Single testis weight (g)			
Immature	8.00 (0.00)	8.00	1
Mature	72.02 (58.90)	19.80 – 200.00	6
Combined testis weight (g)			
Immature	16 (0.00)	16.00	1
Mature	144.03 (122.99)	41.40 – 376.00	6
Mean testis length (cm)			
Immature	6.53 (2.12)	2.10 – 8.40	8
Mature	12.16 (1.41)	10.00 – 14.4	7
Seminiferous tubule diameter (µm)			
Immature	41.70 (15.89)	23.76 – 69.61	7
Mature	74.66 (23.25)	43.54 – 110.58	9

Maturity occurred at a mean testis weight of 72.02g (n=6) and a mean testis length of 12.16cm (n=7) (Table 4.2), and corresponded to a total body length of between 220cm and 230cm (Figure 4.5a). In general, as age and body length increased, testis length gradually increased as well (Figure 4.5). At a testis length greater than 10cm, all individuals were mature, with the exception of the inactive individual (N0289) (Figure 4.5). Only a few individuals had testis weights available, therefore the sample sizes were small for combined testis weights plotted against total body length and estimated age. However, above the combined testis weight of 41g all individuals were mature, with the exception the inactive individual (N0289) with a combined testis weight of 50g (Figure 4.6).

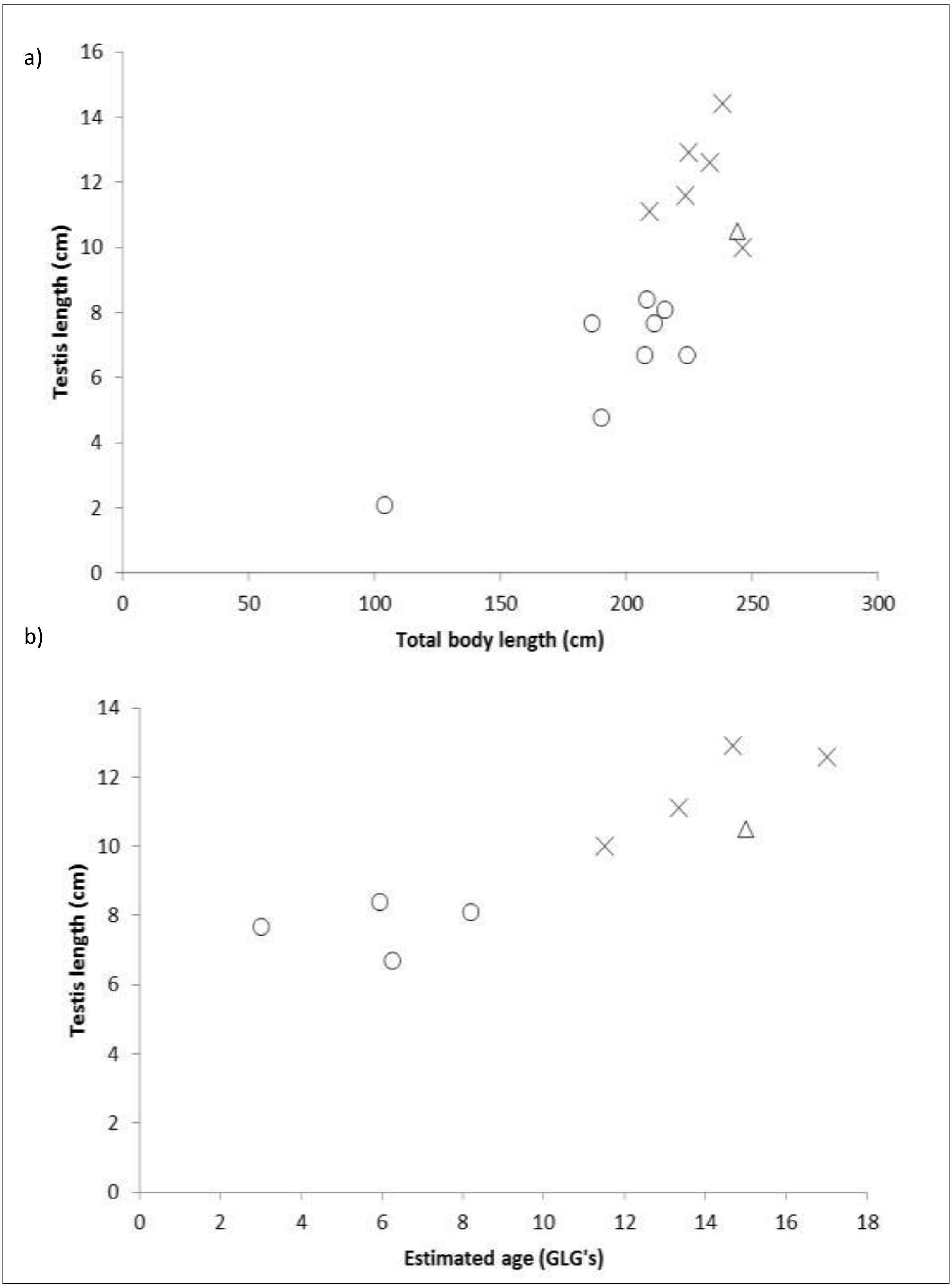

Figure 4.5 Testis length versus a) total body length (n=16) and b) estimated age (GLG's) (n=12) of immature and mature individuals. The crosses represent sexually mature individuals and circles immature individuals. The triangle represents the inactive individual (N0289).

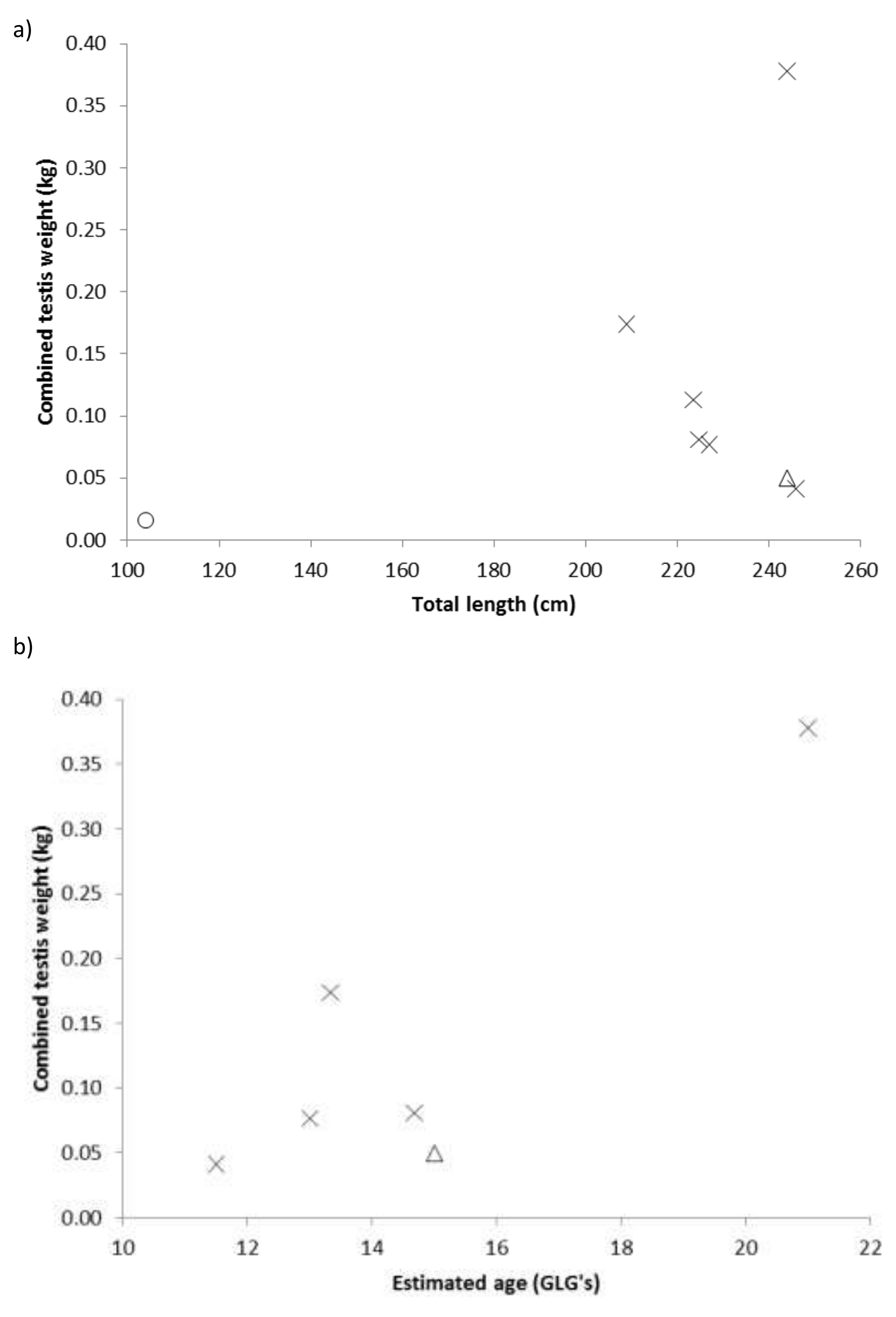

Figure 4.6 Combined testis weight versus a) total body length (n=7) and b) estimated age (GLG's) (n=6) of immature and mature individuals. The crosses represent sexually mature individuals, circles sexually immature individuals and the triangle an inactive individual (N0289).

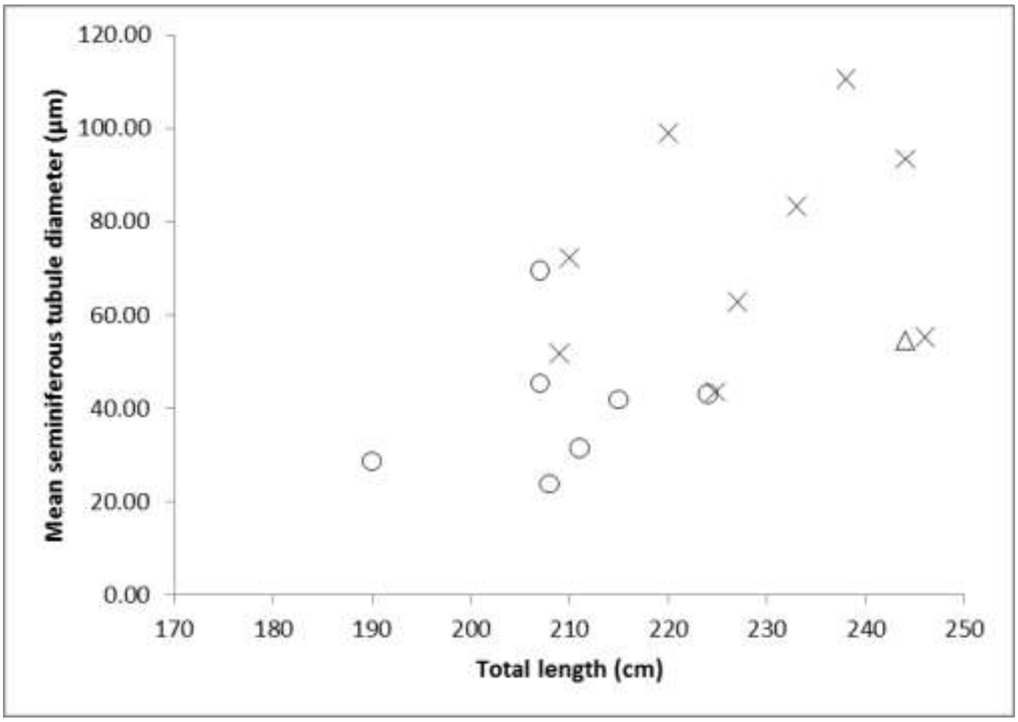

Figure 4.7 Mean seminiferous tubule diameters for male (n= 17) *S. coeruleoalba* of different maturity stages in relation to total body length (cm). Crosses represent sexually mature individuals, circles sexually immature individuals and the triangle a sexually inactive individual.

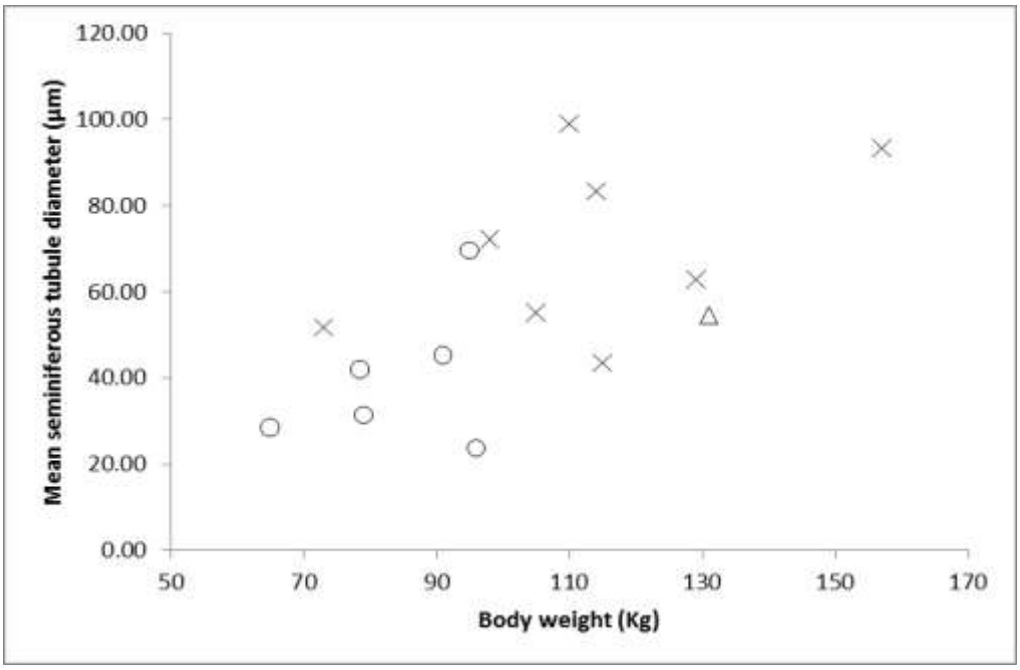

Figure 4.8 Mean seminiferous tubule diameters for male (n= 15) *S. coeruleoalba* of different maturity stages in relation to total body weight (kg). Crosses represent sexually mature individuals, circles sexually immature individuals and the triangle a sexually inactive individual.

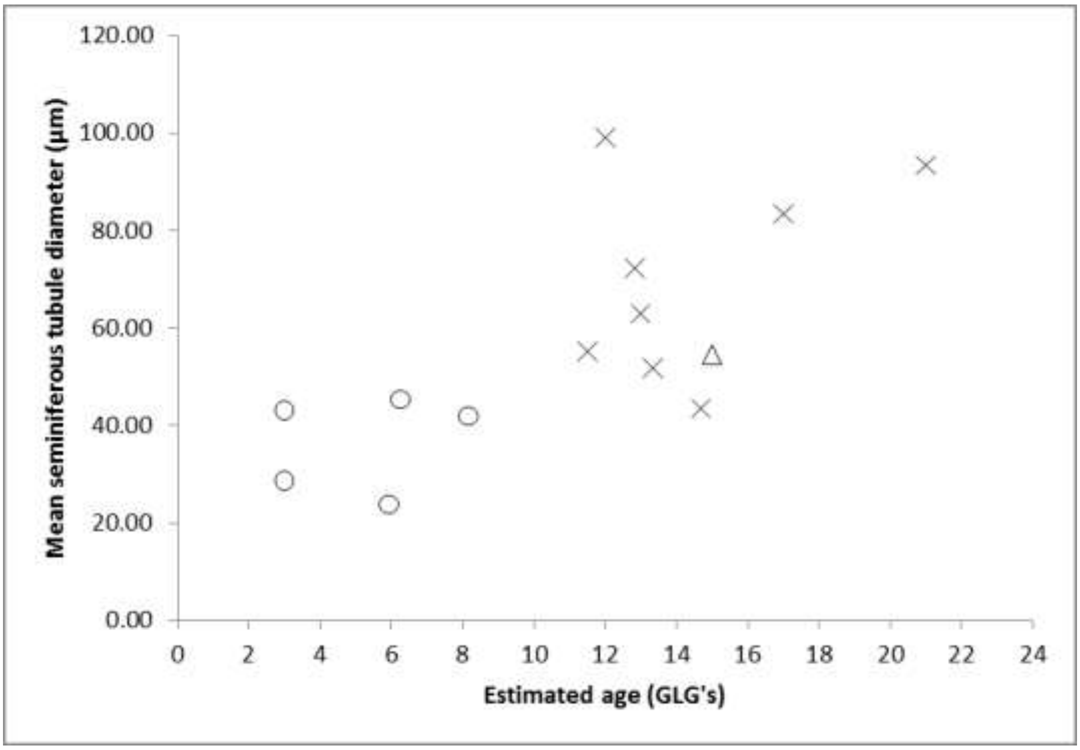

Figure 4.9 Mean seminiferous tubule diameters for male (n=14) *S. coeruleoalba* of different maturity stages in relation to estimated age (GLG's). Crosses represent sexually mature individuals, circles sexually immature individuals and the triangle a sexually inactive individual.

Mean seminiferous tubule diameter was plotted against total body length (Figure 4.7), body weight (Figure 4.8) and estimated age (Figure 4.9). Mature individuals all had a seminiferous tubule diameter greater than 72µm (Figures 4.7; 4.8 and 4.9). Similarly, individuals were mature at a body length greater than 224.8cm, a body weight over 98kg and an age of 10 years or more. A noticeable exception was the inactive individual (N0289), which had a body length of 244cm, a body weight of 131kg and an age of 15 years (Figures 4.7, 4.8 and 4.9).

The sample size was too small to estimate the age at 50% sexual maturity using statistical methods. However, a range of age and length at sexual maturity could be determined. This was done by taking the range between the oldest/longest immature individual and the youngest/shortest mature individual. Using this approach, the ASM occurs between 8 and 11 years of age and at a body length of between 209cm and 224cm (Table 4.3).

A mean age at attainment sexual maturity could also be determined, by using the von Bertalanffy growth curve in Chapter 3. The mean age was determined by reading it off the growth curve using the average body length (227.54cm) and weight (112.63kg) at ASM calculated in the current chapter (Table 4.3). These data correspond to the ages between 10 and 11 years, indicating that the average age at ASM for male *S. coeruleoalba* is between 10 and 11 years of age using this method.

Table 4.3 Summary of the size and estimated ages for different maturity stages for male *S. coeruleoalba*.

Maturity stage	**Mean**	**Range**	**Sample size**
Total Body Length (cm)			
Immature	185.10 (±45.43)	99.00 – 224.00	10
Mature	227.54 (±12.83)	209.00 -246.00	10
Total body weight (kg)			
Immature	76.59 (±47.96)	8.60 – 167.00	9
Mature	112.63 (±24.18)	73.00 – 157.00	8
Estimated age (GLG's)			
Immature	-	0 – 8.17	7
Mature	-	11.5 - 21	8

Seasonality

Seasonal variation of the mean seminiferous tubule diameter, combined testis weight and testis length by month are shown in Figures 4.10 to 4.12. Unfortunately, no individuals were available for the month of March. Mature individuals were found throughout the year with three exceptions: April, September and October (Figures 4.10, 4.11 and 4.12). By looking at the mature individuals, there could be a fluctuation in tubule diameter (Figure 4.10) and testis weight (Figure 4.11) throughout the year, with a peak in May and December.

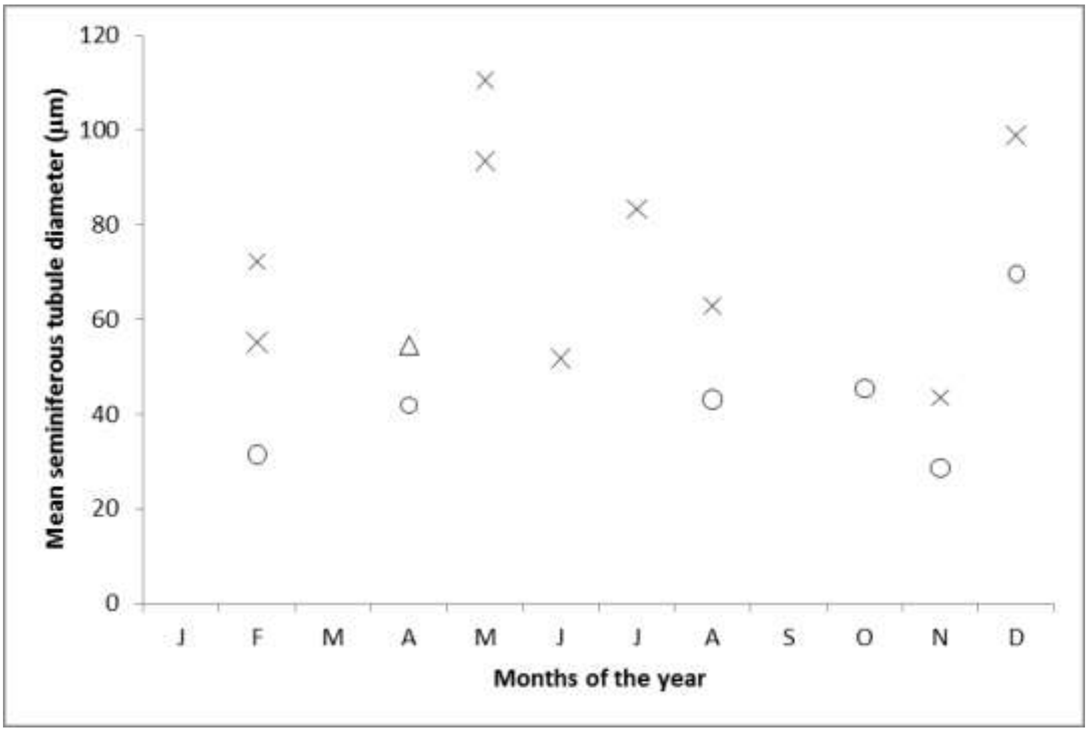

Figure 4.10 Monthly plot of mean seminiferous tubule diameter for mature and immature male *S. coeruleoalba*. Crosses represent sexually mature individuals, circles sexually immature individuals and the triangle the inactive individual (N0289).

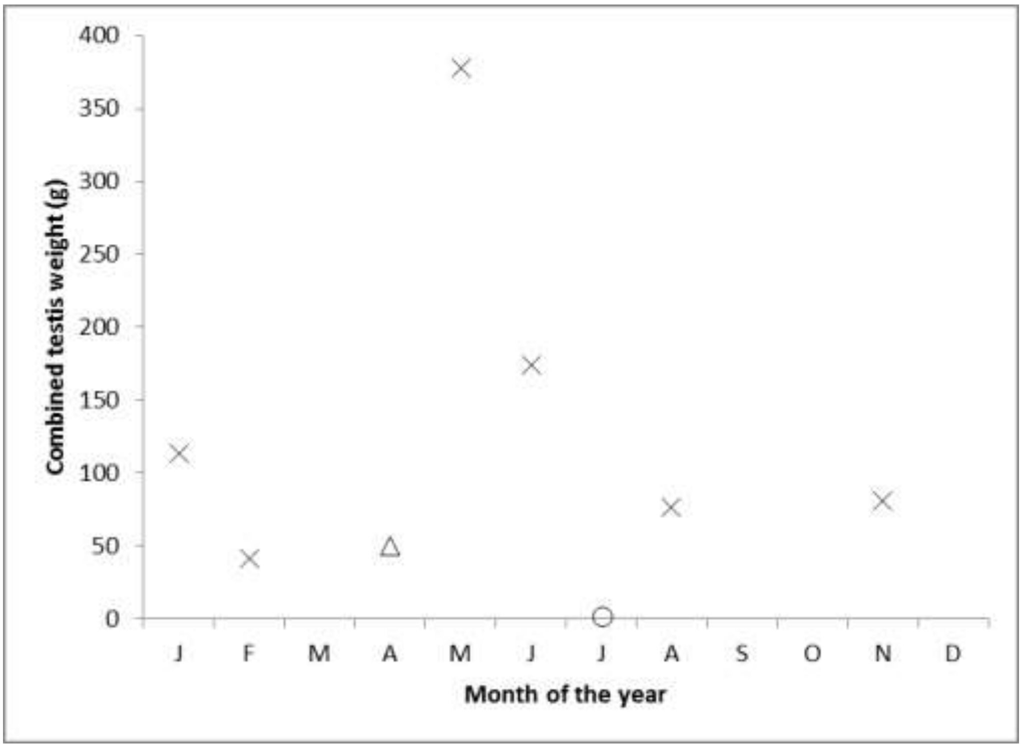

Figure 4.11 Monthly plot of combined testis weight for mature and immature male *S. coeruleoalba*. Crosses represent sexually mature individuals, circles sexually immature individuals and the triangle the inactive individual (N0289).

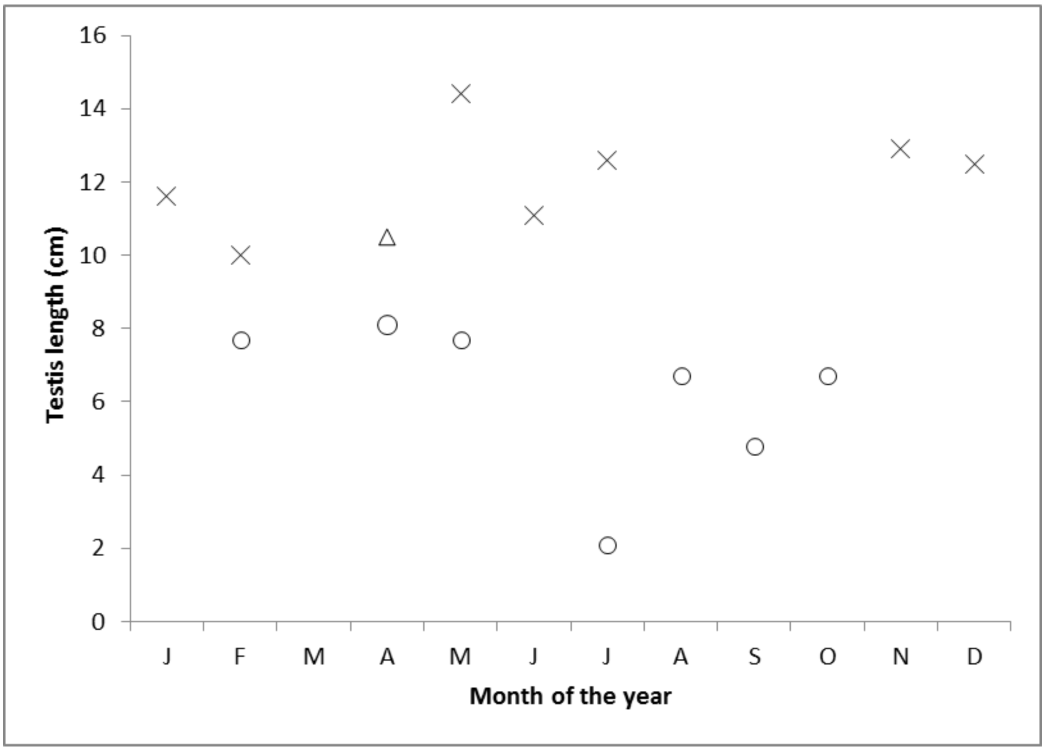

Figure 4.12 Monthly plot of testis length for mature and immature male *S. coeruleoalba*. Crosses represent sexually mature individuals, circles sexually immature individuals and the triangle the inactive individual (N0289).

