

**The status and natural history of pygmy (*Kogia breviceps*)  
and dwarf (*K. sima*)  
sperm whales off Southern Africa**

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## Abstract

For the present study 106 strandings of *Kogia breviceps* and 85 strandings of *K. sima* along the South African coastline between 1880 and 1995 were analysed in order to examine the age and growth, male and female reproduction, diet, stranding patterns, and population genetic structure of both species.

Length and weight at birth were about 120cm and 53kg for *K. breviceps* and about 103cm and 14kg for *K. sima*. Von Bertalanffy growth curves were fitted to the data and indicated that physical maturity was reached at around 15 years in both sexes of *K. breviceps* and at 13 years in female and 15 years in male *K. sima*. Asymptotic length was reached at 306.0 and 286.1cm in female and male *K. breviceps* and 249.14 and 263.75cm in female and male *K. sima*, respectively. Maximum ages were 16 years for male *K. breviceps* and 23 years for females and 17 years for male *K. sima* and 22 years for females. Reversed sexual size dimorphism was suggested for *K. breviceps*, while in *K. sima* males were larger than females.

Attainment of sexual maturity in males occurred at between 2.5 and 5 years of age in *K. breviceps* and 2.6 and 3 years in *K. sima*, corresponding to 241-242cm and 197cm body length, respectively. The maximum combined testis weight comprised 1.04% and 2.00% for *K. breviceps* and *K. sima*, respectively, and a polygynous mating system with a roving male strategy was proposed for both species. The sperm morphology for both *Kogia* species was described and is characterised by 20-25 spherical mitochondria arranged in rows around the midpiece.

Attainment of sexual maturity in females occurred at 5 years in both *Kogia* species, and at 262cm and 215cm body length in *K. breviceps* and *K. sima*, respectively. The ovulation rates were 0.9 and 0.7 per year for *K. breviceps* and *K. sima*, respectively. In *K. breviceps* conceptions occurred from April to September and births from March to August,

while in *K. sima* both conceptions and births occurred from December to March. Annual reproduction and a post-partum oestrus was suggested for both *Kogia* species.

The diet of *K. breviceps* comprised 50 different cephalopod species from 22 families and 17 other prey species, while *K. sima* fed on 32 cephalopod species from 17 families and six others. Although niche overlap indices between the two species and between groups within each species were high, some differences in diet could be determined, which allow these two sympatrically occurring species to share the same ecological niche off the coast of Southern Africa.

An analysis of the stranding patterns revealed that *K. sima* has a closer affinity to the Agulhas current and to higher water temperatures than *K. breviceps*, which is supported by differences in the size of the appendages between the two species.

The population genetic analysis revealed a high haplotype and nucleotide diversity for *K. breviceps* in the Southern hemisphere, but a lack of significant phylogeographic structure, indicating substantial gene flow among populations and inhibiting genetic differentiation of local populations, although the South African population was somewhat isolated from others in the Southern Hemisphere. In contrast the data on the phylogeographic structure of *K. sima* were somewhat restrictive as the majority of the samples originated from South Africa. Nevertheless, both nucleotide and haplotype diversities were markedly lower than in *K. breviceps* and more similar to those for other small cetacean populations, suggesting a smaller population size for *K. sima* than for *K. breviceps*.

Although both *Kogia* species belong to the medium to larger-sized odontocetes their life histories are located near the fast end of the slow-fast continuum of life histories of marine mammals, indicating high mortality rates. The “false-gill” marking and the ability to squirt ink are thought to reflect adaptations to predator mimicry and avoidance.

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*“The cure for anything is saltwater-sweat, tears or the sea”*

*Isak Dinesen (alias Karen Blixen)*

# *Chapter 1: Introduction*

*"It is better to understand a little than to misunderstand a lot"*

-

*Anatole France*



## **1.1 Aim of the present study**

Both pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales are amongst the least studied odontocetes. As with many odontocete species that have not been the target of commercial exploitation, data on their natural history are scarce. Although new and innovative field studies are becoming more frequent, leading to an increase in knowledge of the biology of many marine mammals, both *Kogia* species are elusive creatures and studies in the wild are virtually impossible. However, basic data on the natural history of any species are vital in order to understand their biology and ensure their continued survival. Therefore studying stranded animals is often the only way of obtaining information on the basic ecology of species that are otherwise inaccessible, and while such data are by no means ideal, they remain invaluable in understanding and protecting the biodiversity of our oceans.

Twenty-four species of small odontocetes are found off the South African coastline, including eight ziphiids, 14 delphinids and the two *Kogia* species (Ross, 1984). South Africa appears to have the second highest stranding rate worldwide for both *Kogia* species combined and thus lends itself as an ideal study area. The following research thus aims to investigate the natural history of both species, in particular age and growth, male and female reproduction, diet, strandings and the population genetic structure. These data combined allow an evaluation of the life history strategy employed by both species. Although the present sample size was in some instances too small for some quantitative analyses, it provided an opportunity to determine whether the life histories are as unusual as other parts of their biology. However, it should be kept in mind that the results can only indicate a first idea of *Kogia* biology and that much more extensive and detailed research is needed to understand the biology of the two species fully. In order to put the present results into perspective the emphasis is placed on comparing the results with the available information on the natural histories of other, mainly pelagic, odontocetes.

While each of the chapters as outlined below has a detailed introduction and literature review for the relevant topic, the present chapter provides a general introduction to the biology of the genus *Kogia* and deals in particular with aspects of their biology not covered in the subsequent chapters.

## **1.2 General introduction**

Leatherwood and Reeves (1983), Nagorsen (1985), and Caldwell and Caldwell (1989) have published reviews on the biology of both *Kogia* species. Further summaries, which included reference to a particular geographical location, were provided by Chantrapornsyl *et al.* (1991), Baird *et al.* (1996) and Willis and Baird (1998).

A number of difficulties were encountered in creating this review. In general, the scientific literature available on both species has often been published in journals, which are not easily accessible internationally. Although every attempt has been made here to compile a literature review as comprehensive as possible, there is inevitably a lack of some articles due to these circumstances.

In addition, the fact that two distinct *Kogia* species were only described as late as 1966 means that there is a substantial amount of uncertainty as to which species are discussed in publications prior to that date. This increases the difficulty of an accurate review, but an attempt was made here to assign the publications to the correct species.

Most accounts of the two *Kogia* species are general, and assume information to be true for both species. Although this is often the case, there are differences in biology and an effort has been made to point those out here and to present information specific to either of the two species whenever possible.

## **1.3 Name**

It is unclear from where the genus name *Kogia* is derived. It has been suggested to be a latinised form of the English word “codger”, which means a “miserly old fellow” or could have been derived from Cogia Effendi, a Turk who observed whales in the Mediterranean (Leatherwood and Reeves, 1983; Rice, 1998). The species name *breviceps* originates from the Latin for “short head” and *sima* is also Latin, meaning “flat- or stump-nosed” (Leatherwood and Reeves, 1983).

Rice (1998) proposes that the old species name *K. simus* should be changed to *K. sima* as that would constitute grammatically correct Latin and this has been accepted by the Society for Marine Mammalogy. It appears that an official name change by the International Commission on Zoological Nomenclature is not necessary (P. Tubbs, pers. com.), and most researchers are already using the new nomenclature. In accordance with this, the new name *K. sima* is used throughout this thesis.

The holotype of the pygmy sperm whale (*K. breviceps*) was described by the French naturalist de Blainville in 1838 from a skull found at the Cape of Good Hope (Ross, 1979a). Only the skull was known until the skeleton of a specimen found in Australia was described by Wall in 1951 (Handley, 1966). Together Gray, Krefft and Owen described the external morphology in 1866 (Handley, 1966).

Owen (1866) describes the type specimen of *K. sima* from Madras, India and calls it the “snub-nosed cachalot” *Physeter (Euphysetes) simus*. The specimen had been hunted by local fishermen. He describes the external characteristics as well as skull measurements and compares them with those made from *Physeter breviceps* (de Blainville’s type specimen of *K. breviceps*) and *Euphysetes (Physeter) grayii*, another *Kogia* specimen described by Macleay. However, current knowledge of the distinguishing characteristics such as dorsal fin height as a percentage of total length and dentition indicate that it was indeed a *K. sima*.

#### **1.4 How many species?**

Although apparently Gill recognised the differences between the two species in 1871 and proposed a separate species name for *K. sima* (Rice, 1998), the existence of two distinct species was not confirmed until the works by Yamada (1954), Handley (1966), and Ross (1979a). Rather up to seven different species were described over the years as listed by Hector (1878) and Handley (1966):

<i>Physeter breviceps</i> , de Blainville (1838)	new species
<i>Kogia breviceps</i> , Gray (1846)	new genus for <i>Physeter breviceps</i>
<i>Euphysetes grayii</i> , Wall (1851)	new genus and species
<i>Euphysetes macleayi</i> , Krefft (1865)	
<i>Kogia macleayi</i> , Gray (1866)	new species
<i>Physeter (Euphysetes) simus</i> , Owen (1866)	new species
<i>Kogia floweri</i> , Gill (1871)	new species
<i>Callignathus</i> , Gill (1871)	new genus for <i>Physeter (Euphysetes) simus</i>
<i>Euphysetes pottsii</i> , Haast (1874)	new species
<i>Kogia goodei</i> , True (1884)	new species

Handley (1966) gives a brief summary of the different reasons behind the description of so many species. It appears that the confusion can be put down to scarcity of specimens for comparison and a general similarity between the two species such as individual variation with age and sex, an existing overlap between some morphological characteristics in the two species, and a subsequent confusion between juveniles of one

species in relation to adults of the other species. However, a number of researchers were in favour of two *Kogia* species such as Gill in 1871 and Beddard in 1902 (Handley, 1966; Rice, 1998). But it was only when Ogawa in 1936 proposed two species and other Japanese authors such as Kuroda (1938), Okada (1938) and Yamada (1954) adopted that nomenclature that Handley followed and proposed his account of two definite species in 1966. He was able to examine a large sample size by *Kogia* standards, namely 42 specimens, and provided a list of the distinguishing morphological characteristics between the two species. His morphological studies together with the previous work by Yamada (1954) and work carried out subsequently by Ross (1979a; Ross, 1984) have all led to the now universally accepted nomenclature of two species in the genus *Kogia* (Rice, 1998). No geographical variation was found in Handley's examination of the specimens (Handley, 1966) and no studies have been undertaken on that topic since.

The confusion regarding classification of different *Kogia* specimens into two species prior to 1966 is well reflected in the literature. Allen's account from 1941 states that "...in spite of some half dozen names applied in the past to various individuals all are currently regarded as pertaining to but a single species.". He also remarks on differences in dorsal fin size, but believes there is one species. Other accounts are also clearly confused as to the number of species present (Duguay, 1966). Hale (1947; 1959; 1962; 1963) carried out comparative morphological studies of the skeletons and skulls of the South Australian specimens examined by him (comprising 13 animals and one mandible) and provides external measurements for some of them. He remarks upon the differences in skeletal characters (especially skull measurements) and the variation in dorsal fin size between the individuals (Hale, 1947; 1962; 1963). However, he still maintains that on these grounds he cannot distinguish two different species as had been suggested by Ogawa in 1936 (in: Yamada, 1954), but rather thinks that one species of *Kogia* exists (Hale, 1962). Similarly, Yamada (1954) describes differences in skull morphology between the two species in addition to dental and vertebral formulae, but states that he does not think that the results perfectly distinguish the two species.

Nagorsen (1985) lists a number of cases where the supplied measurements of the animal described made it possible to identify it after Handley's 1966 paper. For example, Allen's (1941) specimen from Virginia, Yamada's animals (1954) and two animals described by Hale (1959) are all *K. sima* (Aitken, 1971; Nagorsen, 1985). These circumstances make a review of the literature difficult and have to be kept in mind when examining publications prior to 1966. However, Willis and Baird (1998) give an overview

of reports in the recent literature, which clarify the species status of some earlier accounts.

## **1.5 Phylogeny**

Although the genus *Kogia* was formerly included in the family Physeteridae (the only other member being the sperm whale *Physeter macrocephalus*) or treated as the subfamily Kogiidae, most recent publications now regard it as a separate family (Kogiidae) within the superfamily Physeteroidea (Heyning, 1997; Rice, 1998). Recent advances in molecular genetics have brought about rapid changes to the phylogenetic tree of Mammalia in general (de Jong, 1998), and led to a controversy about the phylogeny of Cetacea in particular. The origin of Cetacea is unclear due to the fact that many aspects of their anatomy are adaptations to an aquatic lifestyle and thus do not allow conclusions to be drawn about their evolutionary history. Furthermore, the lack of fossils makes the estimation of the time of evolution difficult. However, the fossil and morphological evidence available indicates that Mesonychidae, early artiodactyls (even-toed ungulates), gave rise to the first cetaceans, or Archaeoceti, which in turn gave rise to the modern whales (Shimamura *et al.*, 1997). Recent molecular analyses support this and show that the Cetacea are nested unambiguously within the artiodactyls as a sister group of the hippopotami (Shimamura *et al.*, 1997; de Jong, 1998).

But within the Cetacea the traditional view that the two suborder, the Mysticeti and the Odontoceti, are monophyletic was challenged by a molecular analysis, which led to the suggestion that the sperm whales (Physeteroidea) are in fact a sister group of the mysticetes (Milinkovitch *et al.*, 1993). This would indicate that Physeteroidea are more closely related to Mysticeti than to the other Odontoceti, inferring paraphyly of the odontocetes and concluding that on these grounds the cetacean phylogeny should be revised (Milinkovitch *et al.*, 1993); for a review of the controversy see Cerchio and Tucker (1998). Although subsequent molecular (Arnason and Gullberg, 1994), morphological (Heyning, 1997), and molecular and morphological studies combined (Messenger and McGuire, 1998) could not replicate this result, some molecular evidence supports the view that the odontocetes are paraphyletic and suggests that the sperm whale family could have branched off before the divergence of the other cetacean families and has undergone a long separate evolution (Douzery, 1993). It is apparent that future work is needed to reconcile the morphological and molecular evidence, particularly as the relationship among the sperm whales is unresolved (Cerchio and Tucker, 1998). However, the special status of the sperm whales

among the Cetacea as shown by a unique karyotype and chromosome number (Arnason and Benirschke, 1973) and the unique spermaceti organ (Schenkkan and Purves, 1973) remains. *K. breviceps* and *Physeter* were found to have similar karyotypes with a chromosome number of 42 and the absence of telocentric chromosomes (Arnason and Benirschke, 1973). No data are available for *K. sima*.

### 1.5.1 Fossil record

The fossil record of *Kogia* seems sparse as with so many cetaceans and most fossils are physically incomplete (Kellogg, 1929; Barnes, 1973; Caldwell and Caldwell, 1989). Anderson and Jones (1967) listed the Kogiinae as a separate subfamily from the early Pliocene in North America and the late Pliocene in Japan (in: Caldwell and Caldwell, 1989). Kellogg (1929) proposed a new genus and species (*Kogiopsis floridana*) from the late Miocene or early Pliocene based on the incomplete portion of a lower jaw, since he was not sure whether the specimen was similar enough to be placed in the same genus. Barnes (1973) describes a new genus and species (*Praekogia cedrosensis*) of an extinct pygmy sperm whale from the early Pliocene. The characteristic shape and curvature of the teeth of *Kogia* play a large part in identifying fossil specimens (Pilleri, 1986). Bianucci and Landini (1999), upon describing a specimen of *Kogia pusilla*, believe that the fossil and phylogenetic evidence shows that the separation of the two groups of *Physeter* and *Kogia* may be relatively old. They suggest that the phylogenetic data indicate an origin of Kogiidae older (at least Early Miocene) than that assumed from the paleontological data (late Miocene). The lack of Kogiid records prior to the late Miocene may have been due to the low frequency of these animals in ancient seas (Bianucci and Landini, 1999). Nagorsen (1985) gives a brief synopsis on the fossil record of the genus *Kogia*.

## 1.6 Identification

### 1.6.1 External characteristics

Both pygmy and dwarf sperm whales are medium sized odontocetes, reaching maximum lengths of less than 4m. They resemble the bigger sperm whale *P. macrocephalus*, in their external appearance, and their blunt, squarish heads are proportionately the smallest among the cetaceans (Handley, 1966; Carvan III, 1988) (Figure 1.1 and 1.2). They have a single blowhole, slightly offset to the left, which is characteristic

for the Physeteriids (Price *et al.*, 1984). The underslung, shark-like mouth is set well back from the tip of the snout and makes them easily distinguishable from other small odontocetes (Handley, 1966; Nagorsen, 1985) (Figure 1.1 and 1.2). In fact, both species have a strong resemblance to a shark (Gaskin, 1972; Leatherwood and Reeves, 1983) and stranded animals have been repeatedly mistaken for sharks (present study; Leatherwood and Reeves, 1983; Credle, 1988; Caldwell and Caldwell, 1989; Shirley Pacheco, pers. com.). Fishermen from the porpoise fishery off North Carolina, having seen the animal in the water, gave reports about a shark, which does not have a shark's tail and comes to the surface to breathe (Enders, 1942), most likely referring to a *Kogia* specimen.

Although there are common characteristics with the sperm whale, either *Kogia* species are often described as “porpoise-like” in shape, which makes them easily distinguishable from their larger cousin (Manville and Shanahan, 1961; Nagorsen, 1985; Caldwell and Caldwell, 1989).

Both pygmy and dwarf sperm whales may appear wrinkled, a feature reminiscent of the sperm whales (Leatherwood and Reeves, 1983). There is no diagnostic difference in colour pattern between the two species (Ross, 1979a). Dorsally both species are dark grey and ventrally white (Yamada, 1954) (Figure 1.1. and 1.2), although Yamada (1954) remarks that it appears that *K. sima* has this dark grey colouration, while *K. breviceps* has a more purplish brown colour. Unfortunately, this suggested colour difference between the two species has not been examined further, probably due to the fact that mainly stranded specimens, which discolour quickly, have been available for examination. Caldwell and Caldwell (1989) describe the colour pattern of both species as “bluish steel grey on the back, shading to a lighter grey on the sides and to a dull white or pinkish on the belly”. Hale (1962) remarks on the considerable variation in colouration of the animals examined by him, ranging from blue to brownish-grey, dark grey to light bluish-grey.

A peculiar feature of both *Kogia* species is the “false-gill” marking, which is a white crescent-shaped marking behind the ear, resembling the shape of a fish gill or operculum. Hubbs (1951) is amongst the first to describe the “false-gill” marking. Yamada (1954) further explores and describes this marking, but suggests that the Japanese specimens differ in these markings from those from U.S. Pacific and Atlantic coasts. Hale (1962; 1963) cannot identify a “false-gill” marking in any of the specimens stranded in South Australia, baring one female. Raun *et al.* (1970) state that in an adult specimen from Texas the false gill marking appears rather in a reversed “L” shape than bracket-shaped.

The teeth of both *Kogia* species are thin and pointed and curved backwards into the

mouth, which leaves them reminiscent of those of a python (Handley, 1966). The teeth of *K. breviceps* are proportionately larger and longer, but those of *K. sima* are more sharply pointed (Caldwell and Caldwell, 1989). They have repeatedly been described as lacking enamel (Handley, 1966; Caldwell and Caldwell, 1989; Willis and Baird, 1998), although Flower and Lydekker (1891) state the opposite. This issue is discussed in more detail in Chapter 3. Some researchers suggest that the number of teeth may be the best criterion to distinguish the two species (Robineau and Rancurel, 1981). The sharp and curved teeth in conjunction with the underslung jaw may be the reason why the animal is also known as the “rat porpoise” in the Lesser Antilles (Caldwell *et al.*, 1973).

The body of the two *Kogia* species is very robust, “torpedo-shaped” and tapers rapidly to the tail (Willis and Baird, 1998) (Figure 1.1 and 1.2). The pectoral fins are moderate in size, convex on the upper and lower margins and taper evenly to a rounded apex (Ross, 1979a) (Figure 1.1. and 1.2). The tailstock is elongated and laterally compressed and the flukes are broad, notched in the middle, concave along the rear margin and tapered laterally (Ross, 1979a; Baird *et al.*, 1996). Detailed body measurements for both *Kogia* species are given by Ross (1979a).

No sexual size dimorphism has been reported for either *Kogia* species (Leatherwood *et al.*, 1982) and it is generally believed that the sexes are similar in size (Leatherwood and Reeves, 1983; Credle, 1988). This is examined further in Chapters 3 and 4.

### ***K. breviceps***

*K. breviceps* has a small, falcate dorsal fin, which is lower and located more posteriorly on the back than that of *K. sima* (Handley, 1966; Caldwell and Caldwell, 1989) (Figure 1.1). The size of the dorsal fin is distinctly different between the two *Kogia* species, being less than 5% of the total body length in *K. breviceps* (Ross, 1979a). This feature appears to be the most reliable characteristic to identify a specimen down to species level and has often been used to identify stranded animals from photographs alone (Robineau and Rancurel, 1981; Sylvestre, 1988a). Few authors do not find it a suitable character to distinguish the two species (Sylvestre, 1988b).

In addition, the distance between the tip of the snout and the anterior insertion of the dorsal fin is over 50% of the total body length in *K. breviceps* (Ross, 1979a). There is, however, some overlap in this character between the two species and it should thus be used

with caution for species identification (Ross, 1979a).

*K. breviceps* has a longer snout than *K. sima* as measured by the distance between the tip of the snout and the blowhole (Ross, 1979a). In *K. breviceps* it is usually more than 10% of the total body length (Ross, 1984). This is a good character for species identification as there is no overlap with *K. sima* (Ross, 1979a).

There are no maxillary teeth present in *K. breviceps* and the number of mandibular teeth ranges from 10 to 16 pairs (Handley, 1966; Ross, 1979a; Baird *et al.*, 1996).

The longest specimen recorded in the literature was a 4.25m female from the south-eastern United States (Caldwell *et al.*, 1971). However, Ross (1979a) suggests that that may have been an overestimate and thus incorrect. The longest specimen he recorded from South Africa was 3.28m in length (Ross, 1979a). Eliason and Houck (1986) reported an animal of 3.82m from the records of the Smithsonian Institution. Credle (1988) reports a 4.11m long male from Florida.

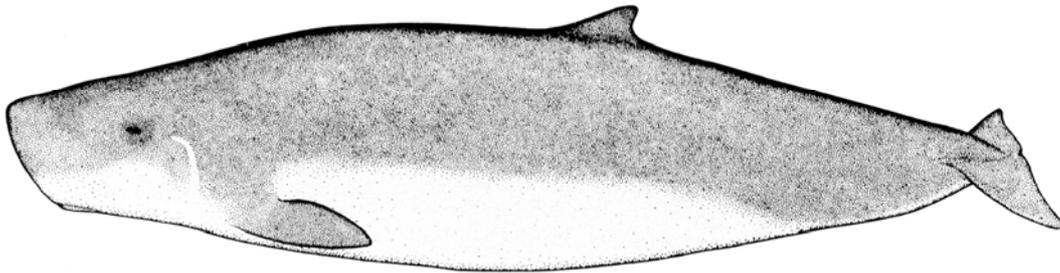


Figure 1.1: External features of an adult female *Kogia breviceps* (from Ross, 1984).

### ***K. sima***

Few authors remark on the throat grooves found in *K. sima*. Allen (1941) reports up to five throat grooves in a foetus and an adult male and female. Caldwell and Caldwell (1989) also remark that *K. sima* may have several short longitudinal grooves on the throat, and Pinedo (1987) reports two throat grooves in a *K. sima* foetus. Leatherwood and Reeves (1983) state that they may only occasionally be present in *K. sima* and later reports do not mention this fact any further. Baird *et al.* (1996), however, suggest this characteristic as a distinguishing feature between the two species as throat grooves are absent in *K. breviceps*.

The dorsal fin is dolphin-like in *K. sima* and located near the midpoint of the back (Caldwell and Caldwell, 1989) (Figure 1.2). Its height is more than 5% of the total body

length and has a slightly longer fin base than that of *K. breviceps* (Ross, 1979a). The distance between the tip of the snout and the anterior insertion of the dorsal fin is under 50% of the total body length in *K. sima* (Ross, 1979a).

The distance between the tip of the snout and the blowhole is less than 10% of the total body length in *K. sima* (Ross, 1979a).

*K. sima* has eight to 12 pairs of mandibular teeth, rarely 13 pairs, and 0-3 pairs of maxillary teeth (Handley, 1966; Ross, 1979a; Baird *et al.*, 1996; Willis and Baird, 1998). The teeth of *K. sima* are shorter and proportionately more slender than those of *K. breviceps* (Ross, 1979a).

The longest *K. sima* reported from South Africa measured 2.64m (Ross, 1979a), which is in agreement with Handley's data of 2.7m as a maximum length for this species (Handley, 1966).

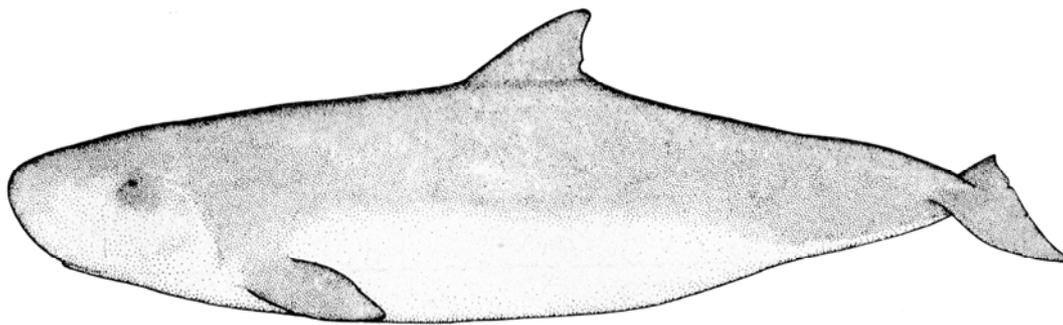


Figure 1.2: External features of an adult *Kogia sima* (from Ross, 1984).

## 1.6.2 Morphology

There have been a number of good reviews of the skeletal structure of the two *Kogia* species, in particular of the skull morphology (Yamada, 1954; Handley, 1966; Ross, 1979a; Nagorsen, 1985). The most distinctive cranial characters of the two *Kogia* species are the shape of the dorsal sagittal septum near the vertex and the dorsal cranial fossae (Handley, 1966). The rostrum of the two *Kogia* species is proportionally the shortest among extant cetacean species, the skull is markedly asymmetrical, has a pronounced supracranial basin and sagittal septum and has an enlarged left naris. Heyning (1997) remarks on the complete lack of nasal bones in the genus *Kogia*, while *Physeter* still possesses one nasal bone. In addition, there is no independent jugal, and the mandibles are fragile and are

described as “paper-thin” (Handley, 1966; Nagorsen, 1985). Allen (1941) also remarks on the fact that the mandibles of a specimen examined by him are paper-thin and stranded animals are often washed up with broken mandibles (Peter Best, pers. com.), which led to speculations whether this could be a result of intra-sexual fighting (see Chapter 4). However, the lack of tooth scars plus the fact that the mandibles are fragile may suggest that they are broken when the animal is dragged over reefs and rocks by the surf.

Handley (1966) describes a number of characters that distinguish *K. breviceps* from *K. sima*, the majority of which refer to features of the cranium and mandible. However, while Handley (1966) uses the position of the foramen magnum to separate the two species, Ross (1979a) is unable to use this character as a distinguishing feature between the two species. Differences in dentition between the two *Kogia* species have often been used as a distinguishing characteristic. Ross (1979a) states that the number of mandibular teeth is distinctive in the two *Kogia* species, ranging from 12-16 in *K. breviceps* and 7-12 in *K. sima*. No maxillary teeth were found in *K. breviceps*, but between zero and six were present in *K. sima*. In contrast, Hückstädt and Antezana (2001) report on a 277cm long female *K. breviceps*, which had a pair of tiny teeth in the upper mandible, a character usually only observed in *K. sima*. This led them to the conclusion that a tooth count is not a reliable diagnostic feature for distinguishing the two *Kogia* species.