4.3.2 Female reproductive activity

Macroscopic examination of the ovaries

Due to the absence of metadata, unfortunately no distinction could be made between the left and right ovaries for the majority of the individuals. In mature animals, one ovary was consistently larger in size and weight compared to the other ovary. In those instances where metadata were available, the left ovary was consistently larger in size and weight than the right ovary. This size difference is indicated in Figure 4.13c. In immature animals, there appeared to be no size difference in the two ovaries.

To ascertain if ovulations occurred equally in both ovaries a paired t-test was conducted on mature individuals where the left and right ovaries were distinguishable (n=9). Results of the analysis indicated that ovulation occurred significantly more often in the left ovary than the right ovary (test statistic = 3.95, p = 0.002) (Table 4.4) Furthermore, CA's were only found in the right ovary in females older than 10 years of age and greater than 220cm in TBL.

A distinct difference in the weight of the two ovaries was also observed, with the left ovary being heavier than the right ovary. This was significant at a 5% level (alpha (α) was set at 5%) (p=0.017) (Table 4.4). A notable exception was specimen N2184, in which the left and right ovary weighed the same (Table 4.4).

Table 4.4 Accumulation of corpora and ovary weight of the left and right ovary of female *S. coeruleoalba.*

PEM number	**Total body length (cm)**	**Number of corpora in the left ovary**	**Number of corpora in the right ovary**	**Weight of the left ovary (kg)**	**Weight of the right ovary (kg)**
N0011	231	9	0	16	4
N0184	226	2	0	4	3
N0264	228	2	0	>1	>1
N0448	228	5	0	6	3
N0708	220	4	0	7	3
N1993	240	1	0	3	2
N2136	228	4	0	5	1
N2184	231.5	3	3	5	5
N4650	219.8	5	0	4	1
n=9	-	*Total=35*	*Total = 3*	*Total =50*	*Total =22*
Mean (±SD)	-	3.89 (±2.37)	0.33 (±1.00)	6.25 (±4.13)	2.75 (±1.39)
P value	-	0.002		0.017	

The external appearance of CL’s and CA’s in the ovary is presented in Figure 4.13. CL’s presented themselves as a protrusion from the surface of the ovaries. The protrusions varied considerably in size, in some cases occupying most of the ovary (Figure 4.13a), whereas in other individuals they presented themselves as small protrusions on the edge of the ovary (Figure 4.13b). In those instances where, left and right ovaries were identified, the CL was always found in the left ovary. CA’s presented themselves as either a small protrusion (Figure 4.13a,b) or as a scar on the surface of the ovary (Figure 4.13c).

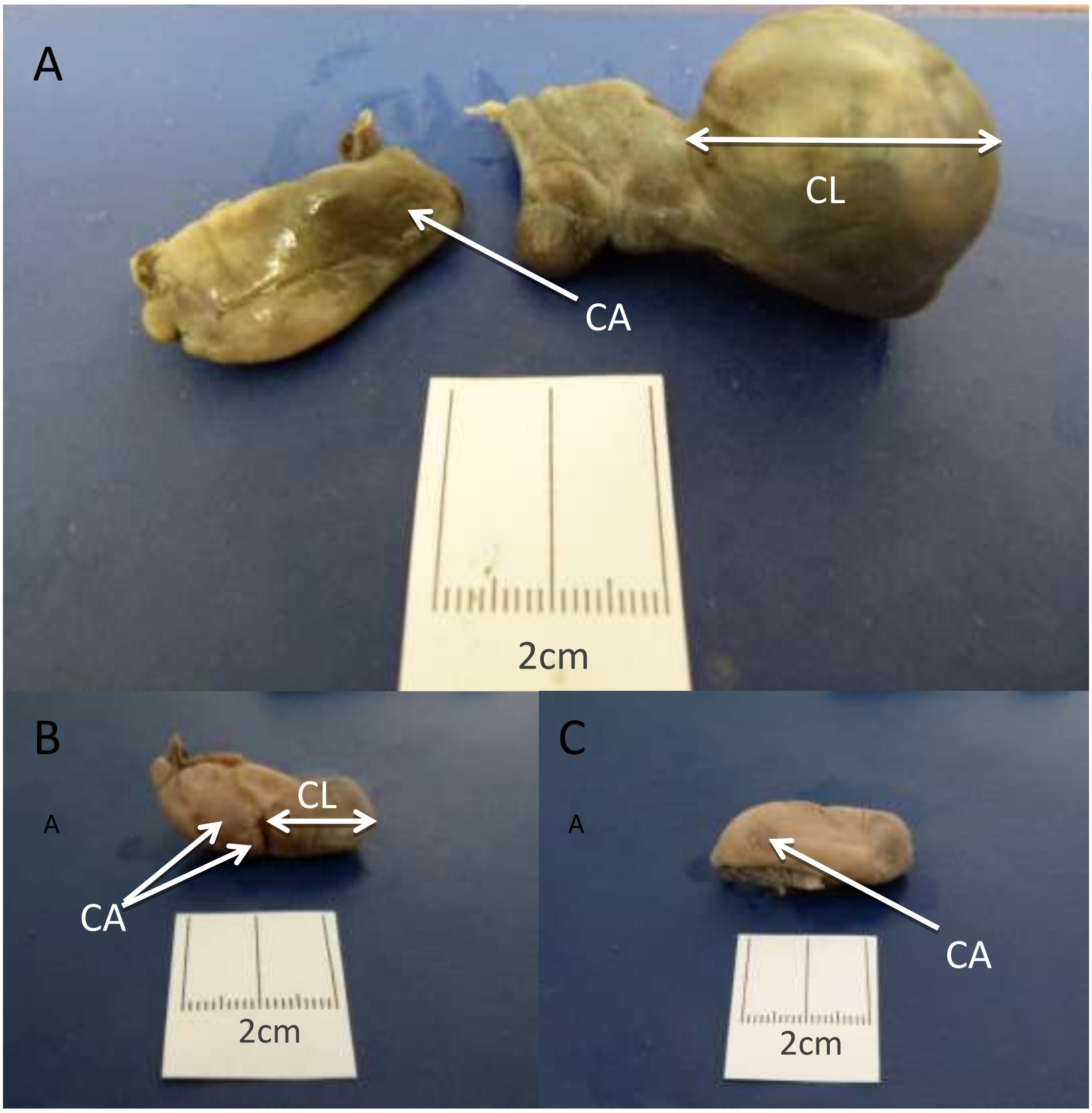

Figure 4.13 Mature ovaries of *S. coeruleoalba*, indicating the outer appearance of a *corpus luteum*(CL) and *corpus albicans* (CA). A – the outer appearance of a far regressed CA, B – an ovary with a small CL, C – indicates the size difference between the two ovaries and shows a large CL.

Figure 4.14 illustrates the internal appearance of CL's and CA's in *S. coeruleoalba*. Figure 4.14a shows two types of CL's, one with no lumen (left) and one with a gelatinous lumen (right). No relationship was found between the type of CL present and the progress of the pregnancy. Figure 4.14b shows two CA's, one (left) is a newly formed CA, while the other one (right) is a regressed CA.

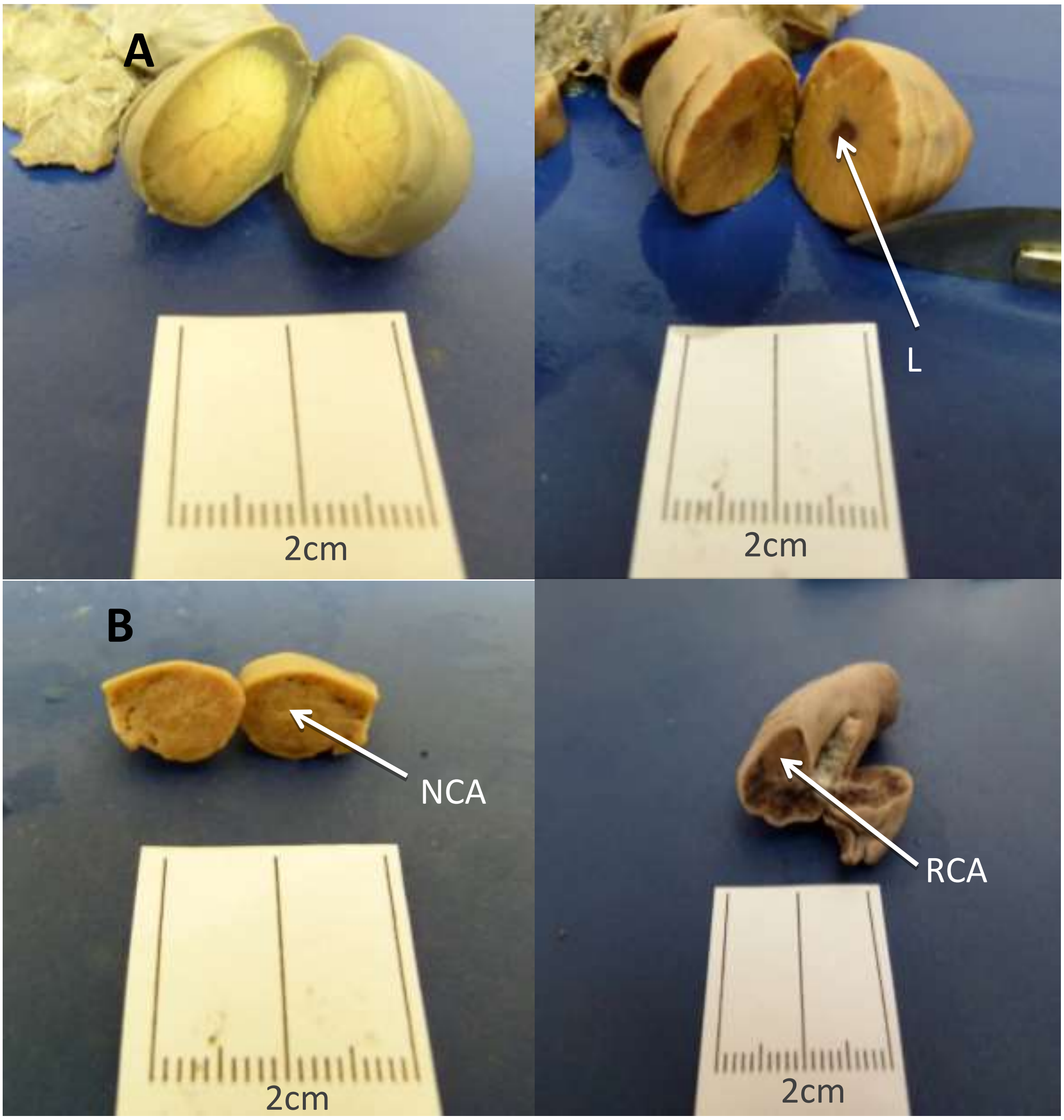

Figure 4.14 Mature ovaries of *S. coeruleoalba*, illustrating the inner appearance of a *corpus luteum* and *corpus albicans*. A – the two types of CL's found (L – lumen), B – a newly formed *corpus albicans* (NCA) (left) and a regressed *corpus albicans* (RCA).

Five specimens had a *corpus atreticum* present in one of their ovaries. These structures were very small (measuring less than 3mm) and appered to be yellow/orange in colour. Figure 4.15 illustrates how the *corpora atretica* appeared in the species.

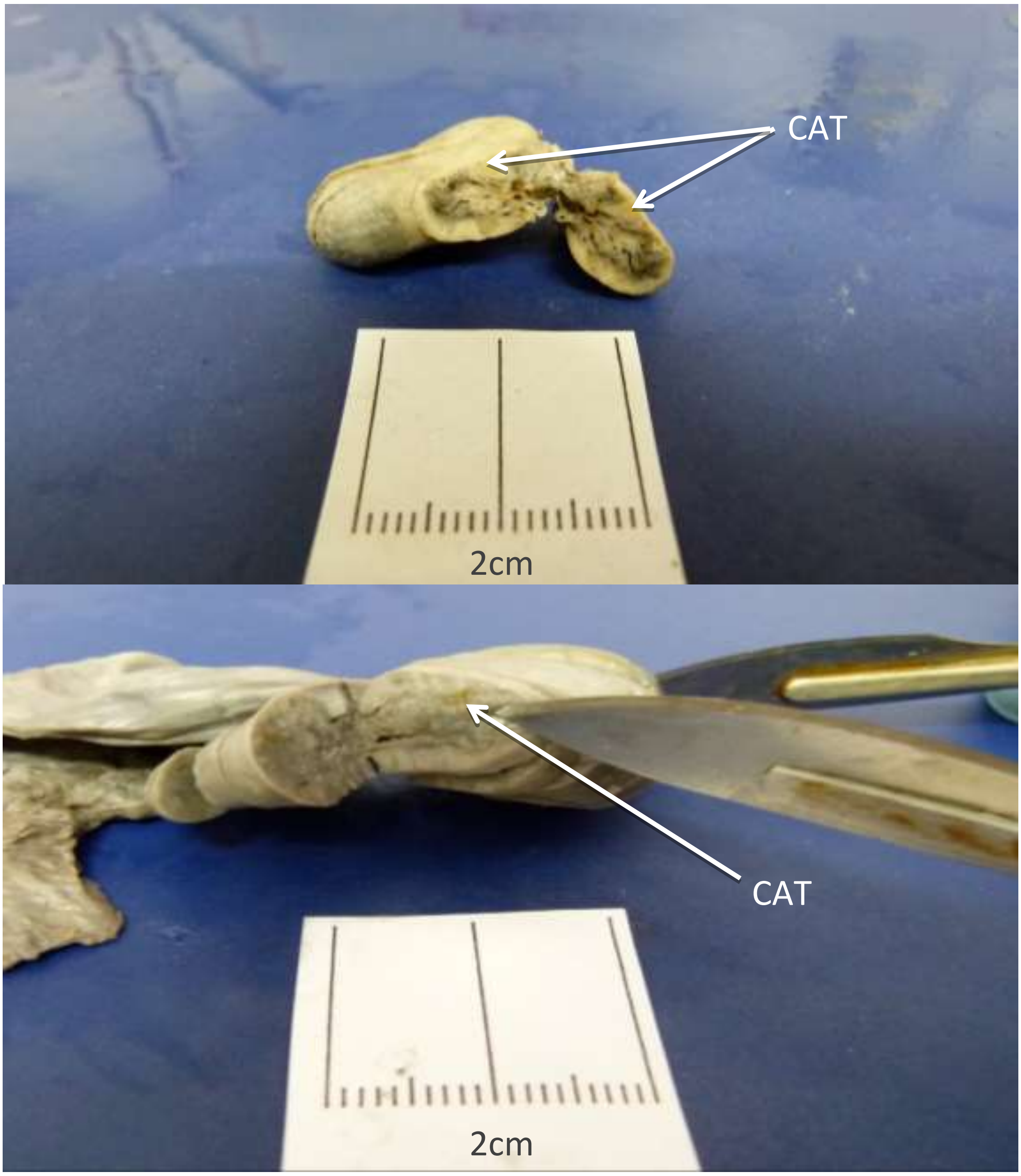

Figure 4.15 Mature ovaries of *S. coeruleoalba*, illustrating the appearance of a *corpus ateticum* (CAT).

Attainment of sexual maturity (ASM)

Ovarian corpora

On the basis of the presence of corpora in the ovaries, six out of the 27 females assessed were immature, seven were mature and pregnant, while a single individual was mature and lactating. The remaining 13 females were mature and resting (neither pregnant nor lactating).

There were five individuals that had only one corpus present in their ovaries, and these individuals ranged from 209.8cm to 240cm in length (Figure 4.16). Two of the five individuals were pregnant based on data from the datasheets, and the corpus present was a *corpus luteum*, suggesting that individuals can fall pregnant on their first ovulation. The maximum number of corpora recorded was nine and this was recorded in a pregnant female measuring 231cm in length (Figure 4.16).

A marked increase in the number of corpora was observed in the ovaries at about 216 cm in body length and at an estimated age of 8 years (Figures 4.16 and 4.17). All individuals above this body length and estimated age were mature (Figures 4.16 and 4.17). The smallest mature female was pregnant and measured 209.8cm in length with an estimated age of 10.83 years (Figures 4.16 and 4.17), while the largest immature female measured 215.5cm in length and was estimated to be 5 years of age (Figures 4.16 and 4.17). Of those individuals for which an age estimate was available, the youngest mature individual was 6.5 years old and pregnant, while the oldest immature individual was 7.5 years old (Figure 4.17).

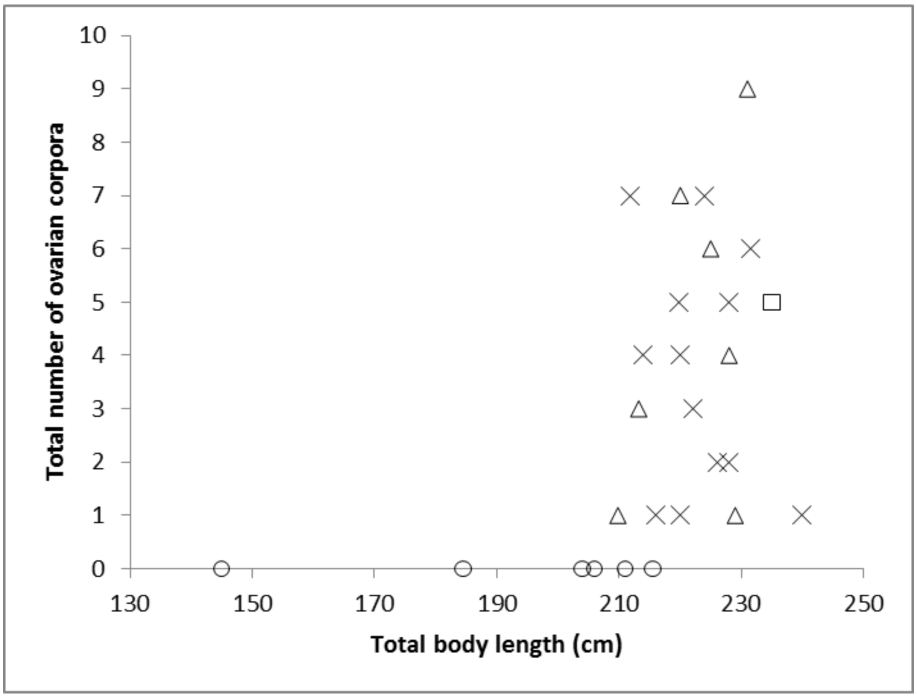

Figure 4.16 Attainment of sexual maturity in relation to total body length (n=27). Circles represent immature individuals, crosses mature resting individuals, triangles mature pregnant individuals and squares mature lactating individuals.

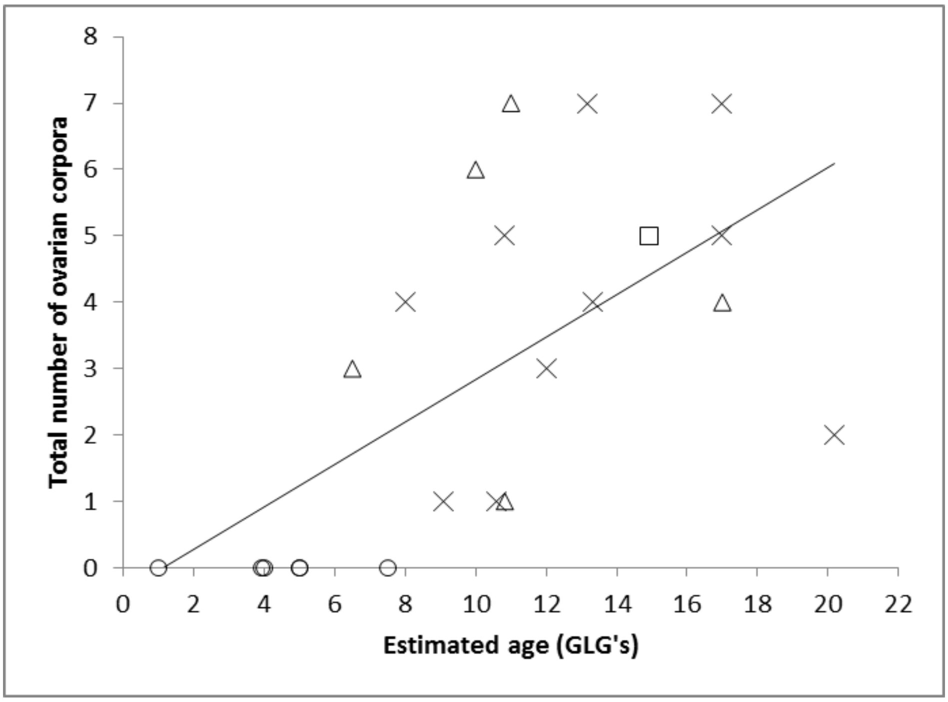

Figure 4.17 Attainment of sexual maturity in relation to estimated age (GLG’s) (n=22). The solid line represents the regression (least squares method) between the number of corpora and the age ($y = 0.3196x - 0.3556$) ($r^2 = 0.3875$). Circles represent immature individuals, crosses mature resting individuals, triangles mature pregnant individuals and squares mature lactating individuals.

There were too few ovaries available to estimate the age at 50% sexual maturity using statistical methods. However, a range of age and length at sexual maturity could be determined using the largest/oldest immature individual and the smallest/youngest mature individual. Table 4.5 summarises the size and estimated ages of mature and immature individuals. For female *S. coeruleoalba*, maturity occurs between a total body length of 209.00cm and 215.50cm, an age of between 6.5 and 7.5 years, and a body weight of between 93kg and 103kg (Table 4.5). Mature individuals had a mean body length of 223.43cm (±7.92), a mean age of 12.59 years (±3.76) and a mean body weight of 123.33kg (±13.00) (Table 4.5). Immature individuals were found to have a mean total body length of 194.33cm (±26.40cm), a mean age of 4.40 years (±2.11) and a mean body weight of 70.80kg (±25.64) (Table 4.5).

Table 4.5 Summary of the size and estimated ages for different maturity stages of female *S. coeruleoalba*.

Maturity stage	**Mean**	**Range**	**Sample size**
Total Body Length (cm)			
Immature	194.33 (±26.40)	145.00 - 215.50	6
Mature	223.43 (±7.92)	209.00 – 240.00	21
Total body weight (kg)			
Immature	70.80 (±25.64)	33.00 – 93.00	5
Mature	123.33 (±13.00)	103.00 – 147.00	14
Estimated age (GLG's)			
Immature	4.40 (±2.11)	1.00-7.50	6
Mature	12.59 (±3.76)	6.50 - 20.17	16

Combined ovary weight

Of the 27 females, two had a combined ovary weight of less than 1g and were omitted. The first one had an estimated age of 1 year, measured 145cm in length and weighed 33kg (N3272), while the other one had an estimated age of 20.17 years, measured 228cm in length and weighed 126.55kg (N0264).

All individuals with a combined ovary weight of 5g (Figures 4.18, 4.19 and 4.20), a body length above 216cm (Figure 4.18), older than 8 years (Figure 4.19) and a body weight above 93kgs (Figure 4.20) were sexually mature. The smallest mature individual was a pregnant female that had a combined ovary weight of 8g, while the largest immature individual had a combined ovary weight of 5g (Figure 4.18). This suggests that maturity occurs between a combined ovary weight of 5 and 8g. The highest combined ovary weight of 20g was attained by a pregnant female measuring 231cm in length.

Of those that had an age estimate available, the youngest pregnant female was 6.5 years old with a combined ovary weight of 11g (Figure 4.19). The oldest immature individual was 7.5 years old and had a combined ovary weight of 3g (Figure 4.19). A lactating female at the age of 14.92 years had the highest combined ovary weight of 13g.

A concurrent increase in combined ovary weight was observed after a body weight of 103kg (Figure 4.21). The largest mature individual weighed 93kg and had a combined ovary weight of 3g, while the smallest mature individual weighed 103kg and had a combined ovary weight of 5g (Figure 4.21). The heaviest individual was pregnant, weighed 147kg and possessed the heaviest ovaries, weighing 20g in total (Figure 4.21).

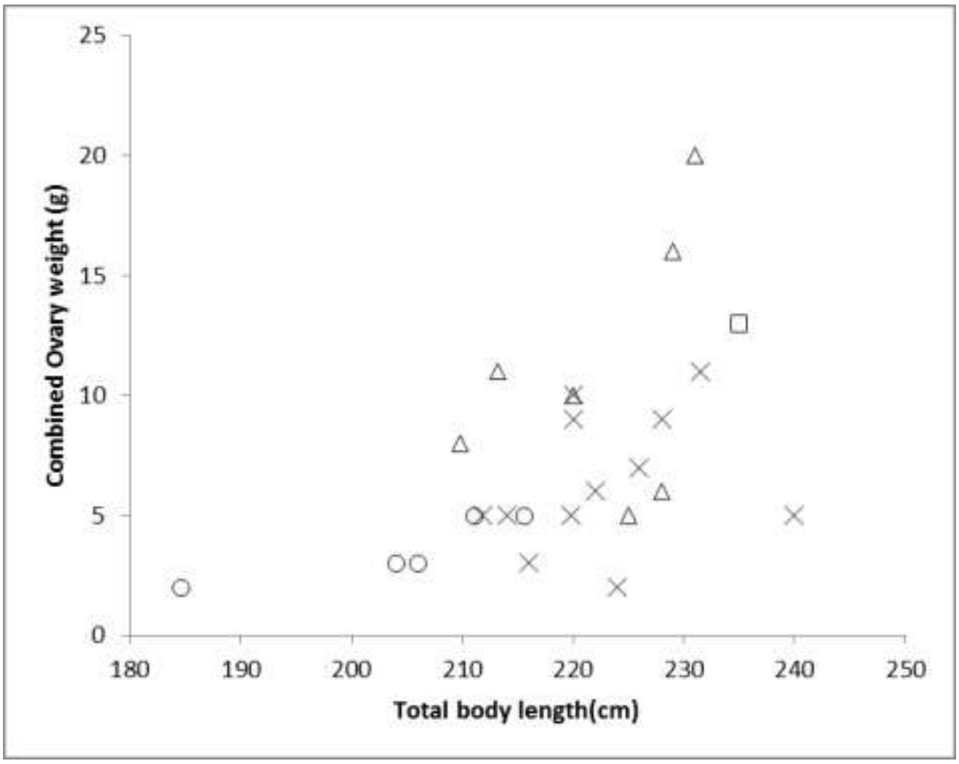

Figure 4.18 Increase in combined ovary weight with body length in female *S. coeruleoalba* (n=25). Circles represent immature individuals, crosses mature, resting individuals, triangles mature, pregnant individuals and squares mature, lactating individuals.

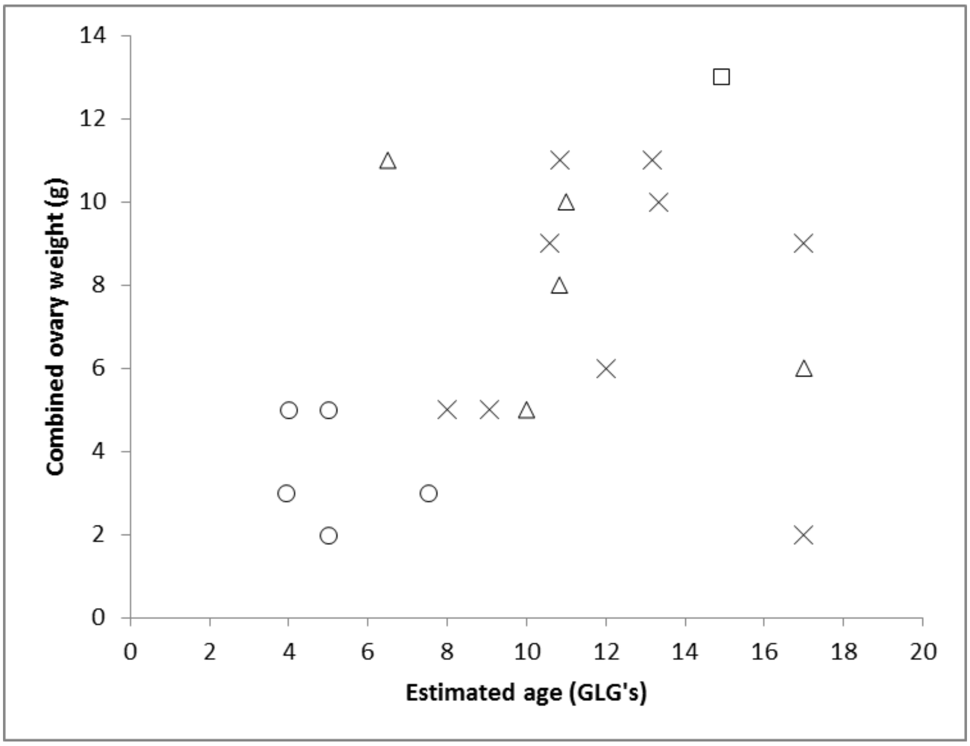

Figure 4.19 Increase in combined ovary weight with estimated age (GLG's) in female *S. coeruleoalba* (n=20). Circles represent immature individuals, crosses mature, resting individuals, triangles mature, pregnant individuals and squares mature, lactating individuals.

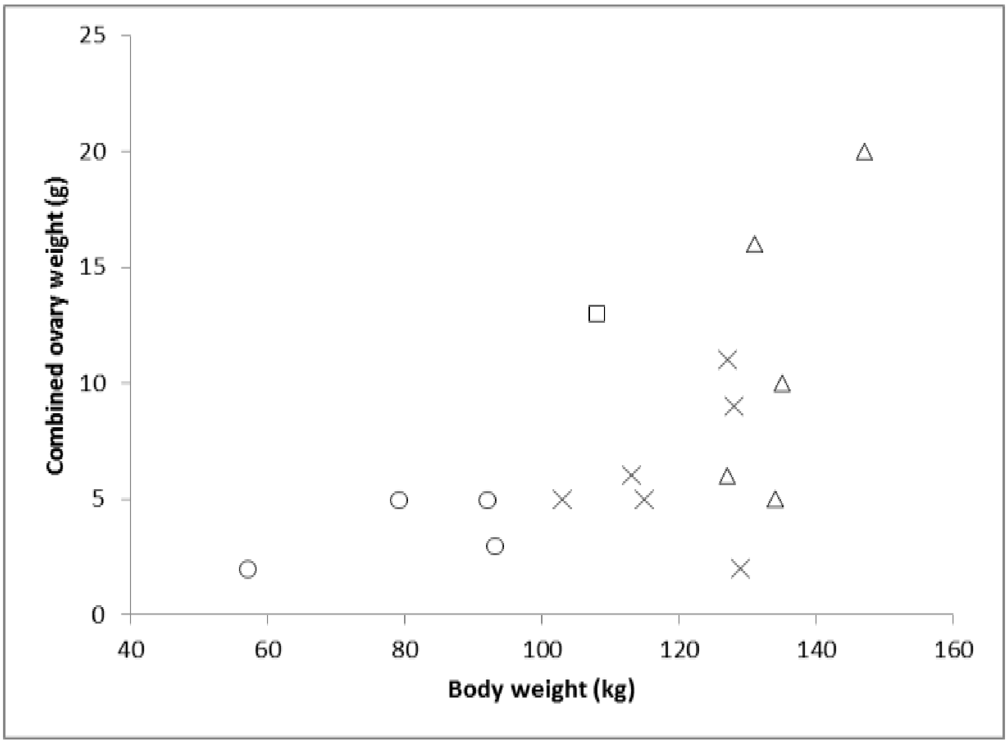

Figure 4.20 Increase in combined ovary weight with body weight in female *S. coeruleoalba* (n=17). Circles represent immature individuals, crosses mature, resting individuals, triangles mature, pregnant individuals and squares mature, lactating individuals.

Reproductive Parameters

In the sample, seven out of the 27 females were pregnant as indicated by the presence of a foetus on the datasheets. Assuming a gestation period of 1 year (Kasuya, 1972; Miyazaki, 1977a), the annual pregnancy rate in the sample was found to be 25.9% (Table 4.6). The calving interval calculated as the inverse of the APR, was estimated at 3.89 years or 46.7 months (Table 4.6). It was not possible to calculate the lactation period due to the unavailability of data. However, the resting period was estimated to be 1.86 years or 22.3 months (Table 4.6).

A regression of estimated age against number of corpora was described by the equation $y = 0.3196x - 0.3556$, which gave an ovulation rate of 0.32 per year (Table 4.6). This suggests that ovulation occurs, on average, every 3.1 years (37.2 months). This estimate is approximately 10 months shorter than the calculated calving interval of 3.86 years (46.7 months). The low coefficient of variance (0.39) between the age and the number of ovarian corpora may indicate that there is either a decrease in the ovulation rate with age or, alternatively, variation in the number of ovulations per oestrus period (Myrick *et al*., 1986).

Table 4.6 Summary of the values obtained for a number of reproductive parameters for female *S. coeruleoalba*.

Reproductive Parameter	**Calculation**	**Value**
Annual Pregnancy rate Proportion pregnant (P)	$APR = P/T_G$ 7/27 = 0.259 (0.259/1) = 0.259 x 100%	25.9%
Calving Interval	$CI = 1/APR$ 1/0.259	3.86 years
Resting period Proportion pregnant (P) Proportion resting (R)	$T_R = T_G \times R/P$ 7/27 = 0.259 13/27 = 0.481 1 x 0.481/0.259	1.86 years
Ovulation rate Regression equation (least squares method)	Figure 4.18. $y = 0.3196x - 0.3556$ Slope of equation = 0.3196	0.32

T_G = length of gestation assumed to be 1 year (12 months)

Seasonality

The occurrence of foetuses, neonates and calves up to an including an age of one year is shown in Figure 4.22. It is difficult to ascertain whether there is seasonality in conceptions and births due to the small sample size. However, there could possibly be two cohorts, one starting in August and the other in December/January. This aligns with the peak in seminiferous tubule diameter during the month of December, however, the peak in seminiferous tubule diameter in May is earlier than the cohort starting in August.

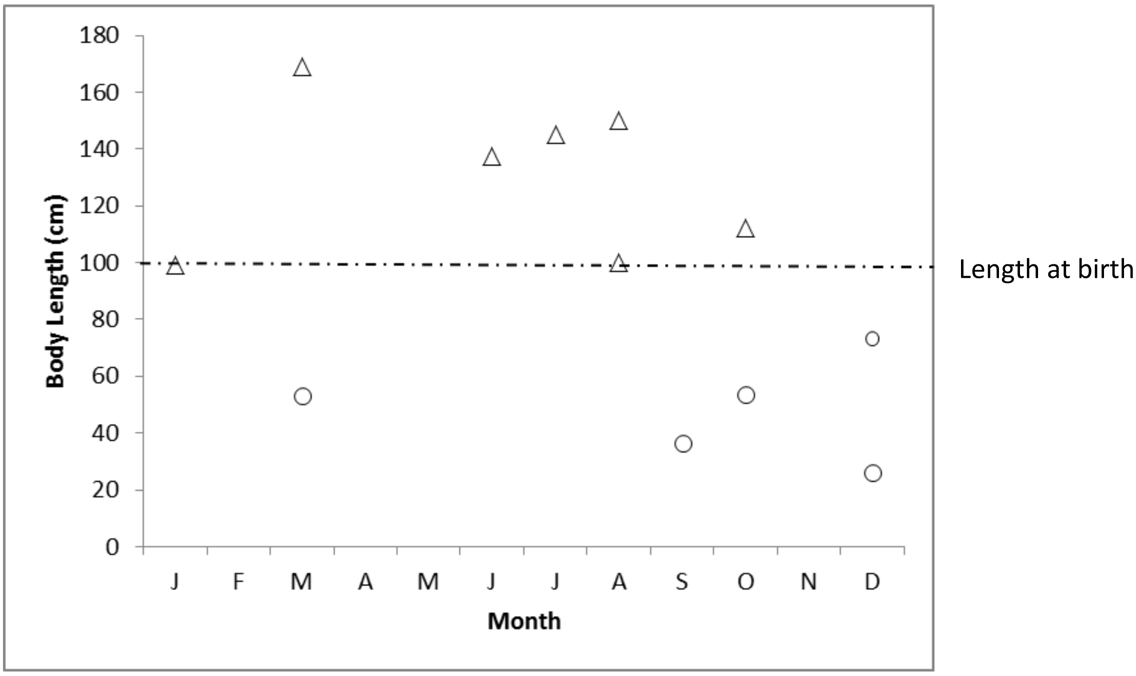

Figure 4.21 Occurrence of *S. coeruleoalba* foetuses (n=5) and calves (n=7) up to and including the age of 1 year. The circles represent foetuses and the triangles neonates and calves.

4.4 Discussion

4.4.1 Attainment of sexual maturity

Testis size and seminiferous tubule diameter

In general, testis size increases as body size increases. Immature *S. coeruleoalba* attains maturity between a combined testis weight of 16.0 and 41.4g (n=8). Mature Individuals have a large range of weights from 41.4 to 376.0g. It is not unusual for mature testes to have such a large range. A large range of between 70.0 and 800.0g was also found in mature *Delphinus delphis* in the eastern north Atlantic (Collet and Girons, 1984). Testis length was less variable, mature testes ranged from 10.0 to 14.4cm in length and immature testes ranged from 2.1 to 8.4cm in length. Therefore the onset of maturity occurs between a testis length of 8.4

and 10.0cm (n=16). The smaller variability and the larger sample size, make testis length a better indicator for sexual maturity.

Seminiferous tubule diameters ranged from 23.8 to 69.6µm in immature testes and from 35.4 to 110.6µm in mature testes (Table 4.2). Therefore maturity occurs between a tubule diameter of 43.5 and 69.6µm. For *S. coeruleoalba* off the Pacific coast of Japan, seminiferous tubule diameters were as follows; immature individuals ranged between 33.0 and 65.0µm, pubertal individuals ranged from 34.0 to 104.0µm and mature individuals ranged from 45.0 to 214.0µm in diameter (Miyazaki, 1977a). This means maturity in the Pacific population of *S. coeruleoalba* occurs at a smaller seminiferous tubule diameter of between 34.0 and 45.0µm than in the present study.

Ovarian symmetry and weight

Both ovaries are not equally functional in *S. coeruleoalba*, the left ovary attains maturity before the right one. Only females older than 10 years and greater than 220cm in length showed corpora in the smaller, right ovary. This prevalence of ovulation from one ovary is not unusual in *S. coeruleoalba* and has been previously reported by Ohsumi (1964) and Hirose *et al*. (1970). Hirose *et al*. (1970) reported that while dolphins are young, they ovulate in the left ovary and only later do ovulations become more frequent in the right ovary. *Stenella coeruleoalba* shows a pattern of asymmetry of sexual maturity, which fits the type III accumulation rate described by Ohsumi (1964).

The onset of sexual maturity in *S. coeruleoalba* occurred at a combined ovary weight of between five and eight grams. Combined ovary weights ranged from two to five grams in immature individuals and from two to 20g in mature individuals. It is clear that ovarian weight was not a good indicator of sexual maturity, due to the high variation resulting from the size of the CL. There was a definite increase in combined ovary weight with an increase in TBL and body weight. This should indicate that ovarian weight would be a good indicator of maturity. However, there was a large overlap of ovarian weights of immature and mature individuals. The variability was high between individuals in the same age and length class.

Length-at-sexual maturity

For male and female *S. coeruleolaba* sexual maturity is reached between 209 and 224cm in TBL and between 209 and 215.2cm in TBL, respectively. This indicates that males and females reach sexual maturity at a similar length off the south-east coast of southern Africa. In the Pacific, Kasuya (1972) found that males reach sexual maturity between 200 to 240cm in TBL and females at a slightly shorter TBL of between 190 and 220cm. It would thus appear that male striped dolphins in South African waters attain maturity at a similar length, whereas the females reach maturity at a greater length compared to the Pacific population. Kasuya (1972) had a large sample size and could calculate the length at which 50% of the population are mature. For males this occurred at 220cm and for females at 212cm, these lengths are within the length at sexual maturity range obtained for males and females, respectively, in the present study. In the Mediterranean Sea, female striped dolphins reach sexual maturity at a shorter length of between 182 and 194cm in TBL and the average length for attainment of sexual maturity was 187cm TBL (Calzada *et al*., 1996). These differences in length at ASM between populations could be due to genetically determined geographic variation or differences in population densities (Perrin and Reilly, 1984).

Age-at-sexual maturity

The age at ASM for *S. coeruleoalba* off the south-east coast of southern Africa is between 8.17 and 11.5 years and between 6.5 to 7.5 years for males and females, respectively. This indicates that females reach sexual maturity at a younger age compared to the males. A number of studies on delphinids have demonstrated that females attain sexual maturity earlier than the males (Kroese, 1993). In the previous study conducted on the same population, it was found that females reached maturity at 8.9 years and males later between 10 and 12 years of age (Kroese, 1993). This could suggest that the age at ASM has decreased slightly for the present population, which could mean that the population is undergoing density dependent changes in life history parameters (Kasuya, 1985). However, caution must be taken with this result due to the small sample size. Alternatively, the difference could be due to differences in the interpretation of GLG's. The changes in population density could be caused by a decrease in food availability or by an increase in human threats. Female striped dolphins were also found to mature earlier than the males in Japanese waters, where maturity was reached between 6.5 and 14.5 years and between 4.5 and 12.5 in males and females, respectively (Miyazaki, 1984). According to these estimates, the Japanese population reaches maturity slightly earlier than the present population. The reason for this is that the Japanese population is highly exploited through directed fishing and the age at ASM has decreased since the 1970's due to overexploitation (Kasuya, 1985).

4.4.2 Annual pregnancy rate, ovulation rate and reproductive cycle

Annual pregnancy rate (APR)

The APR of a population is the proportion of mature females that we expect to give birth in any given year (Myrick *et al*., 1986). In the present study the APR was estimated to be 25.9%. This estimate is similar to that of the Mediterranean Sea population, where it was estimated to be 25% (Calzada *et al*., 1996). Similarily, the APR of *S. attenuata* off the Pacific coast of Japan was and found to be 23.8% (Kasuya *et al*., 1974) and 25.4% (Kasuya, 1976). These estimates are lower than those obtained in a previous study on the same population of *S. coeruleoalba*, where the APR was estimated to be 34% (Kroese, 1993). The decline in the APR of the present population could suggest density dependent changes in the population (Perrin and Reilly, 1984). However, the difference could also be due to discrepancies in GLG interpretation between the studies. These values are even lower than the APR value of *S. coeruleoalba* off the Pacific coast of Japan, where it is estimated at 42.2% (Kasuya, 1976) and 45.5% (Kasuya and Miyazaki, 1976). The reason for this higher APR could be due to larger sample sizes compared to the present study. Alternatively, due to the high exploitation of the Japanese population, the calving interval has declined and this could account for the higher APR in Japan (Perrin and Reilly, 1984; Kasuya, 1985). Higher estimates of 47% and 36% were also obtained for *S. attenuata* (Perrin *et al*., 1976) and *S. longirostris* (Perrin *et al*., 1977), respectively, in the eastern tropical Pacific.

Ovulation rate

Estimates of ovulation rates vary among delphinids and within the species depending on the region (Perrin and Reilly, 1984). In the present study, an ovulation rate of 0.32 per year was obtained from the least squares regression method. Using the same method, the ovulation rate of *S. coeuleoalba* off the Pacific coast of Japan was found to vary between 0.41 and 0.69 per year (Kasuya, 1972; Kasuya, 1976; Miyazaki, 1984). Similarly, in the Mediterranean Sea the ovulation rate was estimated to be 0.40 per year (Calzada *et al*., 1996). It has been suggested that the variable ovulation rates recorded in the Japanese population are a direct result of exploitation (Miyazaki, 1984).

In the present study the correlation between the number of corpora and estimated age was poor (r^2 = 0.39), which could suggest a high variability in ovulation rates. Individual variability in ovulation rates has also been observed in *S. attenuata* (Kasuya *et al*., 1974; Perrin *et al*., 1976; Myrick *et al*., 1986). However the poor correlation could be a due to the small sample size.

Gestation period

In mammals, the breeding cycle has three parts, a gestation period, a lactation period and a resting period (Perrin and Reilly, 1984; Murphy, 2004). As mentioned, the gestation period is the least variable component of the breeding cycle within a species (Perrin and Reilly, 1984). Estimates of gestation periods are available for a number of delphinid species, including *S. coeruleoalba* (Perrin and Reilly, 1984). Due to the small sample size, the gestation period could not be calculated during this study. However, it has been estimated that the gestation period lasts 12 months for *S. coeruleoalba* off the coast of Japan (Kasuya, 1972; Miyazaki, 1977a; Perrin and Reilly, 1984). Therefore, we can assume a similar gestation period for *S. coeruleoalba* off the coast of South Africa.

Lactation period

The lactation period is the most variable component of the breeding cycle (Perrin and Reilly, 1984). In the present study, only one female was lactating in the sample, therefore lactation period could not be calculated due to insufficient data. In a previous study conducted in Japanese coastal waters the lactation period of *S. coeruleoalba* was estimated to be at least 1.25 years (Kasyua, 1972). Since the age estimates and life history parameters seem to be very similar to the Japanese population it can be assumed that the lactation period of the South African population is also similar. For *S. attenuata* in the eastern tropical Pacific the lactation period was estimated to be 1.66 years (Myrick *et al*., 1986), while the lactation period for *S. longirostris* in the eastern tropical Pacific had an estimated lactation period of 1.5 years (Perrin *et al*., 1977).

Resting period

The resting period is the time between weaning and the next pregnancy (Perrin and Reilly, 1984). In the present study the resting period was estimated to be 1.86 years (22.3 months). This value is much higher than that obtained by Kasuya (1972), who estimated a resting period of between 3.6 and 6 months for *S. coeruleoalba* off the Pacific coast of Japan. This short resting interval implies that some females are impregnated in the same mating season as they have weaned their calves (Kasuya, 1972). It is worth noting that the resting period of *S. coeruleoalba* has decreased to between 2.4 and 3.6 months under heavy exploitation in Japanese waters (Kasuya, 1984). In the present study, females rest for almost 2 years before pregnancy occurs again. The difference between the present population and the Japanese population could be a result of varying population densities, geographic variations or the small sample size in the present study (Perrin and Reilly, 1984). The resting period for *S.*

attenuata off the Pacific coast of Japan was longer, lasting 8.1 months (Kasuya *et al*., 1974) and in a later study 9 months (Kasuya, 1976), however, these are still not as long as the resting period estimated for the present population.

Calving interval

The gestation period, lactation period and resting period make up the calving interval, which is an estimate of the mean period between births (Myrick *et al*., 1986). When employing the 1/APR method (1/0.259), a calving interval of 46.3 months (3.86 years) was estimated in the present study. This estimate is similar to that of 4 years for the Mediterranean Sea population (Calzada *et al*., 1996). Kasuya (1972) found a calving interval of around 3 years for *S. coerulaoalba* off the Pacific coast of Japan. In a subsequent study on the same population the calving interval decreased to 2.37 years (Kasuya, 1976). It has been proposed that when a population is depleted through exploitation, such as the Japanese population, the pregnancy rate and the calving interval change in order to increase recruitment (Laws, 1961). Therefore, the calving interval decreased to increase recruitment in the Japanese population.

4.4.3 Seasonality

In an earlier study on *S. coeruleoalba* in South African waters, no conclusion could be made on the seasonality of spermatogenesis due to insufficient data (Reddy, 1996). In the present study more data were available, but still not sufficient for clear conclusions to be made. Mature males were found throughout the year, except in April, September and October. These months could be possible resting periods where spermatogenesis does not occur. Additionally, there is evidence that tubule diameter and testis weight fluctuate throughout the year. The combined data, could suggest that these dolphins are seasonal breeders. In addition, foetal lengths could possibly indicate two breeding seasons, one in August and the other in December/January. However, reproductive seasonality cannot be concluded due to the small sample sizes. In the Japanese population, it was determined that *S. coeruleoalba* reproduce seasonally (Kasuya, 1972; Miyazaki, 1977a; Miyazaki, 1984). Kasuya (1972) reported two breeding seasons for the Japanese population, one in the Northern Hemisphere winter (November - December) and the other in summer (May - June). This was based on age determination by means of dental growth layers, but no gonads were examined. Later, Miyazaki (1977b) discovered three breeding seasons, from February to May, from July to September and in December based on the detailed examination of the testes, ovaries and foetal growth. A number of factors can influence the timing of births, such as food availability and migration (Bronson, 1989).

4.4.4 Comparison with previous studies

In order to set the data obtained for *S. coeruleoalba* in the present study into a larger context, the length and age at attainment of sexual maturity (ASM) were compared with the values available for other *S. coeruleoalba* populations (Table 4.7 and 4.8). The ages-at-sexual maturity from the present study are similar to those obtained by Kasuya (1972) for the population off the Pacific coast of Japan, for both males and females (Table 4.7 and 4.8). The range of ASM for males and females overlaps between the two studies.

A number of studies have been conducted on the *S. coeruleoalba* population off the Pacific Coast of Japan (Kasuya, 1972; Kasuya, 1976; Miyazaki, 1977a and Miyazaki, 1984). The age-at-sexual maturity has been very similar for males and females over the years. However, there was a gradual decrease in the age and length at ASM from 1972 to 1977 (Table 4.7 and 4.8). In 1984, the age and length at which ASM occurs increased for males and females. These fluctuations were suggested to be due to changes in exploitation (Kasuya, 1985). Driving and netting of *S. coeruleoalba* off the Pacific coast of Japan has been carried out since the 19th century, and the population has declined since World War II (Kasuya, 1985). A decline in the striped dolphin population can cause density dependent changes of life history parameters, such as length and age at ASM (Kasuya, 1985).

Table 4.7 Age and length at attainment of sexual maturity (ASM) in males for a number of delphinid species, comparing geographic regions.

Species	Range of age and length at ASM	Length at ASM	Age at ASM	References
Striped dolphin *S.coeruleoalba* NW Indian Ocean	8.17 - 11.5yrs 209-224cm	-	-	Present study
Striped dolphin S.coeruleoalba NW Pacific Ocean	7-11yrs	220cm (50% mature)	9.2yrs (mean)	Kasuya, 1972
Striped dolphin *S.coeruleoalba* NW Pacific Ocean	-	-	9.0yrs (50% mature)	Kasuya, 1976
Striped dolphin *S.coeruleoalba* NW Pacific Ocean	2.5-11.5yrs	210cm (50% mature)	6.7yrs (50% mature)	Miyazaki, 1977a
Striped dolphin *S.coeruleoalba* NW Pacific Ocean	6.5-14.5yrs	-	8.8yrs	Miyazaki, 1984

The range of age at ASM for female *S. coeruleoalba* during the present study is less than that obtained for the Mediterranean Sea population (Table 4.8). Differences between the two populations can likely be ascribed to geographic variability in water temperature and food availability. The Mediterranean striped dolphin attains a much smaller asymptotic length than the striped dolphin off South Africa (Chapter 3), which suggests that the striped dolphin in the Mediterranean Sea does not get as large as the Southern African striped dolphin. Calzada *et al*. (1996) suggested that elevated ASM of striped dolphin in the Mediterranean Sea is the result of food constraints. Calzada *et al*., (1996) also suggested that the striped dolphin population off Japan may reach maturity at a younger age, because there is a large amount of food available due to the decline in the population numbers in recent years.