Extensive morphological studies have been carried out on the nasal anatomy of the Physeteriids, including the two *Kogia* species (Schenkkan and Purves, 1973; Clarke, 2003). Both *Physeter* and the two *Kogia* species are unique among the odontocetes in that the nasal passages remain as separate tubes to just deep of the blowhole, which is considered a primitive character (Heyning and Mead, 1990). Another feature unique to these two genera is that they possess a spermaceti organ, which is not the same as the melon in odontocetes (Heyning and Mead, 1990). There have been many speculations about the function of the spermaceti organ in both *Physeter* (Clarke, 1970) and the kogiids (Karol *et al.*, 1978; Carvan III, 1988). While it is repeatedly speculated that the spermaceti organ functions as an acoustical lens in the genus *Kogia* (Karol *et al.*, 1978; Carvan III, 1988), it may play a role in the absorption of nitrogen in the sperm whale (Schenkkan and Purves, 1973) and is widely accepted to also play a functional role in buoyancy control during diving in *Physeter* (Clarke, 1970). However, there is some critique of the latter (Ridgway, 1971; Schenkkan and Purves, 1973) and it has been ruled out as a buoyancy control mechanism in the two *Kogia* species (Schenkkan and Purves, 1973; Clarke, 2003). Although the similarities in the anatomical structure and the exclusive presence of the spermaceti organ, the cushion

structure and a structure known as the “museau de singe” in both genera have been used to link the two genera into one family, the structure of the forehead in the two *Kogia* species is actually more complex and differently arranged than that of *Physeter* (Karol *et al.*, 1978; Carvan III, 1988; Clarke, 2003), supporting the separation into different families (Rice, 1998) (see above).

Another point of focus in the study of the anatomical structures in the head of the two *Kogia* species have been the sound producing and propagation tissues (Carvan III, 1988; Clarke, 2003), and it has been suggested that the “museau de singe” or “monkey’s muzzle” has the appearance of a sound producer, using movement of air rather than water for sound production (Karol *et al.*, 1978; Heyning and Mead, 1990; Clarke, 2003) (see below).

The postcranial skeleton also reveals some interesting features, including all cervical vertebrae being fused into a single unit, the costal cartilages being unossified, the sternum being reduced to three elements and a low and porpoise-like scapula (Handley, 1966).

Detailed anatomical studies of the external characteristics, the skeletal muscles, and peripheral nerves are described by Schulte and Smith (1918). Their studies were based on a single male foetus of *K. breviceps*, which was 109.7cm long and thus near term. The same animal was the basis for another anatomical study on the respiratory tract, foregut and thoracic viscera, including the heart, lungs, pharynx and ear (Kernan and Schulte, 1918). A detailed anatomical description of the stomach of *K. breviceps* is presented by Rice and Wolman (1990).

Hale (1947) appears to be the only author who describes the presence of rostral hairs in the form of six bristles arranged in a diagonal along the snout in a foetal *Kogia* specimen, a characteristic that is commonly described for foetal and newly born odontocetes.

Further anatomical differences between the two *Kogia* species are described by Yamada (1954), Handley (1966) and Ross (1979a).

### ***K. breviceps***

Detailed descriptions of the skull and/or skeleton are provided by Yamada (1954) and Ross (1979a). The latter also provides a regression equation to predict total body length from condylobasal length for this species.

### *K. sima*

A comprehensive summary of the skull morphology of *K. sima* is given by Nagorsen (1985). There appear to be quite a few inconsistencies between different skeletons of the same species as far as the number of vertebrae and ribs is concerned; this and other discrepancies are summarised by Nagorsen (1985). Further detailed descriptions of the skull and/or skeleton are provided by Yamada (1954), Ross (1979a) and Gallagher and van Bree (1980). Ross (1979a) concluded that *K. sima* has a shorter snout than *K. breviceps*. Regression equations to predict total body length from condylobasal length and body weight from total body length are provided by Ross (1979a).

## **1.7 Biology**

The most comprehensive studies on the general biology of the genus *Kogia* were carried out by Ross in 1979 and 1984. These studies still provide the baseline data on the natural history of the two species to this date.

### **1.7.1 Reproduction**

Very little is known about the reproductive biology of the two species and most estimates of reproductive parameters are based on a small number of individuals examined (Ross, 1979a; Baird *et al.*, 1996; Willis and Baird, 1998). A detailed description of the gonads is found in Ross (1979a). However, this topic is examined in detail in Chapters 4 (Male reproduction) and 5 (Female reproduction).

### *K. breviceps*

Ross estimates the length at birth to be 120cm (Ross, 1979a). Attainment of sexual maturity in females occurs between 270 and 280cm in body length, and between 270 and 300cm in males (Ross, 1979a). Neither the length of gestation nor the lactation period could be estimated for this species by Ross, although he speculates that gestation may last either seven or 11 months (Ross, 1979a). However, mating and calving are thought to extend over a period of seven months from the Austral autumn through to spring (Ross, 1979a). A reasonable proportion of females are simultaneously pregnant and lactating and must therefore conceive in successive breeding seasons (Ross, 1979a). Throughout the literature there have been reports of females being simultaneously pregnant and lactating, suggesting

annual reproduction (Ross, 1979a; Odell *et al.*, 1984; Credle, 1988; Baird *et al.*, 1996). The possibility of post-partum reproduction in *K. breviceps* was first mentioned by Dawson (1985) based on an account of a stranded female, which was lactating, with a three month old calf and a foetus estimated to be about five weeks old. The sex ratios of the foetuses and calves from South Africa are surprisingly disproportionate and skewed towards males (Ross, 1979a). However, the sex ratio for adult and sub-adult animals is 1:1 (Ross, 1979a).

### ***K. sima***

Length at birth is estimated to be 100cm by Ross (1979a), which is the same estimate Pinedo (1987) arrived at. Attainment of sexual maturity is thought to occur between 210 and 220cm in both sexes (Ross, 1979a). Although Ross (1979a) could not estimate the length of gestation, records of the size of foetal and juvenile animals from the Southern Hemisphere in comparison to month indicate a mating season in summer and birth in early summer, with a gestation period of about 9.5 months (Pinedo, 1987). Ross (1979a) suggests an extended calving season of five months. The sex ratio of the stranded animals is not considered to be significantly different from parity (Ross, 1979a).

## **1.7.2 Age determination**

A number of researchers have attempted age determination techniques in *Kogia*, some more successful than others, and these results are discussed further in Chapter 3. As with most odontocetes there is no calibration available to verify the deposition rate of growth layers in the teeth of either *Kogia* species (Baird *et al.*, 1996). No information is available on the longevity of either species (Baird *et al.*, 1996; Willis and Baird, 1998).

### ***K. breviceps***

Ross (1979a) presents the results of age determination for 15 animals from South Africa, although only six teeth were rated sufficiently legible to estimate the age.

### ***K. sima***

Ross (1979a) states that the teeth of *K. sima* are similar in structure to those of *K. breviceps*, but growth layers in the dentine are not very distinct and pose problems for the estimation of age in this species.

### 1.7.3 Diet

In contrast to other aspects of their biology the diet of the two *Kogia* species has been studied in some detail in different geographical areas (Fitch and Brownell, 1968; Ross, 1979a; Martins *et al.*, 1985; Candela, 1987; Pinedo, 1987; Klages *et al.*, 1989; Sekiguchi *et al.*, 1992; Clarke, 1996b; Wang *et al.*, 2002). Stomach content analyses indicate that both species feed mainly on cephalopods, but supplement their basic diet with fish and crustaceans (Ross, 1979a; 1984; Klages *et al.*, 1989). With a few exceptions, the same species of cephalopods are found in the stomachs of either *Kogia* species (Ross, 1979a). Small numbers of salps and deepwater shrimp are also reported from the stomachs of the two species (Candela, 1987). The foraging ranges of the two species off the south-eastern United States broadly overlap, concentrating on the epi- and mesopelagic zones of the deeper shelf and slope (Candela, 1987). A more detailed review and analysis of data on the stomach contents of both *Kogia* species is provided in Chapter 6.

#### *K. breviceps*

The diet of *K. breviceps* off the coast of Taiwan suggests that the species lives seaward of the continental shelf and dives deeper than *K. sima* (Wang *et al.*, 2002). Similarly, the diet of *K. breviceps* off South Africa indicates that adult animals forage over the shelf edge and slope, with juvenile and immature animals feeding closer inshore (Ross, 1979b; Klages *et al.*, 1989). Off the south-eastern United States *K. breviceps* feeds to a greater extent on larger and deeper ranging squid, in contrast to *K. sima*, which take smaller squid and feed at lesser depths (Candela, 1987).

#### *K. sima*

Stomach content analyses off South Africa suggest that juvenile and immature *K. sima* forage closer inshore than adults, probably over the outer part of the shelf and upper part of the slope (Ross, 1979b). In contrast, adult animals are found over deeper water. *K. sima* is thought to feed further inshore than *K. breviceps* off both the coasts of South Africa (Klages *et al.*, 1989) and Taiwan (Wang *et al.*, 2002).

## **1.8 Distribution and abundance**

### **1.8.1 Distribution**

Although they are amongst the most commonly stranded cetaceans in some parts of the world, both species are considered to be rare, mainly because of their offshore distribution (see Section 1.7.2 Habitat). Sightings at sea are still rare and there are no reliable criteria to distinguish sightings of *K. breviceps* and *K. sima* (Leatherwood and Reeves, 1983). Thus knowledge on the distribution of either species is almost exclusively based on stranding records, which often cannot be distinguished to species level (Leatherwood and Reeves, 1983). It has been repeatedly suggested that gaps in the distribution of either *Kogia* species may be due to a lack of observer effort rather than to a lack of strandings (Ross, 1979a; Caldwell and Caldwell, 1989). The frequency of reports on either *Kogia* species is increasing, which may be due to an increased awareness by both the public and scientists alike. There appears to be no evidence that their populations have declined over time, like those of species of commercial importance (Handley, 1966).

Both species are found world-wide in tropical and warm-temperate seas (Carwardine, 1995; Baird *et al.*, 1996; Willis and Baird, 1998) (Figures 1.3 and 1.4). In addition, a number of detailed accounts list the waters from which the two *Kogia* species have been reported (Baird *et al.*, 1996; Willis and Baird, 1998).

Allen (1941) gives a brief overview of the geographical distribution of strandings worldwide. He reports that most specimens of *Kogia* have come from the Indian and Pacific Ocean, particularly from Australian and New Zealand waters. He then goes on to give a more detailed summary of strandings along the Atlantic coast. However, Gunter *et al.* (1955) are among the first to note the distribution pattern of *Kogia* strandings along the western seaboard of the world's oceans.

There are a number of reviews of the distribution of animals of either *Kogia* species in a particular region. Muñoz-Hincapié *et al.* (1998) give a review of strandings of both *Kogia* species and sightings in South American waters. A total of 21 records of *K. breviceps*, 23 of *K. sima* and five of *Kogia* spp. are reviewed in order to analyse the zoogeography of the species (Muñoz-Hincapié *et al.*, 1998). No records exist for Venezuela, Trinidad and Tobago, Guyana, Suriname, French Guiana, and the northern part of Brazil, which may be a reflection of both the Orinoco and the Amazon discharging fresh water and sediments to these regions (Muñoz-Hincapié *et al.*, 1998). Such large river outlets may significantly alter the marine environment in such a way that it does not provide

a suitable habitat for species of *Kogia* (Muñoz-Hincapié *et al.*, 1998). Apart from these regions both *Kogia* species are found along the coast of all other coastal countries of the Caribbean, Atlantic and Pacific (Muñoz-Hincapié *et al.*, 1998). Most records are reported from north of the Tropic of Capricorn (23.5°S) and differences in the distribution range observed between the east and the west coast are ascribed to the prevailing currents and water masses (Muñoz-Hincapié *et al.*, 1998). A review of the two *Kogia* species in the Caribbean is provided by Cardona-Maldonado and Mignucci-Giannoni (1999), listing nine strandings of *K. breviceps* and four of *K. simus* for Puerto Rico and the Virgin Islands between 1976 and 1998. It is not known whether the populations of either *Kogia* species are continuous or discontinuous across the world (Gaskin, 1972; Leatherwood and Reeves, 1983; Klinowska, 1991).

In what is probably the only literary reference to the genus *Kogia* and one of the earliest accounts on their distribution, “The cruise of the cachalot” by Frank T. Bullen, a group of kogiids was apparently observed and hunted off the Aldabra Islands, north of Madagascar (Palmer, 1948).

### ***K. breviceps***

*K. breviceps* appears to be a cosmopolitan species, recorded from nearly all temperate, subtropical and tropical waters (Klinowska, 1991). It appears to most frequently strand along the south-eastern coast of the United States, the southern African coastline, the coast of New Zealand and the south-eastern coast of Australia. Scheffer and Slipp (1948) report that *K. breviceps* is widely distributed in the temperate seas of the world. Gaskin (1972) suggests that the species is fairly common around New Zealand in both the Tasman Sea and along the South Pacific coast. Baird *et al.* (1996) summarize the distribution of the species: it has been reported in the western Pacific from Japan in the north to New Zealand and Australia in the South and in the eastern Pacific from Washington State in the north to Peru and Chile in the south. In the western Atlantic specimens have been reported from Canada in the north to Argentina in the south and in the eastern Atlantic from Ireland in the north to South Africa in the south (Baird *et al.*, 1996). Records from the Indian Ocean are mainly from South Africa and India (Ross, 1979a; Chantrapornsyl *et al.*, 1991). For a map of the species distribution see Figure 1.3.

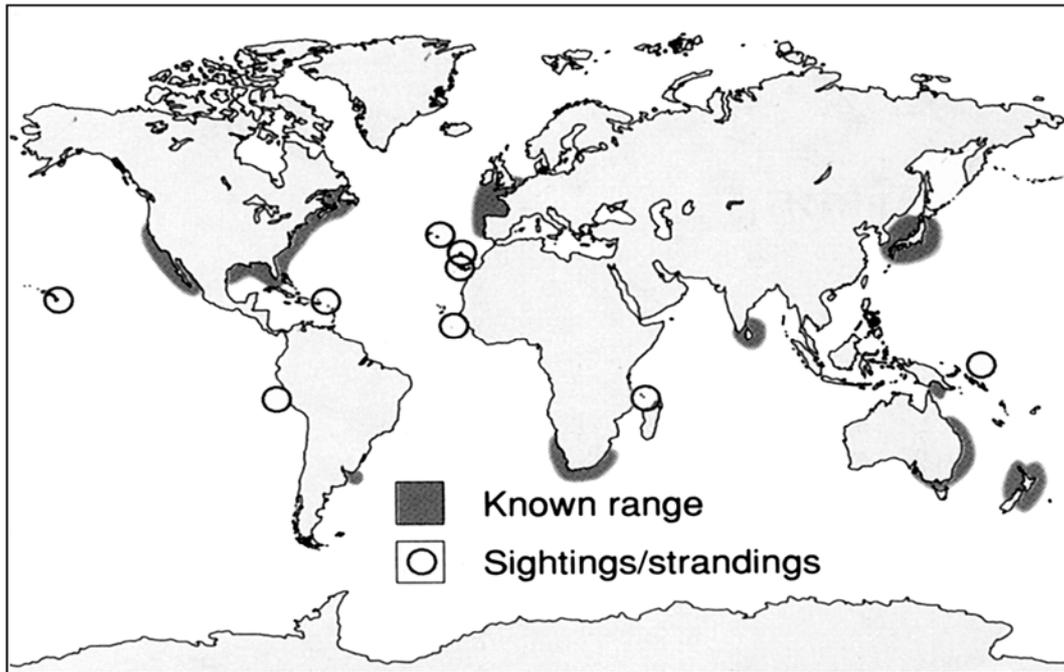


Figure 1.3: Worldwide distribution of *Kogia breviceps* (from Carwardine, 1995).

### *K. sima*

*K. sima* appears to prefer slightly warmer waters than *K. breviceps* (Caldwell and Caldwell, 1989). Nagorsen (1985) gives a detailed review of the distribution of *K. sima* based on stranding data, as do Willis and Baird (1998). In the western Pacific records range from Japan in the north to New Zealand and Tasmania in the south, while in the eastern Pacific the records range from Canada in the north to central Chile (Willis and Baird, 1998). In the western Atlantic *K. sima* has been reported from Virginia (USA) in the north to southern Brazil and in the eastern Atlantic records range from the Mediterranean, off Italy, to South Africa (Willis and Baird, 1998). In the Indian Ocean specimens have been reported from Oman, Sri Lanka, India, Thailand, Indonesia, western Australia and South Africa (Ross, 1979a; Chantrapornsy et al., 1991; Willis and Baird, 1998). For a distribution map of the species see Figure 1.4.

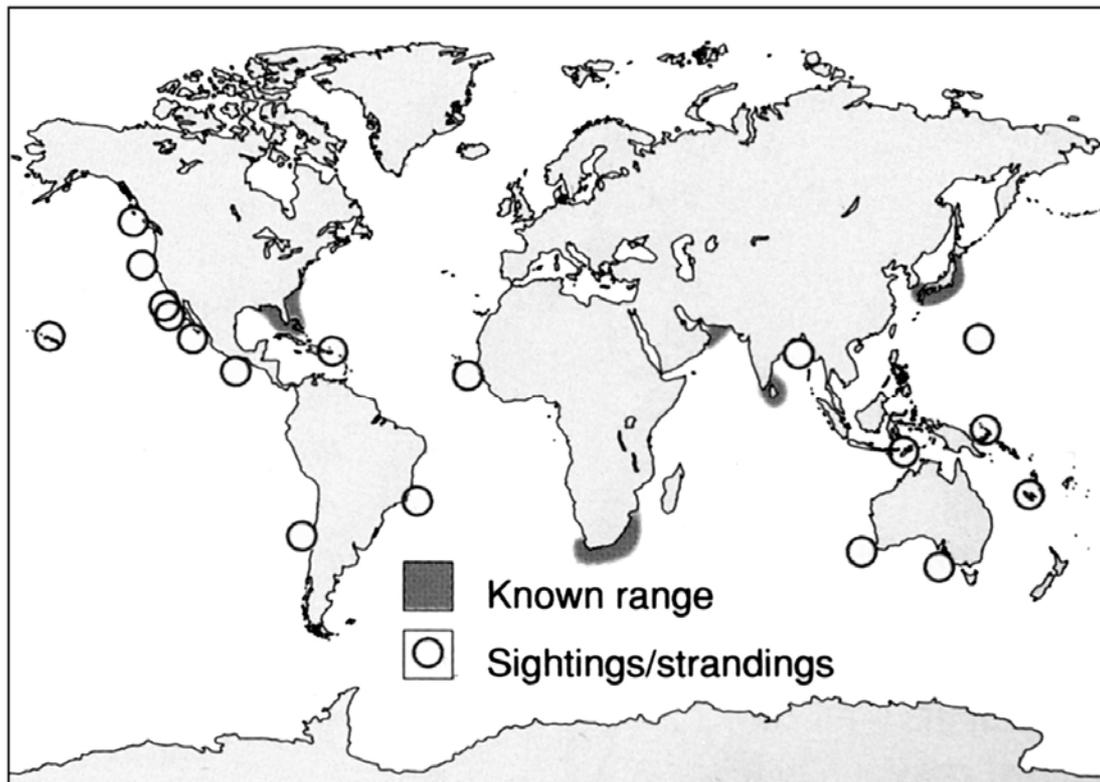


Figure 1.4: Worldwide distribution of *Kogia sima* (from Carwardine, 1995).

## 1.8.2 Habitat

Although data are rare, some authors have made deductions about the habitat of either *Kogia* species from the shape of their anterior-ventrally flattened snout and their small underslung jaw and suggest that the animals feed at or near the bottom at least some of the time (Nagorsen, 1985; Caldwell and Caldwell, 1989). Based on stomach content analyses Ross (1979a) suggests that *K. breviceps* lives further offshore than *K. sima*. However, a subsequent analysis by age group indicates that juvenile and immature animals, particularly of *K. sima*, live closer inshore than do adults (Ross, 1984). He suggests that the younger animals live over the outer part of the continental shelf and upper part of the slope, while adults are found over deeper water. In addition, the continental shelf or slope off Southern Africa appears to be important as a ‘nursery’ area for immature animals of either *Kogia* species (Ross, 1984).

Based on sighting data, Baumgartner (2000) identifies the distribution of the two species in the Gulf of Mexico as restricted to the upper continental slope. There is no information on the ecological relationships of the two species, but they have never been seen together (Klinowska, 1991).

### *K. breviceps*

Klages *et al.* (1989) conclude that both *Kogia* species inhabit waters over the continental slope on the basis of stomach content analysis, but suggest that *K. breviceps* is found more offshore than *K. sima*. Brabyn (1991) suggests that Mahia Peninsula off the east coast of the North Island of New Zealand is a calving area for *K. breviceps* due to the high stranding rate of mother/calf pairs in the area.

### *K. sima*

Stomach content analyses of specimens from South Africa suggest that *K. sima* occurs further inshore than *K. breviceps* (Klages *et al.*, 1989). During a survey in the Eastern Tropical Pacific *K. sima* is reported throughout the survey area, but most frequently near the coast (Wade and Gerrodette, 1993).

## 1.8.3 Abundance estimates

Authors of the early works on *Kogia* considered the animals so rare that a worldwide record of the reported specimens was kept. By 1911 only a dozen specimens of *Kogia* had been reported, by 1917 only 21 and by 1937 (which is a century after its first discovery) about 50 specimens were known (Scheffer and Slipp, 1948; Handley, 1966). Ross in his account from 1979 states that in the 140 years since Blainvilles' description of *K. breviceps* only approximately 150 specimens had been reported.

So "rare" and curious was the occurrence of a *Kogia* specimen anywhere that for a long time, the scientific literature about the two species concentrated on the findings of either one or two animals stranded somewhere in the world: (Pillay, 1926; Harmer, 1927; Hale, 1947; Scheffer and Slipp, 1948; Boschma, 1951; Hubbs, 1951; Gunter *et al.*, 1955; Harrison and Jamuh, 1958; Hale, 1959; Caldwell *et al.*, 1960; Hale, 1962; 1963; Raun *et al.*, 1970; Roest, 1970; Duguy, 1972; Kami and Lujan, 1976; Gallagher and van Bree, 1980; Maigret and Robineau, 1981; Omura and Takahashi, 1981; de Silva, 1987; Baccetti *et al.*, 1991; Nelson *et al.*, 1991; Debrot and Barros, 1992).

However, the size of any cetacean population is not easily determined, especially for pelagic stocks (Geraci and Lounsbury, 1993). In addition, a species abundant in one area may be in peril in another depending on regional conditions such as habitat degradation, patterns of exploitation, and fisheries interactions that might influence food

abundance, health and survival (Geraci and Lounsbury, 1993). Abundance estimates for either *Kogia* species have been attempted in the Eastern Tropical Pacific (ETP) (Wade and Gerrodette, 1993). However, sightings of either species of *Kogia* are difficult unless the sea is calm (between sea state 0-2 on the Beaufort scale) (Figure 1.5). In addition, small schools of animals are more likely to be missed than large ones. Since both *Kogia* species occur either singly or in small groups and are assumed to be deep and long divers, which may not be at the surface when the survey ship passes by, such estimates may not be representative (Wade and Gerrodette, 1993). In addition, ship avoidance behaviour, which was demonstrated for either *Kogia* species in the Gulf of Mexico (Würsig *et al.*, 1998), may bias the abundance estimates in a negative way (Wade and Gerrodette, 1993). Furthermore, the coast and shelf areas (which are preferred habitats for both *Kogia* species) were not systematically surveyed in these studies and may thus have been under-represented, further producing a negative bias (Wade and Gerrodette, 1993). These abundance estimates of *Kogia* in the eastern tropical Pacific revealed 84 *K. sima* sightings and four *K. breviceps* sightings, resulting in a total estimate of 11200 animals for *K. sima*; no abundance estimate was given for *K. breviceps* (Wade and Gerrodette, 1993). All *K. breviceps* sightings were north of 24° N, while the *K. sima* sightings all occurred south of 24° N (Wade and Gerrodette, 1993).



Figure 1.5: *Kogia* at sea off Southern Africa (Photo by V. Cockcroft, courtesy of the PE museum, Port Elizabeth, South Africa).

#### 1.8.4 Migration

Little is known about the seasonal distribution or movements of either species of *Kogia*. Examining the whaling catches off Japan, Yamada (1954) speculates that there may be a seasonal migration, and seasonal differences in stranding events for certain areas led a number of authors to believe in possible seasonal migrations (Allen, 1941; Gunter *et al.*, 1955). However, as strandings off South Africa and the south-eastern United States occur throughout the year, there is no indication for seasonal movements in these regions (Ross, 1979a; Leatherwood and Reeves, 1983; Caldwell and Caldwell, 1989). Odell (1985; pers. com.) suggests that the stranding seasonality in Florida is linked to the inshore-offshore movement of the Gulf Stream. Individual animals may follow warm water plumes shooting off from the stream and travelling towards the coast. They may get confused in the more complex inshore waters and subsequently strand as strandings appear to occur more frequently when the Gulf Stream is positioned further offshore. A few locations have been identified where *Kogia* appear to be local, year-round residents, like the Gulf of California, Mexico, which appears to be a permanent habitat for *K. sima* (Aurioles-G. *et al.*, 1993).

### *K. breviceps*

Sylvestre (1988a) suggests a seasonal movement of *K. breviceps* off the west coast of New Caledonia based on the fact that strandings only occur between June and December. In the North Pacific the majority of records for *K. breviceps* are from the autumn and winter (Eliason and Houck, 1986). Ross (1979a) suggests that the species is non-migratory off South Africa, although the animals may move offshore during summer.

### *K. sima*

Ross (1979a) states that there is little evidence to suggest that *K. sima* migrates onshore or along the shore of South Africa at any season.

## **1.9 Behaviour**

### **1.9.1 Surface behaviour**

Little has been published about the behaviour of the two *Kogia* species (Breese and Tershy, 1993), although one of the earliest accounts on their behaviour from “The cruise of the cachalot” by Frank T. Bullen apparently describes them as “lively” (Palmer, 1948). Subsequently, *Kogia* have been described as slow moving, lethargic and occurring solitarily rather than in social groups (Allen, 1941), while Hale (1962) calls them “sluggish”. Both species spend considerable time lying motionless at the surface, with only the back of the head exposed and the tail hanging down well below the surface of the water, with the dorsal fin submerged (Price *et al.*, 1984; Caldwell and Caldwell, 1989). This behaviour has also been termed “logging” (Carwardine, 1995). Yamada (1954) states that the Japanese name “Uki-Kujira”, meaning “floating whale”, was used by the ancient whalers in the province of Awa. There are also some accounts that *K. breviceps* is easy to approach, basically lying motionless on the surface until touched (Katona *et al.*, 1983 in: Caldwell and Caldwell, 1989). In contrast, whalers in the Lesser Antilles describe the animals as elusive and wary and being difficult to approach and catch (Reeves, 1988). More recent reports portray the two species to be rather shy, avoiding boats (Würsig *et al.*, 1998) and displaying a more porpoise-like behaviour of jumping and swimming vigorously (David Schofield, pers. com.; Bob Pitman, pers. com.). After diving the individuals rise slowly to the surface, produce an inconspicuous blow and dive without showing the flukes by sinking vertically beneath the surface (Leatherwood and Reeves, 1983; Baird *et al.*, 1996; Willis and Baird,

1998).

Both *Kogia* species are very difficult to observe in their natural habitat as they are rather 'cryptic' (Wade and Gerrodette, 1993; Ballance and Pitman, 1998) and avoid vessels (Würsig *et al.*, 1998). Most reliable sightings have occurred at calm seas and excellent visibility (Leatherwood and Reeves, 1983). During surveys in the northern Gulf of Mexico the two *Kogia* species showed the greatest percentage of avoidance reaction of all cetaceans observed by orienting away; none approached the ship or started bow riding (Davis *et al.*, 1995; Würsig *et al.*, 1998). Furthermore, in 40% of the sightings the majority of *Kogia* changed their behaviour from resting to diving in response to a survey airplane (Davis *et al.*, 1995; Würsig *et al.*, 1998). These data indicate that the two *Kogia* species are probably often undercounted during surveys (Davis *et al.*, 1995). In general, cetaceans with greater activity like leaping and splashing and those with a positive reaction to vessels have a greater probability of detection than a school that is rafting at the surface, creating little disturbance, and even avoiding the vessel (Würsig *et al.*, 1998). Due to this behaviour it is unknown how many animals are unseen or unidentified even during surveys.