Table 4.8 Age and length at attainment of sexual maturity (ASM) in females for a number of delphinid species, comparing geographic regions.

Species	**Range of age and length at ASM**	**Length at ASM**	**Age at ASM**	**References**
Striped dolphin *S.coeruleoalba* NW Indian Ocean	6.50-7.50yrs 209-215.5cm	-	-	Present study
Striped dolphin S.coeruleoalba NW Pacific Ocean	8-10yrs	212cm (50% mature)	8.9yrs (mean)	Kasuya, 1972
Striped dolphin S.coeruleoalba NW Pacific Ocean	-	-	8.5yrs (50% mature)	Kasuya, 1976
Striped dolphin *S.coeruleoalba* NW Pacific Ocean	2.5-12.5yrs	209cm	7.1yrs	Miyazaki, 1977a
Striped dolphin *S.coeruleoalba* NW Pacific Ocean	4.5-12.5yrs	-	8.8yrs	Miyazaki, 1984
Striped dolphin *S.coeruleoalba* Mediterranean Sea	10-15yrs 182-194cm	187cm (50% mature)	12yrs (50% mature)	Calzada *et al*., 1996

Chapter 5

External morphology of *Stenella coeruleoalba*: Allometric relationships and sexual dimorphism

5.1 Introduction

5.1.1 Allometry

Allometry describes how the characteristics of living animals change with size (Shingleton, 2010). It also refers to the scaling relationship between the size of a body part and the size of the body as a whole (Shingleton, 2010). Three types of allometry exist, namely, ontogenetic, evolutionary and static allometry (Klingenberg, 1996). Ontogenetic allometry explains the variation of characters during growth, while evolutionary allometry explains the variation of traits between closely related species (Klingenberg, 1996). Static allometry or size allometry, deals with variations between individuals in the same population and age class (Klingenberg, 1996). This chapter deals with static/size allometry to examine whether differences between males and females in the same population and age class exist. It provides information about differing growth rates and patterns between sexes and body parts (Murphy and Rogan, 2006). Static allometric relationships are fundamental in understanding the social structure and life history of a population (Clark and Odell, 1999; Klingenberg, 1996). Additionally, this information can be used to distinguish between races and species (Willig *et al*., 1986).

Allometry can be further divided into three types, namely, positive allometry, negative allometry and isometry. Positive allometry refers to those processes where the body part has a higher growth rate than the body as a whole (Shingleton, 2010). Another type of allometry is negative allometry. This type occurs when the body part has a slower growth rate than the body as a whole (Shingleton, 2010). The phenomenon where the body part grows at the same rate as the whole body is called isometric growth (Shingleton, 2010). A body part that exhibits isometry will maintain a proportionate size to the whole body throughout the organisms' development (Shingleton, 2010). Allometry refers to traits that grow at different rates to the overall body, thus strictly speaking isometry is not a form of allometry. However, allometry is used to refer to scaling relationships in general, of which isometry is a special case (Shingleton, 2010).

Allometric relationships within cetaceans have been little examined and there is a paucity of published literature. Within the genus *Stenella*, allometry has been investigated for *Stenella attenuata graffmani* from Bahia de Banderas, Mexico (Sanvicente-Añorve *et al*., 2004). The results indicated that growth in this species demonstrated negative allometry for most body measurements, especially in the males (Sanvicente-Añorve *et al*., 2004). In addition, the females showed a greater growth coefficient than the males in three out of four measurements considered (Sanvicente-Añorve *et al*., 2004). Significant allometric trends were also observed in most external measurements of *Stenella attenuata* and *Stenella longirostris* from the eastern Pacific Ocean and from Hawaii (Perrin, 1975b; Edwards, 1993). In addition, allometric relationships have been investigated in the short-beaked common dolphin (*Delphinus delphis*) in the Atlantic Ocean, where it was demonstrated that males and females showed a similar pattern of growth for a number of characters (Murphy, 2004). Similarly, it was found that the anterior region of the body exhibited negative allometry, indicating that the anterior portion grows slower than the posterior portion and is smaller in relation to the whole body than other body parts (Murphy, 2004). This trend was also noted in the Dall's porpoise (*Phocoenoides dalli*) (Amano and Miyazaki, 1993) and harbour porpoise (*Phocoena phocoena)* (Read and Tolley, 1997).

5.1.2 Sexual dimorphism

In addition to allometric relationships, sexual dimorphism also plays an important role in the understanding of the life history of *Stenella coeruleoalba*, for example the presence or absence of sexual dimorphism can determine the social structure of the species (Clark and Odell, 1999; Murphy and Rogan, 2006). 'Sexual Dimorphism' is defined as two sexes of a species differing in external appearance, including differences in size, shape, dentition, colour, scent, vocalisations and in the development of appendages (Ralls and Mesnick, 2009). In odontocetes, the most outstanding sexually dimorphic characters are size and shape (Tolley *et al*., 1995; Ralls and Mesnick, 2009). However, the narwhal (*Monodon nonoceros*) exhibits the most extreme form of sexual dimorphism within odontocetes involving dentition, where the male grows a unicorn like tusk (Ralls, 1977; Ralls and Mesnick, 2009). Odontocetes seem to follow the trend of increasing dimorphism with body size (Ralls, 1977). In the largest odontocetes, such as the sperm whale, *Physeter catodon*, the male is more than three times larger than the female (Lockyer, 1981). Conversely, in the smaller odontocetes such as the harbour porpoise, *P. phocoena*, dimorphisim is often reversed and the female is larger than the male (Read and Gaskin, 1990). In medium sized dolphins, such as spotted (*S. attenuata*) and spinner dolphins (*S. longirostris*), dimorphism is more subtle and is shown in shape rather than in total body size (Perrin, 1975b).

The evolutionary significance of sexual dimorphism has been highly debated (Douglas *et al*., 1986). A number of hypotheses have been brought forward concerning the cause of sexual dimorphism within a species (Douglas *et al.*, 1986; Shine, 1989). These include sexual selection, type of mating system, niche utilization and predation pressures (Douglas *et al.*, 1986; Shine, 1989). An argument most commonly cited is that a larger body size in males could have evolved due to the advantage of a larger size promoting success in male-male combat, therefore increasing the success of mating (Shine, 1989). The tusk in the narwhal (*M. nonoceros)* is said to have evolved as a weapon for intraspecific competition for females between males (Ralls, 1977; Ralls and Mesnick, 2009). Similarly, the use of teeth as weapons is not uncommon in the beaked whales (*Mesoplodon* spp. and *Berardius* spp.) (Macleod, 1998). Additionally, in the common bottlenose dolphin (*Tursiops truncatus*) it was suggested that the presence of a larger caudal peduncle, flukes and dorsal fin in males were also related to intraspecific competition (Tolley *et al*., 1995).

Cranial dimorphism has been investigated for *S. coeruleoalba* in South African waters and off the coasts of Portugal, as well as for *S. longirostris* in the eastern tropical Pacific Ocean (Conry, 2012; Amaral *et al*., 2009; Douglas *et al*., 1986). No sexual dimorphism was evident in cranial morphology for *S. coeruleoalba* in both regions (Amaral *et al*., 2009; Conry, 2012). However, for *S. longirostris*, significant sexual dimorphism was found for 13 of the 36 cranial morphological characters (Douglas *et al*., 1986). Sexual dimorphism in external morphology was present in the adults of spinner (*S. longirostris)* and spotted dolphins (*S. attenuata)* in the eastern Pacific Ocean and in Hawaii (Perrin, 1975b). Sexual dimorphism in external morphology has also been described in the short-beaked common dolphin (*D. delphis)* in the Atlantic Ocean, where the males are significantly larger than the females in a number of characters (Murphy, 2004). In contrast, the short-beaked common dolphin (*D. delphis)* in southern Australia, exhibited no sexual dimorphism (Bell *et al.,* 2002). The absence of sexual dimorphism was ascribed to low productivity in the environment (Murphy and Rogan, 2006). A similar trend has been observed in the Dall's porpoise (*P. dalli*), where a higher degree of dimorphism occurred in animals found in the productive Sea of Japan compared to animals found in the less productive North Pacific Ocean (Amano and Miyazaki, 1996). Morphological sexual dimorphism has also been found in the coastal spotted dolphin (*S. attenuata graffmani)* (Sanvicente-Añorve *et al*., 2004), the Dall's porpoise (*P. dalli)* (Jefferson, 1989; Amano and Miyazaki, 1993), the common bottlenose dolphin (*T. truncatus)* (Tolley *et al.,* 1995), the Fraser's dolphin (*Lagenodelphis hosei)* (Perrin *et al*., 2003) and the Killer whale (*Orcinus orca*) (Clark and Odell, 1999).

5.1.3 Aim of the present chapter

To date no study has been conducted to determine the presence of sexual dimorphism in *S. coeruleoalba* occurring of the coast of South Africa. Therefore the aims of this chapter are to examine the presence of sexual dimorphism in external characteristics and to determine the allometric relationships in the size and shape of the striped dolphin off the south-east coast of southern Africa.

5.2 Materials and methods

5.2.1 Sample

Data used for the analyses in this study were obtained from the Graham Ross Marine Mammal collection at the Port Elizabeth Museum. A number of standard external morphometric measurements are taken from every stranded and net caught carcass and noted on data sheets that are stored in the museum (Norris, 1961). These standard measurements are illustrated in Figure 5.1. In some instances, observers did not record all the measurements, therefore sample sizes vary between analyses. All specimens noted as either rotten, shark-bitten, pregnant as well as net caught animals were removed from the data set. Additionally, only measurements from sexually mature individuals were used for the analyses. Males were considered sexually mature if their total body length was > 224cm and females if their total body length was greater than >215.5cm, based on results obtained in Chapter 4. Measurements were available from 49 sexually mature *S. coeruleoalba* specimens. Of these, 27 were males and 22 were females. The size-frequency analysis of the specimens is shown in Chapter 2 (Figure 2.8).

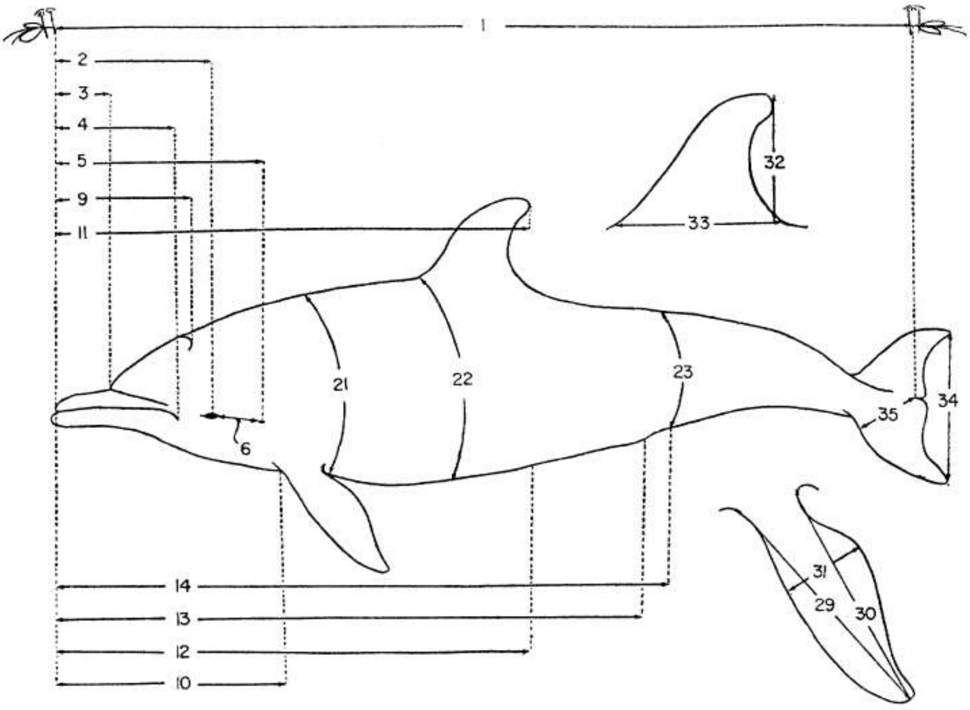

Figure 5.1 Standard external measurements taken from stranded or net caught cetaceans for future analyses (taken from Norris, 1961).

Table 5.1 External measurements used for the analysis of allometric relationships and sexual dimorphism in *S. coeruleoalba.*

Measurement	**Abbreviation**	**Measurement number (Fig 5.1)**
Tip upper jaw, to deepest part of notch (Total body length)	TBL	1
Tip upper jaw, to centre eye	T-E	2
Tip upper jaw, to apex of melon	T-AM	3
Tip upper jaw, to angle of gape	T-AG	4
Tip upper jaw, to centre blowhole	T-B	9
Tip upper jaw, to the anterior insert of the flipper	T-F	10
Tip upper jaw, to the anterior insert of the dorsal fin *	T-ADF	NA
Tip upper jaw, to the tip of the dorsal fin	T-DF	11
Tip upper jaw, to midpoint of umbilicus	T-MU	12
Tip upper jaw, to midpoint of the genital aperture	T-GA	13
Tip upper jaw, to the centre of the anus	T-A	14
Tip upper jaw, to ear	T-EA	5
Centre eye, to ear	E-EA	6
Centre eye, to angle of gape	E-AG	NA
Centre eye, to centre blowhole	E-B	NA
Girth, at axilla	GAX	21
Girth, maximum	GM	22
Girth, at anus	GA	23
Pectoral fin length, anterior insert to tip	AF	29
Pectoral fin length, axilla to tip	AXF	30
Pectoral fin width, maximum	WF	31
Dorsal fin, height	HDF	32
Dorsal fin base, length	LDF	33
Tail flukes width, tip to tip	WTF	34
Tail flukes, anterior boarder to notch	NAB	35
Tail flukes, notch depth	ND	NA

*This measurement was added after Norris (1961) was published.
NA – these measurements are not illustrated in Figure 5.1 but are included in Norris (1961).

5.2.2 Allometry

For the morphometric analyses, 26 standard external measurements were used (Table 5.1). A number of these measurements are illustrated in Figure 5.1. Three measurements namely, centre of eye to angle of gape, centre of eye to centre of the blowhole and the notch depth of the fluke are not illustrated in Figure 5.1, however, they were included in Norris's (1961) list of measurements. One measurement was added to the list of necessary measurements after the publication of Norris (1961), this measurement is tip upper jaw to the anterior insert of the dorsal fin.

Each measurement was converted to the logarithmic scale and plotted against the log of total body length (TBL) for males and females separately (Schmidt-Nielsen, 1993). An outlier analysis was conducted on the data and outliers were removed using the computer package Microsoft Office Excel 2010. A data point was considered an outlier if it deviated from the statistical mean by more than 15%. A linear line of regression was then fitted to the sexes separately using the same program. In order to analyse growth patterns and compare them between the sexes, allometric growth equations were then created in the form of:

$$y = ax^b$$

Where:

y is the character (dependent variable),

a is the intercept,

x is the total body length (independent variable),

b is the growth coefficient (Schmidt-Nielsen, 1993).

The type of allometry was then determined for each measurement by determining whether the growth coefficient (b) was significantly different from one (Read and Tolley, 1997). To test significance, a test statistic was calculated and compared to the value at a 5% level of significance in a t-distribution statistical table.

$$t_s = (b-1)/SE_b$$

Where:

t_s = test statistic,

b=slope,

SE_b = standard error of the slope,

df = n-2

$\alpha = 0.05$

Significant negative allometry was indicated when the growth coefficient was significantly < 1, significant positive allometry was indicated when the growth coefficient was significantly > 1, and isometric allometry was indicated when the growth coefficient was not significantly different from one (Read and Tolley, 1997).

5.2.3 Sexual dimorphism

Each measurement was analysed separately between the sexes by carrying out a univariate analysis of variance (ANOVA) and a univariate analysis of covariance (ANCOVA) using Statistica, version 11. An ANOVA was used to investigate the variation in size, while an ANCOVA was used to investigate sexual variations of body shape (Murphy, 2004). The ANCOVA used total body length (TBL) as a covariate to remove the effect of dolphin size on individual characters (Murphy, 2004). A 95% confidence level was used to determine whether there was a significant difference between males and females.

5.3 Results

5.3.1 Allometry

The results of the regression analyses are shown in appendix B. In general, the correlation coefficients indicated a poor fit to the data for most measurements (Table 5.2). Tip upper jaw to tip dorsal fin (T-DF) had the best fit for the males (r^2 = 0.567) and tip upper jaw to the genital aperture (T-GA) had the best fit to the females (r^2 = 0.713).

Linear body measurements

In males, all linear body measurements exhibited negative allometric relationships ($b<1$), with the exception of tip upper jaw to the tip of the dorsal fin (T-DF), which demonstrated isometric growth ($b=1$) (Table 5.2). This indicates that T-DF grew at a similar rate to the total body length while all other linear body measurements became relatively shorter as length increased. In females, linear body measurements such as T-DF, tip upper jaw to midpoint of the umbilicus (T-MU), tip upper jaw to the genital aperture (T-GA) and tip upper jaw to the anus (T-A) exhibited isometric growth ($b=1$) (Table 5.2). All other linear body measurements demonstrated negative allometry in females. This suggests T-DF, T-MU, T-GA and T-A increased at a faster rate to all other linear body measurements. In males T-DF demonstrated the highest growth coefficient (b) and in females T-GA.

Head measurements

All head measurements demonstrated negative allometry ($b<1$) in both males and females (Table 5.2). One exception was tip upper jaw to centre of the eye (T-E) which exhibited positive allometry (b>1) in females, indicating T-E increases at a faster rate to the total body length. Additionally, T-E demonstrated the highest growth coefficients (*b*) in both sexes.

Girth measurements

The majority of the girth measurements exhibited negative allometry (b<1) for both males and females, with the exception of girth at the axilla (GAX) in females, which demonstrated isometric growth (b=1) (Table 5.2). Indicating that GAX in females increased at the same rate as total body length, while maximum girth (GM) and girth at the anus (GA), scaled smaller than expected in relation to the total body length in females. GAX demonstrated the highest growth coefficient (*b*) in both sexes (Table 5.2).

Appendage measurements

In general, all appendage measurements demonstrated negative allometry (b<1) (Table 5.3). The exceptions were pectoral fin width (WF), which exhibited isometric growth (b=1) in males, fluke length (nearest point on the anterior boarder to notch (NAB)) which exhibited positive allometry (b>1) in females, and fluke notch depth (ND), which exhibited positive allometry (b>1) in both sexes (Table 5.3). This suggests that, in males, WF increased at the same rate as the total body length, while pectoral fin length (both anterior insert to tip (AF) and axilla to tip (AXF)) increased at a slower rate. Additionally, ND increased at a faster rate compared to fluke width (WTF) and NAB in both sexes. Overall, the pectoral fin measurements and fluke measurements demonstrated the highest growth coefficients (*b*) compared to all other external measurements.

5.3.2 Sexual dimorphism

Some sexual size dimorphism was evident in *S. coeruleoalba* when comparing external measurements between males and females using ANOVA. Eight external measurements demonstrated sexual size dimorphism as indicated with an asterix in Tables 5.2 and 5.3. These external measurements were TBL, WF, HDF, LDF, WTF, T-DF, T-GA and T-A (Tables 5.2 and 5.3). The males were significantly longer and wider compared to the females in TBL, WF, HDF, LDF, WTF and T-DF, while the females were significantly longer than the males for T-GA and T-A. Only one external measurement showed sexual shape dimorphism when using ANCOVA. This measurement was T-GA and the females were significantly larger (Table 5.2).

Table 5.2 Allometric relationships for linear body, head and girth measurements regressed against total body length for male and female *S. coeruleoalba*, showing any significant differences between the sexes (where $p<0.05$).

Measurement	Sex	n	Equation	±SE(b)	r^2	b=1	SIZE p ANOVA	SHAPE p ANCOVA
Linear body measurements								
Tip upper jaw, to deepest part of notch (TBL)	Male	22	-	-	-	-	0.021*	-
	Female	14	-	-	-	-		
Tip upper jaw, to anterior insertion of pectoral fin (T-F)	Male	19	$y = 1.7719x^{-0.057}$	0.076	0.0007	< 1	0.424	0.629
	Female	13	$y = 1.0984x^{0.4958}$	0.142	0.0232	< 1		
Tip upper jaw, to tip dorsal fin (T-DF)	Male	17	$y = 1.0133x^{0.8597}$	0.095	0.567	= 1	0.019*	0.592
	Female	13	$y = 1.2477x^{0.615}$	0.275	0.1055	= 1		
Tip upper jaw, to anterior insertion of dorsal fin (T-ADF)	Male	16	$y = 1.059x^{0.7465}$	0.134	0.2397	< 1	0.124	0.566
	Female	12	$y = 1.3843x^{0.4341}$	0.165	0.0932	< 1		
Tip upper jaw, to centre blowhole (T-B)	Male	21	$y = 1.2043x^{0.2619}$	0.063	0.0065	< 1	0.402	0.575
	Female	14	$y = 2.1244x^{-0.391}$	0.107	0.0097	< 1		
Tip upper jaw, to umbilicus (T-MU)	Male	11	$y = 1.1764x^{0.6307}$	0.141	0.2537	< 1	0.235	0.888
	Female	9	$y = 1.1001x^{0.7095}$	0.169	0.2829	= 1		
Tip upper jaw, to genital aperture (T-GA)	Male	20	$y = 1.2964x^{0.5952}$	0.122	0.2931	< 1	0.015*	0.0499*
	Female	13	$y = 0.7519x^{1.2474}$	0.150	0.7132	= 1		
Tip upper jaw, to anus (T-A)	Male	20	$y = 1.276x^{0.641}$	0.121	0.3929	< 1	0.018*	0.285
	Female	12	$y = 0.9313x^{1.0083}$	0.153	0.6525	= 1		
Head measurements								
Tip upper jaw, to centre eye (T-E)	Male	21	$y = 0.8067x^{0.7227}$	0.061	0.0492	< 1	0.684	0.631
	Female	13	$y = 0.4739x^{1.3557}$	0.101	0.1231	> 1		
Tip upper jaw, to apex of melon (T-AM)	Male	20	$y = 12.629x^{-2.887}$	0.031	0.1765	< 1	0.363	0.746
	Female	11	$y = 4.8921x^{-1.823}$	0.039	0.0955	< 1		
Tip upper jaw, to angle of gape (T-AG)	Male	20	$y = 1.4219x^{0.012}$	0.069	0.000008	< 1	0.504	0.785
	Female	12	$y = 0.8888x^{0.5676}$	0.101	0.0165	< 1		
Tip upper jaw, to ear (T-EA)	Male	12	$y = 1.7652x^{-0.128}$	0.107	0.0018	< 1	0.663	0.617
	Female	10	$y = 0.9225x^{0.633}$	0.119	0.0447	< 1		
Centre eye, to ear (E-EA)	Male	11	$y = 0.8426x^{-0.114}$	0.024	0.0002	< 1	0.780	0.259
	Female	9	$y = 45.982x^{-4.78}$	0.015	0.4853	< 1		
Centre eye, to angle of gape (E-AG)	Male	19	$y = 11.382x^{-3.101}$	0.018	0.1144	< 1	0.139	0.823
	Female	10	$y = 6.9305x^{-2.583}$	0.024	0.0836	< 1		
Centre eye, to centre blowhole (E-B)	Male	20	$y = 0.8286x^{0.5422}$	0.031	0.0403	< 1	0.253	0.368
	Female	10	$y = 1.9981x^{-0.491}$	0.049	0.0303	< 1		
Girth Measurements								
Girth, at axilla (GAX)	Male	10	$y = 1.5237x^{0.3278}$	0.269	0.027	< 1	0.533	0.794
	Female	7	$y = 1.1045x^{0.7119}$	0.425	0.0852	= 1		
Girth, maximum (GM)	Male	8	$y = 2.4237x^{-0.198}$	0.130	0.0449	< 1	0.451	0.645
	Female	7	$y = 1.5146x^{0.3543}$	0.301	0.0495	< 1		
Girth, at anus (GA)	Male	12	$y = 1.5733x^{0.198}$	0.246	0.0039	< 1	0.065	0.797
	Female	9	$y = 2.1328x^{-0.171}$	0.170	0.0078	< 1		

Table 5.3 Allometric relationships for appendage measurements regressed against total body length for male and female *S. coeruleoalba*, showing any significant differences between the sexes (where $p<0.05$).