### ***K. breviceps***

*K. breviceps* floats higher in the water with more of its back and head exposed than *K. sima* (Leatherwood and Reeves, 1983). The species has been described as rising slowly to the surface to breathe, producing an inconspicuous blow (Leatherwood and Reeves, 1983). In addition, *K. breviceps* more or less "sinks" below the surface when starting to dive (rather like a submarine), rather than rolling forward like other small odontocetes.

### ***K. sima***

Scott and Cordaro (1987) report on the behaviour of two *K. sima*, a presumed mother/calf pair, in the eastern tropical Pacific. The pair was accidentally encircled in a tuna purse-seine net together with a mixed school of spotted and spinner dolphins, although they did not appear to be associated with the group. The cow was observed to release a cloud of reddish-brown faeces into the net about six to eight times and hide herself and the calf inside it whenever a dolphin was approaching the pair (Scott and Cordaro, 1987). The cloud covered an area of approximately 100 m<sup>2</sup>. Furthermore, some aggressive behaviour was observed in the form of the mother ramming either the purse-seiner or the manned vessel aiding in the release of the dolphins (Scott and Cordaro, 1987). The authors conclude that the aggressive behaviour displayed in this instance is similar to that observed in other

physeterids, that the release of faeces occurs in response to threatening situations, and that it may be used for concealment (Scott and Cordaro, 1987).

### 1.9.2 Diving behaviour

One of the few dive times for wild *Kogia* to date have been reported by Breese and Tershy (1993) for a *K. sima* in the Gulf of California. The dive times ranged from 15 to 43 minutes. The animal rafted between dives, much like a sperm whale (Breese and Tershy, 1993). Willis and Baird (1998) provide some unpublished data for 59 dive intervals of *K. sima* and unidentified specimens of *Kogia* in the Gulf of California. The median dive time was 8.6 minutes and the median surface time was 1.2 minutes, but dives of up to 25 minutes and surface intervals of three minutes were common. Maximum dive times of up to 53 minutes were observed, but may have resulted from missed surfacings of the animal involved (Willis and Baird, 1998). Barlow and Sexton (1996) report the most frequent dive times for *Kogia* spp. in the Gulf of California to be between two and four minutes. They classify both species as “long-diving whales” and model the duration of long dives as 10.9 minutes on average and the duration of surfacing series as 78 seconds on average, based on 59 dive cycles for *K. sima*.

### 1.9.3 Inking

Animals of either *Kogia* species have been observed to emit clouds of reddish-brown faeces, sometimes during excretion (Price *et al.*, 1984), which brought the species its Japanese name “Tsunabi”, roughly translated as “firecracker-whale” (Yamada, 1954). Apparently whales were often observed by Japanese whalers to be basking at the surface, so that they were easily harpooned (Yamada, 1954). Frightened by the sudden attack, they would start to dive, while leaving an emission of reddish-brown faeces behind, which was easily mistaken for bleeding. Sometimes the animals were called the “skunk of the sea” for this habit (Yamada, 1954). This observation is often made when the animal appears startled and thus it has been speculated that it may be some form of camouflage mechanism, acting either as a visual or olfactory decoy, similar to that found in the octopus (Caldwell and Caldwell, 1989). Apparently, a similar reaction can be observed in the sperm whale, *P. macrocephalus*, but reports of that are rare (Yamada, 1954; Bob Pitman, pers. com.).

Caldwell and Caldwell (1989) describe how the lower intestine of both species has

a sac-like expansion, which is filled with a dark reddish-brown liquid. They comment that it is a very sticky and messy substance, which appears to stain clothing readily and has a consistency of chocolate syrup. In contrast, the examination of a South African specimen revealed it to be more like sand granules, which dissolve in water (pers. obs.). Caldwell and Caldwell (1989) estimate that in a large *K. breviceps* there may be up to 12 litres of this fluid present and initial laboratory tests of two samples reveal that the liquid contains large amounts of carbon (61.5% and 43.2%). Interestingly, the substance was found in a *K. breviceps* foetus from the coast of Oregon, which was near term, and has also been reported for a newborn male *K. breviceps*, which had not been nursed, but force-fed on milk formula for a day (Caldwell and Caldwell, 1989). These findings suggest that the animals synthesize the substance themselves rather than extract it from their prey of cephalopods.

When stranded this liquid may exude from the anus (Caldwell *et al.*, 1971) and may lead to reports from observers that the animal is bleeding (Manville and Shanahan, 1961). In Sri Lanka the species are called *lie mulla*, which literally translates into “blood dolphin” (Leatherwood, 1985).

#### 1.9.4 Sound production

The nasal apparatus in both *Physeter* and the two *Kogia* species appears more complicated than in most other cetaceans (Backhouse, 1972; Karol *et al.*, 1978), which suggests that it is probably used for sound production. A large melon composed of fatty tissue in front of a fat-filled spermaceti organ described for the two *Kogia* species is suggested to play a similar role to the melon found in other odontocetes and thus aid in echolocation (Karol *et al.*, 1978). At the rear of the spermaceti organ the “museau de singe” is located, which is thought to be a sound generator (Karol *et al.*, 1978). The results of the lipid analysis from these two organs together with anatomical and acoustical considerations suggest that the combined melon/spermaceti organ system functions to generate and focus echolocative sound (Karol *et al.*, 1978). While most authors believe that this is the source of sound production in the two species of *Kogia* (Caldwell *et al.*, 1966; Karol *et al.*, 1978; Carvan III, 1988; Clarke, 2003), it has also been suggested that the echolocation pulses are produced by the epiglottic spout of the larynx (Schenkkan and Purves, 1973).

Caldwell and Caldwell (1987) report that *K. breviceps* is capable of producing pulsed sounds, which might serve in echolocation. In addition, Caldwell *et al.* (1966) report on four isolated *K. breviceps*, which produced echolocation-type clicks with a high degree

of directionality. Recordings in air by Caldwell *et al.* (1966) and underwater by Caldwell and Caldwell (1987) from stranded animals showed low-amplitude echolocation-like clicks of varying repetition rates with peak frequencies below 13kHz. The fact that no recordings were made even when the animal was facing the hydrophone led Caldwell and Caldwell (1989) to suggest that the directionality of the emitted sounds must be greater than that found in *T. truncatus*. No sounds were recorded from *K. sima* to date and *K. breviceps* is said to vocalise infrequently (Caldwell and Caldwell, 1989). Thomas *et al.* (1990) describe an attempt to record sounds of a wild *K. breviceps* by following it for about 30 minutes with a towed array of hydrophones without any success. In addition, they report recordings from a stranded *K. breviceps* female, which produced a low-frequency, low amplitude sound of short duration, but no echolocation-clicks. It rather emitted a short sweep or cry, starting at a frequency of around 1.36kHz and ending with a frequency of 1.48kHz. These sounds may have been distress calls and occurred either singly or in pairs (Thomas *et al.*, 1990). Only ultrasonic click trains, most of them inaudible, are reported from a 179cm long male *K. breviceps* stranded in Monterey Bay, U.S.A. in August 1989 (Marten, 2000). The click trains ranged from 20kHz to over 200kHz, peaking at 125kHz (Marten, 2000). No other sounds were recorded for this specimen (Marten, 2000). Click duration varied and was on average 600µsec (Marten, 2000). Most of the click trains had a rising repetition rate, starting at 20kHz and rising like a “closure click train” observed in delphinids like killer whales *Orcinus orca* and bottlenose dolphins *Tursiops truncatus* (Marten, 2000). Sound recordings of “Inky”, a *K. breviceps* calf rehabilitated at the Baltimore Aquarium (see below) yielded sounds of 185kHz, the highest peak frequency from a whale at the time (Carder *et al.*, 1995; David Schofield, pers. com.).

Attempts to record the vocalisations of either *Kogia* species in the wild have not been very successful to date and clicks around 30-35kHz were recorded in close proximity to *Kogia* only once (Jay Barlow, pers. com.). This may suggest that acoustic census methods, which are very useful to support poor sightings data in other species, such as sperm whales *P. macrocephalus* and some delphinids (Oswald *et al.*, 2003), may not be very promising for either *Kogia* species. Sound recordings carried out during a survey in the north-central and western Gulf of Mexico yielded only one recording that was positively identified as belonging to a *Kogia*, although it was unknown to which species (Davis *et al.*, 1995). The frequency of the recording was not specified, but the analysis frequency range was 0-20kHz (Davis *et al.*, 1995). While limited knowledge exists about the vocalisations

of either *Kogia* species, it is known that their vocalisations differ from those of sperm whales *P. macrocephalus* by being of a higher frequency and shorter duration (Norris, pers. obs. in: Davis *et al.*, 1995).

### 1.9.5 Group size

The fact that two distinct species were only recognised as late as 1966 (Handley, 1966) makes many of the accounts published prior to this date unclear as to which species is the one concerned (Palmer, 1948). Yamada (1954) reports on a sighting of six or seven animals of what appear to be *K. breviceps* and two to three *K. sima*. Vidal *et al.* (1987) comment on a “loosely-formed” group of three *K. breviceps*.

Stranding data from Florida and South Africa suggest that there are different types of groups in both species, namely solitary adult animals of both sexes, cow/calf pairs and small groups of immature animals (Ross, 1979a; Leatherwood and Reeves, 1983; Credle, 1988). However, the most common groups, judging from data from stranded animals, seem to be solitary animals or cow/calf pairs (Ross, 1979a; 1984; Credle, 1988) (see also Chapter 7).

#### *K. breviceps*

Sighting data from the Eastern Tropical Pacific with identification to species level suggest that *K. breviceps* occurs solitarily (Wade and Gerrodette, 1993; Ballance *et al.*, 1996a), while sighting data from the Gulf of Mexico indicate that *K. breviceps* occurs in groups of one to two animals, with a mean group size of 1.2 (Davis *et al.*, 1995).

The highest number of animals stranded at the same time is three adult-sized animals (one male and two females) for *K. breviceps* (Credle, 1988; Caldwell and Caldwell, 1989).

#### *K. sima*

Although it is frequently stated that *K. sima* occurs in groups of up to 10 animals (Handley, 1966; Leatherwood and Reeves, 1983; Nagorsen, 1985; Carwardine, 1995; Willis and Baird, 1998), real evidence for this is rare. Recent observations in the Bahamas did indeed show that *K. sima* occurs in small groups of up to 10 animals and shows as yet unrecorded behaviour such as bow-riding, breaching and jumping (Colin MacCleod, unpubl. data). Most authors provide group size estimates of one to four animals for the

species (Ross, 1979a; 1984; Willis and Baird, 1998), while most sighting data indicate slightly larger group sizes. Group sizes range from one to five animals in the ETP and western tropical Indian Ocean (Wade and Gerrodette, 1993; Ballance *et al.*, 1996a), to one to seven in the Gulf of Mexico (Davis *et al.*, 1995). However, the mean group size in the ETP is 1.7 (Wade and Gerrodette, 1993), 1.6 in western tropical Indian Ocean (Ballance *et al.*, 1996b), and 2.1 in the Gulf of Mexico (Davis *et al.*, 1995).

The highest number reported of animals stranded at the same time is four immature animals (one male and three females) for *K. sima* (Ross, 1979a).

### **1.10 Predators**

Although Leatherwood and Reeves (Leatherwood and Reeves, 1983) state that no predators are known for *K. breviceps*, there has been one report of a shark bite thought to originate from a great white shark *Carcharodon carcharias* on a *K. breviceps* in northern Californian waters (Long, 1991). In addition, remains of both *K. breviceps* and *K. sima* were found in the stomachs of great white sharks (Heithaus, 2001). As the ranges of white sharks and the two *Kogia* species overlap in the coastal areas of eastern and western North America, south-eastern and western South America, north-western Europe, north-western and southern Africa, southern Australia and New Zealand and north-eastern Asia and Japan, other incidences of shark attacks may be observed in these areas in the future (Long, 1991). A number of dead stranded animals are also reported with shark bites, however, in these cases it is unclear whether the bites have occurred prior to or after the death of the animal. McAlpine and Murison (1997) also report possible signs of a healed wound inflicted by a shark. Furthermore, they suggest that indirect indications of shark attacks on animals of either *Kogia* species may be more common than indicated by the available literature, based on reports of infections with the cestode *Phyllobothrium delphini* (Caldwell and Caldwell, 1989; McAlpine and Murison, 1997), which is thought to mature in elasmobranchs. Remains of a *Kogia* specimen have also been found in the stomach of a shark (species unknown) caught off Cuba (Caldwell *et al.*, 1973).

Jefferson *et al.* (1991) in reviewing killer whale interactions with other marine mammals, report that *K. breviceps* remains have been found in the stomach of killer whales, but animals have not been observed being attacked and may therefore have been already dead. However, ecological interactions between killer whales and their prey as well as a number of shark species and their marine mammal prey have not been studied

systematically and in fact either predator may have a greater impact on *Kogia* populations than previously thought (Jefferson *et al.*, 1991) (see Chapter 9).

### **1.11 Additional studies**

Although specimens of either *Kogia* species may be quite shy and remote, the fact that they strand frequently in the south-eastern United States and are often taken into rehabilitation makes them available for a number of studies, which are usually not carried out on other cetacean species. Cronin (1998), for example, carried out studies on videophotoretinoscopy in both the bottlenose dolphin *T. truncatus* and *K. breviceps* and found that the latter had a near perfect eye-sight (emmetropic) in water, but was myopic (or near-sighted) in air.

Carballeira *et al.* (1987a) used the pygmy sperm whale to carry out a study on the adrenal gland morphology, hormonal content and biosynthesis of corticosteroids as well as the mitochondrial steroid enzyme activity of the adrenal gland (1987b).

### **1.12 Parasites and diseases**

#### **1.12.1 Parasites**

Parasitism appears to be prevalent in both *Kogia* species. In particular, large amounts of nematodes can be found in the stomach region and encysted tapeworms in the blubber (Zam *et al.*, 1971; Pinedo, 1987; Caldwell and Caldwell, 1989; McAlpine and Murison, 1997). At times the parasite load seems extreme and some authors have wondered whether a stranded whale was not spending more time and energy feeding the parasites than itself (Caldwell and Caldwell, 1989). While Raga (1994) gives an overview of all the parasites reported for *K. breviceps* in European waters and Nagorsen (1985) summarizes the species of internal parasites found in the two *Kogia* species, there have been no quantitative studies on parasitism in the genus *Kogia*. A number of parasites not commonly found in other marine mammals have been reported for either *Kogia* species (Pendergraph, 1971). Allen (1941) reports a calf with a goose-barnacle (*Penella* sp.) attached to the skin and blubber and trailing behind and another *K. breviceps* with a goose-barnacle attached was reported by McAlpine (1997). Raun (1970) found the skin of a stranded *K. breviceps* pocked with irregular holes 25-100mm in diameter and between 12 and 50 mm deep, but otherwise did not see any evidence of any external parasites. Dawson (1985) states that

many of the *K. breviceps* specimens stranded along the New Zealand coast were found to be seriously ill from disease and parasite infestations. Baker (1983) also notes that most animals stranded in Australia and New Zealand are extensively diseased.

### **1.12.2 Diseases**

Bossart *et al.* (1985) found both macroscopical and microscopical changes in the hearts of stranded adult specimens of either *Kogia* species, which were consistent with heart failure. This condition was considered to be a major factor in the stranding of those animals. All adult animals stranded along the south-eastern United States showed cardiomyopathy, leading Credle (1988) to conclude that it is probably a primary factor responsible for mortality in the two species, either at sea or on the beach.

### **1.13 Captivity**

Few stranded specimens of either *Kogia* species survive for long in captivity (Bossart *et al.*, 1985). Out of 33 animals kept in captivity most died within five days (Sylvestre, 1983). The longest time a stranded specimen of either *Kogia* species survived in captivity was 79 days reported for a male and a female *K. breviceps* kept at Ocean World Florida in 1966 (Sylvestre, 1983).

One stranded *K. breviceps*, a young male, was rehabilitated at the Long Marine Lab in Santa Cruz for five weeks. He produced high frequency clicks at a slow rate all the time, which were recorded by hydrophone and the click rate increased when the animal was startled (Dave Casper, pers. com.). The young animal was emaciated and cold. Once the tank was heated up to 72°F (22.3°C) he started shedding heat from his flippers (Dave Casper, pers. com.). Only when the water temperature had reached 76°F (24.5°C) could a blood sample be obtained and warming the water allowed the animal to start gaining weight. He was transferred to Marine World Africa after five weeks, where the heat was turned off as the animal gradually gained weight and started swimming around the pool (Dave Casper, pers. com.). Unfortunately the antibiotics given to him were stopped and he died of a pleural abscess (Dave Casper, pers. com.).

To date probably the longest surviving pygmy sperm whale in captivity and the only one that has been released successfully into the wild is “Inky” (Figure 1.6). “Inky” was a young female, that stranded on the 25/11/1993 in Egg Harbour in southern New Jersey

(Bob Schoelkopf, pers. com.). She was 182.9cm long and weighed 79.4kg at the time of her stranding (Bob Schoelkopf, pers. com.). She showed the behaviour typical for *Kogia* of emitting reddish-brown faeces into the water, which resulted in her name. Her teeth were erupting and she was therefore thought to be of weaning age (Schofield, 1996). Apparently a wind surfer had supported her on the beach until she was transported to the Animal Stranding Centre in Atlantic City, New Jersey (David Schofield, pers. com.), where she was stabilized throughout the night. The following day she was airlifted by helicopter to the National Aquarium in Baltimore. There she was measured and weighed again and reported to measure 182.9cm and weigh 93.9kg (David Schofield, pers. com.). The discrepancy in these data from one day to the next can only be explained by the difficulties encountered in weighing a live animal.

Inky was found to be regurgitating her food initially, until a series of endoscopic examinations yielded small pieces of plastic from her stomach (Schofield, 1996). There have been a number of incidences when plastic was found in the stomachs of specimens of either species of *Kogia* (see below). Inky was found to only consume what was thought to be half of her nutritional requirement initially, but after the plastic pieces were removed from her stomach her behaviour made a dramatic positive change (Schofield, 1996).

Inky was kept in Baltimore for almost six months until the 5/5/1994, when she was flown to Florida to be released (Schofield, 1996). She grew 35.6cm and gained 56.8kg during her time in Baltimore (Schofield, 1996).

Inky was released on the 30/5/1994, equipped with a time-depth recorder (TDR) attached to her dorsal fin (David Schofield, pers. com.). This was the first time a TDR was ever attached to an animal of either *Kogia* species and it might have led to a lot more information and insight to the life of these elusive animals. She was tracked for four days for 100 miles north along the western edge of the Gulf Stream (David Schofield, pers. com.). Her dive times seemed to increase to 15 minutes during the evening hours, which might suggest night time feeding. Unfortunately no data were obtained about the diving depth as the TDR seemed to have come off and could not be retrieved subsequently (David Schofield, pers. com.).

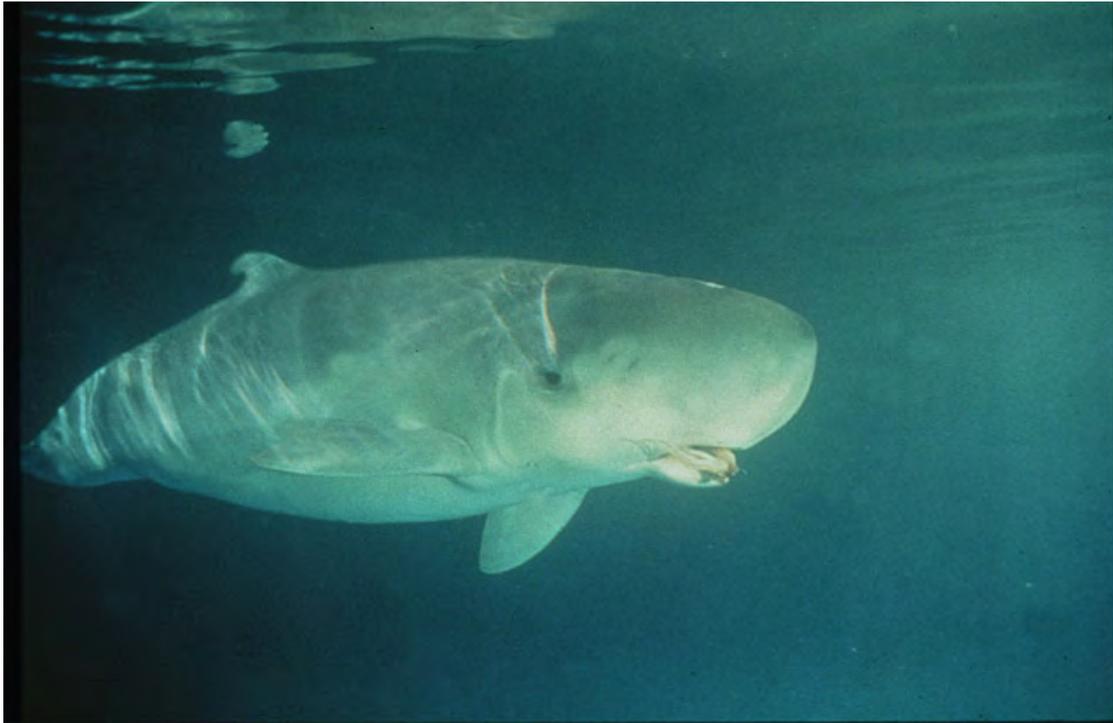


Figure 1.6: “Inky” feeding on squid (Photo by David Schofield, National Aquarium, Baltimore, USA).

Jenness and Odell (1978) give data on the milk composition for a lactating *K. breviceps* female that stranded with a calf in apparent good body condition. The sample had a pH of 6.2 and contained more water, lactose and whey protein and less fat and calcium compared to other cetaceans, including the sperm whale *P. macrocephalus*, which is also teuthophagous (Jenness and Odell, 1978). However, individual specimens vary greatly, which may also be due to the changes in composition occurring during the lactation period. Gorzelany *et al.* (1995) provide a formula that was successfully administered to a *K. breviceps* calf in captivity; Price *et al.* (1984) also provide a formula, but the calf died within five days.

### **1.14 Human consumption**

Some researchers remark that the meat of *Kogia* is good to eat. “Reports ranged from disgust to enthusiasm” by members of Scripps Institution, although the *Kogia* meat was stronger in flavour and less delectable than an Andrew’s beaked whale *Mesoplodon bowdoini* that they had tried some time earlier (Hubbs, 1951). Hale (1962) remarks that the meat makes “an excellent hot meal and provided some of the most tender steak”, although it

was “not so palatable when cold”. Yamada (1954) reports that around ten *Kogia* used to be caught in the Japanese whaling port of Taiji annually. However, animals were only caught during the summer season and Yamada speculates that this may be due to their migratory nature. In contrast, Handley (1966) states that the flesh is edible, but not the aim of a major commercial operation.

Recent incidents of accidental capture of specimens of either *Kogia* species in gillnets and other fisheries are reported to have resulted in consumption in at least some areas (Klinowska, 1991; Muñoz-Hincapié *et al.*, 1998). Both *K. breviceps* and *K. sima* are hunted in the Philippines (Leatherwood *et al.*, 1992), where they are either used for human consumption or as bait to catch sharks (Anonymous, 1996).

### ***K. breviceps***

Although Dawson (1985) states that a few specimens of *K. breviceps* are taken every year by Japanese whalers, no such indication was found in the literature. Furthermore, the International Fund for Animal Welfare (IFAW) database on whale meat identified from the markets of Japan and Korea contains only one *K. breviceps* specimen (Merel Dalebout, pers. com.), which indicates that these species do not seem to be targeted. In Peru the remains of a subadult *K. breviceps* were discovered in a rubbish dump amongst carcasses of cetaceans frequently caught and sold for human consumption (van Waerebeek *et al.*, 1987).

### ***K. sima***

Kami and Lujan (1976) report on a stranded *K. sima* in Guam, which was apparently eaten by local people. Muñoz-Hincapié *et al.* (1998) also report that a dwarf sperm whale was captured by fishermen off Brazil and consumed.

## **1.15 Threats**

### **1.15.1 Interactions with fisheries**

Probably one of the first references to *Kogia* being hunted appears in “The cruise of the cachalot” by Frank T. Bullen, in which the author refers to a group of five animals being taken, averaging apparently wrongly seven barrels of oil each (Palmer, 1948). However, it appears that there have been no major threats to either species of *Kogia*, although they have been reported to be hunted off St. Vincent in the Lesser Antilles (Caldwell *et al.*, 1973), the

Phillipines (Leatherwood *et al.*, 1992), and have been seen occasionally in the fish markets in Sri Lanka (Leatherwood, 1985). Chantrapornsyl *et al.* (1991) report that a number of calves and sub-adults are by-caught in the Sri Lankan gillnet fishery. They are also possibly taken accidentally in other fisheries (Klinowska, 1991) and there is a recent report of both *Kogia* species being by-caught in fishing gear in Taiwan (Wang *et al.*, 2002). In most other nations in South-east Asia from which the species are reported the only threats identified are possible encroachment on habitat by fisheries and plastic bag ingestion (Anonymous, 1996).

### ***K. breviceps***

A few specimens appear from time to time in the local small cetacean fisheries off southern Japan and Indonesia (Klinowska, 1991).

One specimen of *K. breviceps* was taken by a spear fisherman in Kahului Harbour, Maui, Hawaii, in 1942 (Edmondson, 1947). In April 1947, while fishing near Lahaina, Maui, Hawaii with a hand line baited with *aku* meat, a fisherman caught a seven foot, 300 pound *K. breviceps* (Edmondson, 1947).

A female *K. breviceps* calf measuring 173cm, was accidentally taken by a driftnet in the high seas of the North Pacific (Omura *et al.*, 1984). Apparently several other, larger animals of the same species were taken at the same time, but no record of the age, sex or size of these was kept (Omura *et al.*, 1984).

### ***K. sima***

A few specimens appear from time to time in the small cetacean fisheries off southern Japan, Indonesia, and St. Vincent in the Lesser Antilles (Caldwell *et al.*, 1973; Klinowska, 1991). In addition, *K. sima* get caught in drift gillnet fishery off California, which operates between 37-370km offshore (Barlow and Cameron, 2003).

## **1.15.2 Plastic ingestion**

Both species of *Kogia* are frequently reported to ingest plastic in the wild (Ross, 1979a; Caldwell and Caldwell, 1989; Tarpley and Marwitz, 1993; Willis and Baird, 1998; David Schofield, pers. com.). It seems to be a common occurrence in these teuthophagous species, which might confuse pieces of plastic with squid (Caldwell and Caldwell, 1989; Tarpley and Marwitz, 1993). Whether or not this behaviour can lead to certain death has not

yet been established, but one would assume that it may prevent digestion and lead to starvation.

### **1.15.3 Pollution**

Few studies have analysed the pollutant load in either *Kogia* species. A detailed study on the organochlorines in both *K. breviceps* as well as bottlenose dolphins *T. truncatus* from south-eastern Florida was carried out by King (1987) in order to test whether there are intraspecific differences in concentration in relation to body length and sex and interspecific differences in relation to distribution and diet. The results indicate significantly higher concentrations of chlorinated pesticides and PCB's for males than for females and there is no significant correlation with body length (King, 1987). Furthermore, bottlenose dolphins show higher overall concentrations of organochlorines than *K. breviceps* as anticipated by the differences in distribution and diet between the two species (King, 1987). While *T. truncatus* off Florida is believed to have a more inshore distribution with a predominantly piscivorous diet, *K. breviceps* is a pelagic species and mainly teuthophagous. However, comparison with a 1976 study on DDT levels in *K. breviceps* from the same area shows that the levels are not considerably different almost ten years later (King, 1987). Overall, both species are within the low range of global contamination for DDT's and while *K. breviceps* is within the low range for PCB levels, *T. truncatus* is in the high range, particularly the males (King, 1987). Two *K. breviceps* specimens stranded in New Caledonia show high levels of cadmium and iron in the liver, which were thought to be associated to the diet of fish and cephalopods (Bustamante *et al.*, 2003). Iron is the only metal having a higher concentration in *K. breviceps* than in the pilot whales examined at the same time (Bustamante *et al.*, 2003).

### **1.16 Conservation status**

Both the pygmy and the dwarf sperm whale are currently listed under Appendix II of the Convention for the International Trade in Endangered Species (CITES) (date: 28 May 2003). This means that the two species are currently not necessarily threatened with extinction, but may become so unless trade is closely controlled. The International Union for the Conservation of Nature (IUCN) assigned the status "insufficiently known" to both *Kogia* species in its 1991 "Red Book" (Klinowska, 1991). Although not currently listed on

the threatened species list of the IUCN, the status of both species remains “data deficient”. The main reason for this is that the abundance and status for both species are unknown, although neither appears to be subject to any significant known threats (Klinowska, 1991). The Red Data book points out that hardly any basic information on either species’ biology is available and that there is a need for more data to be gathered on its abundance, biology and behaviour (Klinowska, 1991).

### **1.17 This study**

At the end of Handley’s classic account of the two *Kogia* species is a short dialogue under the “Comments” section (Handley, 1966). An excerpt from this reads as follows:

Question: Should there not be some ecological and behavioural differences between these two species?

Dr. Handley: That seems very likely, but it is not known to me.

Although subsequent studies by Ross have managed to shed a substantial amount of light on this issue, one of the major aims of the present study is not just to examine the life histories of both species in more detail, but also to investigate differences found between these two confusingly alike species. Due to the limited knowledge on the natural history of the two *Kogia* species, researchers have often suggested that the biology of *Kogia* is similar to that of *Physeter* because of their status as sister taxa (LeDuc *et al.*, 1999). The present work will help to indicate that such an assumption is not valid, as it appears that the environment in which these animals live has a bigger influence on the shaping of their life histories than their genetic make-up. Not only are *Physeter* and the two *Kogia* species very different from each other in their biologies, but similarly *K. breviceps* and *K. sima* are quite different in their ecologies and life history strategies as well as will be shown in the present work.

### **1.18 Thesis structure**

Due to the diverse nature of the present research, each of the following working chapters (with the exception of Chapter 2) is presented as a study in itself and thus has its individual Introduction and Materials and Methods sections. In addition, the results are presented and discussed individually for each chapter as well. An overall summary and

discussion of the combined results is presented in the last chapter.

The following is an outline of the structure of the present thesis:

Chapter 2 gives information on the sample and study area.

Chapter 3 examines the age and growth of the two *Kogia* species.

Chapters 4 and 5 concentrate on the reproductive biology of males and females, respectively.

Chapter 6 examines the diet of the two *Kogia* species.

Chapter 7 presents information on the stranding patterns of both species along the Southern African coastline.

Chapter 8 examines the population structure of the two *Kogia* species off South Africa in relation to others in the Southern Hemisphere.

Chapter 9 summarizes the main results and presents conclusions about the life history strategies of the two *Kogia* species.

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## *Chapter 2: Sample and Study Area*



## **2.1 Introduction**

The present study is based on samples obtained from animals, which stranded over a period of 115 years over an approximately 3000 km long stretch of coastline. Although definite numbers are unavailable, a comparison with published data from Florida (Credle, 1988) suggests that South Africa has the second highest stranding rate for both *Kogia* species worldwide after Florida. This presents a great opportunity to study these little known species in more detail.

## **2.2 Sample**

For the present study records and samples of pygmy (*Kogia breviceps*) and dwarf (*K. sima*) sperm whales stranded along the Southern African coastline between 1880 and 1999 were examined. Basic information on every stranding record used in the present study is listed in Appendix A by species in reverse chronological order. Each stranding event has a Port Elizabeth Museum (PEM; now Bayworld) or South African Museum (SAM) number and information on the date (day/month/year), sex, length, latitude and longitude of the stranding site, the location and the type of event and condition of the animal assigned to it. In some instances the reproductive status is also noted (e.g. pregnant, lactating). The total length of the animal is given in centimetres and measured from the tip of the snout to the notch of the flukes (Norris, 1961). The latitude and longitude is given in degrees and minutes and coordinates have been taken from a gazetteer for those localities where only a name was provided (Anonymous, 1992). The type of event was also noted i.e. single, cow/calf, or multiple (double/triple).

Material for age determination, assessment of reproductive status in males and females, stomach content analysis as well as analysis of stranding patterns (see Chapters 3 to 7) was provided by the Port Elizabeth Museum, Port Elizabeth, South Africa, as well as the South African Museum, Cape Town, South Africa. Since the material was sampled over a considerable time span by a variety of sources the data sets are not always complete for each individual (see Appendix B), which explains discrepancies in sample sizes between tables and figures.

The availability of organ samples for a specimen, as indicated in Appendix B, does not necessarily mean that the whole organ was available as, in some cases, only a

sub-sample was preserved. Also organ measurements, such as testes weights and lengths, may have been indicated on the data sheets in some instances, but no tissue sample was available for histological examination. All the organ and tissue samples used in this study had been fixed and stored in 10% buffered formalin, while teeth and bones were stored dry.

In order to increase the sample size, material examined previously on the same population by Ross (Ross, 1979; 1984) was included in the present study. For this purpose, the original data sheets located at the Port Elizabeth Museum as well as the publications were consulted. This explains occasional differences in the data presented here and the ones published previously.

Additional material and information was obtained for 28 *K. breviceps* and one *K. sima* stranded along the Australian coastline (see Appendix C). For the majority of these animals, however, only teeth could be obtained for age determination and genetic analysis of population dynamics and thus the resulting data could only be included in Chapters 3 and 8.

For the population genetic analysis (see Chapter 8) an attempt was made to obtain samples from the entire Southern Hemisphere in order to compare the South African populations with those from other geographical locations. For this purpose the South African as well as the Australian samples were analysed. In addition, samples were obtained from New Zealand, Chile, Peru and New Caledonia (see Appendix C).

### **2.3 Sample bias**

The size-frequency analysis for *K. breviceps* (Figure 2.1) showed a bimodal distribution, which indicates that this sample was biased towards males of a total length between 200 and 220cm and females between 280 and 320cm. An analysis of the reproductive organs showed that males are still immature at that length, while females are mature (see Chapters 4 and 5). Therefore the sample for *K. breviceps* is probably not representative of the whole population.

In contrast, the size-frequency distribution for *K. sima* indicated that the sample was normally distributed (Figure 2.2). Most males that stranded were between 200-220cm in body length, while females were slightly larger (between 220-240cm). As reported in Chapters 4 and 5, both male and female *K. sima* are mature at that stage.

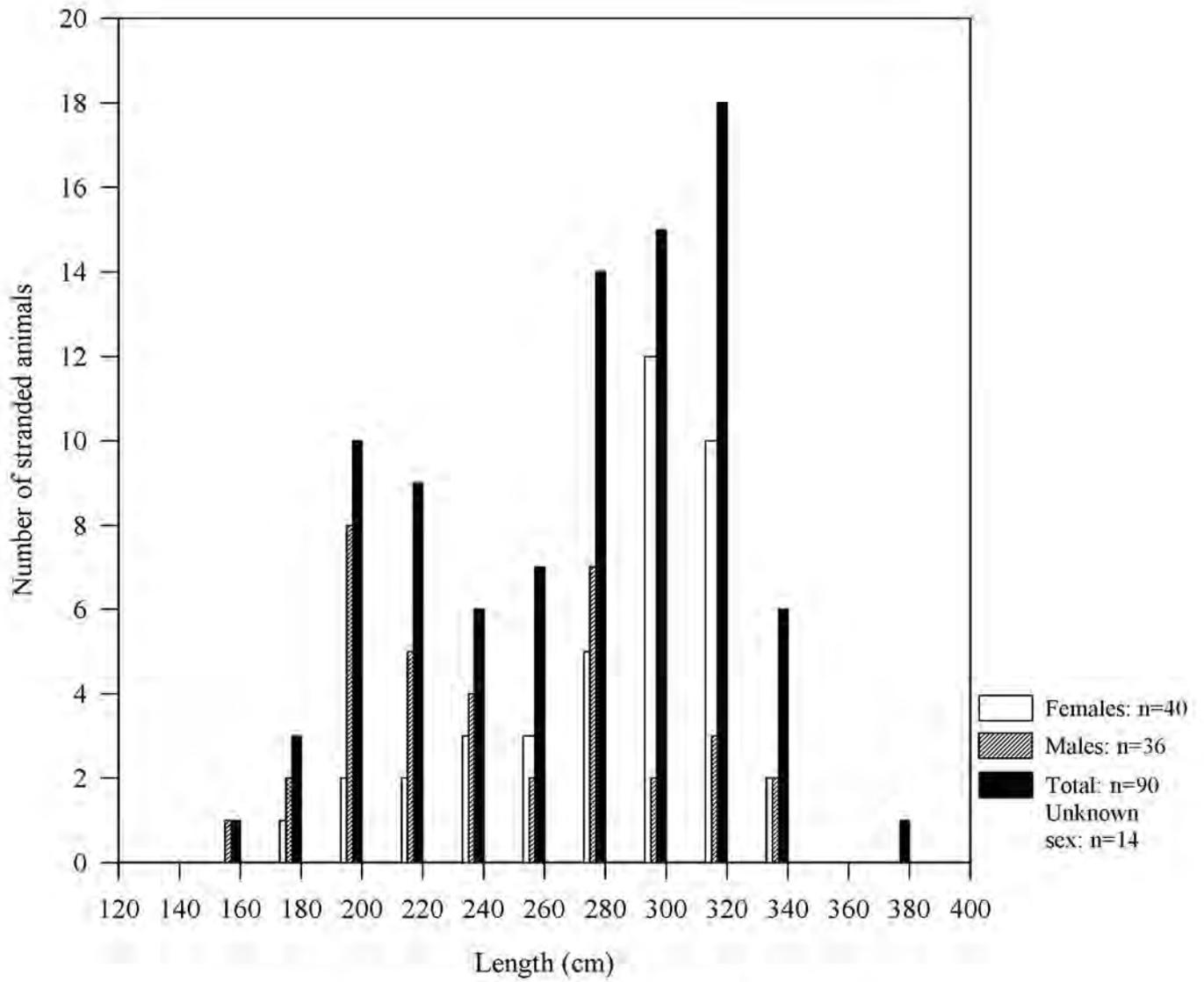


Figure 2.1: Size-frequency of *Kogia breviceps* strandings.

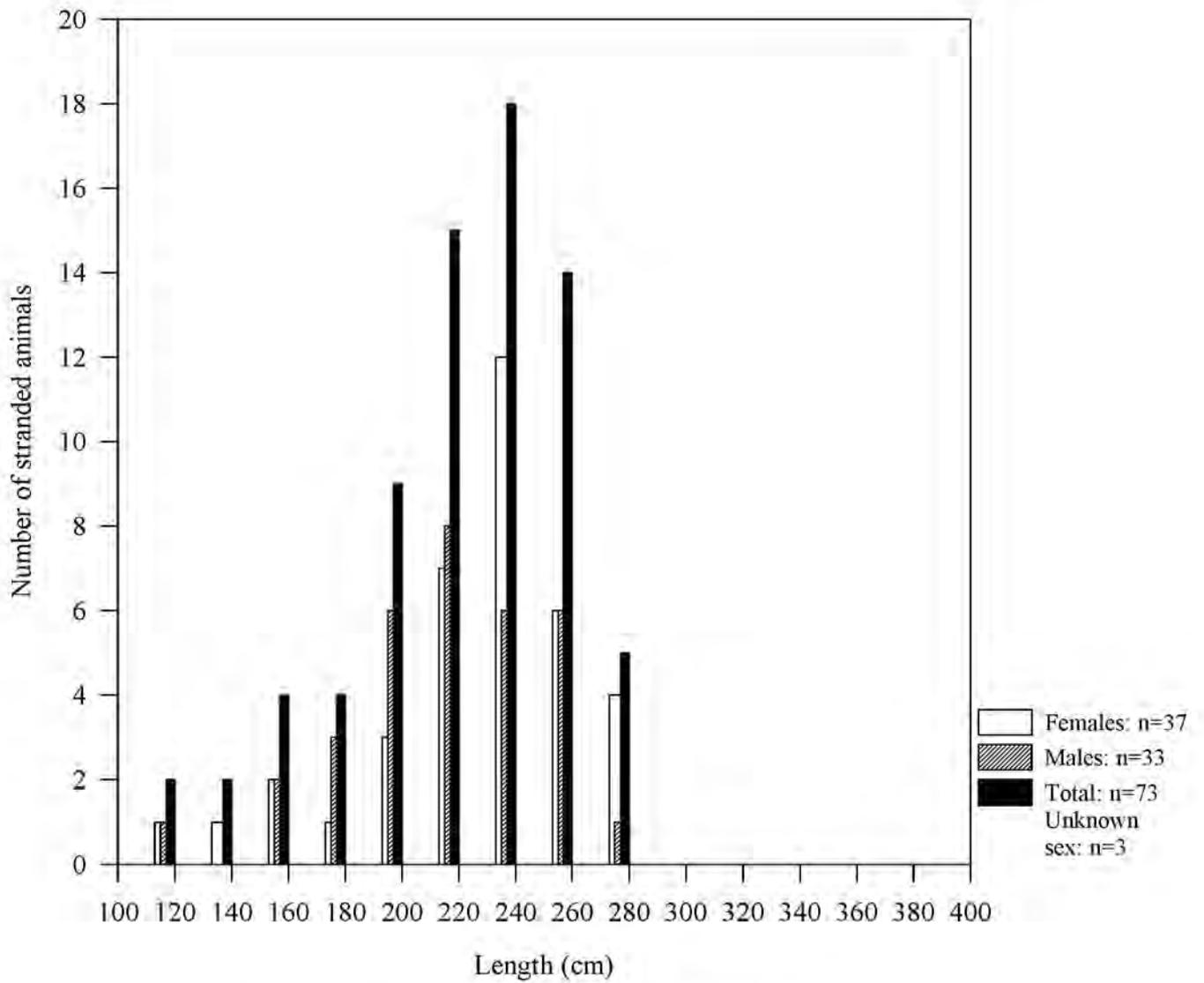


Figure 2.2: Size-frequency of *Kogia sima* strandings.

Neonates also stranded, but in low numbers (Figure 2.2).

It is interesting to compare these data with the ones available from Credle (1988) for the south-eastern United States. Plotting the size-frequency distribution for her sample of stranded *K. breviceps* the females were slightly larger, showing a peak between 280-320cm of body length. In contrast, the males were much larger than in the present sample, showing a peak between 310-330cm.

The size-frequencies of *K. sima* in Credles' sample indicated that both males and females of this species showed a similar size-frequency distribution as in the present sample, with peaks at 230cm for the females and at 190-230cm for the males, respectively (Credle, 1988). Thus the males of this species are slightly smaller in the present sample than those that stranded along the south-eastern United States.

One concern with the analysis of cetacean strandings is the bias that invariably accompanies such studies. This bias is due to the fact that studies on stranded whales and dolphins often include animals, which were recovered over a long period of time as well as a wide geographic area. In addition, animals may either have died at sea and subsequently stranded or stranded first and then died as a result. In most cases the cause of death is unclear and stranded animals may not reflect the "normal" biology of a species. In addition, it means that such studies are of a deductive nature rather than dealing with directly observed results. This scenario is also prevalent in the present study, and although most of the specimens may have succumbed to disease, predation or aggression, a large number of *Kogia* carcasses probably never wash ashore due to the offshore habitat of these species (see Chapters 1, 6 and 7). Thus the sample analysed here can possibly not be assumed to be a true representation of the *Kogia* populations off Southern Africa. This is rather unlucky and in many ways unsatisfactory, but due to the cryptic behaviour and lack of field data on the two species of *Kogia* (see Chapter 1) there is little likelihood of obtaining better data at present. As it is unlikely that similar data as gathered here will be obtained from free-ranging animals in the near future, the results of the present study present a first insight into the biology of *K. breviceps* and *K. sima* off Southern Africa and hence justify the acceptance of a certain, although unknown, bias in the sample set.

## **2.4 Study area**

For the present study samples and data from strandings of the two *Kogia* species along the entire South African coastline as well as a part of the Namibian coast were analysed. The location of the strandings extend from Durrissa Bay in Namibia on the western Southern African coastline (21°15'S and 13°14'E) to Central Beach, Durban, on the east coast of South Africa, approximately 500km south of the border with Mozambique (29°50'S and 31°02'E) (Figure 2.3, Appendix A).

The oceanography of this region is determined by two major current systems found off the subcontinent: the cold, northward flowing Benguela current on the west coast and the warm, southward flowing Agulhas current on the east coast (Figure 2.3). Both currents meet at Cape Agulhas on the southern Cape coast.

The topography of the region is also shown in Figure 2.3. The continental shelf along the west coast is relatively wide, with a distance of 180km off the Orange River (28°35'S, 16°25'E), but narrows to about 40km off the Cape Peninsula. South of the Cape the shelf widens rapidly to form the Agulhas Bank, which stretches to about East London at the Eastern Cape coast. The topology of the Agulhas Bank is characterised by rocky capes and shallow sandy bays, which are usually below 50m in depth (Findlay, 1989). Then the shelf narrows again drastically to less than 10km in width. This provides little resistance to the fast flowing Agulhas current (Gründlingh, 1983). The oceanographic conditions of the study area are described in more detail in Chapter 7.

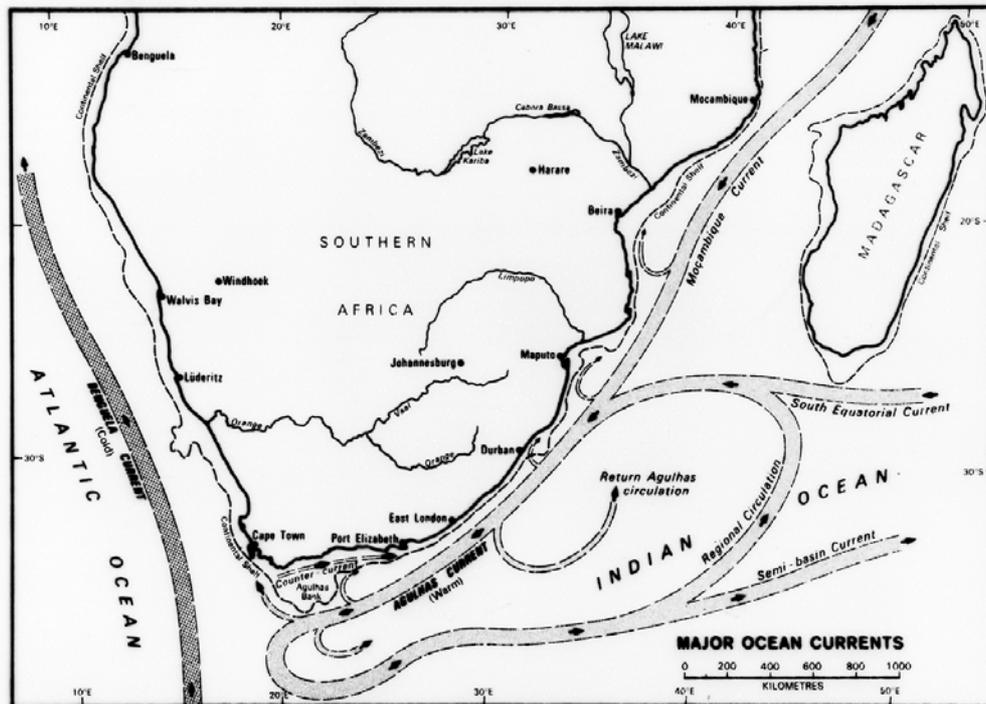


Figure 2.3: Map of Southern Africa showing the major ocean currents off the coastline and the topography of the continental shelf (map by the Department of Geography, Rhodes University, Grahamstown, South Africa).

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## *Chapter 3: Age and Growth*



### **3.1 Theoretical background**

Being able to determine the age of an animal is a fundamental requirement in many areas of ecological and physiological research (Langvatn, 1995) and data on age and growth in relation to reproductive parameters present vital information about the potential survival of a given species (Hohn *et al.*, 1996). The use of age determination of marine mammals, based on the layered structures in their teeth, has become a standard procedure in stock assessment and management decisions (Scheffer and Myrick, 1980) as age-specific estimates for fecundity or mortality are used to project population growth (Hohn, 2002). In addition, changes in parameters such as age at sexual maturity can be interpreted as reflecting changes in the population abundance or resource availability (Hohn, 2002). Age determination enables general conclusions to be drawn on the life span of the animals, the growth curves of males and females, and the ages at sexual and physical maturity (Mikhalev, 1982). In addition, reproductive parameters are important for an understanding of the basic life history of a species as well as to demonstrate continued survival or possible threats. Studies on the age and growth and related life history parameters in odontocetes have mainly concentrated on small cetaceans incidentally caught in fishing gear (Perrin *et al.*, 1977; Myrick *et al.*, 1986; Read and Gaskin, 1990; Sooten, 1991; Read and Hohn, 1995; Hohn *et al.*, 1996; Read and Tolley, 1997; Ferrero and Walker, 1999), animals from directed fisheries (Sergeant, 1962; Kasuya, 1972; Kasuya *et al.*, 1974; Kasuya, 1978; Kasuya and Marsh, 1984; Bloch *et al.*, 1993; Kasuya *et al.*, 1997), incidental catches in shark nets (Kasuya and Brownell, 1979; Cockcroft and Ross, 1990), and dead specimens from epizootics (Calzada *et al.*, 1994; Calzada *et al.*, 1996). Few studies have concentrated on stranded specimens (Ross, 1984; Mendolia, 1989; Sooten, 1991; Di-Méglio *et al.*, 1996).

In order to determine basic life history parameters such as age at sexual maturity and reproductive rate it is essential to determine the age of individuals with known reproductive status. The present chapter deals with the aspects of age and growth of both *Kogia breviceps* and *K. sima*, while Chapters 4 and 5 present results on the reproductive biology of male and female *Kogia*, respectively.

### 3.1.1 Teeth, dentition and mode of feeding

Teeth are amongst the most rigid and lasting structures in an organisms' body, but are still dynamic enough to reflect cyclic and metabolic events in the life of an individual (Langvatn, 1995). In addition, they are readily available from dead animals and easy to preserve and store for later processing and analysis (Langvatn, 1995) (see Chapter 8).

Odontocetes have a homodont dentition, which means that all teeth have the same shape and are not differentiated into incisors, premolars and molars (heterodont) (Peyer, 1968; Myrick, 1991). Homodont dentition is commonly found in fish, amphibians and reptiles, but presents an exception among mammals (Peyer, 1968; Myrick, 1991). The teeth of odontocetes are either conical or peg shaped (Myrick, 1991). In addition, they are far more numerous in most delphinid species than in any other mammal (Myrick, 1991). Odontocetes are furthermore monophodont, meaning that they do not possess deciduous teeth (milk teeth) (Peyer, 1968) and thus their teeth contain a complete growth record from the time of birth to the animals' death.

The differing dental formulae of the two *Kogia* species have often been used as a distinguishing characteristic (Handley, 1966; Ross, 1979; Carwardine, 1995) and further details were presented in Chapter 1. Both species of *Kogia* exhibit reduced dentition, which is a phenomenon commonly seen in teuthophagous odontocetes (see Chapter 6). It has long been suggested that a number of odontocetes may feed by means of suction feeding, which does not involve the need of teeth for chewing or even grasping of the prey (Norris and Møhl, 1983). Recent morphological evidence suggests that ziphiids and possibly also both families of sperm whales (Physeteridae and Kogiidae) employ this mode of feeding (Heyning and Mead, 1996). This is discussed in more detail in Chapter 6.

### 3.1.2 Tooth morphology and age determination

Reviews on age determination in mammals have been provided by Klevezal' and Kleinenberg (1967) and, more recently, by Langvatn (1995). Klevezal' and Kleinenberg (1967) present a general description of the annual layers in the tissues of teeth and bone, including a general description of mammalian teeth, their histology and growth. In addition they give an overview of the methods for selecting, processing and reading teeth

and bone for age determination. Langvatn (1995) presents a summary of the structure and chemical composition of teeth, regulation of calcium and phosphate metabolism and, the process of mineralisation (Langvatn, 1995). A review on the history of age determination in marine mammals is given by Scheffer and Myrick (1980).

### **3.1.2.1 Tooth morphology and histology**

A number of authors review the histological structures of odontocete teeth (Boyde, 1980; Myrick, 1980; Langvatn, 1995), as well as the use of these structures in age determination (Klevezal', 1980; Pierce and Kajimura, 1980; Myrick, 1980). A multitude of methods have been developed over the years in order to optimally visualize the layered structures in the teeth. Techniques include acid etching (Pierce and Kajimura, 1980), polarizing light microscopy (Myrick, 1980), aspartic acid racemization (Bada *et al.*, 1980), micro radiography and scanning electron microscopy (SEM) (Hohn, 1980a). Scheffer and Myrick (1980) give a review of age determination results by species.

Mammalian teeth are composed of a crown and a root, the former protrudes out of the jaw, while the latter is concealed in the tooth alveolus of the jaw (Klevezal' and Kleinenberg, 1967). Most of the tooth is made up of dentine, with the crown being covered by enamel and the root having an outer coat of cementum (Klevezal' and Kleinenberg, 1967). Newly erupted teeth in mammals are composed of a thin-walled dentine cap already covered with enamel, encapsulating a papilla of soft tissue, known as the pulp cavity (or tooth canal) (Klevezal' and Kleinenberg, 1967). The pulp contains odontoblasts, which give rise to new dentine (Klevezal' and Kleinenberg, 1967). As the tooth grows, dentine is deposited from the side of the pulp cavity in such a way that the dentine layers formed earlier are situated closer to the outer walls of the tooth and those formed most recently are closer to the pulp cavity (Klevezal' and Kleinenberg, 1967). The general pattern of tissue differentiation in the tooth into dentine, enamel, and cementum in odontocetes is described by Perrin and Myrick (1984).

Dental and periosteal tissues of dolphins and other vertebrates are composed of the mineral hydroxyapatite (Myrick, 1980; Lockyer, 1995a; Outridge *et al.*, 1996). Because growth is inconstant, layers of various optical densities are formed, and crystal lattices of hydroxyapatite are deposited within the layers in orientations that tend to differ from increment to increment, but which have a common alignment within a given growth increment (Myrick, 1980). The laminations in the dentine and cementum have

generally been defined in terms of differing mineralization density or quality (Lockyer, 1993). Contiguous pairs of such laminae comprise a growth-layer group (GLG), 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). GLGs consist of thin layers that are deposited with lunar monthly regularity (Hohn, 1980a; Myrick, 1991). This means that they usually show 13 accessory layers, which are thought to be related to lunar cyclicity (there are thirteen lunar months in a year) (Myrick, 1980; Myrick *et al.*, 1984; Myrick and Cornell, 1990). Within the accessory layers of the postnatal dentine one can distinguish a system of minute incremental growth layers called “lines of von Ebner”; these are thought to reflect daily growth (Myrick, 1980).

The formation of layers comprising GLGs is thought to occur seasonally in most mammals, including odontocetes (Klevezal’ and Kleinenberg, 1967). Klevezal’ and Kleinenberg (1967) list a number of reasons for the differences in optical density found between the layers comprising a GLG. In general it is assumed that one band is related to slower growth and thus more calcified, while the other band is representative of faster growth and less calcified (Klevezal’ and Kleinenberg, 1967). While the layers are thought to be linked to seasonal changes in food and feeding of the animal or changes in regular growth rate, the mode of life (i.e. terrestrial, aquatic or semi-aquatic) does not appear to have an influence (Klevezal’ and Kleinenberg, 1967).