Measurement	**Sex**	**n**	**Equation**	**±SE(b)**	**r^2**	**b=1**	**SIZE p ANOVA**	**SHAPE p ANCOVA**
Pectoral fin measurements								
Pectoral fin length, anterior insert to tip (AF)	Male	22	$y = 1.2853x^{0.1699}$	0.067	0.0021	< 1	0.054	0.561
	Female	14	$y = 2.8791x^{-0.79}$	0.069	0.0637	< 1		
Pectoral fin length, axilla to tip (AXF)	Male	21	$y = 0.6508x^{0.8254}$	0.049	0.0458	< 1	0.266	0.381
	Female	14	$y = 2.6127x^{-0.803}$	0.056	0.0394	< 1		
Pectoral fin width, maximum (WF)	Male	19	$y = 0.4226x^{0.9985}$	0.018	0.0541	= 1	0.014*	0.737
	Female	14	$y = 0.7274x^{0.3395}$	0.030	0.0032	< 1		
Dorsal fin Measurements								
Dorsal fin, height (HDF)	Male	18	$y = 1.2969x^{-0.017}$	0.045	0.00002	< 1	0.046*	0.990
	Female	13	$y = 1.5234x^{-0.237}$	0.074	0.0016	< 1		
Dorsal fin, base length (LDF)	Male	19	$y = 1.365x^{0.1112}$	0.066	0.0011	< 1	0.044*	0.780
	Female	12	$y = 1.9708x^{-0.34}$	0.110	0.0061	< 1		
Fluke measurements								
Tail flukes width, tip to tip (WTF)	Male	20	$y = 0.8789x^{0.7692}$	0.118	0.0475	< 1	0.028*	0.596
	Female	13	$y = 1.5675x^{0.0795}$	0.148	0.0006	< 1		
Nearest point on anterior boarder to notch (NAB)	Male	18	$y = 0.7839x^{0.4487}$	0.058	0.0032	< 1	0.060	0.461
	Female	12	$y = 0.1593x^{2.2879}$	0.035	0.2687	> 1		
Notch depth (ND)	Male	17	$y = 0.0089x^{4.2988}$	0.020	0.0055	> 1	0.320	0.950
	Female	13	$y = 0.0058x^{4.7709}$	0.017	0.0178	> 1		

5.4 Discussion

5.4.1 Allometry

Allometry describes the occurrence of some body parts growing at different rates to the overall growth of the body (Murphy, 2004). In the present study the type of allometry exhibited (positive/negative/isometry) varied between the sexes. For example, in some measurements, males and females demonstrated a different type of allometry. Variations in the type of allometry between male and female delphinids have been demonstrated in previous studies on the spotted dolphin (*S. attenuata graffmani*) (Sanvicente-Añorve *et al.*, 2004) off the Mexican coast and on the short-beaked common dolphin (*D. delphis*) in the north east Atlantic Ocean (Murphy, 2004). Our results show that *S. coeruleoalba* off the south-east coast of southern Africa exhibit negative allometry in most of their external measurements. A number of cetaceans appear to demonstrate mainly negative allometry. These include the spotted dolphin (*S. attenuata graffmani*) (Sanvicente-Añorve *et al*., 2004), the short-beaked common dolphin (*D. delphis*), the killer whale (*O. orca*) (Clark and Odell, 1999), the harbour porpoise (*P. phocoena*) and the Dall's porpoise (*P. dalli*) (Amano and Miyazaki, 1993). However, the Dall's porpoise (*P. dalli*) only exhibited negative allometry in the flipper measurements and isometric or positive growth in all other characters (Amano and Miyazaki, 1993). The anterior portion of the harbour porpoise (*P. phocoena*) in the Bay of Fundy demonstrated negative allometry and it was suggested that this reflected the importance of the early development of the cranium, meaning cranial characteristics reach their maximum size before the skeleton has stopped growing (Read and Tolley, 1997).

The linear body measurements of *S. coeruleoalba* exhibited both negative and isometric allometry. Isometry implies that the feature is growing at a similar rate to the total length. In the present study most of the linear body measurements demonstrated negative allometry, which could suggest that these characters reach their final size before the skeleton stops growing (Read and Tolley, 1997). It is important to note that there is no measurement taken from the anus to the tail fluke. Therefore, this portion of the body could exhibit positive allometry/isometry which would increase the length of the posterior portion, increasing thrust during swimming.

The head dimensions of male and female *S. coeruleoalba* generally demonstrated negative allometry. Similarly, the harbour porpoise (*P. phocoena*) from the Bay of Fundy exhibited negative allometry in the head measurements (Read and Tolley, 1997). This means the cranium reaches its maximum size before overall growth stops. The early development of the cranium is important for the development of the brain.

The girth measurements also exhibited negative allometry, except for GAX in the females which exhibited isometric growth. This suggests that the girth also reaches it maximum before length stops increasing. It has been reported that posterior muscle development is important for sexual maturity (Tolley *et al*., 1995; Murphy and Rogan, 2006). A larger girth has been attributed to a greater muscle mass and strength (Tolley *et al.*, 1995; Clark and Odell, 1999; Murphy and Rogan, 2006). According to this study *S. coeruleoalba* reach sexual maturity before physical maturity, therefore it is important that the girth reaches its maximum before total length to ensure the appropriate muscle development for sexual maturity.

One notable exception that demonstrated positive allometry in both males and females was the fluke notch depth (ND). This section of the fluke increases in depth faster than the rest of the fluke increases in size. However, in females fluke length (NAB) also demonstrates positive allometry. A rapid increase in both of these measurements may help increase surface area. It has been found that the dorsal fin and tail fluke have a superficial venous system which plays an important role in counter-current heat exchange associated with the testis and uterus of the common bottlenose dolphin (*T. truncatus*) (Rommel *et al*., 1992, 1993). Therefore, by increasing surface area, thermoregulatory efficiency also increases. This is essential for a tropical/subtropical oceanic species like *S. coeruleoalba* that experiences a wide range of temperatures.

All other appendage measurements exhibited negative allometric relationships, suggesting the significance of the early development of these features (Read and Tolley, 1997). Additionally, in the present study, the dorsal fin measurements and the tail fluke measurements demonstrated the highest growth coefficients. This could further suggest the importance of these appendages in thermoregulation. However, caution must be taken with this result due to the small sample size. Large growth coefficients were also noted for fluke and girth measurements in the Dall's porpoise (*P. dalli)* (Amano and Miyazaki, 1993). Amano and Miyazaki (1993) suggested that the rapid development of the flukes and associated muscles is necessary for fast swimming and diving. Therefore in addition to thermoregulation, the rapid development of the appendages in *S. coeruleoalba* is vital for propulsion and maneuverability while swimming and diving (Tolley *et al*., 1995).

5.4.2 Sexual dimorphism

Sexual dimorphism is generally expressed in variations in overall body size and shape, the size and shape of the tail flukes and the dorsal fin, the presence of a postanal hump in the short-beaked common dolphin (*D. delphis*) and differences in pigmentation (Murphy, 2004). In the present study sexual size dimorphism (Tables 5.2 and 5.3 - ANOVA) was evident in eight out of 26 characters, namely, pectoral fin width (WF), dorsal fin height (HDF), dorsal fin base length (LDF), fluke width (WTF) and tip upper jaw to the tip of the dorsal fin (T-DF), tip upper jaw to genital aperture (T-GA) and tip upper jaw to the anus (T-A). The females had a significantly longer distance from the tip upper jaw to the genital aperture and anus than males. This is expected, as the genital slit is further forward in males than females in most cetaceans (Tolley *et al*., 1995; Murphy and Rogan, 2006). In a study on spotted dolphins (*S. attenuata graffmani*) in Mexico, the relative position of the umbilicus, genital slit and anus were the main differences between males and females (Sanvicente-Añorve *et al*., 2004). Additionally, the position of the genital slit and anus were found to be sexually dimorphic in the short-beaked common dolphin (*D. delphis*) (Murphy, 2004; Murphy and Rogan, 2006) in the Atlantic Ocean. These differences were also attributed to differing positions (Murphy, 2004; Murphy and Rogan, 2006).

The males had significantly larger dorsal fins (HDF and LDF), wider flukes (WTF), wider pectoral fins (WF) and a greater distance for T-DF compared to the females. Significantly longer pectoral fins, from the axilla to tip, have been observed in male spotted dolphins (*S. attenuata*) in the eastern tropical Pacific (Perrin, 1975b) and in Mexico (Sanvicente-Añorve *et al*., 2004). It has already been discussed that larger appendages assist with thermoregulation as well as maneuverability and propulsion when swimming and diving (Tolley *et al*., 1995). It has also been suggested that larger appendages assist in male on male encounters during intraspecific competition for females (Tolley *et al.,* 1995). It has been proposed that dolphins use their flukes during aggressive encounters (Connor *et al*., 2000).

Only one character in the present study displayed sexual shape dimorphism (Tables 5.2 and 5.3 -ANCOVA), where the females had a greater distance from the tip of the upper jaw to the genital aperture (T-GA). Similarly, for the short-beaked common dolphin (*D. delphis*), sexual size dimorphism was evident in 20 characters, while sexual shape dimorphism was only evident in two characters (Murphy, 2004).

During the current study sexual size dimorphism was evident while sexual shape dimorphism was not. Eight out of 26 characters demonstrated sexual size dimorphism. In a recent study on the same population, sexual dimorphism was not evident in cranial shape and size between males and females (Conry, 2012). This was confirmed in the present study where no significant differences were observed in any of the external head measurements between the sexes. Two of the characters that demonstrated sexual size dimorphism (T-GA and T-A) were expected due to differences in anatomy (Tolley *et al*., 1995; Murphy and Rogan, 2006). The main difference was that males possessed significantly larger appendages than the females. More extreme sexual size dimorphism was found in the short-beaked common dolphin (*D. delphis*), where 20 out of 25 characters demonstrated sexual dimorphism (Murphy, 2004). The common bottlenose dolphin (*T. truncatus*) also exhibited sexual dimorphism for a large number of characters (Tolley *et al*., 1995). In addition, the Dall's porpoise (*P. dalli*) demonstrated distinct sexual dimorphism, where most of the characters measured were significantly different (Jefferson, 1989). The males were larger and heavier than the females (Jefferson, 1989). Generally, in species where the male is larger, it has been suggested that there is intrasexual competition for females in a polygynous mating system (Jefferson, 1989). In fact, where there is extreme dimorphism, it is said to be a very good predictor of extreme polygyny (Ralls, 1977). *Stenella coeruleoalba* off the south east coast of South Africa does not show distinct sexual dimorphism in shape and size. However, the males possess significantly larger appendages. The absence of extreme sexual dimorphism and the presence of larger appendages in males suggesting intraspecific competition for females, indicates that *S. coeruleoalba* practices a less extreme form of polygyny (Ralls, 1977).

Chapter 6

General Discussion

The striped dolphin is frequently found stranded along the south east coast of South Africa, with the total number of specimens analysed increasing from 46 individuals in 1984 (Ross, 1984) to 101 individuals in 1993 (Kroese, 1993) and to 128 individuals in the present study. However, there is a lack of information on its biology and ecology in this region (Kroese, 1993). A number of aspects of the biology of the striped dolphin were assessed in this study, including age and length at physical and sexual maturity, growth rates, length at birth, pregnancy rates, components of the calving interval, reproductive seasonality, sexual dimorphism and allometric relationships in body size and shape. Using this information, inferences could be made about population parameters.

6.1 Stranding patterns

Stenella coeruleoalba strandings took place in seven hotspots along the south-east coast of southern Africa (n=96), as highlighted in Chapter 2 (Figure 2.2). This does not necessarily mean *S. coeruleoalba* have not stranded along other parts of the south-east coast, but that they may not have been discovered. Certain parts along the South African coast are remote and strandings are less likely to be found and reported. This is supported by the fact that the strandings that were reported are all from well-developed areas. The highest frequency of strandings were in the areas of Port Elizabeth (n=27) and Jeffery's Bay (n=26) (Figure 2.2). Along the east coast of southern Africa the northern Agulhas Current flows swiftly and closely along the narrow continental shelf with no regular meandering (Lutjeharms *et al.*, 1989). Once the current reaches Port Elizabeth, the continental shelf widens and forms the Agulhas Bank and regular shoreward meanders form (Lutjeharms *et al.*, 1989). Therefore, Algoa Bay and Jeffery's Bay are strongly influenced by the Agulhas current and represent a special situation in the course of the current (Goschen and Schumann, 1988). The broadening of the continental shelf and formation of meanders may partially explain why Algoa Bay and Jeffery's Bay have the highest stranding records of *S. coeruleoalba.*

6.2 The sample

In the sample each length class was represented by at least one individual, with the exception of female dolphins measuring between 160 and 179cm (Chapter 2, Figure 2.3). The sample consisted of fewer smaller individuals (between 80 and 199cm (n=25)) than expected, while the majority of males and females fell within a TBL of 200 to 239cm (n=62) (Chapter 2, Figure 2.3). The distribution of the different size classes suggests that sexually and physically mature individuals strand more frequently than juveniles. Additionally, there was a higher frequency of male strandings (Chapter 2, Figure 2.3). The length frequency of the sub-samples used for age determination and morphometric analysis were similar to the length frequency of the whole sample meaning that there were more males and an absence of calves and juveniles in the samples (Chapter 2, Figures 2.5 and 2.7). However, the length frequency of the reproductive sample had only three individuals smaller than 180cm (Chapter 2, Figure 2.6). The majority of the individuals fell within 180 and 259cm, indicating that this sample contained mostly mature individuals (Chapter 2, Figure 2.6). This was reflected in the reproductive analysis where fewer immature individuals were present.

The largest stranded individual was a male measuring 265cm in length, while the smallest stranded individual was a female measuring 93cm. This suggests that *S. coeruleoalba* along the south-east coast of southern Africa can reach lengths of up to 265cm, and calves can be born at lengths as small as 93cm, which is similar to that estimated for the Mediterranean population (92.5cm) (Aguilar, 1991).

6.3 Life history parameters

6.3.1 Temporal and geographic variations

Teeth from 59 *S. coeruleoalba* were used for age determination during this study. There was a good correlation between dentinal and cemental age estimates up to an age of about 11 years, after which the pulp cavity starts to become occluded. In an earlier study on the same population it was suggested that the average age of occlusion is approximately 14 GLG's (Kroese, 1993). For the population off Japan, occlusion occurred from about 11 years of age (Kasuya, 1976). During this investigation, the von Bertalanffy growth equation gave the best fit to the data based on the correlation coefficient. Predicted lengths at birth by the two growth models of 117cm and 112cm for males and females are higher than in other populations elsewhere in the world (present study, Kroese, 1993) (Table 6.1). They are also in disagreement with the length for the smallest individual that stranded, which was 93cm long, indicating that *S. coeruleoalba* off the south-east coast of southern Africa are born at lengths smaller than the predicted values (Table 6.1). The high predicted length at birth may be an artefact of the study, due to the paucity of calves in the sample. *S. coeruleoalba* off the south east coast could actually be born at lengths closer to that of the Mediterranean Sea population (Calzada *et al*., 1996; Di-Meglio *et al*., 1996) (Table 6.1).

The maximum length in the sample (265cm) is at least 20cm greater than the maximum lengths reported for other populations (Table 6.1). However, the maximum age estimates of 21 and 20.2 years in the present study for males and females, respectively, are slightly lower (up to 8 GLG's) than that of the other populations (Table 6.1). The present maximum ages are in the range reported for those of the Mediterranean Sea population (Calzada *et al*., 1996; Di-Meglio *et al*., 1996) and north-east Atlantic Ocean (Di-Meglio *et al*., 1996) (Table 6.1). The maximum ages of the previous study on the south-west Indian Ocean population (Kroese, 1993) are almost double those estimated for other populations (Table 6.1). Simarily, the maximum ages for the Japanese population are much greater (Kasuya, 1976) (Table 6.1). These estimates could possibly be over-estimated as *S. coeruleoalba* teeth have numerous accessory lines and as a result it is easy to misinterpret GLG's in this species (Hohn *et al.*, 1989). However, by using dentinal age estimates, maximum ages of 29 and 27.5 years were obtained for males and females, respectively, in the Japanese population (Miyazaki, 1977a).

Table 6.1 Temporal and geographic variations in life history parameters of *S. coeruleoalba*

Life history Parameter	Sex	SW Indian Ocean[1] (previous study)	SW Indian Ocean[2] (Present study)	NW Pacific Ocean[3,4,5,6]	NE Atlantic Ocean[7]	Mediterranean Sea[7,8,9]
Length at birth (cm)*	♂	107.7	117	100.5	-	~95
	♀	91.2	112	100.5	-	~95
Maximum length (cm)	♂	244.7	265	245	240	210
	♀	229.7	240	235	210	208
Maximum age (GLG's)	♂	46	21	50	29	25
	♀	41	20.2	49	23	22
Length at physical maturity (cm)	♂	245.9	231	236	216.07	191.20
	♀	229.8	224	225.3	200.10	194.75
Age at physical maturity (GLG's)	♂	25	21	21	8-9	-
	♀	20	18	17	5-6	-
Length at sexual maturity (cm)	♂	210 -230	209 - 224	218.3	-	190
	♀	200-240	213 - 215.5	211.5	-	182-194
Age at sexual maturity (GLG's)	♂	10-15	8.17 – 11.5	6.5-14.5	-	11.3
	♀	8.9	6.5 – 7.5	4.5-12.5	-	10-15
Gestation period (months)		-	12 – 13 (1 -1.08 years)	12-13	-	12
Annual pregnancy rate (%)		34	25.9	34.8	-	25
Ovulation rate/year		0.43 (2.3 years)	0.32 (3.1 years)	0.50 (2 years)	-	0.401 (2.5 years)
Calving Interval (years)		2.3	3.86	3.17	-	4
Reproductive seasonality		No	Unknown	Yes	-	-
Sexual dimorphism		-	Limited	-	-	-

[1]Kroese (1993), [2]Present study, [3]Kasuya (1976), [4]Kasuya and Miyazaki (1976); [5]Miyazaki, (1977b), [6]Miyazaki (1984), [7]Di-Meglio *et al.* (1996), [8]Calzada *et al.* (1996); [9]Aguilar (2000).

*The values for length at birth were determined by the growth models

Reproductive organs from 20 male and 27 female *S. coeruleoalba* were examined to determine the reproductive state of the individual animals. Due to poor preservation of the testes, males could only be classified as either immature or mature based on the presence or absence of spermatozoa. The attainment of sexual maturity (ASM) for males occurred between 8.17 and 11.5 years, 209 - 224cm total body length, and a mass between 73 - 167kg (Table 6.1). ASM occurred at a combined testis weight of between 16 and 41.2g, 8.4 - 10cm testis length, and 43.54 - 69.61μm seminiferous tubule diameter (Chapter 4, Table 4.2). In general, cetaceans possess testes that comprise more than 1% of their total body weight (Kenagy and Trombulak, 1986). This was not true in the present study as the maximum combined testis weight comprised only 0.24% of the total body weight. The humpback dolphin (*Sousa chinensis*) and the common bottlenose dolphin (*Tursiops truncatus*) possess relatively small testes of 0.7% and 1% of their total body weight, respectively (Cockcroft, 1993). Other odontocetes, such as the harbour porpoise (*Phocoena phocoena*) (Gaskin *et al*., 1984; Read 1990), short-beaked common dolphin (*Delphinus delphis*) (Cockcroft, 1993), vaquita (*Phocoena sinus*) (Hohn *et al*., 1996) and dusky dolphin (*Lagenorhynchus obscurus*) (van Waerebeek and Read, 1994), all possess testes that comprise more than 1% of their total body weight. This suggests that *S. coeruleoalba* have small testes in relation to their body size compared to other odontocetes. It has been suggested that species with relatively small testes have uni-male breeding systems, either monogamous or polygynous (Harcourt *et al*., 1981). However, species with relatively large testes have multi-male breeding systems and exhibit promiscuity (Jefferson, 1990). The small testis size suggests that *S. coeruleoalba* off the south east coast of southern Africa do not display multi-male breeding systems.

In females ASM occurred earlier than in the males at between 6.5 and 7.5 years of age, 213.2 – 215.5cm in length and a body weight of 93 – 103kg (Table 6.1). As with physical maturity, the age and length at sexual maturity is variable between various geographic populations (Table 6.1). The present populations' age and length at sexual maturity are similar to the north-west Pacific Ocean population (Miyazaki, 1984) (Table 6.1).

Macroscopic examination of the ovaries revealed that in most cases ovulations only occurred in the left ovary. Ovulations only occurred in the right ovary in individuals older than 10 years of age (n=4). An ovulation rate of 0.32 per year was calculated, indicating that on average ovulations occur every 3.1 years (37.2 months). This estimate is lower than the previous estimate for the present population, which was 0.43 per year (Kroese, 1993). The ovulation rate in the present study is also lower than that of other populations of *S. coeruleoalba* in the north-west Pacific Ocean and Mediterranean Sea, which range from 2 to 2.5 years (Table 6.1). A calving interval of 3.86 years was estimated in the present study (Table 6.1). This is similar to the calving interval of the north-west Pacific Ocean (Miyazaki, 1984) (3.2 years) and Mediterranean Sea populations (Calzada *et al*., 1996; Di-Meglio *et al*., 1996) (4 years) (Table 6.1). However, the present estimate of 3.86 years is higher than the previously estimated 2.3 years for the South African population (Kroese, 1993). It is worth noting that the previous estimate of 2.3 years was suggested to be an underestimate (Kroese, 1993). In the present study, the resting period for the South African population was estimated to be 1.86 years. Unfortunately, there were too few individuals in the present study to accurately estimate the lactation period.

Assuming that the sample is a good representative of the free ranging population, 25.9% of *S. coeruleoalba* females in the population off southern Africa would be pregnant at any one time. This estimate is slightly less than that estimated for the same population in 1993, which was 34% (Kroese, 1993) (Table 6.1). The higher pregnancy rate in 1993 could be due to differences in GLG interpretation or the inclusion of west coast animals in Kroese's (1993) study. However, it could also indicate that population density or food availability has decreased and females do not have enough energy to give towards foetus development. Alternatively the decrease in pregnancy rate could be due to the presence of pollution such as organochlorines with endocrine disrupting chemicals (Fossi, 2003). These chemicals detrimentally affect foetal development by interfering with important hormones (Fossi, 2003). The annual pregnancy rate (APR) differs by only 10% between populations, ranging from 25% to 34.8% (Table 6.1), suggesting that the APR is relatively invariable between separate populations. For example, in the overexploited Japanese population, the APR was only 10% higher than other less exploited populations, indicating that APR changes marginally with environmental conditions (Kasuya, 1985).

With regard to reproductive seasonality, the small sample size made it impossible to make any definite suggestions. In the present study, spermatogenesis seemed to occur all year round, however, testis weight and seminiferous tubule diameters fluctuate throughout the year and there is a possibility that there are two resting periods in April and September/October (Chapter 4, Figures 4.10 – 4.12). Additionally, by examining foetus and calf lengths, there is a possibility that there are two cohorts, with conceptions occurring in both August and December/January and births a year later (Chapter 4, Figure 4.22). These data for males and females could suggest that these dolphins reproduce seasonally, however, a larger sample size is needed to make any clear conclusions. In a previous study on the same population, diffuse breeding with peaks in births at certain times of the year was observed (Kroese, 1993). Similarly, this study was based on small sample size. Diffuse breeding, with peaks at certain times of the year, is known for other delphinids within the subregion, such as the common bottlenose dolphin (Cockcroft and Ross, 1990). On the other hand, clear reproductive seasonality was observed for the north-west Pacific population of *S. coeruleoalba* (Kasuya, 1972; Miyazaki, 1977a; Miyazaki, 1984) (Table 6.1). Three breeding seasons were observed for this population, one from February to May, another from July to September and the last one in December (Miyazaki, 1977a). The differences observed in reproductive seasonality are likely due to geographic variations in environmental conditions, such as food availability, water temperature etc. (Bronson, 1989).

Morphometric measurements were available from 104 stranded dolphins, 63 males and 41 females. Statistical analyses indicated that *S. coeruleoalba* along the south-east coast of southern Africa do not exhibit distinct sexual dimorphism for the majority of physical characters (Chapter 5, Table 5.2). This is consistent with studies on *S. coeruleoalba* skull morphology off the coast of South Africa and in the eastern tropical Pacific Ocean (Conry, 2012; Amaral *et al*., 2009). Sexual dimorphism was, however, displayed in the girth at the axilla and maximum girth, flipper length from the axilla to tip and from the centre of the eye to the ear. In the first three cases, the males were significantly larger, presumably to aid during mating and intraspecific competition for females (Tolley *et al*., 1995). This suggests that this population displays polygyny and not monogamy. The relationship between testis size, sexual dimorphism and mating strategy are so strong that both sexual dimorphism and testis size can be used an indicator of the type of mating system employed (Gomenido *et al*., 1998). The lack of distinct sexual dimorphism together with their small testis size, suggests that this population practises a less extreme form of polygyny (Ralls 1977; Gomenido *et al*., 1998), meaning that *S. coeruleoalba* off the south-east coast of southern Africa has a mating system in which one male copulates with many females (Ralls, 1977).

6.3.2 Comparison with similar sized delphinids

Tables 6.2 and 6.3 summarize the age and length at attainment of physical and sexual maturity of other delphinids around the world. The age and length at attainment of physical maturity for both males and females varies considerably between different species (Table 6.2 and 6.3). In general, the spinner dolphin (*S. longirostris*) appears to reach physical maturity at the youngest age and smallest length (Table 6.2 and 6.3) compared to other delphinids. While the striped (*S. coeruleoalba*) and spotted (*S. attenuata*) dolphins appear to reach physical maturity at the greatest age and length (Table 6.2 and 6.3). Male and female striped dolphins

(*S. coeruleoalba*) examined in the present study reach physical maturity at a similar age and length to the spotted dolphin (*S. attenuata*) in the NW Pacific Ocean (Kasuya, 1976) (Table 6.2 and 6.3).

In the present study, for both males and females the length at ASM for the striped dolphin (*S. coeruleoalba*) is higher than those obtained for the spotted (*S. attenuata*) and spinner (*S. longirostris*) dolphins in the Pacific Ocean and for the long-beaked common dolphin (*Delphinus capensis*) in the SW Indian Ocean (Table 6.2 and 6.3). However, the age at which males reach sexual maturity is similar to the spotted (*S. attenuata*), spinner (*S. longirostris*) and common (both *D. capensis* and *D. delphis*) dolphins (Table 6.2). In general, female striped dolphins (*S. coeruleoalba*) in the SW Indian Ocean, attain sexual maturity at a younger age compared to the spotted (*S. attenuata*) and common (*D. capensis* and *D. delphis*) dolphins (Table 6.3). However, they attain sexual maturity at a similar age to the spinner dolphin (*S. longirostris*) in the eastern tropical Pacific (Perrin *et al*., 1977; Perrin and Henderson, 1984) (Table 6.3).