Both the numbers and the character of the layers found in the teeth are similar in all the teeth of an individual (Mikhalev, 1982; Myrick, 1991). It appears that both the sex and the age of the animal have an influence on the rate of deposition of the GLGs (Nielsen, 1972; Hohn, 1980b; Myrick *et al.*, 1984; Myrick and Cornell, 1990). In addition, the layers in odontocete teeth appear to decrease in width with age (Kasuya, 1972; Best, 1976; Hohn, 1980b; Myrick and Cornell, 1990), although this is less pronounced than in other mammals (Klevezal’ and Kleinenberg, 1967). Although the layered pattern in the dentine appears to be largely under endogenous control, being unaffected by conditions of captivity, including changes in water temperature or salinity, physical activity, some kinds of short-term stress and type of food consumed, variations in depositional rates of dentine have been related to periods of sickness of the animal (Myrick *et al.*, 1984; Myrick and Cornell, 1990). In addition, increased depositional rates were recorded in spring and summer and decreased ones in autumn and winter (Myrick and Cornell, 1990). Deeper staining layers in the GLGs of two *Stenella* species were

correlated with parturition (Klevezal' and Myrick, 1984), and the deposition of optically different types of dentine in dusky dolphins *L. obscurus* off Peru has been attributed to changes in mineral composition related to an El Niño event (Manzanilla, 1989). As this was not observed in other cetacean species at the same time it was thought that the presence of the hypocalcified layer is related to their dietary dependence on anchoveta, the stocks of which were dramatically reduced during the El Niño event (Manzanilla, 1989). A review of factors involved in the zonation of odontocete teeth is given by Lockyer (Lockyer, 1995a), in addition to a detailed classification of anomalies found in teeth, such as pulp stones, marker lines, mineralization interference, dentinal resorption and cemental disturbance (Lockyer, 1993). Anomalies are of the same type and pattern in different teeth from the same individual and occur at the same age, proving that they are of systemic origin (Lockyer, 1993). Comparisons with known-history captive short-finned pilot whales *Globicephala macrorhynchus* indicate that likely stressors, which may either be directly or indirectly responsible for certain mineralization anomalies, may include sexual maturation, pregnancy and/or parturition, periods of starvation or nutritional stress and changes in health and lifestyle (from free-living to captive) (Lockyer, 1993).

### **3.1.2.2 Age determination**

In order to use GLGs for age determination the rate of deposition of an individual GLG has to be verified. Incremental growth layer groups in the dentine and cementum appear as successive pairs of opaque and translucent layers in sectioned teeth examined in transmitted light, or as alternate light and dark stained layers when the section is decalcified and stained with haematoxylin. Klevezal' (1980) found two layers per year deposited in the hard tissues of both terrestrial and marine mammals.

Another form of calibration is to examine teeth from known-age animals. Minimum ages are usually known for captive animals and tetracycline labelling has benefited from that (Myrick *et al.*, 1984). Tetracycline marking has verified an annual deposition rate per GLG in dusky dolphins *L. obscurus* (Best, 1976), spinner dolphins *S. longirostris* (Myrick *et al.*, 1984), bottlenose dolphins *T. truncatus* (Myrick and Cornell, 1990), and short-finned pilot whales *G. macrorhynchus* (Lockyer, 1993). However, the technique did not contribute to an understanding of the deposition of cemental layers (Best, 1976; Myrick and Cornell, 1990).

A few studies have been able to examine free-ranging animals by having a record of the birth of individuals to identifiable mothers and by marking and recapturing individuals and performing multiple tooth extractions (Hohn *et al.*, 1989). One such study carried out on bottlenose dolphins *T. truncatus* confirmed an annual deposition rate of the GLGs in teeth (Hohn *et al.*, 1989).

However, the use of growth layers in age determination has generally been accepted even when they have not been calibrated for a species based on the facts that 1) growth layers are very common and have been identified in most mammalian species examined, 2) the appearance and structure of growth layers have been similar among different species within the same tissues (e.g. teeth and bone), and 3) in each species for which data are available, growth layers have been calibrated to real time showing the existence of annually occurring layers (Hohn *et al.*, 1989).

#### 3.1.2.2.1 Dentine

The neonatal line is thought to demarcate the point of parturition, recording post parturitional trauma of the neonate as it is confronted with the external environment and a new mode of feeding (Myrick, 1980). Experiments with tetracycline-marked animals verified that the neonatal line forms at or near the time of birth (Myrick and Cornell, 1990). Polarized light microscopy shows that this line is composed of an alternating series of three or more pairs of opaque and translucent layers bounded on either side by a rather bright translucent layer (Myrick, 1980). As a dolphin matures and dentine continues to accumulate at the wall of the pulp cavity, the volume of the pulp cavity decreases gradually and successive GLGs become thinner (Myrick *et al.*, 1983). Once the pulp cavity occludes one may not be able to age the animal accurately (Myrick *et al.*, 1983).

Osteodentine (also referred to as secondary dentine or ‘pulp stones’) is made up of discrete nodules containing concentric rings in the dentine (Lockyer, 1995a). The occurrence of all anomalies tends to increase with age as a result of their persistence in the teeth (Lockyer, 1995a). However, the pattern of increase is not regular for pulp stones and the generally low incidence suggests that occurrence may be both uncommon and spontaneous. Only 6.8% of the total sample in a study of harbour porpoises *P. phocoena* had pulp stones (Lockyer, 1995a). The cause of these stones is not understood (Lockyer, 1995a), although they are associated with the age at which puberty occurs in

long-finned pilot whales *G. melas* (Lockyer, 1993). In captive short-finned pilot whales *G. macrorhynchus* these anomalies coincide with a period of weight loss (Lockyer, 1993). Klevezal' and Kleinenberg (1967) observe intensive deposition of secondary dentine, resulting in many accessory bands being formed in the molars of rodents and suggest that this is caused by big mechanical load (presumably from heavy chewing in this group of mammals).

#### 3.1.2.2.2 Enamel

Enamel is deposited prenatally and contains growth lamellae, which are thought to represent daily records of prenatal growth; it does not, however, yield any information for age determination purposes of the animal (Myrick, 1980).

#### 3.1.2.2.3 Cementum

Because cementum is deposited externally of the tooth and apparently unconfined, it is thought to form a continuous record representing a dolphin's entire life. Cementum, then, may be used to estimate the maximum age of older dolphins for which maximum dentinal age estimates are not possible (Myrick *et al.*, 1983). In short-finned pilot whales *G. macrorhynchus* readings from dentinal and cemental GLGs are equal and thus either may be used in age determination (Lockyer, 1993). However, GLGs within the cementum are often difficult to distinguish due to the extreme thinness and poor layering of the tissue (Myrick, 1980). Marsh and Kasuya (1986) conclude that cemental and dentinal readings together give more accurate determination of age, especially for older animals, but cemental readings by themselves are less accurate than dentinal readings (Kasuya and Brownell, 1979). The number of cemental layers appears to correspond to the number of dentine layers in species where it is easily countable (Klevezal' and Kleinenberg, 1967). However, Myrick and Cornell (1990) fail to demonstrate a relationship between annual GLGs deposited in the dentine and cemental layers of captive bottlenose dolphins *T. truncatus*. The thickness of the cementum appears to be related to the mechanical load exerted on the teeth (Klevezal' and Kleinenberg, 1967). One indication of the size of the load is the rate of wear. In many species the intensive wear of the crown of the tooth is accompanied by the formation of broad layers of cement on the root, like the sperm whale *Physeter macrocephalus*

(Klevezal' and Kleinenberg, 1967). However, intensive wear does not always entail the formation of thick cement depositions (Klevezal' and Kleinenberg, 1967).

It has to be emphasized that the criteria and approaches used in age determination show varying degrees of accuracy and applicability and that ideally a combination of criteria should be used on the same material in order to get the best possible age estimate (Langvatn, 1995). The current methods employed for age determination in mammals, and specifically in odontocetes, have obvious shortcomings and should be used with a clear understanding of the limitations inherent in the methods available (Langvatn, 1995).

### 3.1.3 Age determination in sperm whales (*P. macrocephalus*)

The pattern of dentine deposition in both *Physeter* and the two *Kogia* species differs to that observed in most other odontocetes. It has been described as a 'herringbone' pattern by Klevezal' and Kleinenberg (Klevezal' and Kleinenberg, 1967), while it is usually referred to as a chevron pattern by other authors (Ross, 1979; Perrin and Myrick, 1980). It is characterized by each layer of dentine being deposited at an angle to the longitudinal axis of the tooth.

There has been a relatively long period of use of age determination as a tool in the study of the biology and management in the sperm whale *P. macrocephalus*, not at least due to its long history of exploitation (Ohsumi *et al.*, 1963; Bow and Purday, 1966; Best, 1970; Berzin, 1972; Perrin and Myrick, 1980; Donovan *et al.*, 1982). For a long time body length was the only criterion used for comparison of specimens (Berzin, 1972). Later the number of corpora present in the ovaries as well as ossification of the vertebral column were used to estimate age in sperm whales (Best, 1967; 1970; Berzin, 1972). Ohsumi (1965) uses both dentinal layers and corpora in the ovaries as an indication of age in sperm whales (in: Best, 1967).

Most researchers assume an annual deposition rate in the teeth of sperm whales (Ohsumi *et al.*, 1963; Best, 1970; Berzin, 1972; Perrin and Myrick, 1980; Mikhalev, 1982; Rice *et al.*, 1986) and a comparison with an independently arrived at age estimate based on the number of corpora found in the ovaries confirmed this (Best, 1970). Ohsumi *et al.* (1963) describe variation in the thickness of the GLGs with age, sex, and between different individuals. Berzin (1972) observes that the size of the tooth is directly

proportional to the number of dentine layers and therefore can be used in old animals with occluded pulp cavities to determine the age. He states that the layers diminish only slightly in thickness with age and thus one can assume that the thickness of a layer that has completed growth is equal to the thickness of the preceding layer (Berzin, 1972). In addition, a seasonal pattern of dentine formation is reported for sperm whales (Best, 1970; Berzin, 1972). To reduce inaccuracy of age estimates, Mikhalev (1982) suggests rejecting those teeth, which do not show the layers clear enough and as a result yield readings, which differ significantly.

The “Report of the workshop” on age determination held by the International Whaling Commission (IWC) includes a comprehensive section on sperm whales, including guidelines for the interpretation of layers in the teeth (Perrin and Myrick, 1980). It was remarked that cemental layers form in a similar pattern to dentinal layers in sperm whales and cemental GLGs should be examined in teeth in which the pulp cavity is closed (Perrin and Myrick, 1980).

### 3.1.4 Age determination in *Kogia*

Although it has been reported before that the teeth of either *Kogia* species have an enamel cap (Flower and Lydekker, 1891), more recent studies conclude that *Kogia* teeth characteristically lack enamel (Handley, 1966; Ross, 1979). Enamel was also reported to be lacking in sperm whales *P. macrocephalus* (Flower and Lydekker, 1891).

Not much previous work has been carried out on age determination in the two *Kogia* species. Handley (1966) in his analysis of *Kogia* species uses the degree of closure in the pulp cavity, the degree of ossification of the mesethmoid in the mesorostral region and the closure of the epiphyses of the vertebrae and of the pectoral girdle to determine relative ages for his specimens.

Ross (1979) describes the histology of the teeth of the two *Kogia* species and makes an attempt to determine the age of 15 *K. breviceps* specimens from South Africa. *K. sima* teeth are shorter and proportionately more slender than *K. breviceps* teeth and Ross suggests that teeth over 30mm in height and 4.5mm in diameter are indicative of *K. breviceps* (Ross, 1979). He finds an enamel cap to be lacking in *K. breviceps*, but describes a clear, narrow neonatal line (about 15µm thick in *K. breviceps*), which delineates the postnatal dentine easily from the distinctly homogenous prenatal dentine in both species; the latter is often worn away in older *K. breviceps*. The pulp cavity

appears to remain open at the base throughout life in both *Kogia* species, although half the teeth of a *K. breviceps* had closed pulp cavities, while the other half had open pulp cavities (Ross, 1979). Growth layers in both the dentine and cementum appear as alternating opaque and translucent bands in both species, however, the distinctness of the laminae is very variable in the dentine and teeth vary in opacity, with some being almost translucent (Ross, 1979). In *K. sima* the dentinal growth layers are not very distinct and the postnatal dentine appears to become progressively more obtuse in older teeth (Ross, 1979). Ross also describes a number of accessory layers within a GLG in *K. breviceps* and a number of teeth had laminae that were too uniform to allow observation of GLGs. Although he obtained some good results from his age determination for *K. breviceps*, the majority of sections had poor legibility. For *K. sima* he obtained age estimates that he thought were too high to present annual layers and thus left any further attempts due to the large risk of inaccurate counts (Ross, 1979).

Other attempts at age determination in *K. breviceps* include Bossart *et al.* (1985), who use length and reproductive status to categorise animals into age classes, unaware that chronological age determination methods had been established for the species. Eliason and Houck (1986) determine the age of a 327cm long female *K. breviceps* as 8.5GLGs. Bustamante *et al.* (2003) determine the age of a 310cm long *K. breviceps* male as six GLGs and that of a 300cm long female *K. breviceps* as 19GLGs; both specimens stranded in New Caledonia. The maximum age estimate obtained for *K. breviceps* specimens stranded in New Zealand is 12.5GLGs for a female and 16+ for a male (Tuohy *et al.*, 2001).

Age determination in *K. sima* includes a study by Nagorsen and Stewart (1983), who sectioned a tooth of a 230cm long female *K. sima* stranded on Vancouver Island, which revealed 12+ “annuli”. Muñoz-Hincapié *et al.* (1998) report a stranding of a 238cm long *K. sima* in Colombia. Age determination revealed eight GLGs in the teeth and the animal was found physically immature based on the lack of fusion of cranial sutures, vertebrae and intervertebral discs. However, Valverde and Caminas (1996) conclude that a 212cm long male *K. sima* from Spain was probably below one year of age as they failed to see any GLGs in the teeth. This age estimate appears unrealistic compared to the results of the present study and indicates that a suitable technique needs to be found to illustrate the GLGs in the two species of *Kogia*.

### 3.1.5 Length at birth and foetal growth rate

Estimates of birth size are valuable as they present the starting point for growth curves (Perrin and Reilly, 1984). Length at birth has been reported for a number of odontocete species (Fisher and Harrison, 1970; Perrin *et al.*, 1976; Cockcroft and Ross, 1990; Aguilar, 1991; van Waerebeek and Read, 1994) and, in delphinids, ranges from 75cm for the tucuxi *Sotalia fluviatilis* to 276cm for the killer whale *Orcinus orca* (Perrin and Reilly, 1984). Any mammalian species has a range of birth sizes (Frazer and Huggett, 1973) and differences may occur between populations of the same species as seen in different populations of harbour porpoises *P. phocoena* (Fisher and Harrison, 1970; Read and Gaskin, 1990; Sørensen and Kinze, 1994). The length of neonates in cetaceans ranges between 20-50% of maximum adult length depending on the species, with 25-30% in the mysticetes (Scott, 1949; Evans, 1987) and 40-48% in odontocetes (Chivers, 2001). This is a higher percentage than for most terrestrial mammals and the main reason for this may be that it presents a more favourable surface area-to-volume ratio when the calf enters the cool aquatic environment (Evans, 1987). Odontocetes have relatively large offspring in comparison with adult size and the size of newborns in relation to adult body size tends to increase with decreasing adult size of the species (Ohsumi, 1966; Ralls, 1976; Sooten, 1991). Scott (1949) reports a constant relationship between neonatal length and maternal length for 10 cetacean species. Marine mammals bear young which are much larger than the young of large terrestrial mammals, which was thought to be a result of a prolonged gestation period, resulting in the young being born in an advanced state of development (Laws, 1956). However, more recent studies indicate that cetaceans differ from terrestrial mammals in that species differences in birth size are achieved mainly by altering the rate of growth rather than the length of the intrauterine phase (Bryden, 1972).

Prenatal growth is difficult to determine in cetaceans, because direct observations are generally not possible (Laws, 1956). However, most foetal growth in mysticetes occurs in the last two months of the pregnancy (Laws, 1959) In addition, growth rates for mysticetes are higher than those for odontocetes (Huggett and Widdas, 1951; Laws, 1959; Frazer and Huggett, 1974). The generally higher foetal growth rates in cetaceans compared to terrestrial mammals was thought to be a result of the increased size (and thus higher volume to surface area ratio) at birth being advantageous in the aquatic environment as well as the increased weight being supported by the aquatic medium

(Frazer and Huggett, 1974).

### **3.1.6 Growth**

Mammals have determinate growth, which means that the external form changes continually during the period of growth and as soon as the form becomes constant, growth ceases (Bryden, 1972). Physical maturity is thus defined as the point when all vertebral epiphyses are fused to their respective vertebrae (Laws, 1956). Growth patterns may vary among species depending on their life history and their environment (Case, 1978).

#### **3.1.6.1 Growth rate**

Much interspecific variability in growth rates can be observed in reptiles, birds and mammals, even in species of similar adult size (Ricklefs, 1969; Case, 1978). Thus no allometric relationship appears to exist between body size and growth rate, but it has been suggested that different physiological constraints, like the evolution of endothermy, have played a role in the variation of growth rates among animals as growth rates of endotherms are on average an order of magnitude higher than those of ectotherms (Case, 1978).

The concept of growth rate is complex and a number of factors have been suggested to influence growth rates in mammals. However, not all of these factors are completely understood and little is known about their interrelationships. The metabolic rate increases proportionally to body weight at roughly the same rate as the growth rate (Ricklefs, 1969; Case, 1978) and thus the growth rate of mammals is thought to be influenced or even set by the metabolic rate (McNab, 1980). Among mammals the fastest growing species are found within the artiodactyls, perissodactyls, cetaceans, pinnipeds, canids and lagomorphs (Case, 1978). Growth rates appear to be adapted to certain environmental conditions such as infant mortality rates (resulting from predation pressure) and food availability (Case, 1978). Mortality rates have been suggested to have a strong influence on growth rate, because adaptations that reduce the period in which the young are vulnerable due to exposure to the environment and predators (such as a high growth rate) should strongly be favoured in evolution through increased survival of the young (Ricklefs, 1969). A further advantage would be that rapid growth results in a

shortened developmental period of the young and thus enables adults to reproduce more often in a given time period (Ricklefs, 1969). Thus an increased growth rate could also be regarded as resulting from high adult mortality rates.

Furthermore, fast growing mammals have relatively larger offspring and smaller litter sizes, which may indicate that the selective forces influencing birth weight and postnatal growth could be very similar (Case, 1978). A larger offspring is favoured when infant mortality rates are high and resources are abundant and evenly distributed (Case, 1978). These two demographic and environmental factors appear to be associated with rapid growth in many birds and mammals and usually the sex with the fastest growth rate has the highest mortality rate (Case, 1978).

### **3.1.6.2 Growth in marine mammals**

Bryden (1972b) gives a review of growth and development in marine mammals in general as well as overviews by family. Whenever available, length-weight relationships for the mysticetes are presented (Bryden, 1972). Although most mammals have determinate growth, and the same was assumed for marine mammals in general and cetaceans in particular (Bryden, 1972), recent results on the growth of the long-finned pilot whales off the Faroese indicate that these animals may continue growing past the stage previously taken as the asymptotic length (Bloch *et al.*, 1993). However, these results are closely related to the continuing problems encountered in the age determination of cetaceans. In this respect, growth rates are still difficult to obtain for mysticetes due to the continuing problems involved in the age determination of some species (George *et al.*, 1999). Early studies on growth using animals from commercial whaling operations were hindered by the lack of age determination techniques, as one needs to assess the age of individuals in order to determine growth rates (Laws, 1956).

Rapid growth during the early postnatal period is especially characteristic for marine mammals (Laws, 1956; Bryden, 1972). The rapid growth of young during the lactation period appears to be related to the very high fat and protein content of the mother's milk (Bryden, 1972). It is generally believed that both the fast increase in body size, which will decrease the surface area to volume ratio, and the rapid growth of the blubber layer both aid to conserve body heat and are adaptations to the aquatic life style of cetaceans (Bryden, 1972). No difference in growth between the sexes is observed at this stage.

Both growth rates and age at sexual maturity in cetaceans vary within species and appear to depend largely on the environment (Laws, 1956). In a number of species larger body sizes and higher growth rates for certain schools or populations within a species have been related to waters with greater productivity (Bryden, 1972; Read and Gaskin, 1990; Bloch *et al.*, 1993; Di-Méglio *et al.*, 1996; Read and Tolley, 1997).

### 3.1.6.3 Size at attainment of sexual maturity (ASM)

The body size of marine mammals at sexual maturity appears large in comparison with terrestrial mammals (Bryden, 1972). Laws (1956) determines that sexual maturity occurs at 86% of maximum body size in marine mammals as opposed to 30% in most laboratory and farm mammals, probably in order to avoid competition for nutrients between the mother and offspring.

While in many species growth appears to slow down with the onset of sexual maturity (Kasuya and Marsh, 1984; Slooten, 1991; Kasuya and Tai, 1993), in some species the male exhibits a so-called “secondary growth spurt” at this stage (Sergeant, 1962; Best, 1970; Kasuya *et al.*, 1988a; Cockcroft and Ross, 1990). The earlier physical maturation of female sperm whales *P. macrocephalus* (at 28-29yrs) compared to male sperm whales (over 35yrs) appears to be a direct result of this accelerated growth of males at puberty (Best, 1970). A secondary growth spurt is characteristic of males of polygynous species, where there is a great difference in size between the sexes (Best, 1970).

The onset of physical maturity is when an organism has completed its growth (Berzin, 1972). Growth comes to an end when ankylosis (=ossification) of the greater part of the vertebral column ceases (Berzin, 1972). The length at physical maturity is also often referred to as the asymptotic length and may vary between different populations of a species, possibly depending on environmental factors, particularly temperature (Cockcroft and Ross, 1990), or the social system (Tolley *et al.*, 1995).

### 3.1.6.4. Growth models

A number of growth models have been used to describe growth in both mammals in general and cetaceans in particular. The von Bertalanffy growth model has been used extensively to describe both mysticete and odontocete growth and appears to

be the most frequent model used (Cockcroft and Ross, 1990; Bloch *et al.*, 1993). However, the Gompertz equation is also widely used (Perrin and Henderson, 1984) and seems to describe phocoenid growth in particular very well (Read and Gaskin, 1990; Hohn *et al.*, 1996; Read and Tolley, 1997; Ferrero and Walker, 1999). The main difference between the two models is the growth rate constant ( $k$ ). The von Bertalanffy function increases progressively more slowly as the asymptotic length is reached, while the Gompertz function does not necessarily have its maximum growth rate at  $t_0$  (the age corresponding to zero length), and thus can approximate more sigmoid patterns (Bloch *et al.*, 1993). Due to the confusion and difficulties with interspecific comparisons some authors are now presenting results obtained from both models (Bloch *et al.*, 1993).

### 3.1.7 Sexual dimorphism

A recent review on sexual dimorphism in marine mammals is given by Ralls and Mesnick (2002) and covers the many forms of sexual dimorphism found in these animals. For the purpose of brevity only sexual size dimorphism is reviewed here.

Sexual size dimorphism refers to the fact that one of the sexes of a species is significantly larger in body size than the other. Most cetaceans lack secondary sexual characters and their dimorphism is more commonly expressed by differences in size and shape (Tolley *et al.*, 1995). In the 13 species of mysticetes we can observe a so called “reversed” sexual size dimorphism with the females attaining asymptotic lengths that are on average 5% longer than males (Bryden, 1972; Ralls and Mesnick, 2002). It is thought that due to the long migrations that these animals undertake, during which they do not feed, females need to store additional energy due to the demands of pregnancy and lactation in the form of blubber and thus gain larger body sizes (Ralls and Mesnick, 2002). In contrast, odontocetes appear to follow the general mammalian pattern of an increase in sexual size dimorphism with larger body size (Tolley *et al.*, 1995). Males are longer than females in many species, the most pronounced dimorphism being seen in the sperm whale *P. macrocephalus*, killer whale *Orcinus orca*, bottlenose whales (genus *Hyperoodon*), narwhals *Monodon monoceros*, belugas *Delphinapterus leucas* and pilot whales (genus *Globicephala*) (Sergeant, 1962; Bryden, 1972; Bloch *et al.*, 1993; Ralls and Mesnick, 2002). The sperm whale *P. macrocephalus* displays one of the most extreme cases of sexual size dimorphism found among mammals with adult females measuring up to 11 metres and weighing 15 tons, whereas males measure up to 16

metres and weigh up to 45 tons (Ralls and Mesnick, 2002). However, in most moderate sized odontocetes the sexes are visually indistinguishable and only the size and shape of the dorsal fin or the flukes may vary (Tolley *et al.*, 1995; Ralls and Mesnick, 2002). In the smallest odontocetes, such as the harbour porpoise *P. phocoena*, vaquita *P. sinus*, or the Hector'dolphin *C. hectori*, the dimorphism is again reversed and females are larger than males (Slooten, 1991; Tolley *et al.*, 1995; Hohn *et al.*, 1996). Some of these traits may be important for females and their offspring as bigger females make better mothers (Ralls, 1976; Ralls and Mesnick, 2002). Other dimorphic traits may reflect ecological differences between the sexes, for example differences in beak length may reflect differences in diet (Hersh and Duffield, 1990; Ralls and Mesnick, 2002).

Based on studies of terrestrial mammals the amount of sexual dimorphism displayed by a species can be used as an indicator of the mating system: the greater the amount of sexual dimorphism the bigger the deviation of the breeding system from monogamy (Ralls and Mesnick, 2002). This has been shown to be true across pinniped taxa and in highly polygynous species males were found to compete for access to females (Ralls and Mesnick, 2002). However, species that lack sexual size dimorphism do not necessarily lack competition among males for mates (Ralls and Mesnick, 2002). Sexual size dimorphism and testis size in relation to the mating system in the two *Kogia* species is discussed in more detail in Chapter 4.

In his review, Bryden (1972b) points out that growth, as he discusses it, is measured in terms of linear dimensions, as it is easier to obtain data and compare them between species. The difference in size between the sexes develops after the attainment of sexual maturity (hereafter referred to as ASM) (Bryden, 1972). Before puberty the two sexes of a species are generally the same length, but a growth spurt occurs in the male between the attainment of sexual maturity and social maturity (which is the beginning of reproductive activity) (Bryden, 1972). However, in some species females attain sexual maturity at an earlier age and at a lesser length and mass than males (Sergeant, 1962; Cockcroft and Ross, 1990), and males have higher growth rates after sexual maturity (Sergeant, 1962) and a longer growth period, subsequently reaching their asymptotic length later than females (Di-Méglio *et al.*, 1996). In species where females are larger than males this pattern appears to be reversed: males have slower growth rates than females after sexual maturity (Anli and Kaiya, 1992) and females have a longer growth period, attaining asymptotic length later than the males (Read and Tolley, 1997).

### 3.1.8 Observations of morphological differences in appendage size between *K. breviceps* and *K. sima*

As part of the examination of sexual size dimorphism in the two *Kogia* species some interesting observations were made with respect to the size of their appendages, which needed further examination. Although these are briefly discussed here, they are elaborated on in more detail in Chapter 7 and 9 together with some other evidence that aids in illuminating basic ecological differences between the two species.

According to the laws of scaling, smaller species are expected to have smaller appendages and larger species are expected to have larger appendages in relation to their body size. Cetaceans are no exception and thus harbour porpoises *P. phocoena* are expected to have smaller dorsal and pectoral fins and flukes than, for example, killer whales *O. orca*, and indeed they do. However, examination of some body measurements in the two species of *Kogia* lead to the observation that not only the dorsal fin is larger in the smaller of the two species, namely *K. sima*, but in addition the length and width of the pectoral fins and the width of the flukes appear larger in *K. sima* than *K. breviceps* (personal observation based on Ross' 1979 measurements). This is contrary to what one would expect in terms of scaling i.e. the larger animal should also have the larger appendages to aid in manoeuvrability. In order to test whether *K. breviceps* has proportionally larger appendages than *K. sima* measurements from Ross' (1979) were re-analysed.

### 3.1.9 Aim of the present chapter

The aim of this part of the study was not only to obtain age estimates for the animals, but also to define a GLG in either species in order to help standardise age estimation techniques for both *Kogia* species in the future. Growth curves were established for both *K. breviceps* and *K. sima* and foetal and adult growth rates were determined. Furthermore, parameters such as length at birth, length, age and body weight at physical maturity, maximum body length, maximum body weight and longevity were determined. Such basic life history parameters are necessary in establishing a picture of the life history strategies employed by the two species (see Chapter 9). Length and age at sexual maturity are determined in Chapter 4 (Male reproduction) and Chapter 5 (Female reproduction) and are discussed again in Chapter 9. Data on sexual dimorphism in the

two species as well as morphological differences between the two *Kogia* species were examined.

## **3.2 Materials and methods**

### **3.2.1 Sample**

Teeth of both *K. breviceps* and *K. sima* from the marine mammal collections of the Port Elizabeth Museum, Port Elizabeth, and the South African Museum in Cape Town were used for age determination (see Chapter 2, Appendix B). Teeth usually originated from stranded animals and the normal procedure was to leave them to macerate. As the teeth from the stranded specimens were collected by a number of individuals with varying levels of experience the exact location in the tooth row from which the teeth were taken and whether they were mandibular or maxillary (in the case of *K. sima*) is not known. However, the largest tooth available was generally chosen for age estimation to prevent underestimation of ages due to underdevelopment of the tooth. As a rule only one tooth was used per animal for age determination. Teeth for sectioning were selected on the basis of greatest size, least curving (in no more than one plane) and least wear, although in some instances extensive wear was found in all teeth present.

In addition to the South African samples, teeth were also available for 27 *K. breviceps* and one *K. sima* from Australia; these were included in the analyses (see Appendix C).

### **3.2.2 Age determination**

Standard methods used for age determination in delphinids, such as decalcification and etching with formic acid, proved to present unsatisfactory results in *Kogia*. Oosthuizen and Bester (1997) got similarly poor results using thin sections of decalcified teeth stained with haematoxylin for age determination of Cape fur seals *Arctocephalus pusillus pusillus*. Thus the following method, which was used successfully for Cape fur seals (Oosthuizen, 1997), was chosen. Due to the curvature of *Kogia* teeth better results were obtained when teeth were ground down from either side to the midline by hand (rather than embedded in resin and sectioned). The teeth were initially ground down to yield a final 300µm thick section along the midline. A Buehler

“Isomet” low speed saw was used for grinding. The saw blade was replaced with an aluminium disc onto which disposable discs of waterproof silicon carbide paper were clamped. The catch container of the saw was filled with water through which the water paper rotated at controlled speed. The initial grind down to a thickness of 1300 $\mu$ m was done using coarse water paper with a grit size of P120. Then finer water paper with a grit size of P320 was used to grind the sections down to 500 $\mu$ m. Finally, water paper with a grit size of P400 was used to grind the sections down by hand to a thickness of 300 $\mu$ m.

Ground sections were stored in absolute alcohol overnight, cleared in xylene for five minutes and mounted on slides using DPX mounting medium. A binocular microscope with transmitted, polarized light was used to examine the sections. The use of the polarizing light microscope assists in overcoming some of the difficulties in distinguishing any regular layering by expressing structural and histological differences as highly contrasted patterns of light. (i.e. different colours or shades) (Myrick, 1980).

*K. breviceps* teeth were examined at 6x magnification and *K. sima* teeth at 12x magnification due to the different sizes of the teeth. Dentinal layers were read as complete GLGs plus an increment consisting of the last incomplete layer. In order to calculate the increment, measurements of the last complete GLG were done using a micrometer under 12x magnification in *K. breviceps* and 25x magnification in *K. sima* and the increment was calculated as a percentage of the last complete GLG. Cemental GLGs were read at a magnification of 40x.

Although some *Kogia* teeth showed either extensive wear at the tip or osteodentine formation they were still included in the analysis as small sample sizes prevented exclusion of the material. However, in future analyses such teeth should be excluded if possible in order to obtain better age estimates. Age estimation for teeth with osteodentine formation was attempted by measuring the length of the part of the tooth occupied by secondary dentine. The mean width of the last three complete GLGs prior to osteodentine formation was taken as an estimate of the mean GLG width and the area (length) of osteodentine then could be divided by the mean GLG width to give an estimate of the number of GLGs occupied by the osteodentine. In addition, counts of cemental GLGs were also carried out in those teeth. No estimation could be made for the amount of tooth wear that had occurred, but cemental layer counts possibly provided a good estimation of the age of these animals. Similarly, for specimens with a closed pulp cavity age was estimated from the layers in the cementum.

In order to obtain age estimates for animals that had less than one GLG present

in the dentine, the average width of the first GLG was determined from animals between one and two years of age. Then the increment of dentine laid down after the neonatal line was measured and used to calculate the age as a percentage of an average GLG.

The teeth were read five times by each of two independent observers and the trimmed mean values of both dentine and cementum readings were calculated. Only estimates within 15% of each other were used (others were neglected). If no clear neonatal line was visible due to tooth wear, the first layer was taken as the first GLG. Cemental layers were only read by a second observer (Herman Oosthuizen) when osteodentine was present. In these cases the cemental readings were used as age estimates.

If GLG counts were not within 15% of each other revised counts were carried out by the two observers and an agreement on the age estimate was reached. Estimates were made without any reference to body parameters, such as body length, which could have influenced the counts.

Two methods for age estimation were examined. Method 1 examined the correlation between cemental and dentinal readings where only complete GLGs were counted. Method 2 examined the correlation between cemental readings and complete GLGs plus an increment. The increment was composed of the dentine laid down after the last complete GLG, calculated as a percentage of the last complete GLG. In teeth where the pulp cavity was closed the cemental reading was taken as an estimate of age. The percentage closure of the pulp cavity was calculated by measuring the length of the open pulp cavity as a percentage of the total length of the tooth. For this exercise only animals with pulp cavities that appeared just closed were included; no animals with extensive osteodentine were included.

There is to date no calibration of GLGs available for either *Kogia* species and for this reason it has been assumed that the deposition rate of dentinal GLGs is the same as that found in all other odontocetes for which calibration has been carried out: one GLG per year. Therefore GLGs and years may be used interchangeably in the rest of the study. However, it has to be kept in mind that this is only an assumption and the results can only be treated as estimates until calibration of the deposition rate of dentinal GLGs is possible in this species.

### 3.2.3 Growth curves

In order to obtain growth curves for either species, the estimated ages of the animals were plotted against the body length. The computer package 'PC-Yield II', Version 2.2 (Punt, 1992) was used to establish which growth equation gave the best fit for the data. The growth model was used to provide data on asymptotic length (or length at physical maturity) and age.

## 3.3 Results

### 3.3.1 Age determination

Figure 3.1 shows the longitudinal section of a *K. breviceps* tooth viewed under translucent, polarized light. The bars on the photograph indicate the neonatal line as well as five GLGs present. The neonatal line in teeth of the two species of *Kogia* is clearly distinguishable from the rather "fuzzy" appearance of the prenatal dentine. In comparison, the postnatal dentine is more layered in structure. Since the GLGs in the dentine vary in colour and brightness with the rotation of the polarizing filter it is difficult to define a GLG in *Kogia* when using this technique. In general, GLGs were composed of a broad opaque band and a narrow translucent band. *Kogia* teeth show quite conspicuous accessory layers as opposed to the teeth of dolphins, which have finer accessory layers. As a result the width of a clear GLG was used as a guideline to identify other GLGs in the same tooth. In order to become familiar with the pattern, teeth were viewed whole under the dissecting microscope and scanned a number of times before counting commenced. Although GLGs have not been calibrated in either species of *Kogia* it is assumed that one GLG is laid down per year as this was found to be the case in all other odontocete species for which calibration of GLGs have been carried out.

Although 90 *K. breviceps* and 48 *K. sima* teeth were available for age determination purposes, nine *K. breviceps* and three *K. sima* teeth had to be discarded. This was due to either bad sections or the presence of extensive osteodentine, both preventing clear readings, or because the two independent observers could not agree on an age estimate for the individual. As a result 80 *K. breviceps* and 45 *K. sima* teeth were used in the age determination.

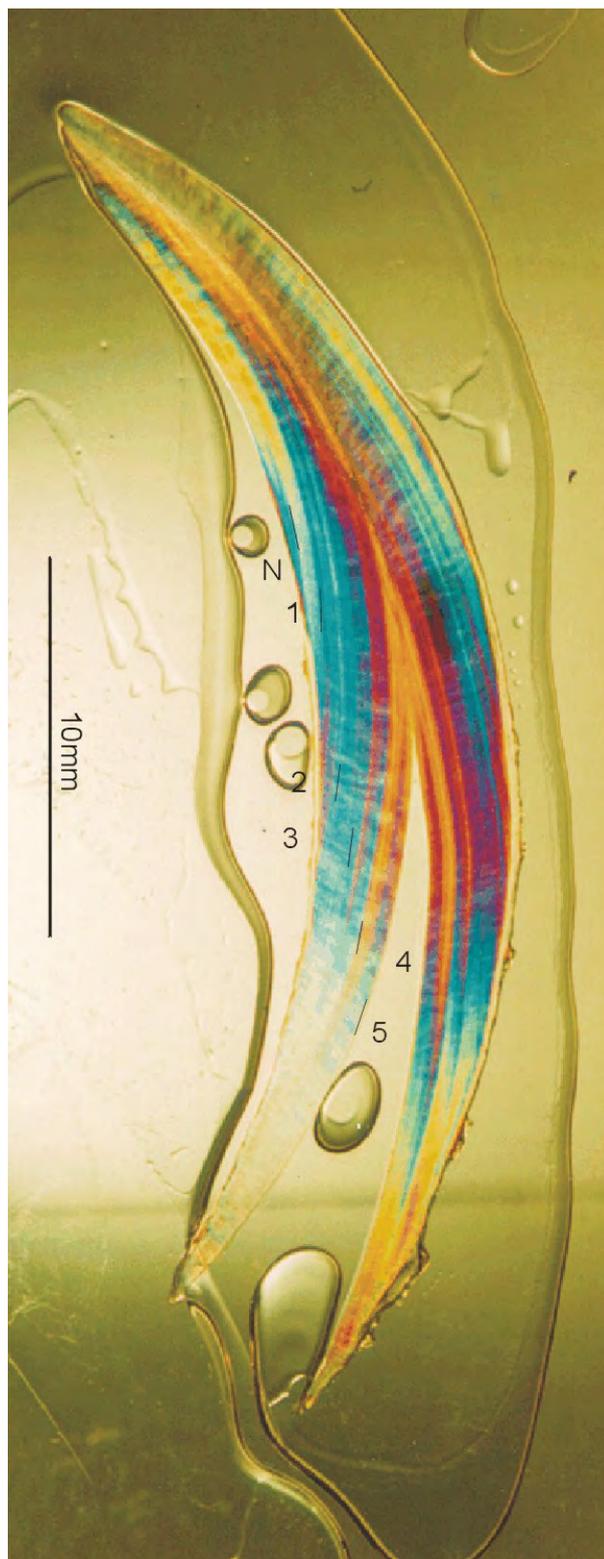


Figure 3.1: Longitudinal section of a *Kogia breviceps* tooth viewed under translucent and polarized light (magnification: x12). The bars on the photograph indicate the neonatal line (N) as well as the five GLGs (1 to 5, respectively). The animal was estimated to be five years old.

As adult *Kogia* teeth are curved it appeared that the side of the tooth with less curvature (i.e. the one that would have been facing the outside rather than towards the inside of the mouth) was easier to read than the other. This may be a result of the fact that GLGs appeared more spaced out on that side and were thus easier to identify. In young animals the teeth are still rather straight, much like those of delphinids and there appears to be no difference in GLG layering between the outside and inside of the tooth.

The neonatal line and other laminae in the teeth of *K. sima* appeared fainter than in *K. breviceps*, which together with its smaller size made teeth of *K. sima* more difficult to read than those of *K. breviceps*.

Contrary to other reports on the two *Kogia* species an enamel cap was found in some of the teeth of younger animals. Interestingly, this was only observed in one *K. sima* from South Africa (South African Museum (SAM) specimen 76/09), which had two GLGs present in the dentine. However, this phenomenon appeared to be more common in the Australian specimens. An enamel cap was found in two Australian *K. breviceps* female specimens (Australian Museum (AM) specimen M 25869 and Queensland Museum (QM) specimen JM 11587), which showed 0.37 and 0.18GLGs, respectively (L: 160cm and 157cm, respectively). In two Australian *K. breviceps* males the enamel cap was partly worn away (South Australian Museum (SAUSM) specimens M 6156 and M 6257); these animals showed 0.92 and 0.69GLGs, the former measuring 172cm while for the latter no length data were available. Thus it appears that by approximately one year of age the enamel cap is worn away. One *K. sima* from Australia (Western Australian Museum (WAM) specimen M 4519) showed an enamel cap with a GLG reading of eight (L: 216cm); however, in comparison with other animals of similar age this appears to be an outlier.

In general the tooth sections obtained from the Australian specimens were much more readable as the GLGs appeared much clearer and more distinct. The reason for this is unclear; possible explanations may be a difference in overall condition between the Australian and South African population, possibly as a direct result from differences in diet. Another possibility may be different methods in the storage of the teeth.

Little holes in the dentine were observed in two adult male Australian *K. breviceps* specimens (Museum of Victoria (MOV) specimens C24972 and C24976). These may either be a result of a tooth disease or mineralization anomalies as described by Lockyer for pilot whales (Lockyer, 1993). It is intriguing that both animals originate from the same geographical area. Mineralization anomalies have previously been linked

to a number of stress factors, including sexual maturation, pregnancy and/or parturition, periods of starvation or nutritional stress and changes in health and lifestyle (from free-living to captive) (Lockyer, 1993). However, which factors caused the anomalies in the teeth of the two *Kogia* species cannot be discerned from the information at hand.

Table 3.1 shows the measurements obtained for the mean width of the first GLG for animals between one and two GLGs. The mean was then used to calculate an age estimate for animals, which had less than one GLG, present in their dentine.

Table 3.1: Width of the first GLG for *Kogia breviceps* and *Kogia sima* between one and two GLGs.

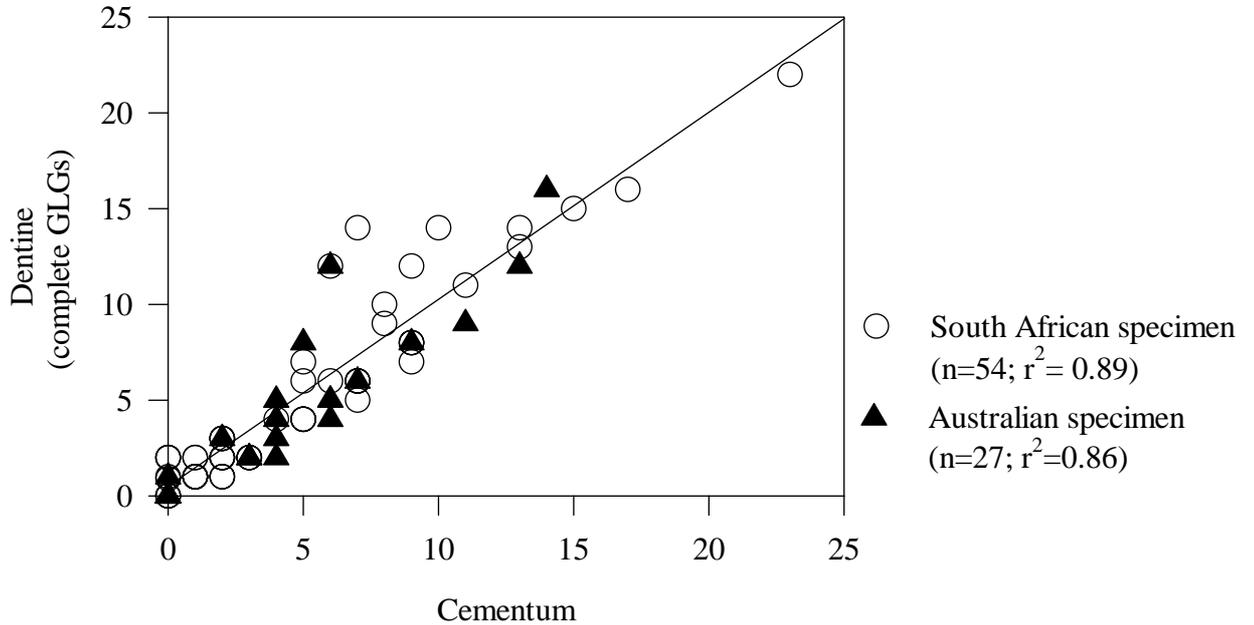
	PEM/SAM #	estimated age	width of first GLG (µm)
<i>Kogia breviceps</i>	N854	1.00	500
	76/17	1.17	666
	76/24	1.25	625
	N1863	1.25	666
	N177	1.33	583
	76/19	1.5	666
	86/22	1.6	666
	84/26	1.67	541
	93/14	1.71	500
<i>Kogia sima</i>	N228	1.4	541
	-	1.67	500
	N2041	1.73	541
	N236	1.92	500

PEM= Port Elizabeth Museum, Port Elizabeth Museum  
 SAM= South African Museum, Cape Town

***K. breviceps***

Figure 3.2 shows the results of methods 1 and 2 for *K. breviceps*. Correlation coefficients for both the South African (method 1:  $r^2=0.89$ ; method 2:  $r^2= 0.90$ ) and the Australian (method 1:  $r^2=0.86$ ; method 2:  $r^2=0.88$ ) specimens were high, indicating a good correlation between cemental and dentinal age estimates. This indicates that age estimations from cemental layers may prove useful in cases where the pulp cavity is closed and osteodentine prevents reading of dentinal GLGs. However, the correlation coefficients for both groups were higher for method 2, indicating perhaps a slightly

Method 1:



Method 2:

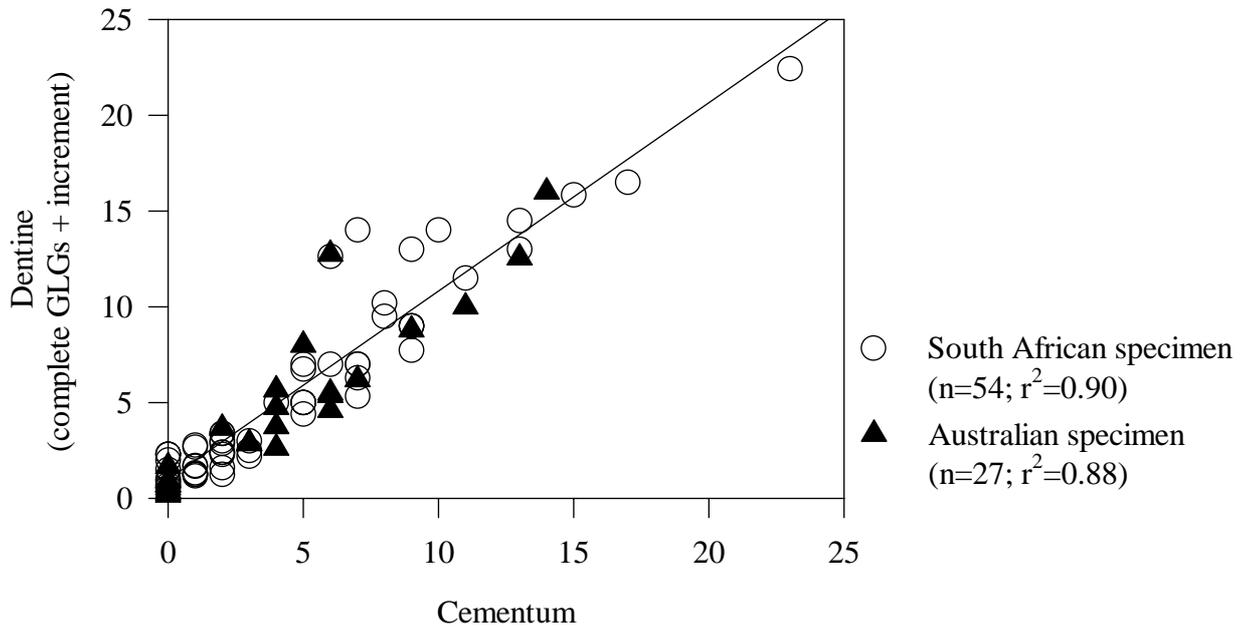


Figure 3.2: Results for the two different reading methods of teeth for *Kogia breviceps*. Method 1: Correlation between cemental and dentinal readings consisting of only complete GLGs. Method 2: Correlation between cemental readings and dentinal readings consisting of complete GLGs plus an increment of the last incomplete layer.

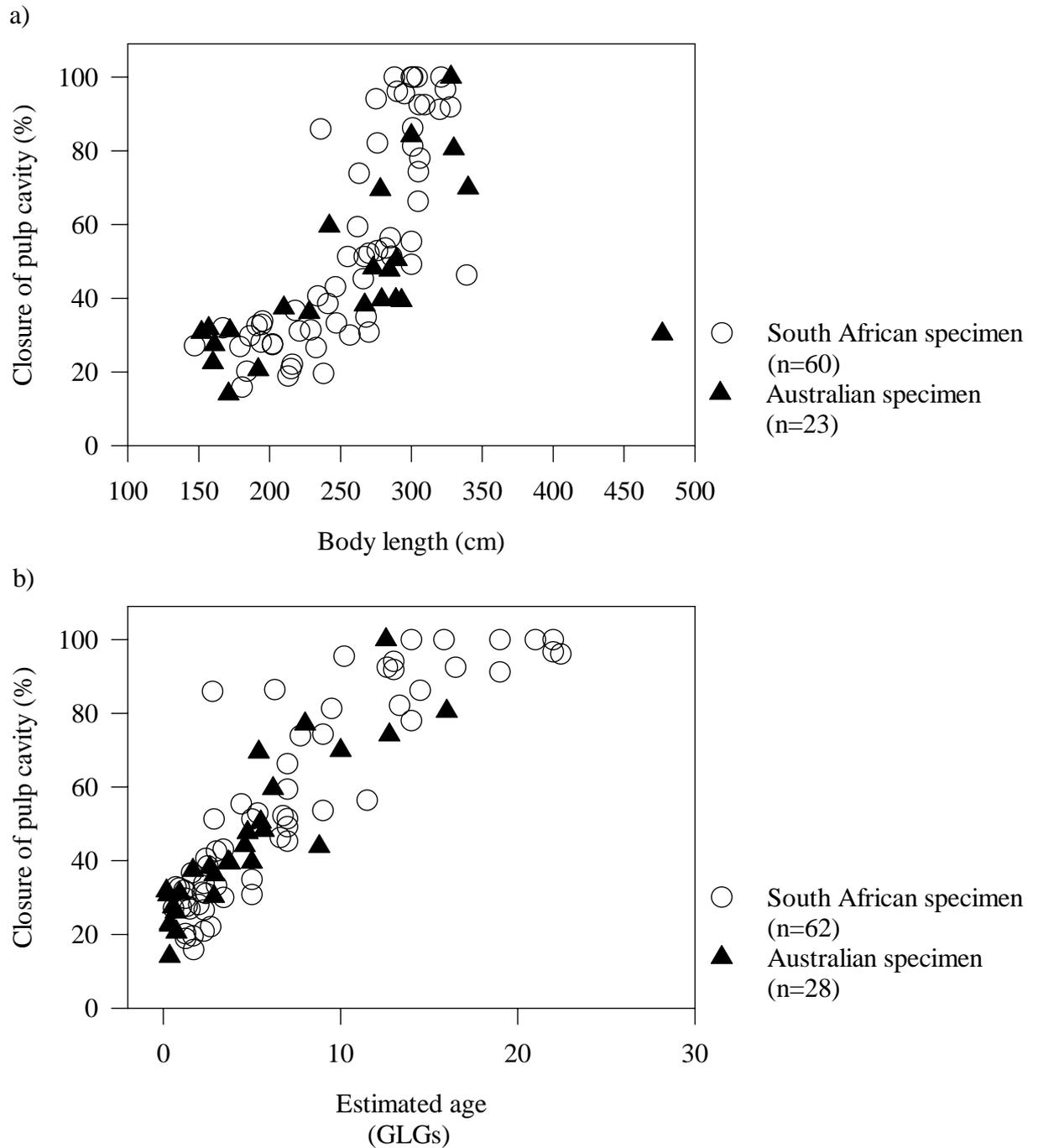


Figure 3.3: Closure of pulp cavity in relation to body length (a) and estimated age (b) in *Kogia breviceps*.

better method for age determination. Therefore only the results from method 2, which is the dentinal age estimate including the last incomplete layer, are subsequently used. In addition, they are hereafter only referred to as GLGs.

A Mann-Whitney-U test between the age estimates from Ross' 1979 study and the ones from the present study (Table 3.2) indicated that there was no significant difference between the two sets of age estimates (p=0.856).

Table 3.2: Comparison of Ross' (1979) results from age determination of *Kogia breviceps* with the results from the present study.

<b>old PEM/ELM/ SAM # (current number)</b>	<b>Length of animal (cm)</b>	<b>Ross' estimate (GLGs + increment)</b>	<b>Present study (GLGs + increment)</b>
SAM 35550 (68/13)	194.5	0.75	0.71
PEM 1517/92 (N179)	197	1	-
PEM 1517/90 (N177)	202	1.5	1.33
PEM 1511/10 (N40)	211	1	-
PEM 1519/12 (N225)	234	2.25	2.5
SAM 36980 (74/08)	236	2.75	2.75
SAM 35522 (66/08)	266.5	4.75	5
PEM 1511/13 (N42)	270	4	5
ELM 674 (N424)	275	12.75	12
PEM 1517/28 (N152)	289.5	9*	-
SAM 35795 (69/15)	305	7	6.97
PEM 1516/48 (N138)	305	8.5	9
PEM 1517/89 (N176)	305.5	11.5	9.69
PEM 1517/91 (N178)	309.5	17.75*	15.5
PEM 1516/08 (N132)	325	10+	-

NB: Ross gave a range for the completion of the last layer in %; only the lower point of the range is used here as decimal values.

PEM= Port Elizabeth Museum, Port Elizabeth

ELM= East London Museum, East London

SAM= South African Museum, Cape Town

\*=Ross indicated some doubt in these results in his 1979 publication.

An attempt was made to plot the width of the increment versus the month in which the animal died in order to determine any seasonal pattern in the deposition of layers, however, no clear trend was visible.

There was high variation in the closure of the pulp cavity (in %) in relation to

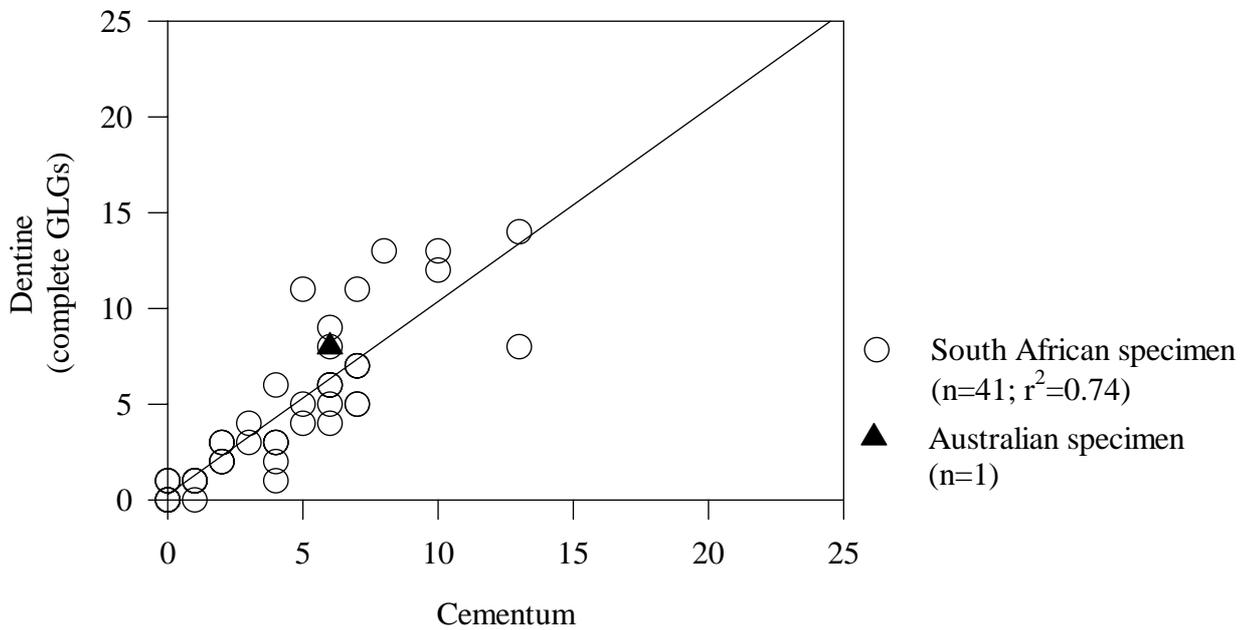
body length and estimated age in *K. breviceps* (Figure 3.3). The pulp cavity was 100% closed in animals ranging in length between 288cm and 321cm in South African *K. breviceps*, which is in agreement with the data from one Australian specimen with a closed pulp cavity, measuring 323cm in length (Figure 3.3a). In relation to age, the pulp cavity in *K. breviceps* became occluded as early as 14GLGs in South African specimens, although other animals with occluded pulp cavities were 19, 21 and 22 years old (Figure 3.3b). The Australian specimen with an occluded pulp cavity had a GLG reading of 12.56.