Table 6.2 Comparison of age and length at attainment of physical and sexual maturity for similar sized male delphinids

Species and region	**Age at Physical maturity (years)**	**Length at physical maturity (cm)**	**Age at ASM (years)**	**Length at ASM (cm)**	**References**
Striped dolphin *S. coeruleoalba* SW Indian Ocean	21	231	8.17 – 11.5	209 - 224	Present study
Spotted dolphin *S. attenuata* NW Pacific Ocean	11.5	203.3	10.3[1]	197[1]	Kasuya *et al*., 1974
Spotted dolphin *S. attenuata* NW Pacific Ocean	21	236	7.5-15.5 11.8[2]	-	Kasuya, 1976
Spotted dolphin *S. attenuata* Eastern tropical Pacific	26	206	12	200.7	Perrin *et al.*, 1976
Spotted dolphin *S. attenuata* Eastern tropical Pacific	-	-	13.2[1]	186.4[1]	Hohn *et al.*, 1985
Spinner dolphin *S. longirostris* Eastern tropical Pacific	~ 13	179.46	6-11.5	174 - 176	Perrin *et al.*, 1977
Long-beaked common dolphin *D. capensis* SW Indian Ocean	-	-	10-12	200	Mendolia, 1989
Short-beaked common Dolphin *D. delphis* Atlantic Ocean	-	-	11 -13	200	Murphy, 2004
Short-beaked common dolphin *D. delphis* Atlantic Ocean	11	211.6	-	-	Murphy and Rogan, 2006

[1] Mean, [2] 50% mature

Table 6.3 Comparison of age and length at attainment of sexual and physical maturity for similar sized female delphinids

Species and region	**Age at Physical maturity (years)**	**Length at physical maturity (cm)**	**Age at ASM (years)**	**Length at ASM (cm)**	**References**
Striped dolphin *S. coeruleoalba* SW Indian Ocean	18	224	6.5 – 7.5	209 – 215.5	Present study
Spotted dolphin *S. attenuata* NW Pacific Ocean	11	194.9	7.5 - 9.5 8.2[1]	187[1]	Kasuya *et al.*, 1974
Spotted dolphin *S.attenuata* NW Pacific Ocean	17	225.3	7.5 - 11.5yrs 9[2]	-	Kasuya, 1976
Spotted dolphin *S. attenuata* Eastern tropical Pacific	18	190	9	187.3	Perrin *et al.*, 1976
Spotted dolphin *S. attenuata* Eastern tropical Pacific	-	-	11.4	-	Myrick *et al.*, 1986
Spotted dolphin *S. attenuata* Eastern tropical Pacific	-	-	7 - 16 [3] 6-11[4]	-	Chivers and Myrick, 1993
Spinner dolphin *S. longirostris* Eastern tropical Pacific	~ 11	170.91	5.6[2]	152-182 164.1[2]	Perrin *et al.*, 1977
Spinner dolphin *S. longirostris* Eastern tropical Pacific	~ 8.5	174.9	6.7[2]	157-188 167.2[2]	Perrin and Henderson, 1984
Long-beaked common dolphin *D. capensis* SW Indian Ocean	-	-	8-9	213	Mendolia, 1989
Short-beaked common dolphin *D. delphis* Eastern tropical Pacific	~ 26	197.2	5 - 12 7.8[1]	-	Danil and Chivers, 2007
Short-beaked common dolphin *D. delphis* NE Atlantic	-	-	10 - 12	-	Murphy, 2004
Short-beaked common dolphin *D. delphis* NE Atlantic	9	197.4	-	-	Murphy and Rogan, 2006

[1] Mean, [2] 50% mature, [3] Northern population, [4] Southern population

6.3.3 Comparison with other delphinids in the subregion

The life history parameters of some delphinids occurring along the southern coast of Africa are listed in Table 6.4. It is important to make these comparisons as these species inhabit a similar region with the same environmental conditions and may show some similarities in life history parameters. The gestation period of some delphinids in the subregion ranges from 10 to 13 months (Table 6.2). There is no indication that gestation period increases with an increase in size, but rather varies between the species. There is an indication, however, that the age at which sexual maturity is reached increases with size, with the exception of the Risso's dolphin (*Grampus griseus*) (Table 6.2). Although there is limited data on physical maturity, it would seem that a larger delphinid, such as the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), reaches physical maturity at a younger age and greater length than the smaller striped dolphin (*S. coeruleoalba*) (Table 6.2). This indicates that the larger Indo-Pacific bottlenose dolphin (*T. aduncus*) has a faster growth rate compared to the striped dolphin (*S. coeruleoalba*).

In general, delphinids found in the subregion do not exhibit seasonal reproduction, but there are peaks in the number of births at certain times of the year (Table 6.2). In all cases, these peaks fall within spring and summer, when the ocean warms and food is readily available. One notable exception is the long-beaked common dolphin (*D. capensis*), for which seasonal reproduction was observed in the subregion (Reddy, 1996) (Table 6.2). These dolphins are migrants within the subregion, which may account for the difference. Additionally, the striped dolphin (*S. coeruleoalba*) appears to also demonstrate seasonal breeding within the subregion.

Table 6.4 Life history parameters of Delphinids in the subregion. The species are listed from smallest to largest.

Species	Maximum TBL (cm)	Distribution	Coastal/ Oceanic	Physical maturity	Sexual maturity	Gestation length	Pregnancy rate	Seasonal reproduction	Sexual dimorphism
Spotted dolphin (*Stenella attenuata*)[1,6]	225cm	Tropical, subtropical and some warm temperate waters	Oceanic & coastal	?	?	11.3-11.5months	?	?	?
Striped dolphin (*Stenella coeruleoalba*)[4]	265cm	Warm temperate to tropical waters	Oceanic	21 GLGs 231cm ♂ 18 GLGs 224cm ♀	8.17-11.5GLGs 209-224cm ♂ 6.5-7.5GLSs 213-215.5cm ♀	12-13months	25.9%	Possibly seasonal?	Limited
Long-beaked common dolphin (*Delphinus capensis*)[1,2,3]	275cm	Warm temperate and tropical waters	Oceanic	?	10-12 GLG's 200cm ♂ 8-9 GLG's 213cm ♀	10months	36.5%	Yes (Migrators)	?
Humpback dolphin (*Sousa chinensis*)[1,6,7,8]	279cm	Indian Ocean and SW Pacific Ocean	Coastal	?	12-13 years ♂ 10 years 235cm ♀	10-12months	?	No Peak of births in spring and summer	Limited
Bottlenose dolphin (*Tursiops aduncus*)[1,5]	330cm	Temperate and tropical waters	Oceanic & coastal	12-15GLGs 245.6cm ♂ 12-15GLGs 239.9cm ♀	`~14.5 years ~240cm ♂ 9.5-11 years ♀	12.3months	5.2%-27%	No Peak of births in summer (Nov-Feb)	Yes
Risso's dolphin (*Grampus griseus*)[1,6]	341cm	Tropical and temperate waters	Oceanic	?	10-12 years ♂ 8-10 years ♀	10-11months	?	No Peak of births in spring and early summer	Proposed?

[1]Ross (1984), [2]Mendolia (1989), [3]Reddy (1996), [4]Present study, [5]Cockcroft and Ross (1990), [6]Best (2007), [7]Jefferson and Karczmarski (2001), [8]Weston (2011).

6.4 Limitations

It is important to remember that the dolphins examined in this study are stranded dolphins and, as a result, the study likely contains several biases. These are due to the fact that the animals may have died at sea and subsequently stranded or stranded and subsequently died. In addition, the animals have been collected over a long time period and wide geographic area. The cause of death is usually unknown and it is thought that stranded dolphins may not reflect the 'normal' population, as the animal may not be healthy, leading to stranding. Nevertheless, the information from the present study is in accordance with that of other striped dolphin populations, where the dolphins were captured at sea, for example the population off Japan. This suggests that the results from the present study truly reflect the life history of the southern African striped dolphin population.

Limitations to age determination were that some pulp cavities were almost occluded and it was difficult to read the last few dentinal GLG's. These counts may therefore be underestimated. The greatest source of error in age determination is the misinterpretation of GLG's (Hohn *et al*., 1989). Most age estimate errors are due to accessory lines or badly prepared sections (Hohn *et al.,* 1989). *Stenlla coeruleoalba* teeth have numerous accessory lines, therefore, it is important to standardise age estimation techniques in order to compare results from other studies.

Lastly, preservation of the testes was poor and this limited the ability to classify individuals as pubertal. Instead, both immature and pubertal individuals were categorised as immature. It would have been advantageous to be able to classify individuals as either immature or pubertal for comparative purposes and to better understand when sexual maturity occurs. Additionally, ovary weights and testis lengths were not recorded at the time of the dissections. Therefore, these had to be weighed and measured after preservation. This presents a limitation because the ovary weights and testis lengths may not be the same as they were at the time of the dissection.

6.5 Future studies

Further studies on the life history and reproductive seasonality of *S. coerulaoalba* off the coast of southern Africa should be conducted with larger sample sizes. It is also important that *S. coeruleoalba* populations are monitored long term. Changes in life history parameters can indicate changes in population dynamics, such as a decrease in population density. This will then have implications for the conservation and management of the species. Additionally, comparative life history studies should be conducted on *S. coeruleoalba* found on the west and east coast of South Africa. This is important due to the difference in cranial morphology between west and east coast animals (Conry, 2012). As west and east coasts of southern Africa pose very different environments oceanographically, this may be reflected in geographic variation of life history parameters, suggesting that different management strategies need to be implemented for the two populations.

6.6 Conclusions

In conclusion, the age, growth and reproductive parameters of the striped dolphin vary geographically between populations. In the present study, age and length at sexual and physical maturity is similar to that of the north-west Pacific population where *S. coeruleoalba* are captured at sea. This suggests that the life history parameters estimated during this study are a true reflection of the population off the south-east coast of southern Africa. It can also be concluded that the *S. coeruleoalba* off the coast of southern Africa do not display distinct sexual dimorphism, which confirms earlier studies on cranial morphology.

Appendix A

Stenella coeruleoalba records and available samples

PEM No.	Sex	Date	Lat (S)	Long (E)	Location	Teeth	Reproductive organs	Weight (Kg)	Total Body length (cm)
N0011	F	24/12/1979			-	-	X	147	231
N0026	-	-			-	X	-	-	-
N0053	-	-			-	X	-	-	-
N0071	-	-			-	X	-	-	-
N0079	-	-			-	X	X	-	-
N0108	-	-			-	X	-	-	-
N0114	M	10/04/1972	33^{0}45’	26^{0}24’	btwn woody cape and cape padrone	X	-	-	178
N0121	-	-			-	X	X	-	-
N0131	-	-			-	X	-	-	-
N0166	M	01/12/1972	34^{0}11’	24^{0}50’	Cape St francis	X	-	68.04	161.3
N0169	M	14/2/1972	33^{0}55’	24^{0}34’	Port Elizabeth	-	-	-	180.34
N0184	F	08/12/1972	34^{o} 01’	24^{o} 55’	Kabeljous River mouth (Jbay)	-	-	-	226
N0187	M	11/07/1972	33^{o} 41’	25^{o} 49’	Sundays River mouth	X	-	-	237
N0188	M	11/01/1972	33^{o} 57’	25^{o} 03’	Gamtoos River mouth	-	-	-	206
N0190	F	10/12/1972	34^{o} 02’	24^{o} 55’	Jefferies Bay	-	-	-	-
N0203	-	27/7/1973	34^{O}11’	24^{0}50’	Cape St francis	-	-	-	165.1
N0210	F	15/3/1974	33^{o} 41’	25^{o} 49’	Sundays River mouth	-	X	-	216
N0229	M	18/2/1975	33^{o} 51’	25^{o} 35’	Swartkops River mouth	-	X	87.09	196
N0245	F	10/07/1975	33^{o} 51’	25^{o} 35’	Sundays River mouth	-	-	-	221
N0264	F	26/12/1975	33^{o} 58’	25^{o} 38’	Humewood beach	X	X	126.55	228
N0269	-	01/01/1976			-	-	-	-	230
N0279	M	-			-	-	-	-	224
N0280	M	09/03/1976			-	-	-	145	239
N0288	F	02/11/1975	34^{o} 01’	22^{o} 48’	Sedgefield	X	X	-	206
N0289	M	11/04/1976			-	X	X	131	244
N0291	M	08/10/1969	34^{o} 01’	25^{o} 22’	Kini-Bay	-	-	113.6	228.6
N0300	M	13/12/1976	34^{o} 02’	23^{o} 22’	Plettenburg Bay	-	X	106	218
N0321	-	-			-	-	-	-	-
N0346	-	29/3/1978	34^{o} 10’	24^{o} 39’	Oyster bay	X	-	-	198
N0349	M	19/4/1978	34^{o} 04’	24^{o} 54’	Aston Bay	X	X	78.5	215

N0351	M	23/4/1978	34° 01’	24° 55’	Kabeljous River mouth (Jbay)	X	-	-	230
N0354	M	05/07/1978	34° 01’	25° 40’	Cape Recife	X	-	-	238
N0363	M	21/5/1978	28° 22’	32° 25’	St Lucia (Natal)	X	X	167	186
N0393	M	27/4/1979	33° 58’	25° 13’	Van Stadens River mouth	X	-	-	241
N0427	-	-			-	-	-	-	-
N0431	-	-			-	-	-	-	-
N0439	M	29/4/1975	32° 58’	27° 52’	East London	X	-	-	234.3
N0443	M	03/12/1980	33° 51’	25° 35’	Swartkops River mouth	-	X	-	cut off tail
N0446	-				-	-	-	-	-
N0447	M(N)	17/6/1980	33° 58’	25° 38’	Kings Beach	X	-	25.9	137.5
N0448	F	17/7/1980	34° 01’	24° 55’	Kabeljous River mouth (Jbay)	X	X	128	228
N0708	F	29/6/1981	34° 02’	25° 29’	Sardinia Bay	X	X	-	220
N0711	M	20/7/1981	33° 58’	25° 13’	Van Stadens River mouth	-	-	-	238
N0763	M	13/12/1979	29° 51’	31° 01’	Durban	-	-	-	232.5
N0775	M	09/07/1981	33° 44’	26° 33’	Boknes River mouth	X	-	87	210
N0781	M	10/10/1981	33° 47’	25° 40’	Coega River Mouth	X	X	91	207
N0785	M	11/10/1981	33° 38’	26° 44’	Kasouga River mouth	-	-	-	265
N0838	-	-			-	X	-	-	-
N0843	M	07/03/1982			-	X	-	42	169
N0849	F	07/09/1982			-	-	X (P)	131	229
N0865	F	09/06/1981	34° 02’	25° 29’	Sardinia Bay, PE	X	X	113	218
N0880	M	10/03/1982	34° 10’	24° 39’	Oyster bay	X	-	-	202
N0891	M	16/10/1982	33° 57’	25° 03’	Gamtoos River mouth	X	-	-	240
N0935	M	04/11/1983	29° 31’	31° 12’	Balito Bay, Natal	X	-	130	235
N0936	F	04/11/1983	28° 46’	32° 02’	Richards Bay, Natal	X	X	108	235
N0993	-	10/10/1983	34° 01’	22° 52’	Goukamma, South Cape court	X	X	-	-
N1019	M	18/12/1983	33° 41’	25° 49’	Sundays River mouth	X	-	-	240
N1046	M	-			Natal	X	X	96	208
N1053	M	24/7/1984	30° 24’	30° 40’	Sezela, Natal	X	X	114	233
N1119	M	01/05/1985	33° 58’	25° 38’	Kings Beach	X	X	157	244
N1145	F	18/4/1985			-	-	-	-	135
N1246	F	10/03/1985	33° 55’	25° 34’	Port Elizabeth	X	X	92	211
N1288	F	08/05/1986	34° 01’	24° 55’	Kabeljous River mouth (Jbay)	-	-	22.9	136

N1318	-	25/10/1984	33^{o} 41’	25^{o} 49’	Sundays River mouth	X	-	-	235
N1324	M	12/08/1986	34^{o} 02’	24^{o} 55’	Jefferies Bay	-	-	85	200
N1378	F	19/6/1987	34^{o} 02’	24^{o} 55’	Paradise Beach, Jefferies bay	X	X	129	224
N1471	M	22/2/1988			-	-	X	79	211
N1533	M	25/04/1988	34^{o} 01’	25^{o} 40’	Cape Recife	-	-	-	178
N1545	F (N)	08/06/1988	27^{o} 33’	32^{o} 40’	Sodwana Bay, Natal	-	-	11.1	110
N1568	F	02/04/1989			Natal	X	P	-	233
N1569	-	20/2/1989	33^{o} 41’	25^{o} 49’	Sundays River mouth	X	-	-	244
N1574	M	23/2/1989	30^{o} 50’	30^{o} 21’	Ramsgate, natal	X	X	98	210
N1585	F	02/05/1989	32^{o} 58’	27^{o} 52’	East London	X	X	113	222
N1640	F (N)	09/05/1989	32^{o} 58’	27^{o} 52’	East London	-	-	10	100
N1650	M	11/12/1989	34^{o} 02’	24^{o} 55’	Jefferies Bay	X	X	110	220
N1652	F	01/08/1990	34^{o} 11’	24^{o} 50’	Cape St Francis	X	X	103	214
N1775	M	08/08/1990	28^{o} 22’	32^{o} 25’	St Lucia (Natal)	X	-	134	258
N1776	M	08/08/1990	28^{o} 06’	32^{o} 33’	Cape Vidal, Natal	X	-	30	150
N1782	M	31/8/1990	33^{o} 55’	25^{o} 34’	PE Oceanarium	X	X	-	224
N1899	F (N)	19/10/1992	32^{o} 58’	27^{o} 52’	East London	-	-	7	93
N1991	M	05/03/1992			Lower south coast, Natal	-	-	-	240
N1993	F	10/09/1992	34^{o} 02’	24^{o} 55’	Jefferies Bay	X (3)	X	115	240
N1995	F (N)	20/10/1992	32^{o} 58’	27^{o} 52’	East London	X	-	13	112
N1997	M	29/6/1992	29^{o} 31’	31^{o} 12’	Salmon bay, Ballito	X	-	67	184
N1998	M(N)	15/7/1992	30^{o} 02’	30^{o} 52’	Amazintoti, Durban	-	-	11.25	113
N2028	-	02/08/1993	33^{o} 47’	25^{o} 40’	Coega River mouth	X	-	-	221
N2030	M(N)	25/2/1993			-	-	-	14.2	108
N2040	F	13/05/1993	34^{o} 02’	23^{o} 22’	Plettenburg Bay	X	X (P)	-	-
N2111	F	22/6/1993	30^{o} 58’	30^{o} 16’	Impenjata-Palm Beach, Transkei	X	X	57	184.5
N2112	F	06/09/1993	30^{o} 11’	30^{o} 46’	Umkomaas, Natal	X	X	79	215.5
N2136	F	12/06/1994	33^{o} 40’	26^{o} 40’	Kenton-on-sea	X	X	127	228
N2138	F	01/11/1994	32^{o} 58’	27^{o} 52’	East London	X	X	93	204
N2173	M	13/10/1993			Natal	X	-	102	220
N2174	M	12/06/1993			-	-	-	83.5	203
N2184	F	15/3/1994	34^{o} 00’	25^{o} 21’	Seaview, PE	X	X	127	231.5
N2245	M	02/06/1994	33^{o} 12’	27^{o} 36’	Kaysers	-	-	30.5	140

					Beach, East London				
N2306	M	22/8/1994	27^{o} 33’	32^{o} 40’	Sodwana Bay, Natal	X	X	129	227
N2462	M	01/12/1996	33^{o} 40’	26^{o} 40’	Kenton-on-sea	-	X	95	207
N2483	M(N)	17/1/1996			Natal	X	X	8.6	99
N2486	F	27/2/1996	34^{o} 02’	24^{o} 55’	Jefferies Bay	X	X	134	225
N2516	-(N)	15/04/1997	34^{o} 02’	24^{o} 55’	Jefferies Bay	X	-	-	107
N2524	M	10/11/1996	34^{o} 01’	25^{o} 40’	Cape Recife	-	-	32.4	142
N2525	-	-			-	-	-	-	-
N2530	-	31/1/1997			-	-	-	-	110
N2624	F	01/02/1996			South coast	-	-	32	146
N2632	-	-			-	X	-	-	-
N2640	F (N)	30/07/1997	33^{o} 57’	25^{o} 03’	Gamtoos River mouth	-	-	16	96.4
N2838	M	08/09/2000	34^{o} 10’	22^{o} 07’	Mossel Bay	X	X	65	190
N2868	M(N)	20/7/1999	31^{o} 03’	30^{o} 13’	Port Edward, KZN	-	X	9.2	104
N3240	M	24/06/2005	29^{o} 51’	31^{o} 01’	South beach, Durban	X	X	73	209
N3272	F	24/07/2006			Natal	X	X	33	145
N3446	M(N)	??/08/2007	32^{o} 58’	27^{o} 52’	East London	X	-	15	100
N3474	F	07/03/2009	30^{o} 11’	30^{o} 46’	Umkomaas, Natal	X	X (P)	135	220
N3553	F	29/1/2010	33^{o} 59’	25^{o} 17’	Maitlands River mouth	-	X	-	223.6
N3566	M	04/05/2010	34^{o} 09’	24^{o} 49’	St Francis Bay	-	X	-	238
N3587	M	18/11/2009			-	X	X	115	224.8
N4350	-	01/04/2010	30^{o} 56’	30^{o} 17’	San Lameer, Natal	X	-	31	140.2
N4520	F	24/12/2010	33^{o} 40’	26^{o} 38’	Bushmans River mouth	X	X (P)	-	209.8
N4545	F	16/4/2011	34^{o} 09’	24^{o} 49’	St Francis Bay	X	X	-	220
N4547	F	02/10/2011	34^{o} 02’	24^{o} 55’	Jefferies Bay	X	X (P)	-	213.2
N4550	M	02/10/2011	34^{o} 09’	24^{o} 49’	St Francis Bay	X	-	-	204
N4603	M	04/08/2011	33^{o} 58’	24^{o} 59’	Btween Gamtoos and Kabeljous	-	-	-	226.4
N4604	M	12/03/2011	34^{o} 11’	24^{o} 50’	Cape St francis	-	-	-	241
N4612	M	30/01/2012	34^{o} 02’	23^{o} 04’	Knysna	-	-	-	208.3
N4633	F	18/03/2012	34^{o} 02’	25^{o} 29’	Sardinia Bay	-	P	-	220
N4648	M	02/02/2012	29^{o} 51’	31^{o} 01’	Durban	X	X	105	246
N4649	F	30/03/2011			-	X	X	-	211.8
N4650	F	10/01/2011	28^{o} 06’	32^{o} 33’	Cape Vidal, Natal	X	X	103	219.8

Appendix B

Results of the morphometric regression analysis

Linear Body measurements

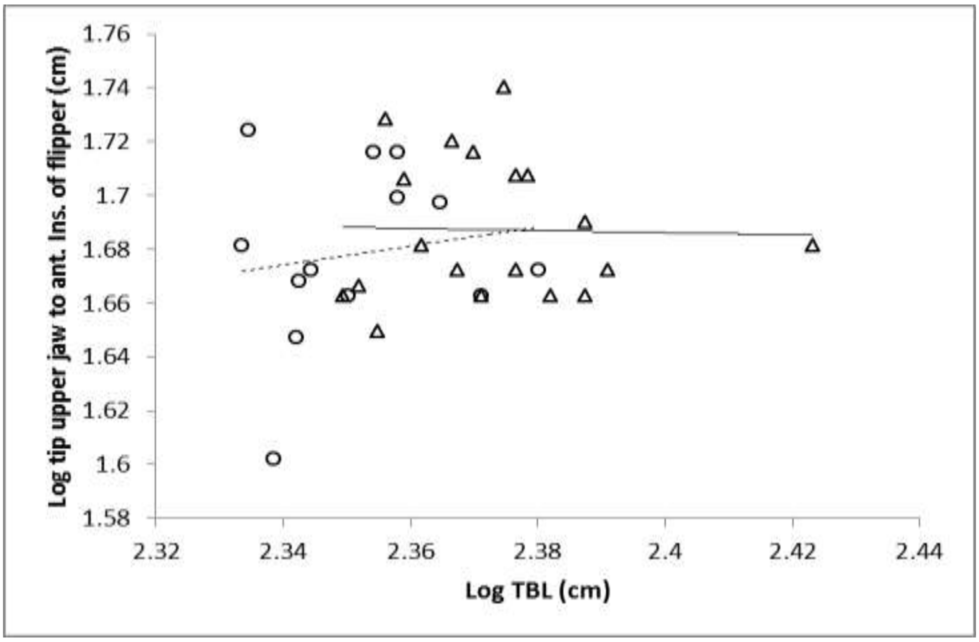

Figure 1 Total body length plotted against the tip of the upper jaw to the anterior insert of the flipper for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0007$ (male); 0.0232 (female).

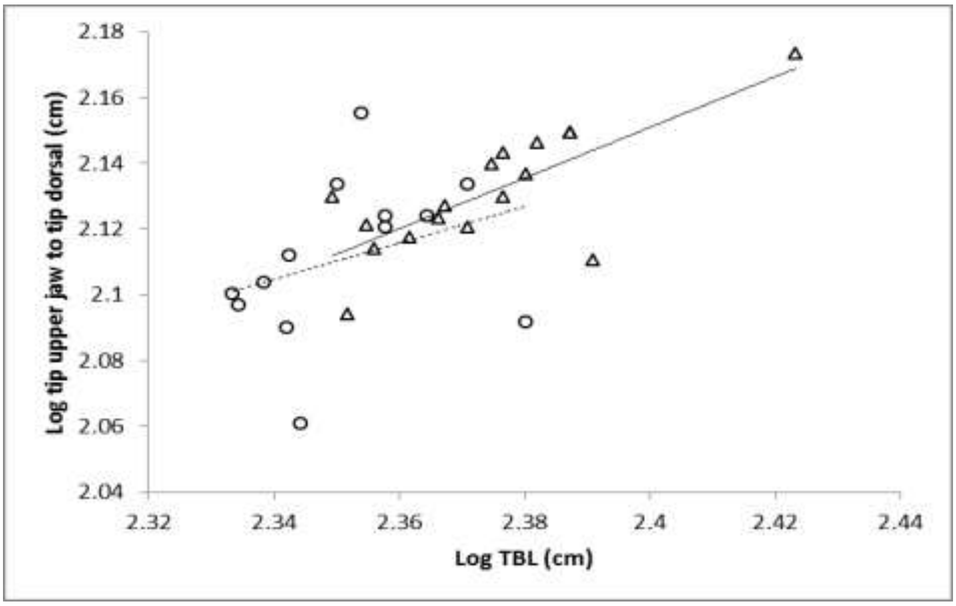

Figure 2 Total body length plotted against the tip of the upper jaw to the tip of the dorsal fin for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.567$ (male); 0.1055 (female).