### ***K. sima***

In contrast to the results for *K. breviceps*, the results for *K. sima* were slightly better for method 1 ( $r^2=0.74$ ) than method 2 ( $r^2=0.73$ ) (Figure 3.4). The lower correlation coefficient compared to *K. breviceps* indicates that cemental readings may not be as reliable in *K. sima* as they are for *K. breviceps*. Overall there appears to be little difference between method 1 and 2, but method 2 has been used for the following analyses.

Body length and age at occlusion of the pulp cavity was similarly variable in *K. sima* as in *K. breviceps* (Figure 3.5). The shortest animal with an occluded pulp cavity measured 196cm in length, while most other animals with closed pulp cavities ranged between 254 and 256cm (Figure 3.5a). While there were three animals with estimated ages of three, five and seven years, respectively, with occluded pulp cavities, the oldest animal in the sample, a 21.5yr old female, had a pulp cavity that was only 83.8% closed (Figure 3.5b). While this animal may represent an outlier, two other animals, a 14yr old female and a 13yr old male, had pulp cavities that were 96.7% and 84.3% occluded, respectively. Thus it appears that the pulp cavity closes between 11.83 and 17, which are the ages estimated for the remaining individuals with occluded pulp cavities (Figure 3.5b).

Method 1:



Method 2:

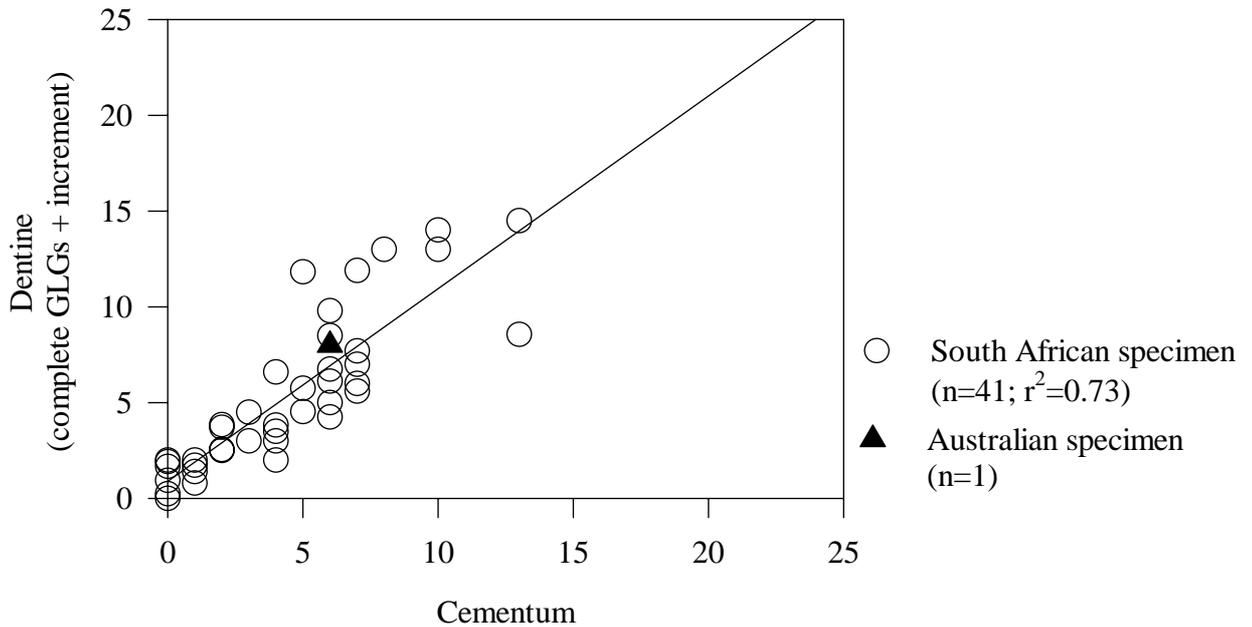


Figure 3.4: Results for the two different reading methods of teeth for *Kogia sima*. Method 1: Correlation between cemental and dentinal readings consisting of only complete GLGs. Method 2: Correlation between cemental readings and dentinal readings consisting of complete GLGs plus an increment of the last incomplete layer.

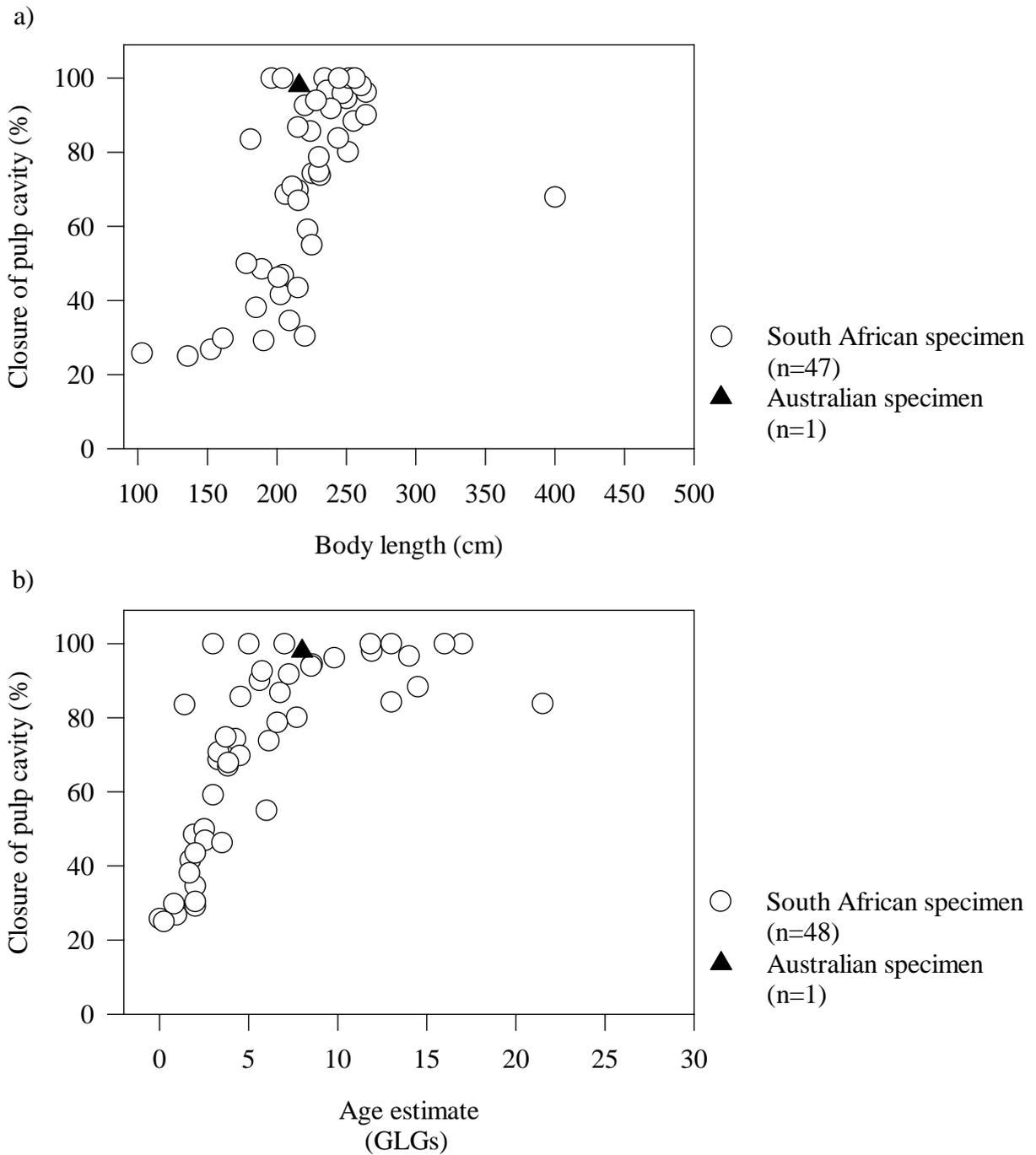


Figure 3.5: Closure of pulp cavity in relation to body length (a) and estimated age (b) in *Kogia sima*.

### 3.3.2 Growth

After trying several growth models it was found that the von Bertalanffy equation gave the best fit for the data based on the smallest residual sums of squares values. The von Bertalanffy equation describes the growth curve as follows:

$$l(t) = L_{\text{inf}} (1 - e^{-k(t-t_0)})^p$$

where:

$L_{\text{inf}}$  is the asymptotic length or mass

$k$  is the constant of metabolism or growth constant

$t_0$  is the age corresponding to zero length

$p$  is the power constant

Table 3.3 provides a summary of the main parameters obtained from the von Bertalanffy growth model for males and females of *K. breviceps* and *K. sima*.

Table 3.3: Parameters derived from a von Bertalanffy growth equation for male and female *Kogia breviceps* and *Kogia sima*.

<i>K. breviceps</i>	Parameter	Males		Females	
		Length (cm)	Mass (kg)	Length (cm)	Mass (kg)
	$L_1$	147	69	184	158.76
	$L_2$	304	374.03	324	480
	$t_0$	-16.09	-0.76	0.33	1.56
	$L_{\text{inf}}$	286.03	412.11	306.04	536.31
	$k$	0.44	0.17	0.199	0.02
	$Lt_0$	142.6	52.84	120	52.8
	$n$	25	14	29	8
<i>K. sima</i>	$L_1$	103	14.5	181	31.5
	$L_2$	260.4	303	264	264
	$t_0$	-4.39	-30.31	-0.39	-1.43
	$L_{\text{inf}}$	263.75	294.89	249.14	208.74
	$k$	0.34	0.25	0.15	0.49
	$Lt_0$	106.51	57.41	103	30.71
	$n$	21	13	23	13

$L_1$  = Smallest length or mass in the sample

$L_2$  = Largest length or mass in the sample

$t_0$  = Age corresponding to zero length or weight

$L_{\text{inf}}$  = Asymptotic length or mass

$k$  = Constant of catabolism (or growth constant)

$Lt_0$  = Estimated length or mass at birth

$n$  = Sample size

*K. breviceps*

For *K. breviceps* von Bertalanffy growth curves were fitted to the length-at-age data for males and females separately (Figure 3.6). Animals of unknown sex and Australian specimens were plotted into the same graph, but not included in the calculations for the growth curves. Individuals were considered physically mature if they had a standard length equal to or greater than the asymptotic value generated by the von Bertalanffy equation. The curve estimates the length at birth to be at 120cm for females and 142.6cm for males. The latter may be quite an overestimate, resulting from the fact that only larger calves were available for males. The longest foetus measured 113cm, whereas the shortest calf measured 147cm with an estimated age of 0.57GLGs (see also Figure 5.4, Chapter 5). The data were too scanty to calculate foetal growth rates or conception dates using the Huggett and Widdas method (1951). However, Scott (1949) developed an equation describing the relationship between the maximum body length of adult animals (both males and females) ( $x$  in cm) and neonatal length ( $y$  in cm) for both mysticetes and odontocetes. His equation:  $y=0.2411x + 44.3$  would predict a neonatal length of 123.63cm for *K. breviceps*, using a mean maximum body length of 329.05cm for both sexes in this study (calculated as the mean of the maximum body length recorded for each sex; see below). This agrees well with the estimated length at birth of 120cm for the present study.

In order to determine foetal growth rates Kasuya's (1977) equation describing the relationship between neonatal length ( $x$  in cm) and daily foetal growth rate for the linear part of the foetal growth phase ( $y$  in cm/day) for several Delphinid species was used. The formula is as follows:  $y=0.001462x + 0.1622$ . Using 120cm as length at birth in *K. breviceps* the foetal growth rate is 0.338cm per day.

The asymptotic length for *K. breviceps* females was calculated as 306.04cm ( $r^2=0.81$ ) by the growth model and for males as 286.08cm ( $r^2=0.84$ ) (Figure 3.6). It is difficult to discern whether this result reflects true sexual size dimorphism in *K. breviceps* or is a result of the skewed sample for this species (see Chapter 2). However, it appears that both sexes reach physical maturity at about the same age of 15 years.

The longest female *K. breviceps* in the sample measured 327.6cm and the longest male 330.5cm. The oldest female *K. breviceps* in the sample was estimated to be 22.4 years old. The oldest *K. breviceps* male from South Africa was estimated to be 13.33 years old and the oldest Australian male was 16 years old. However, an animal of

unknown sex (SAM specimen 87/10), which was possibly male according to the data sheet, was estimated to be 19 years old. This may indicate that the life expectancy may actually lie between 16 and 23 years in *K. breviceps*.

Only a reduced number of samples had details on the body weight of the animals (see Appendix B), which is probably due to the logistical problems encountered when wanting to weigh an animal the size of *K. breviceps*. However, a regression of body length on body weight for the 19 males and 13 females for which data were available yielded a good correlation of 0.91 and 0.96, respectively (Figure 3.7a). Although a smaller sample of animals with body length and age estimate data was available for the females than the males, a von Bertalanffy growth model could only be fitted to the female data due to the distribution of the sample (Figure 3.7b). The model estimated the weight at birth as 52.8kg and the asymptotic weight at 536.3kg ( $r^2=0.94$ ), although the latter might be an overestimate as no clear asymptote was reached. For males the weight at birth was again estimated at 52.84kg, but the asymptotic weight was estimated at 412.11kg ( $r^2=0.83$ ). The longest foetus weighed 23kg, whereas the shortest calf weighed 69kg and had an age estimate of 0.57GLGs (see also Figure 5.4, Chapter 5). In this respect the birth weight estimate of around 53kg for both sexes calculated by the model appears to fit in well with the available data.

The heaviest females in the sample were 320cm and 321cm in length, with no age estimate and an estimate of 19GLGs, respectively, and both weighed 480kg. For the males the heaviest animal had an age estimate of 13.33, measured 276cm and weighed 374.03kg.

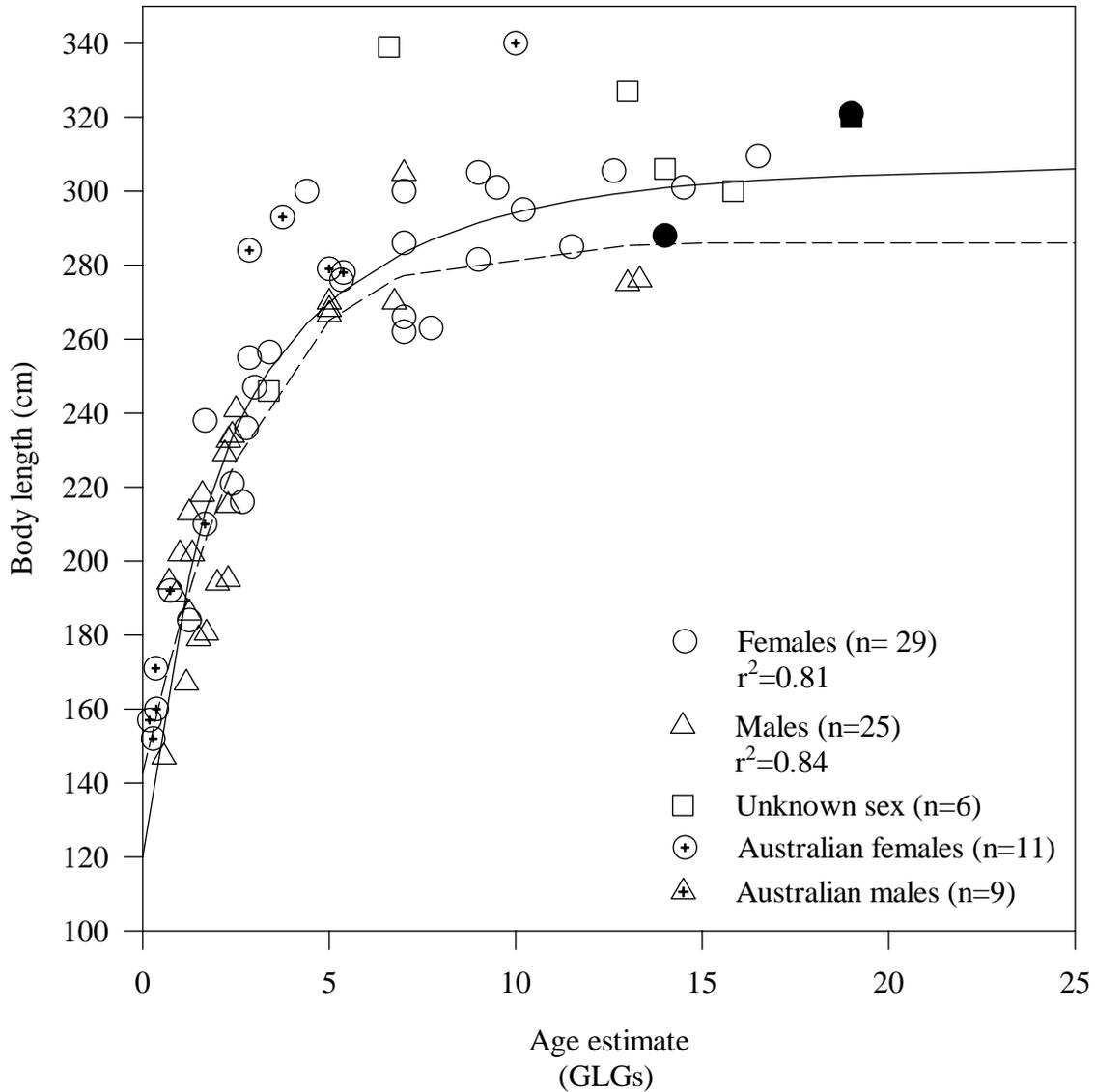


Figure 3.6: Von Bertalanffy growth curve for *Kogia breviceps*. The solid line shows the fit for females, the dotted line for males. Australian specimens and animals of unknown sex were not included in these calculations, but plotted afterwards. Filled symbols represent specimen for which cemental readings were used as an age estimate.

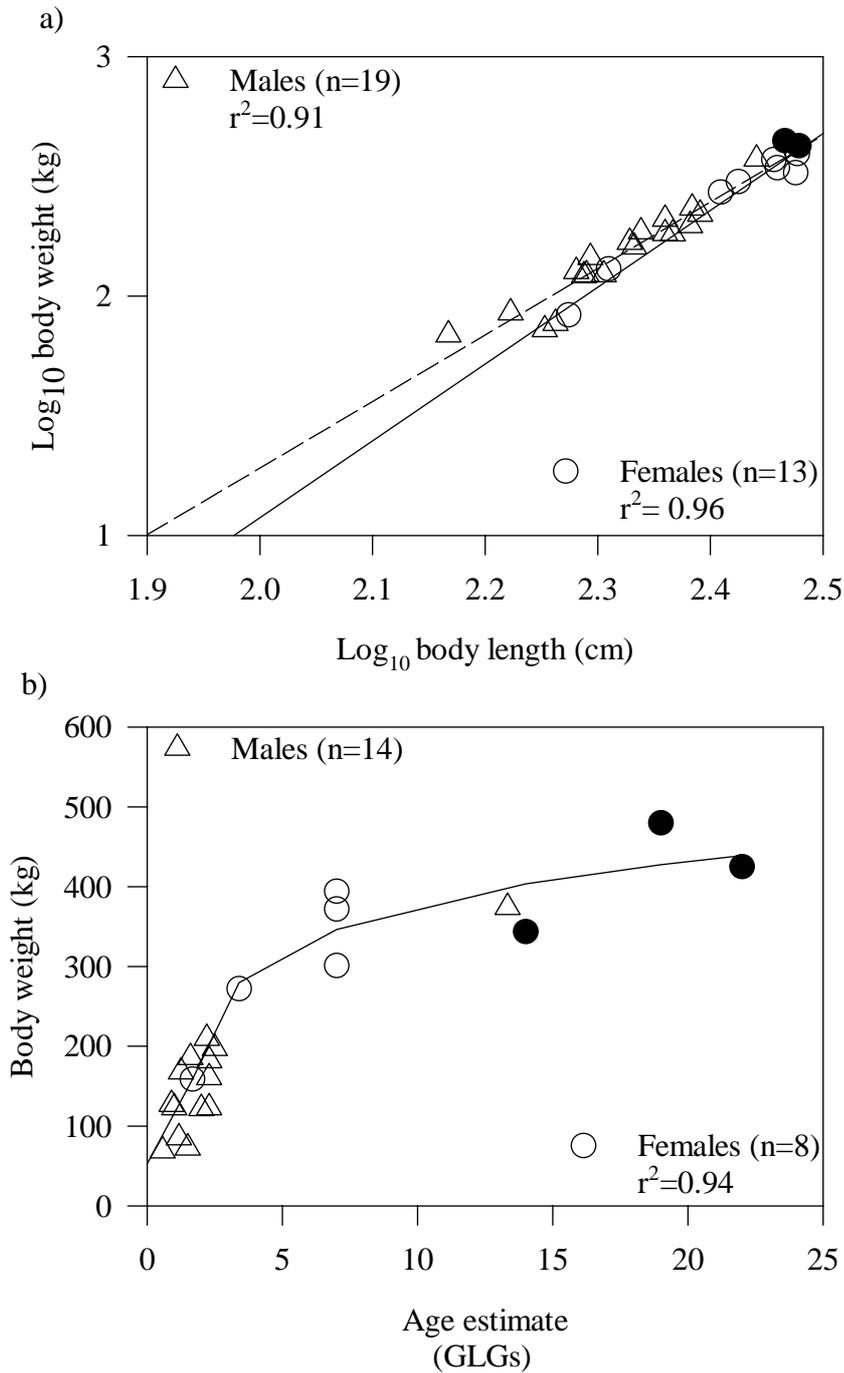


Figure 3.7: Body length (a) and age (b) in relation to body weight in *Kogia breviceps*. Filled symbols represent specimens for which cemental readigs were used as an age estimate. A von Bertalanffy growth curve could only be fitted to the female data (b).

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*K. sima*

The von Bertalanffy growth curves fitted to the length-at-age data for *K. sima* males and females are shown in Figure 3.8. In this species the intercept with the y-axis, representing size at birth, was estimated to be at 106.52cm for females and 103cm for males by the growth model. Both estimates appear realistic as the longest foetus measured 108cm, while the two shortest calves measured 103cm and 103.5cm (see also Figure 5.8, Chapter 5). The 103cm long calf had a GLG reading of zero. This indicates that birth occurs between 103cm and 108cm. The data were too scanty to calculate foetal growth rates or conception dates using the Huggett and Widdas method (1951). However, using Scott's (1949) equation and a mean maximum adult length of 267.35cm for both sexes of *K. sima* in the present study (calculated as the mean of the maximum body length recorded for each sex; see below), a neonatal length of 108.75cm can be calculated. This is somewhat longer than the 103cm estimated from the lengths of foetuses and calves. In addition, Kasuya's (1977) formula gave a foetal growth rate of 0.313 cm/day, based on a length at birth of 103cm in *K. sima*.

The asymptotic length calculated by the growth model is reached at 249.14cm in *K. sima* females ( $r^2=0.9$ ), while the males appear to reach physical maturity at a slightly larger body size of 263.75cm ( $r^2=0.84$ ) (Figure 3.8, Table 3.3). This corresponds to 13 and 16 years of age for females and males, respectively.

The longest animal in the sample was a 274.3cm long female with no age estimate. The longest female for which the age could be determined measured 264cm and for male *K. sima* the longest animal measured 260.4cm. The oldest female was 21.5 years and the oldest male was estimated to be 17 years old. These data indicate a life expectancy of 17-22 years in *K. sima*.

As for *K. breviceps*, only a few specimens of *K. sima* had accompanying data on body weight (see Appendix B). The regression of body length on body weight gave a similarly good regression coefficient for both sexes ( $r^2=0.95$  and 0.96 for males and females, respectively) (Figure 3.9a). The von Bertalanffy model calculated weight at birth at 30.71kg for female *K. sima* and the asymptotic weight at 208.7kg ( $r^2=0.92$ ) (Figure 3.9b, Table 3.3). For males the model calculated weight at birth at 57.41kg and the asymptotic weight at 294.9kg ( $r^2=0.88$ ) (Figure 3.9b, Table 3.3). However, as the growth curve for the male data does not reach a plateau this may be a substantial overestimate. The longest foetus present in the sample weighed 12.98kg, while the two

shortest calves weighed 31.5kg and 14.5kg (see also Figure 5.8, Chapter 5). Thus birth weight probably lies between 13kg and 15kg in this species. The GLG reading of the calf weighing 31.5kg was 0, indicating that it was a neonate and possibly only a few weeks old, but weight increases rapidly after birth.

The heaviest female in the sample was a 9.8year old animal, measuring 264cm with a weight of 264kg (Figure 3.9b, Table 3.3). The heaviest male was estimated to be 16 years old, measured 256cm in body length and weighed 303kg (Figure 3.9b, Table 3.3).

### 3.3.2.1 Comparison with other species

In order to compare the data obtained from the growth curves for both *Kogia* species Table 3.4 lists growth rate constants (k) for both the Gompertz and the von Bertalanffy model for other cetaceans found in the literature. Most studies of growth in odontocetes appear to use the Gompertz model and thus the growth rate constants (k) for males and females from different odontocete species were plotted (Figure 3.10). While the data do not have a good regression coefficient ( $r^2=0.62$  for females and 0.45 for males), a general trend of higher growth rate constants in smaller species can be observed. For both males and females the data for *K. breviceps* appear to fit in better with the general trend observed in odontocetes than the data for *K. sima* (Figure 3.10). While female *K. sima* have a higher growth rate constant than female *K. breviceps*, this trend is not visible in the males (Figure 3.10). Compared to another odontocete of similar body length, the bottlenose dolphin *T. truncatus*, the growth constants for both male *K. breviceps* and female *K. sima* are remarkably higher (Figure 3.10, Table 3.4).