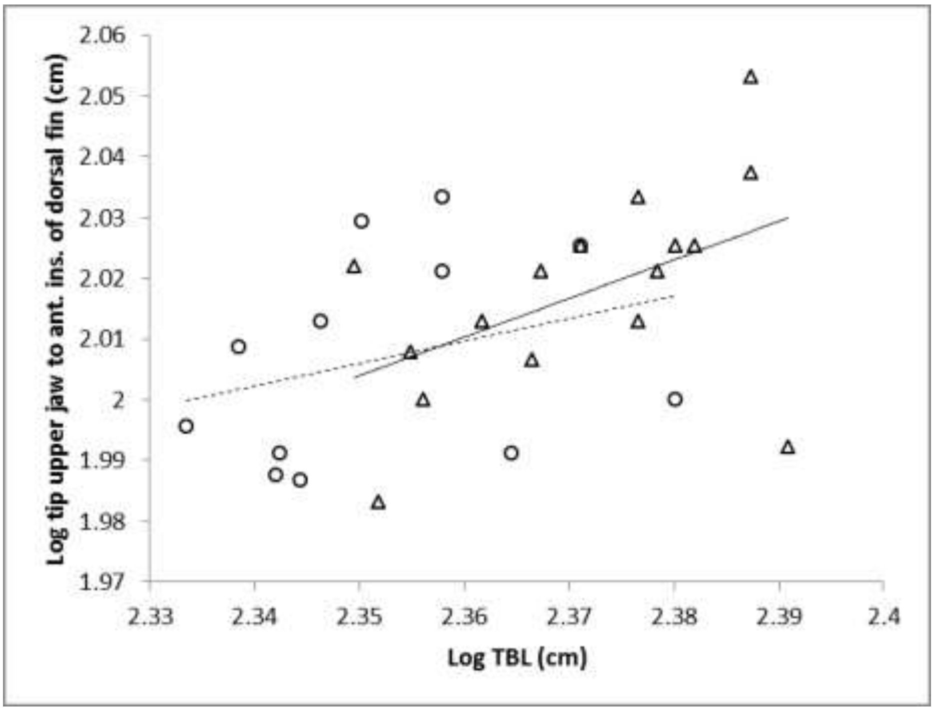

Figure 3 Total body length plotted against the tip of the upper jaw to the anterior insert of the dorsal fin for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.2397$ (male); 0.0932 (female).

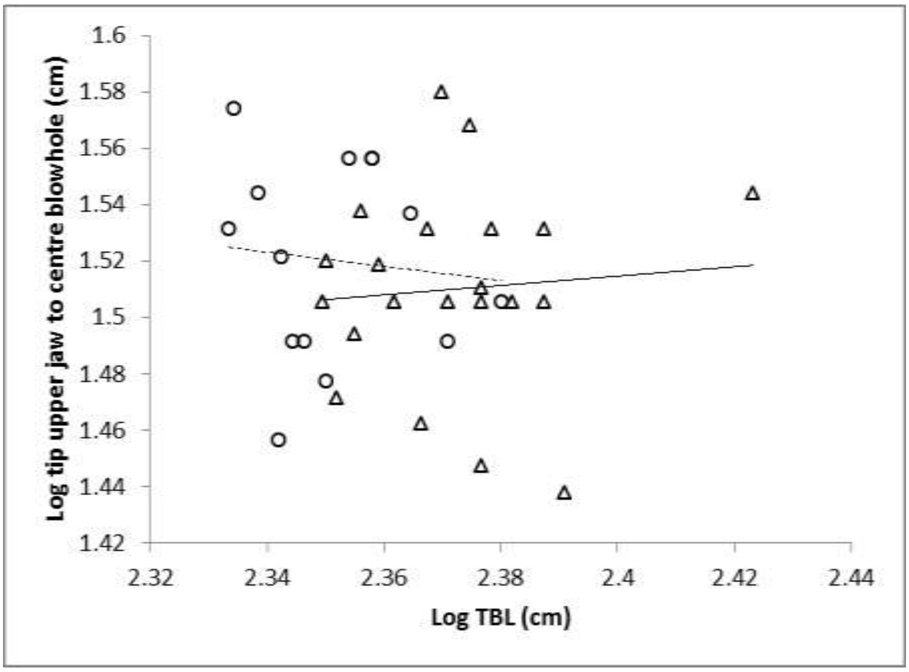

Figure 4 Total body length plotted against the tip of the upper jaw to the centre of the blowhole for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0065$ (male); 0.0097 (female).

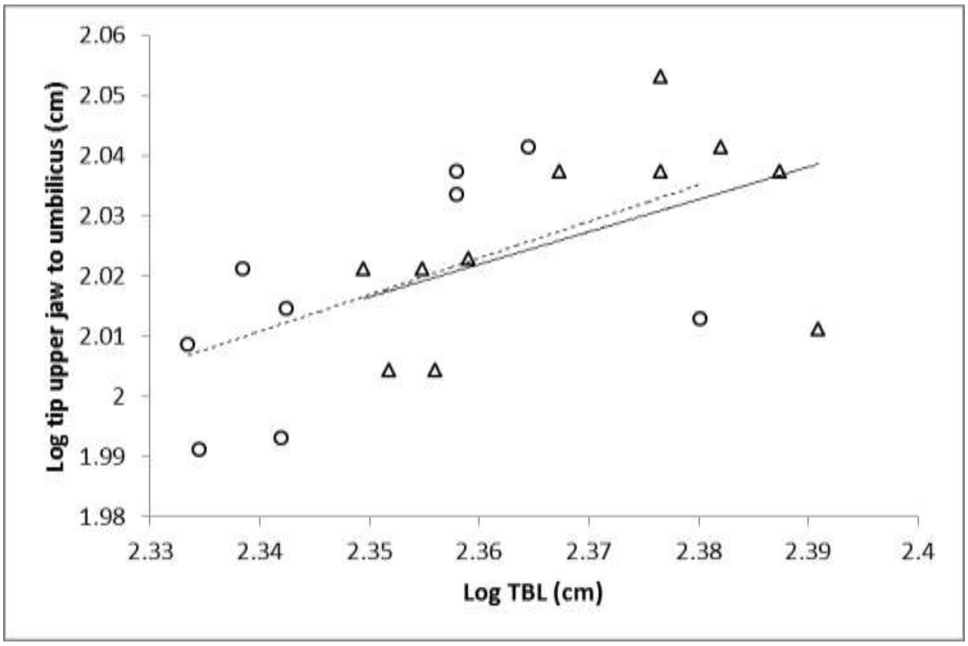

Figure 5 Total body length plotted against the tip of the upper jaw to the midpoint of the umbilicus for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.2537$ (male); 0.2829 (female).

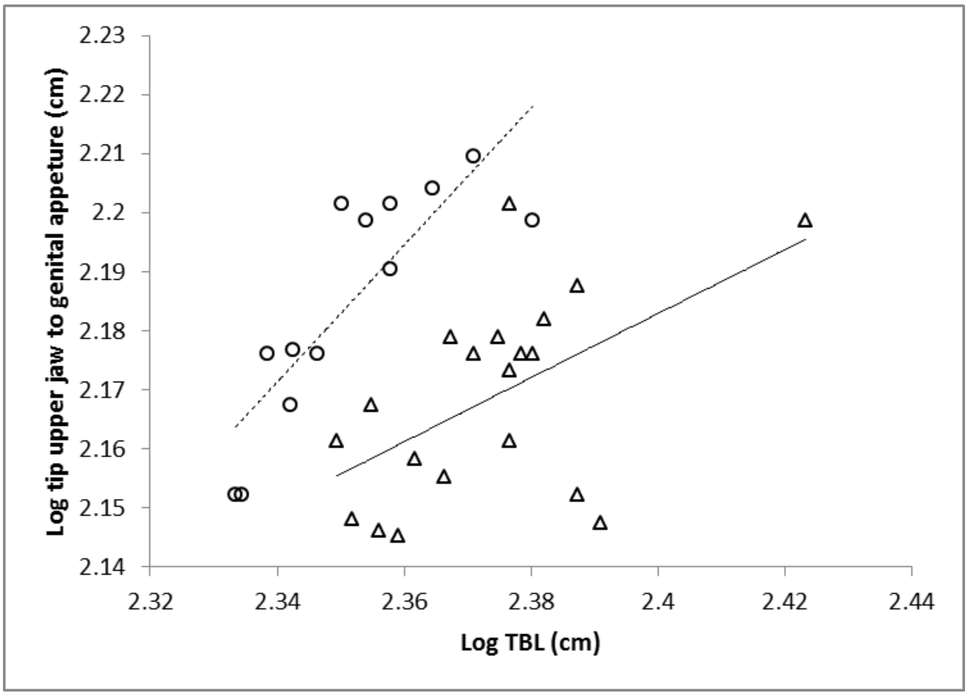

Figure 6 Total body length plotted against the tip of the upper jaw to the genital aperture for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.2931$ (male); 0.7132 (female).

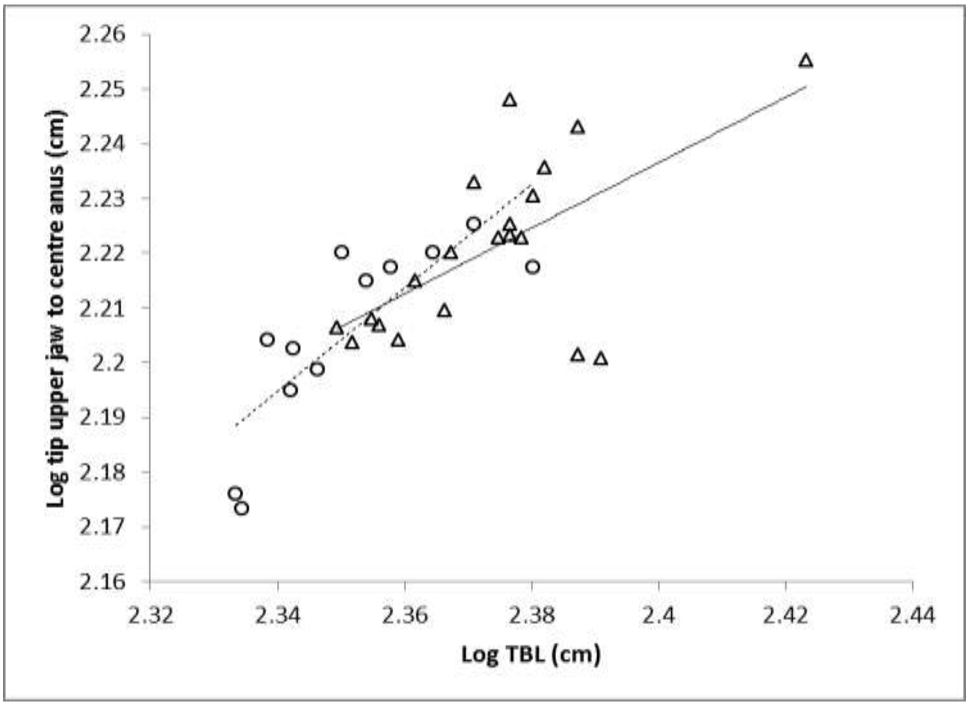

Figure 7 Total body length plotted against the tip of the upper jaw to the centre of the anus for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.3929$ (male); 0.6525 (female).

Head measurements

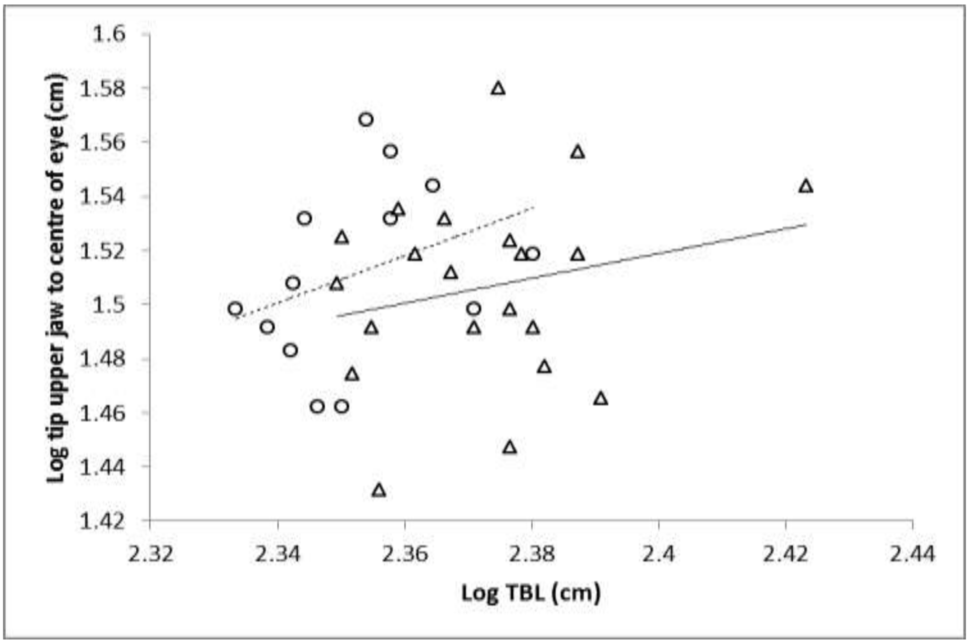

Figure 8 Total body length plotted against the tip of the upper jaw to the centre of the eye for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0492$ (male); 0.1231 (female).

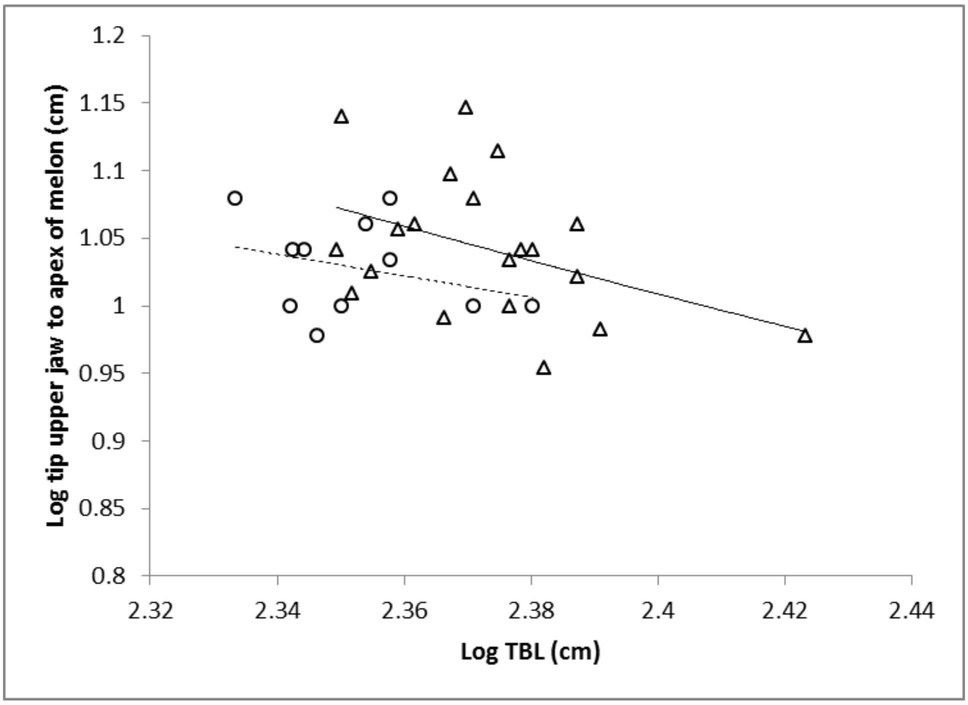

Figure 9 Total body length plotted against the tip of the upper jaw to the apex of the melon for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.1765$ (male); 0.0955 (female).

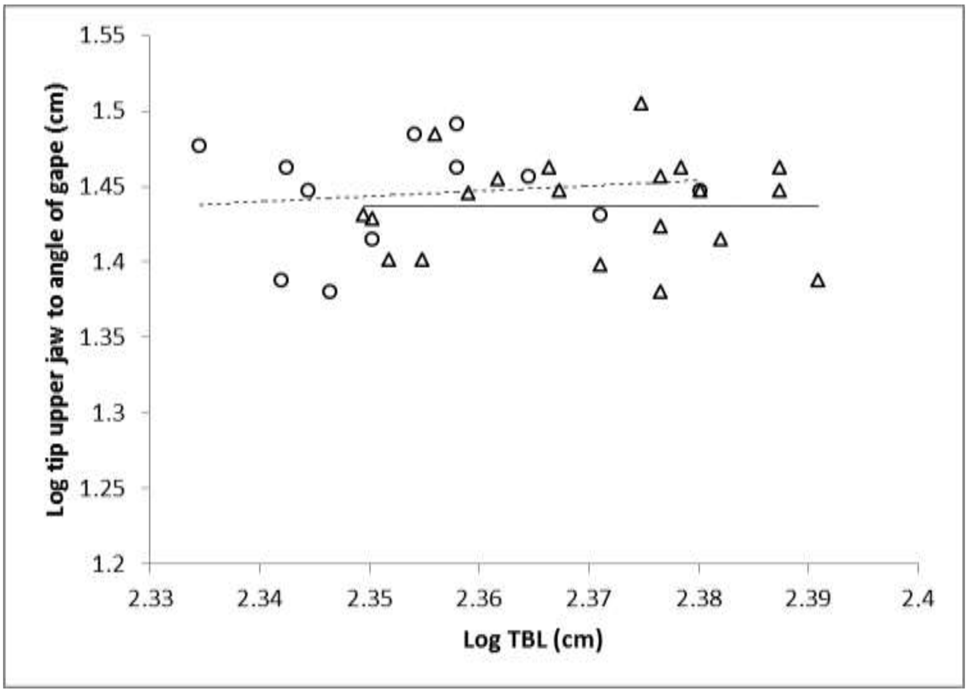

Figure 10 Total body length plotted against the tip of the upper jaw to angle of gape for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.000008$ (male); 0.0165 (female).

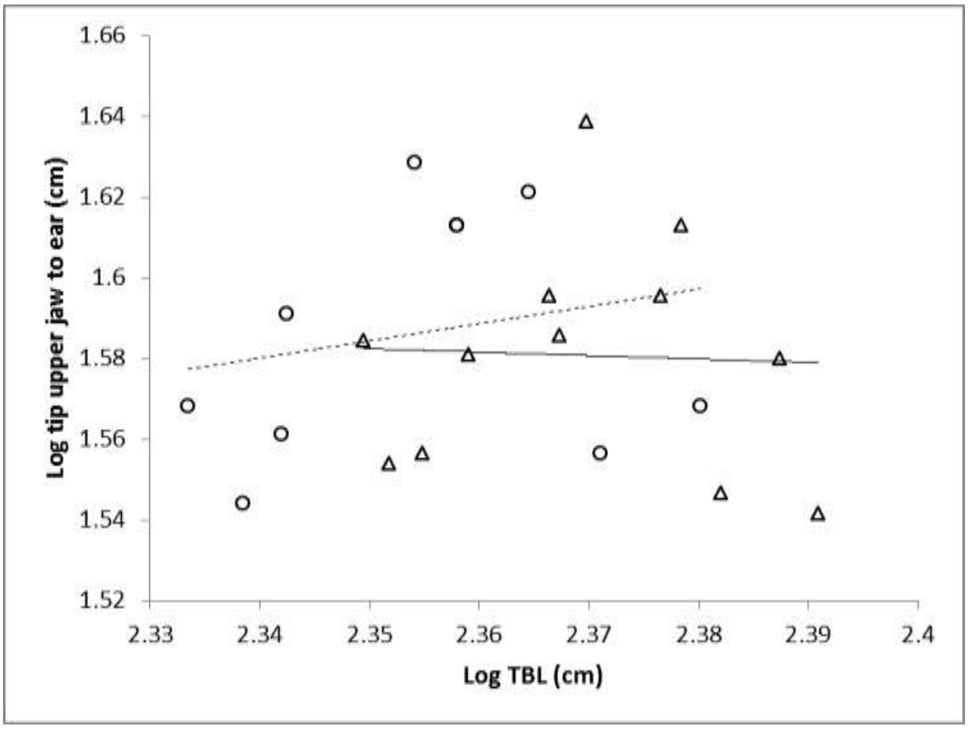

Figure 11 Total body length plotted against the tip of the upper jaw to the centre of the ear for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0018$ (male); 0.0447 (female).

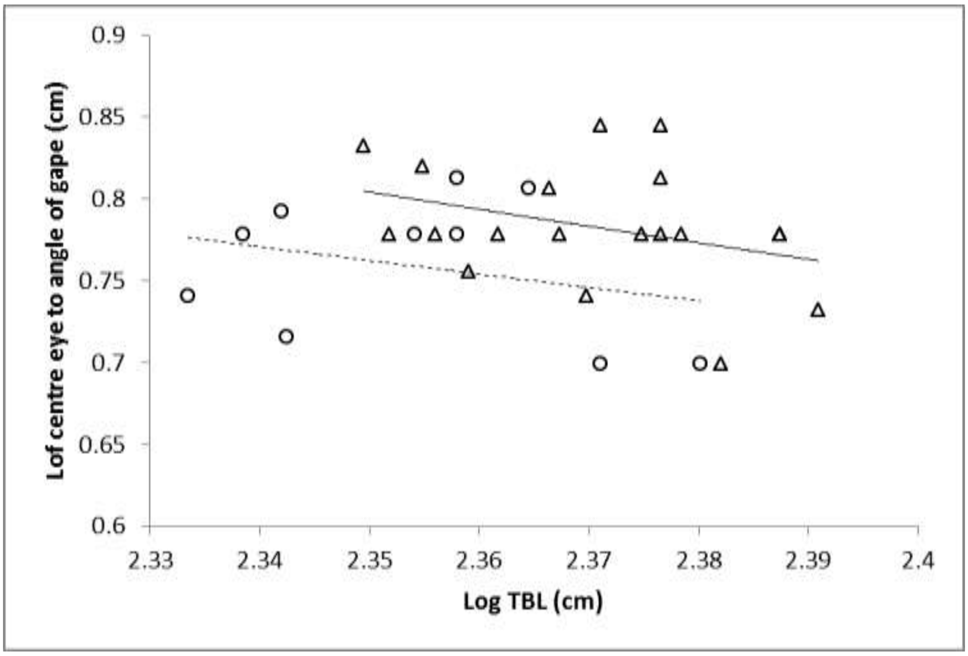

Figure 12 Total body length plotted against centre of the eye to the angle of gape for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.1144$ (male); 0.0836 (female).

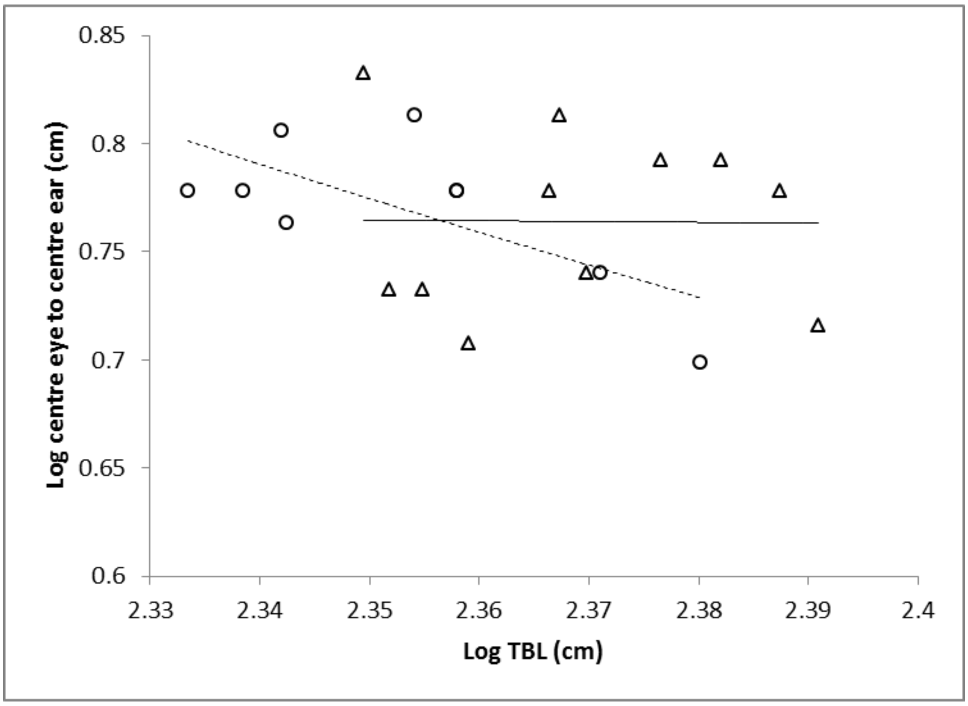

Figure 13 Total body length plotted against centre of the eye to the ear for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0002$ (male); 0.4853 (female).

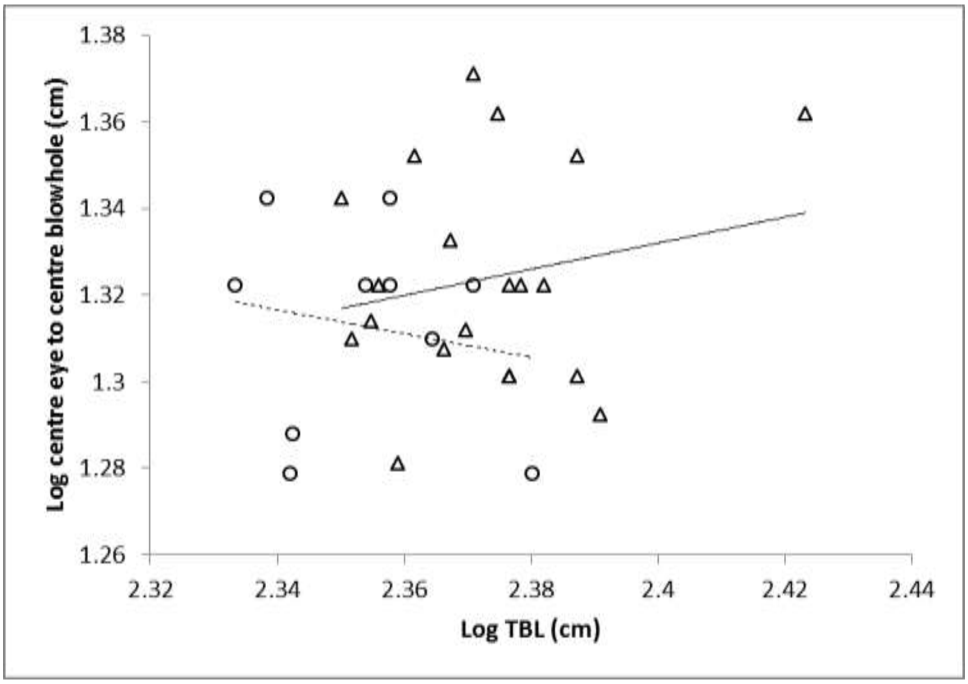

Figure 14 Total body length plotted against centre of the eye to the centre of the blowhole for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0403$ (male); 0.0303 (female).

Girth measurements

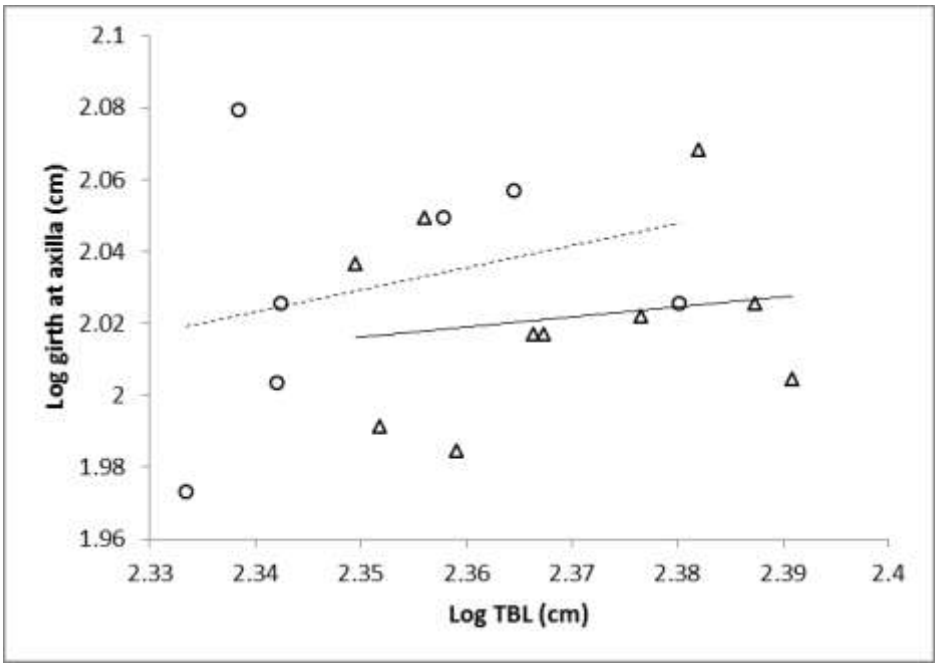

Figure 15 Total body length plotted against the girth at the axilla for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.027$ (male); 0.0852 (female).

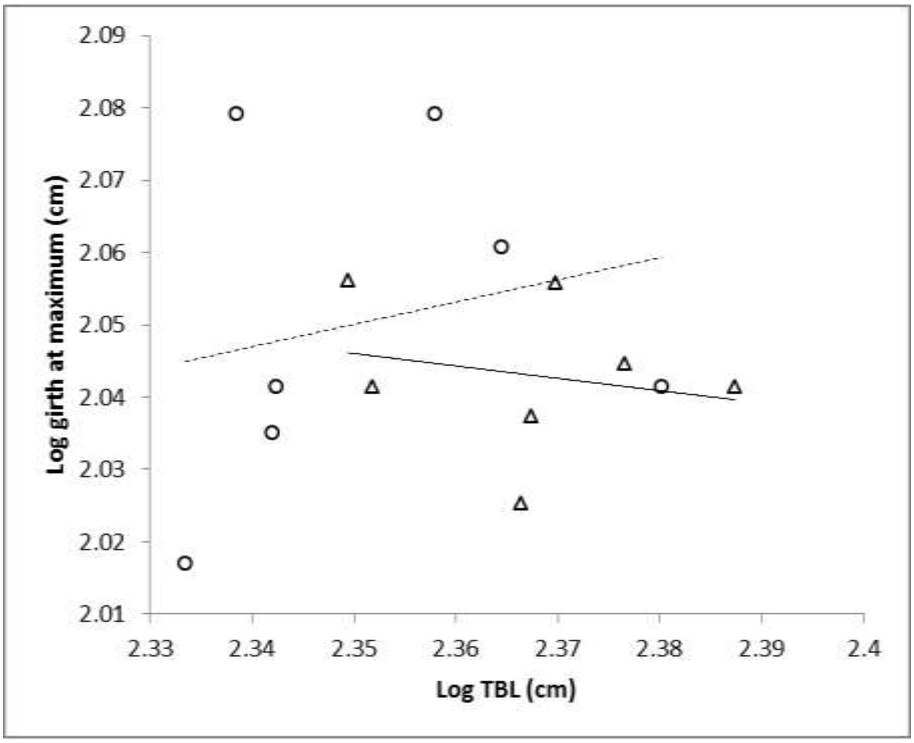

Figure 16 Total body length plotted against the girth at maximum for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0449$ (male); 0.0495 (female).

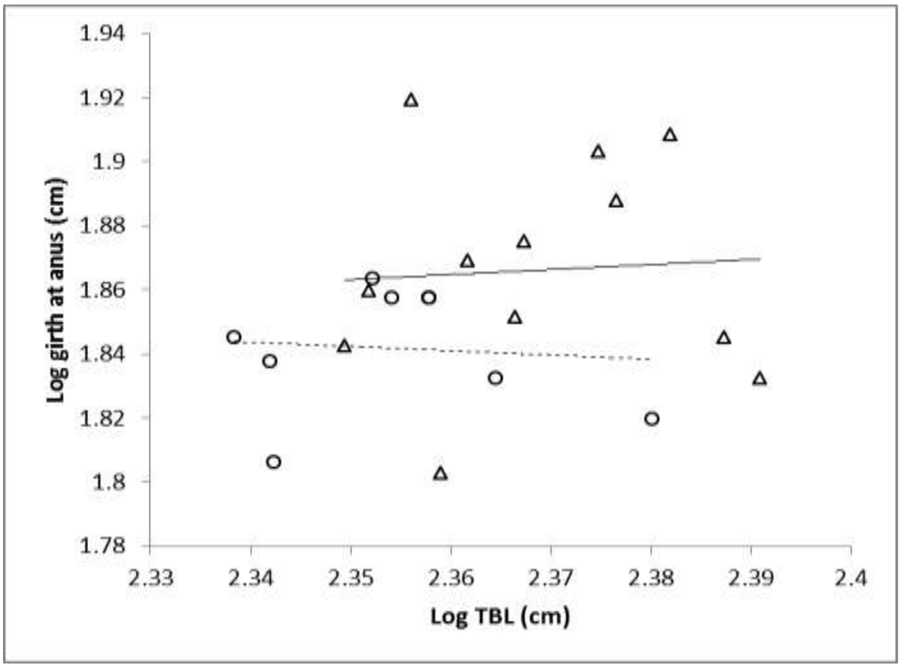

Figure 17 Total body length plotted against the girth at the anus for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0039$ (male); 0.0078 (female).

Appendage measurements

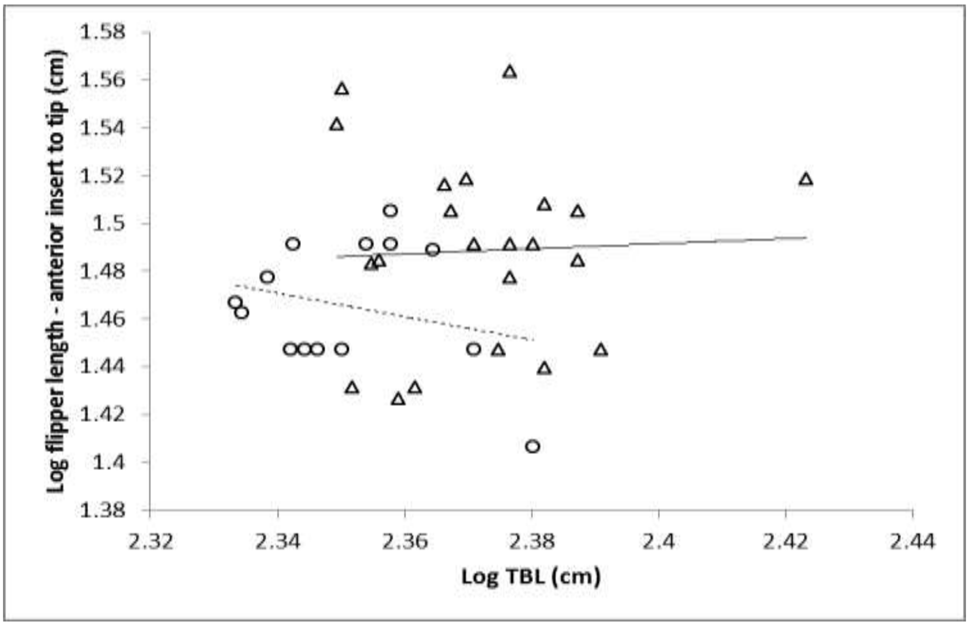

Figure 18 Total body length plotted against flipper length from the anterior insert to the tip for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0021$ (male); 0.0637 (female).

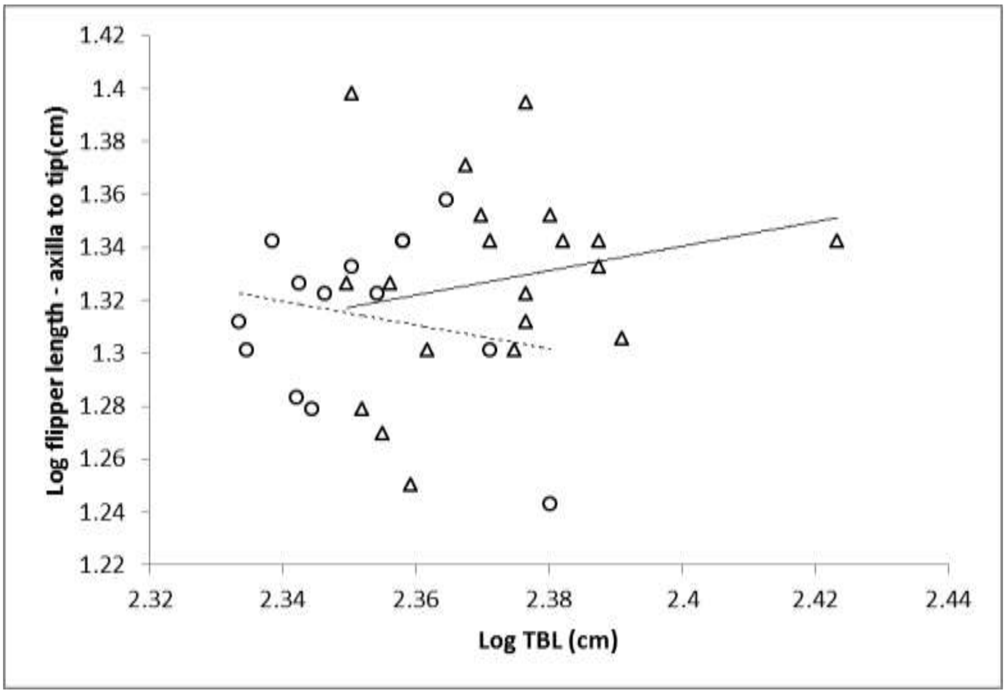

Figure 19 Total body length plotted against flipper length from the axilla to the tip for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females., $r^2 = 0.0458$ (male); 0.0394 (female).

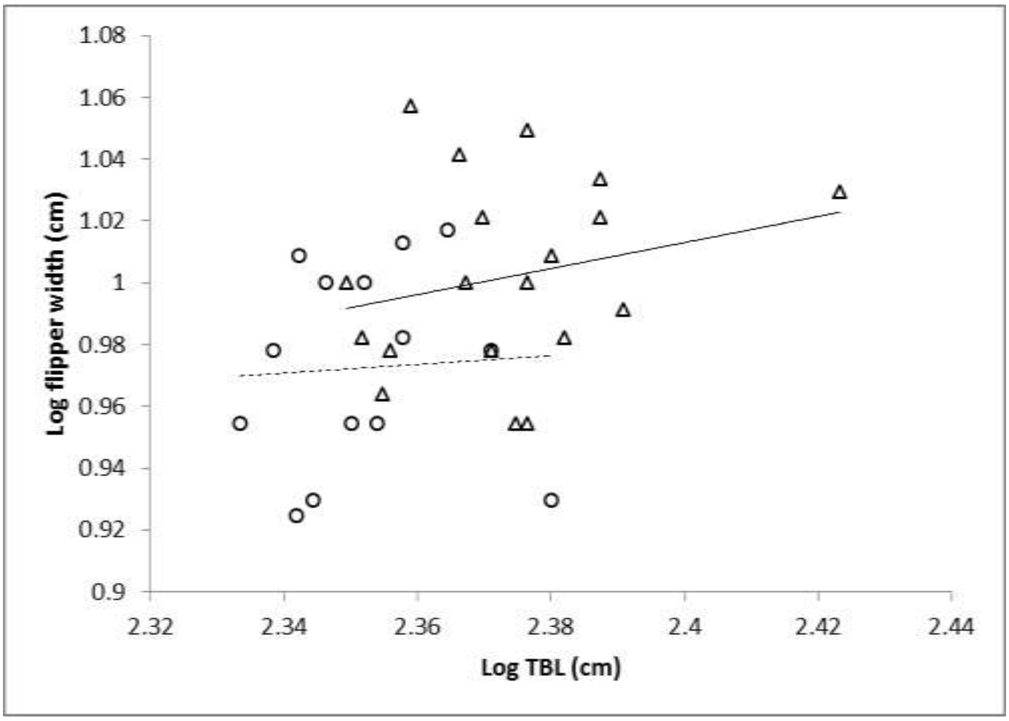

Figure 20 Total body length plotted against the maximum flipper width for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, r^2 = 0.0541 (male); 0.0032 (female).

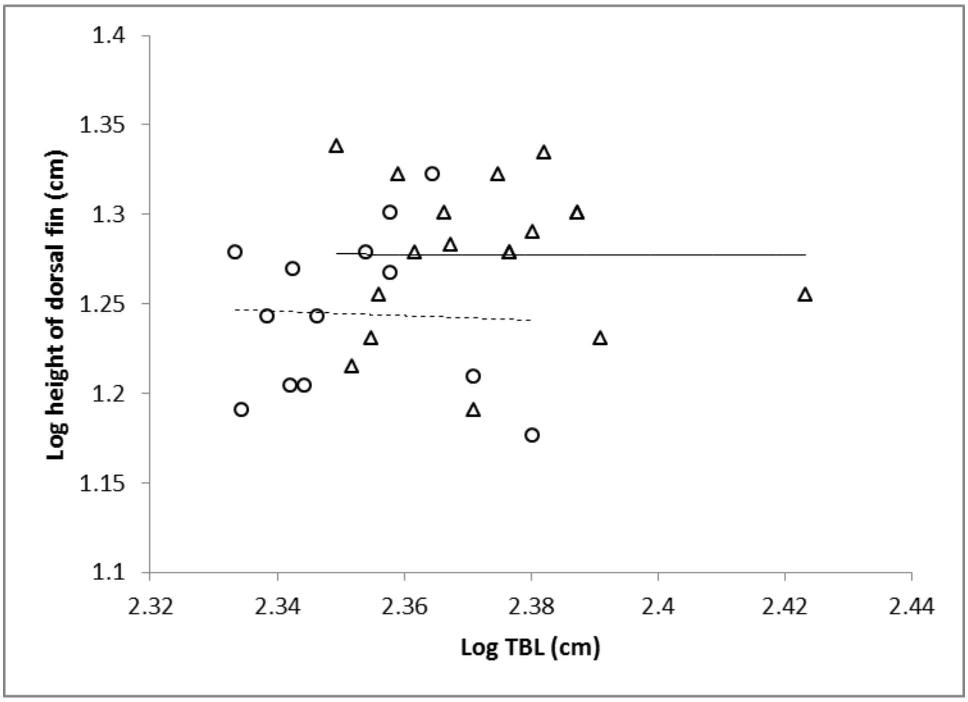

Figure 21 Total body length plotted against the height of the dorsal fin for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, r^2 = 0.00002 (male); 0.0016 (female).

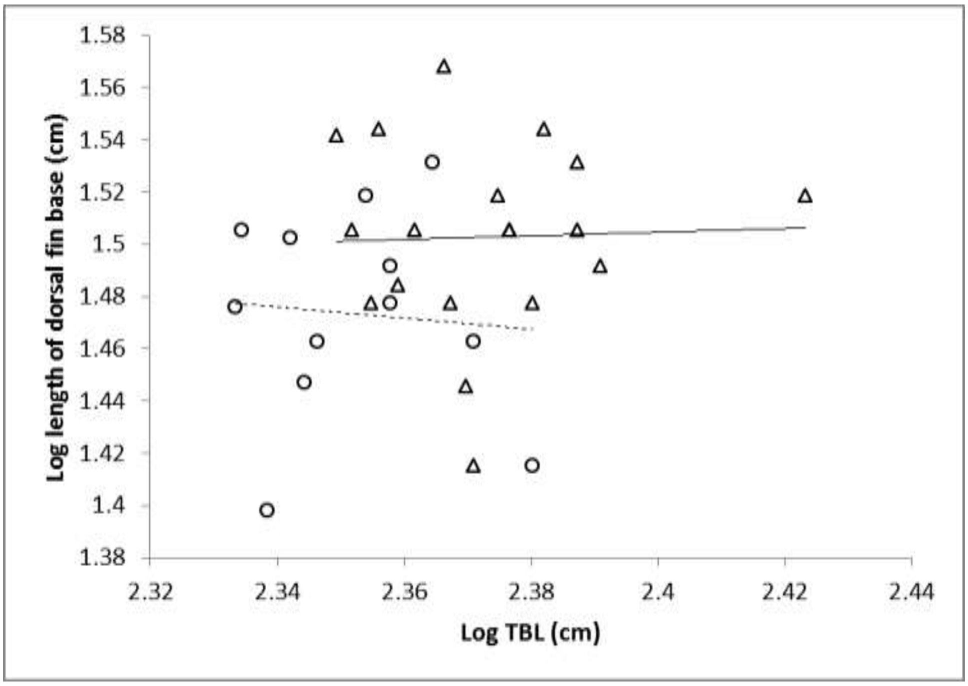

Figure 22 Total body length plotted against the length of the dorsal fin base for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0011$ (male); 0.0061 (female).

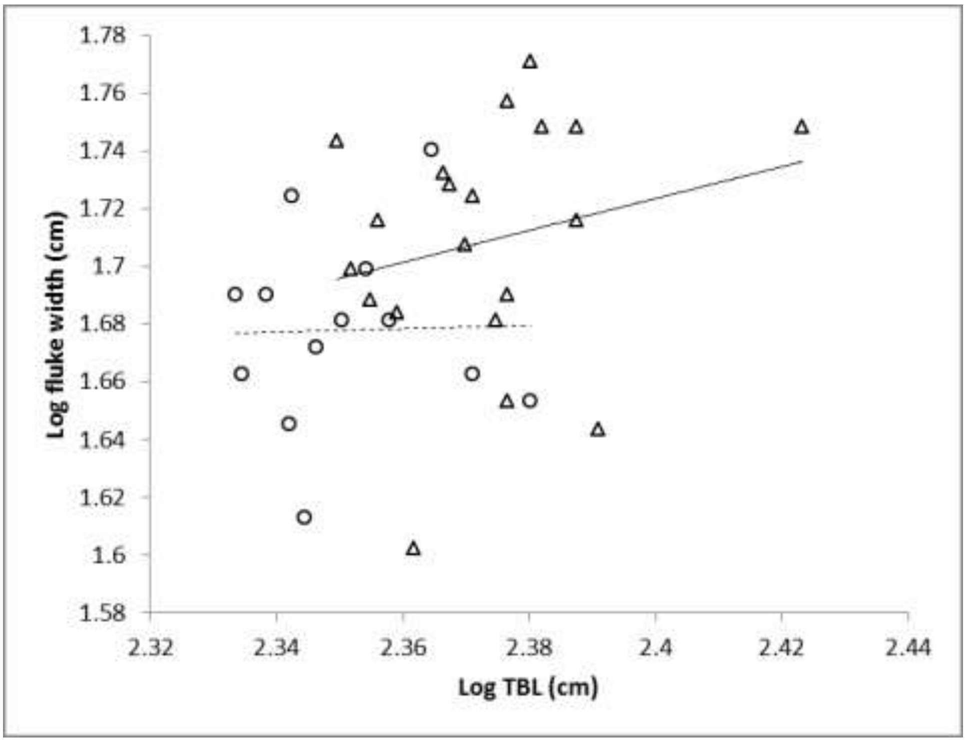

Figure 23 Total body length plotted against the fluke width for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0475$ (male); 0.0006 (female).

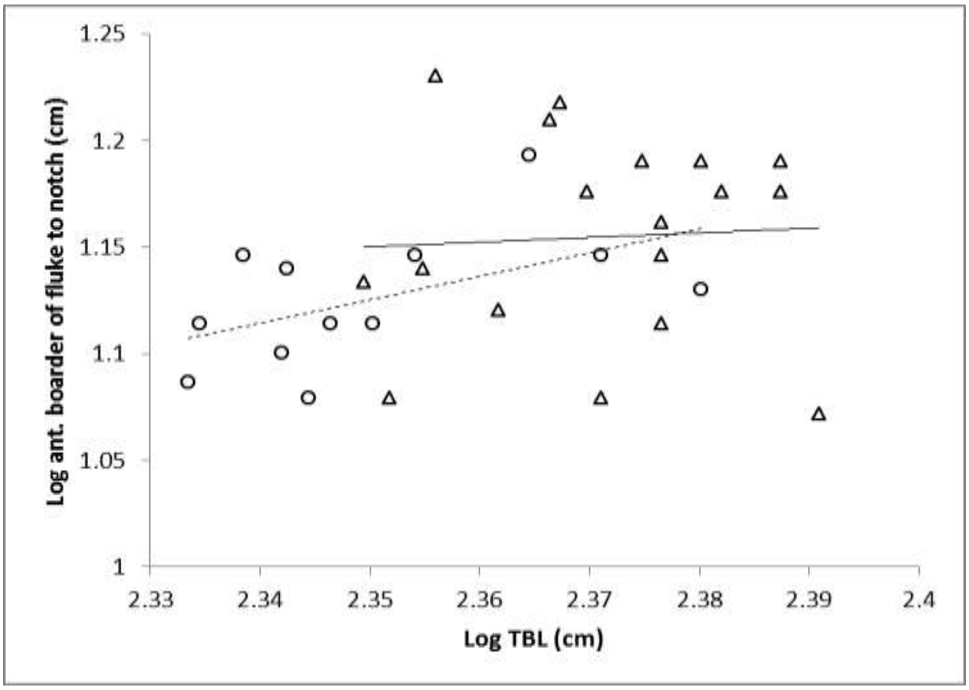

Figure 24 Total body length plotted against the anterior boarder of fluke to the notch for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0032$ (male); 0.2687 (female).

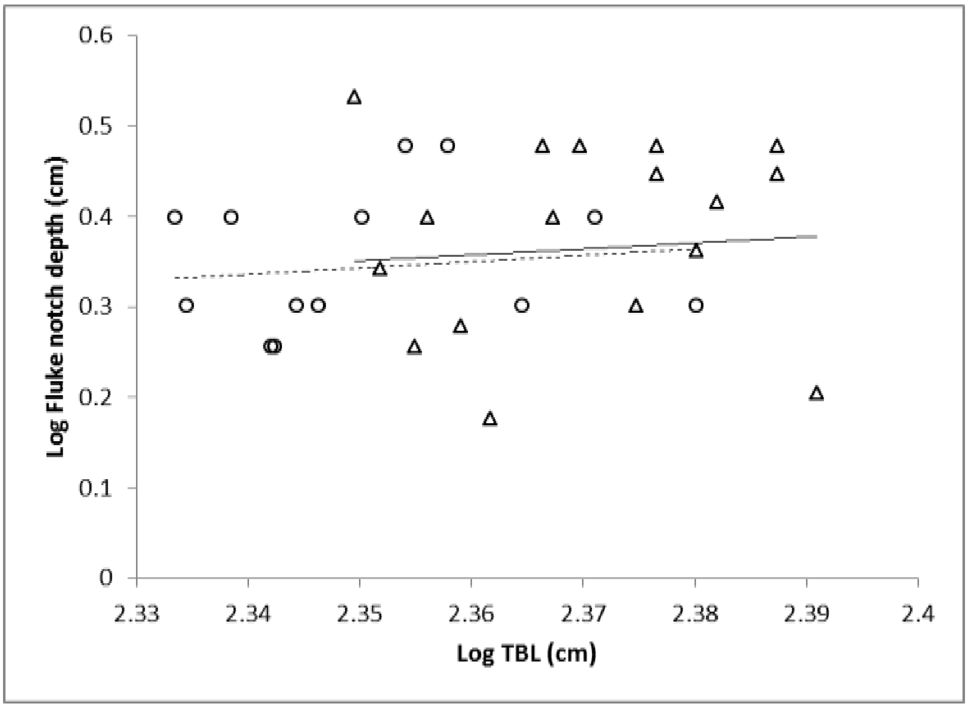

Figure 25 Total body length plotted against fluke notch depth for male (represented by triangles) and female (represented by circles) *S. coeruleoalba* specimens. The solid line represents the linear regression for the males and the dotted line, the linear regression for the females, $r^2 = 0.0055$ (male); 0.0178 (female).

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