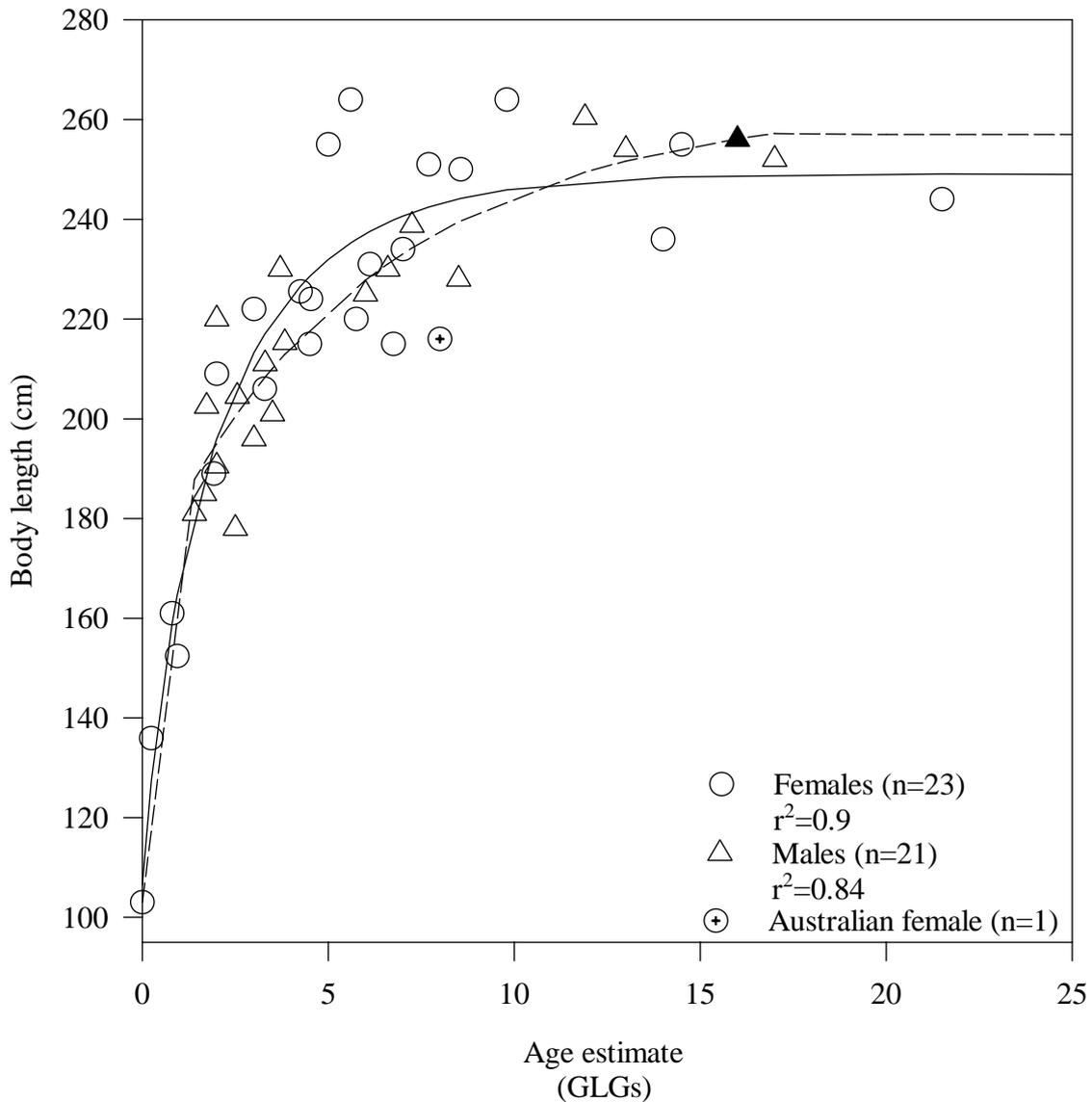


Figure 3.8: Von Bertalanffy growth curve for *Kogia sima*. The solid line shows the fit for females, the dotted for males. The Australian female was not included in these calculations. The filled symbol represents a specimen for which cemental readings were used as an age estimate.

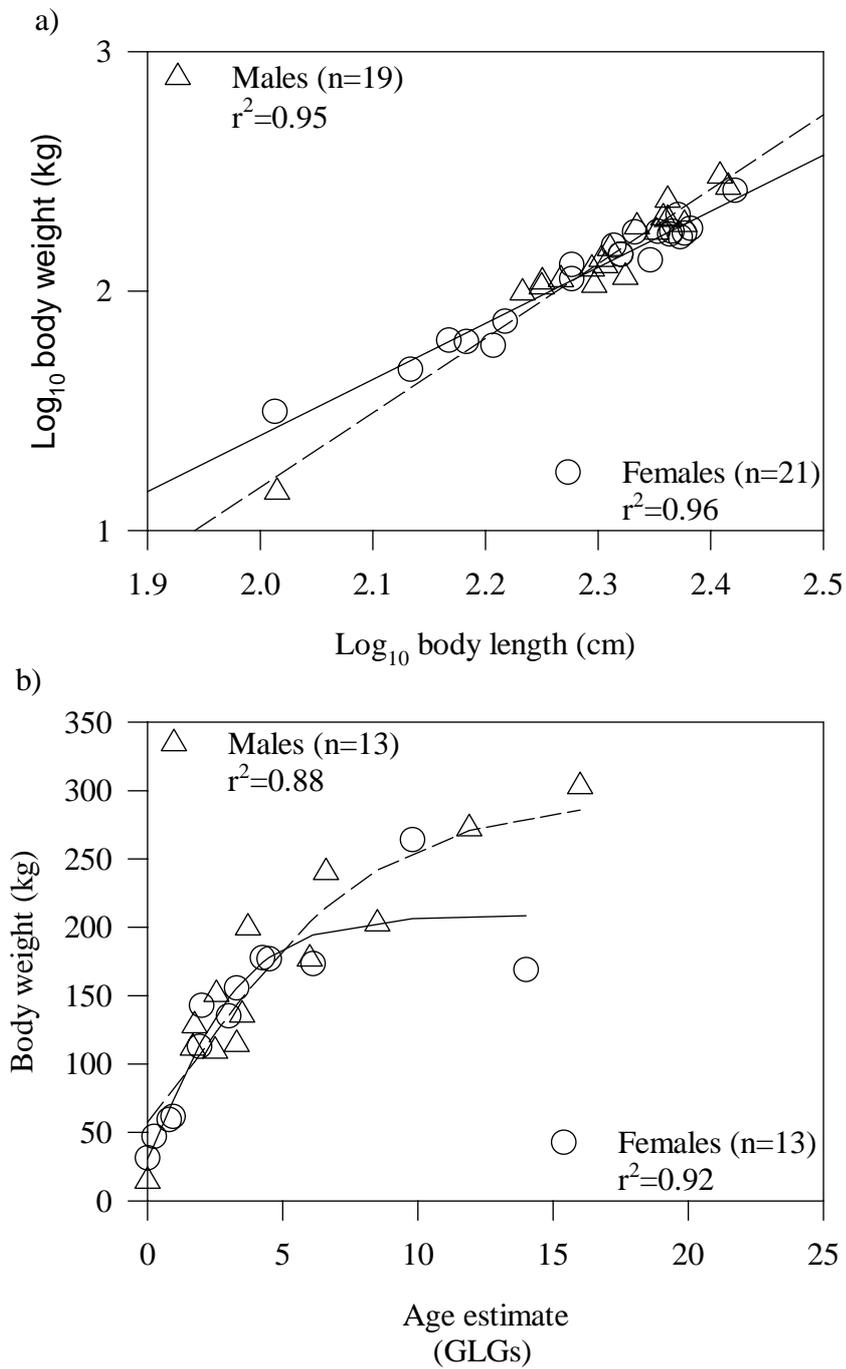


Figure 3.9: Body length (a) and age (b) in relation to body weight in *Kogia sima*. The solid line shows the fit of the von Bertalanffy model for females, the dotted line for males.

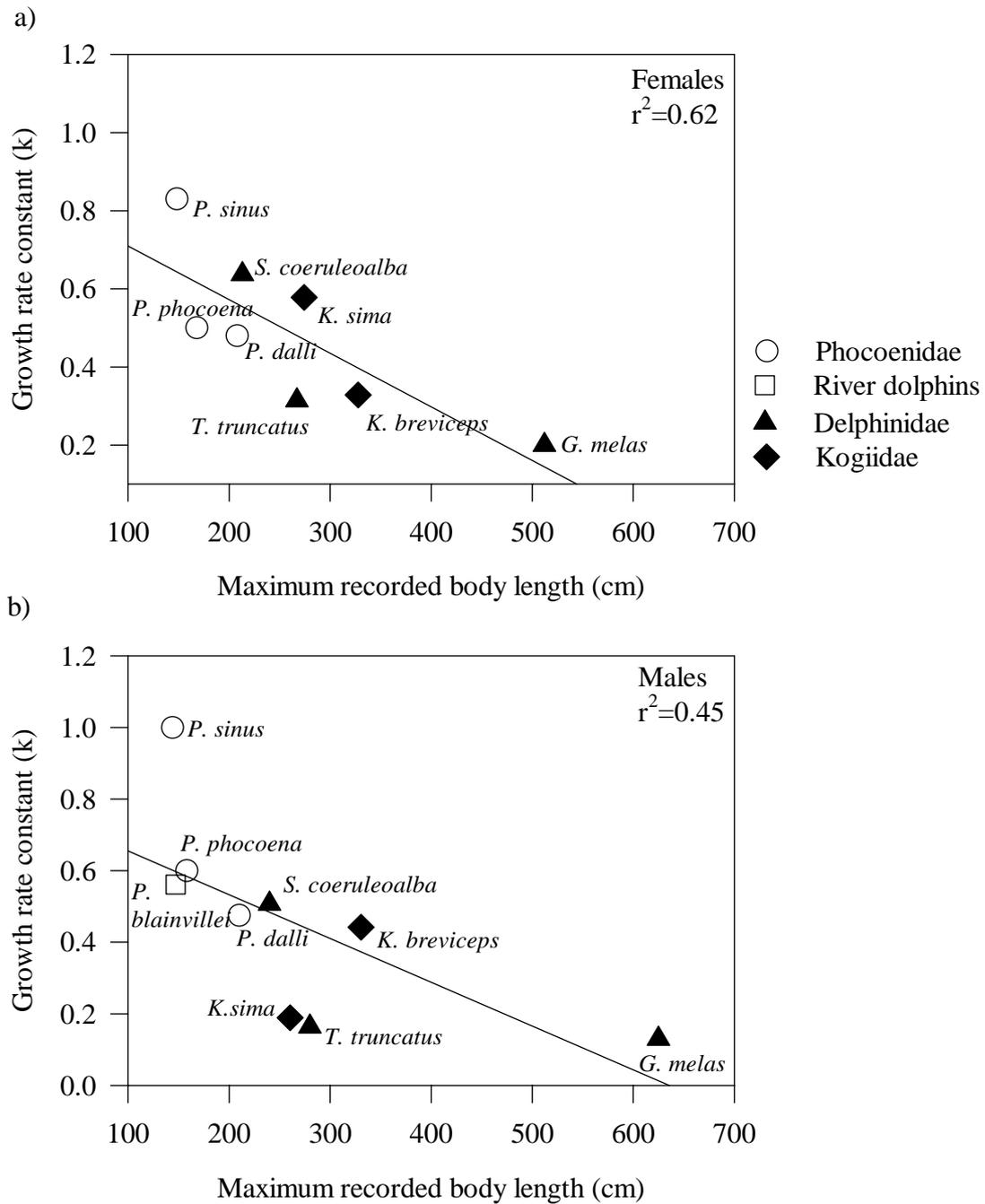


Figure 3.10: Body length versus growth rate constants (k) obtained from Gompertz growth models for different species of odontocetes. Data are from Ferrero and Walker, 1999; Read and Tolley, 1997; Di-Méglio *et al.*, 1996; Hohn *et al.*, 1996; Read *et al.*, 1993; Kasuya and Brownell, 1979.

Table 3.4: Growth rate constants (k) for different species of cetaceans (for length-age relationships).

Species	Growth rate constant (k)		Model used	Reference
	Males	Females		
Vaquita <i>Phocoena sinus</i>	1.00	0.83	Gompertz	Hohn <i>et al.</i> , 1996
Dall's porpoise <i>Phocoenoides dalli</i>	0.48	0.48	Gompertz	Ferrero and Walker, 1999
Harbour porpoise <i>Phocoena phocoena</i>	0.6	0.5	Gompertz	Read and Tolley, 1997
Harbour porpoise <i>Phocoena phocoena</i>	0.54	0.48	Gompertz	Read and Gaskin, 1990
Harbour porpoise <i>Phocoena phocoena</i>	0.55	0.55	Gompertz	Read and Gaskin, 1990
Franciscana <i>Pontoporia blainvillei</i>	0.56	-	Gompertz	Kasuya and Brownell, 1979
Striped dolphin <i>Stenella coeruleoalba</i>	0.51	0.64	Gompertz	Di-Méglio <i>et al.</i> , 1996
Striped dolphin <i>Stenella coeruleoalba</i>	0.65	0.38	Gompertz	Di-Méglio <i>et al.</i> , 1996
Bottlenose dolphin <i>Tursiops truncatus</i>	0.16	0.31	Gompertz	Read <i>et al.</i> , 1993
Bottlenose dolphin <i>Tursiops truncatus</i>	0.09	0.17	v. Bertalanffy	Cockcroft and Ross, 1990
Dwarf sperm whale <i>Kogia sima</i>	0.15	0.34	v. Bertalanffy	present study
Dwarf sperm whale <i>Kogia sima</i>	0.19	0.58	Gompertz	present study
Pygmy sperm whale <i>Kogia breviceps</i>	0.44	0.20	v. Bertalanffy	present study
Pygmy sperm whale <i>Kogia breviceps</i>	0.44	0.33	Gompertz	present study
Long-finned pilot whale <i>Globicephala melas</i>	0.13	0.20	Gompertz	Bloch <i>et al.</i> , 1993
Long-finned pilot whale <i>Globicephala melas</i>	0.07	0.04	v. Bertalanffy	Bloch <i>et al.</i> , 1993
Baird's beaked whale <i>Berardius bairdii</i>	0.56	0.54	v. Bertalanffy	Kasuya, 1977
Minke whale <i>Balaenoptera acutorostrata</i>	0.18	0.22	v. Bertalanffy	Masaki, 1979

Minke whale <i>Balaenoptera acutorostrata</i>	-	0.20	v. Bertalanffy	Lockyer, 1981
Minke whale <i>Balaenoptera acutorostrata</i>	-	0.25	v. Bertalanffy	Mitchell and Kozicki, 1975
Humpback whale <i>Megaptera novaeangliae</i>	0.23	0.21	v. Bertalanffy	Chittleborough, 1965
Fin whale <i>Balaenoptera physalus</i>	-	0.1-0.13	v. Bertalanffy	Mitchell and Kozicki, 1975

### 3.3.3 Sexual size dimorphism

Table 3.5 gives a summary for length and age at both sexual (see Chapters 4 and 5 for details) and physical maturity for *K. breviceps* and *K. sima*. These data show that in *K. breviceps* age at ASM and age at physical maturity is the same between the two sexes. In contrast, length at both sexual and physical maturity is shorter in males than in females. Although this result may again reflect the skewed sample towards younger males (see Chapter 2) in this species one would expect to see that reflected in the age as well. Thus these results would indicate that females are larger in body size than males in *K. breviceps*.

A different pattern can be seen in *K. sima*, where females are both older and longer at ASM, but males “overtake” them and are older and longer at physical maturity. This a pattern commonly observed in odontocetes species in which males are larger than the females. Both the later attainment of age and length at physical maturity are indicators for sexual dimorphism in this species.

Although a series of measurements such as maximum girth, maximum length of pectoral fins and maximum width of flukes are available in the datasheets for both *K. breviceps* and *K. sima* (Ross, 1979), the majority of these measurements are from physically immature specimens. Therefore an analysis of sexual size dimorphism between the sexes of either species was not possible. Although some results of the growth analysis appear to indicate that females may be larger in *K. breviceps* and males in *K. sima*, these data would need to be supported with a more detailed analysis of sexual size dimorphism. This highlights the importance of detailed measurements of body dimensions to be taken from specimens in the future, in particular physically mature ones.

Table 3.5: Length and age at sexual and physical maturity for *Kogia breviceps* and *Kogia sima*.

		<i>K. breviceps</i>	<i>K. sima</i>
<b>Length at sexual maturity (cm)</b>	Females	262	215
	Males	242	197
<b>Age at sexual maturity (GLGs)</b>	Females	~5	~5
	Males	2.5-5	2.55-3
<b>Length at physical maturity (cm)</b>	Females	306	249.1
	Males	286	263.8
<b>Age at physical maturity (GLGs)</b>	Females	15	13
	Males	15	16

### 3.3.4 Morphological differences between *K. breviceps* and *K. sima*

As the lack of body measurements for physically mature specimens of either *Kogia* species also affects the determination of differences in the size of appendages between the two species, no definite conclusion can be drawn here. However, considering Ross' 1979 results (1979), the length ( $\bar{x}=10.0$  in *K. breviceps*,  $\bar{x}=14.7$  in *K. sima*) and height ( $\bar{x}=3.6$  in *K. breviceps*,  $\bar{x}=7.5$  in *K. sima*) of the dorsal fin, flipper length ( $\bar{x}=13.9$  in *K. breviceps*,  $\bar{x}=15$  in *K. sima*) and the width of the flukes ( $\bar{x}=23.8$  in *K. breviceps*,  $\bar{x}=26.1$  in *K. sima*) are larger in *K. sima* than *K. breviceps* (measurements are percentages of body length). Although there is some overlap between the two species the means for these body measurements are consistently larger in *K. sima*. This may be a good indication that appendages such as pectoral fins, dorsal fin and flukes are larger in *K. sima* than *K. breviceps*. However, again more detailed measurements need to be taken for physically mature specimens in order to test this in more detail in the future.

## 3.4 Discussion

### 3.4.1 Tooth morphology and age determination

#### 3.4.1.1 Tooth morphology and histology

The general description of the histology of longitudinal sections of *K. breviceps* teeth is in agreement with Ross' (1979) results. The prenatal dentine is easily distinguishable from the postnatal dentine by a clear, narrow neonatal line. In addition, the growth layers in the dentine can be distinguished into GLGs. However, it appears

that the present technique may give a better resolution than the one employed by Ross (1979). His sections were of the same thickness or thinner (200µm) than the ones in the present study (300µm). Grinding down the teeth to very thin sections may have resulted in loss of resolution and hence inability to distinguish between laminae as he mentioned in his work. In addition, the use of polarized light in the present study appears to improve the resolution of the laminae significantly. A similar result is presented for Cape fur seal *A. pusillus pusillus* teeth (Oosthuizen, 1997). This technique uses the refractive properties of the apatite crystals in the teeth of these animals and thus enables distinction between layers, which would not be possible with normal light microscopy. However, the reason why results with stains such as haematoxylin (present study) or toluidine blue (as employed by Ross (1979)) did not yield good results for teeth of either *Kogia* species is unclear.

Contrary to Ross' findings (1979) an enamel cap was found in some young animals in the present study. All of the *K. breviceps* with an enamel cap were below one year of age and originated from Australia, indicating that perhaps the presence of an enamel cap may be more prevalent in Australian *K. breviceps*. For *K. sima* an enamel cap was found for a South African specimen with two GLGs; the age estimate of eight GLGs for the *K. sima* from Australia, which had an enamel cap is considered to be an overestimate. This indicates that something causes wear or grinding down of the teeth and thus loss of the enamel cap in older animals, which is supported by the worn tooth tips found in many adult animals of either species of *Kogia*. In addition, the diet or environmental conditions to which the Australian animals were exposed may result not only in a clearer GLG pattern in the teeth, but also facilitate the formation of an enamel cap.

The high degree of tooth wear found in the two *Kogia* species is puzzling. It is unlikely that this would result from feeding as cephalopods are relatively soft and would not cause increased abrasion of the teeth (see Chapter 6). Furthermore, the redundancy of teeth in teuthophagous odontocetes and subsequent reduction in the number of teeth would suggest that they are not used excessively (Heyning and Mead, 1996; MacLeod, 1998). Thus the extensive wear of teeth in the two *Kogia* species may have an alternative, as yet unknown origin. Tooth wear may vary between individuals, especially between sexes due to differences in diet (see Chapter 6), as well as between populations. As the rate of tooth wear is unknown and cannot be determined from the current sample no attempt can be made to correct the estimate of age at sexual maturity presented here

for both *Kogia* species. Therefore results from the present study cannot be directly compared with age estimates from other populations.

#### 3.4.1.2 Age determination

The lack of significant difference between the age estimates from the present study and the ones made by Ross (1979) supports the fact that the interpretation of the GLGs was the same by both observers. The greatest source of error in age determination of *T. truncatus* is the misinterpretation of GLGs (Hohn *et al.*, 1989). Errors are predominantly due to accessory layers and poorly prepared sections (Hohn *et al.*, 1989). Any guide or “model” for estimating age from odontocete teeth must take into account that accessory layers are often a part of the GLG pattern (Hohn *et al.*, 1989) and this is particularly the case with *Kogia* teeth as the number of accessory layers present is high in the two species. This highlights the need to standardise age estimation techniques for *Kogia* in order to compare results from different studies.

Age estimation in *K. sima* seems less reliable than in *K. breviceps*. Ross (1979) indicates that the number of accessory layers present in the teeth in addition to the smaller tooth size and the resulting compression of GLGs make age estimation in this species exceedingly difficult. Although Klevezal' and Kleinenberg (1967) report that the method of preservation of the teeth does not appear to make a difference to the visualisation of the GLGs, there is some evidence that it might (pers. obs.; Peter Best, pers. com.). In addition, the readability of the teeth varies with the species examined (Kasuya *et al.*, 1988a). Perrin *et al.* (1977) report that postnatal dentine in spinner dolphins *S. longirostris* has a better readability than in spotted dolphins *S. attenuata*, two species that also belong to the same genus. Bloch *et al.* (1993) state that the teeth of long-finned pilot whales *G. melas* originating from one school are easier to read than those from other schools. Genetic similarity, post-mortem changes in tissues, predisposition to disease, and environmental stress, such as malnutrition, are all possible reasons for this variation (Bloch *et al.*, 1993). As mammalian teeth from species inhabiting colder areas show a clearer definition of laminae than those from animals inhabiting warmer areas (Grue and Jensen, 1979 in: Lockyer, 1995a; Langvatn, 1995), the differences in distribution patterns between the two *Kogia* species, with *K. breviceps* inhabiting cooler waters than *K. sima* (see Chapter 7) may be reflected in the teeth. These factors combined with the high number of accessory layers, smaller tooth size and

resulting compression of GLGs in *K. sima* would explain the differences in readability between the teeth of *K. breviceps* and *K. sima*.

It should be kept in mind that for both *Kogia* species the present results on age determination can only be viewed as an estimate. Estimates of age are imprecise for most cetacean species as the definite rate of dentine and cementum deposition is not known for the majority of species. Furthermore, the age estimation is subjective and based on the observers' interpretation of GLGs. This imprecision tends to increase with the age of the animals. Although the present study presents the first age estimates for a comparatively large sample of *Kogia* and thus a good start into exploring the life history strategy of both species, the technique may be refined and perfected once teeth and age estimates from more animals become available. In particular, reading teeth from animals originating from different geographical locations may aid in defining the GLG patterns in the teeth of the two *Kogia* species as was found with the Australian samples in the present study.

The high correlation between dentinal and cemental layers for both *K. breviceps* and *K. sima* leads to the conclusion that both are deposited at the same rate in both species, but after the closure of the pulp cavity only cemental layers continue to be deposited. Similar results have been observed in other odontocetes (Sergeant, 1962; Kasuya and Marsh, 1984; Cockcroft and Ross, 1990; Bloch *et al.*, 1993) and in most odontocetes age estimation from dentinal layers alone has been hindered by the occlusion of the pulp cavity at some stage during the life of the animal (Sergeant, 1962). In general, dentinal counts are considered to be more reliable, with cemental counts only being used after occlusion of the pulp cavity (Cockcroft and Ross, 1990; Bloch *et al.*, 1993). Without direct evidence it is assumed that the cemental deposition is homogenous throughout life (Kasuya *et al.*, 1988a).

On average about 12 layers are laid down in the dentine of long-finned pilot whales *G. melas* before occlusion of the pulp cavity (Sergeant, 1962) and in bottlenose dolphins *T. truncatus* the pulp cavity closes at about 12 years, which almost coincides with the age at attainment of sexual maturity (Cockcroft and Ross, 1990). Thus the start of the occlusion of the pulp cavity in *K. breviceps* at 14 years and in *K. sima* at 11 years appears to agree well with data for other odontocetes.

Similarly cemental layers are used as an age estimate when osteodentine formation prevents age estimates to be made from dentinal layers (Miyazaki, 1984). Teeth of the two *Kogia* species appear to have an unusually high percentage of

osteodentine compared to other odontocetes (Sergeant, 1962; Bloch *et al.*, 1993). As expected the occurrence of osteodentine increases with age in long-finned pilot whales *G. melas*, albeit in an irregular manner (Lockyer, 1995a). This is due to the fact that it may form at an early age, but not embed in the dentine until later, if at all (Lockyer, 1995a). The cause of osteodentine formation is not understood (Lockyer, 1995a). It has, however, been suggested for terrestrial mammals that a big mechanical load results in intensive deposition of secondary dentine and as a result many accessory bands form in the dentine (Klevezal' and Kleinenberg, 1967).

### 3.4.2 Length at birth and foetal growth rate

Based on the data from the present study the length at birth for *K. breviceps* lies around 120cm and the weight around 53kg, while it is around 103cm and 14kg for *K. sima*. However, the largest foetus ever reported for a *K. breviceps* was 125cm from a stranded female in California, USA (Eliason and Houck, 1986), while the shortest neonate reported for a *K. sima* in the literature is 95cm for an animal, which was thought to be less than a week old (Caldwell and Caldwell, 1989). Some variation of birth length is expected within a species, especially when comparing animals from different geographical locations and possibly different populations. The present results agree well with Ross' (1979) estimate of the length at birth of 120cm for *K. breviceps* and 100cm for *K. sima*. These data indicate that *K. breviceps* neonates are born at 40.5% of mean adult asymptotic length (296cm), whereas it is 40.2% in *K. sima* (mean adult asymptotic length: 256.5cm). This is in agreement with Scott's (1949) estimate that the length of neonates ranges between 20-50% of maximum adult length depending on the species, with 25-30% for the mysticetes. A more recent estimate for mysticetes is 25% (Evans, 1987) and 40-48% in odontocetes (Chivers, 2001).

The data calculated here for length at birth for the two *Kogia* species using Scott's (1949) equation (*K. breviceps*: 123.6cm, *K. sima*: 120cm) differ somewhat from the estimated length at birth based on actual calf and foetus lengths (*K. breviceps*: 120cm; *K. sima*: 103cm). As he based his equation on both mysticetes and odontocetes together some inaccuracies are to be expected. In addition, he used maximum recorded body length in his formula rather than average or mean adult body length. However, if only considered as a rough estimate of length at birth the data are not too far off from the observed length at birth for either species of *Kogia* in the present study.

The results for the foetal growth rate in cm/day during the linear part of the growth curve using Kasuya's (1977) formula indicate that growth is slightly faster in *K. breviceps* (0.34cm/day) than *K. sima* (0.31cm/day). Although Kasuya derived his equation from data on delphinids, this is to be expected as it was found that those species of cetaceans that produce a larger full-term foetus also exhibit a higher foetal growth rate rather than a prolonged gestation period (Huggett and Widdas, 1951; Laws, 1959; Frazer and Huggett, 1974). In comparison, the Ganges dolphin *Platanista gangetica*, the harbour porpoise *P. phocoena* and the bottlenose dolphin *T. truncatus* all have lower specific foetal growth rates of 0.23, 0.28 and 0.28, respectively (Frazer and Huggett, 1974). Larger odontocetes such as the beluga *D. leucas* and Baird's beaked whale *Berardius bairdii* have specific foetal growth rates of 0.56 and 0.95 (Frazer and Huggett, 1974; Kasuya, 1977). A similar foetal growth rate to *Kogia* was seen in the long-finned pilot whale *G. melas* with 0.33 (Frazer and Huggett, 1974). Interestingly, data presented on *K. breviceps* indicate a specific foetal growth rate of 0.8 (Frazer and Huggett, 1974), which does not conform with those of the present study. The main reason for this appears to be that the estimated gestation period was only 270 days or nine months (Frazer and Huggett, 1974), which is in contrast to 12 months in the present study (see Chapter 5). Considering the trend in increased foetal growth rate with increased length at birth (and thus increased adult length) the data from the present study are in better agreement than those presented by Frazer and Huggett (1974).

### 3.4.3 Growth

The growth curves generated for both *K. breviceps* and *K. sima* show a rapid increase of length with age. This is in agreement with other data as cetaceans show rapid growth subsequent to birth, especially in terms of mass, and growth rate decreases gradually with age (Hohn, 1980b; Cockcroft and Ross, 1990). The growth rate of bottlenose dolphins *T. truncatus* off South Africa is greatest during the first year of life (Cockcroft and Ross, 1990). Mass increases by 255% in the first year, but only by 49%, 13.5% 10.6 and 3.8% in the following years (Cockcroft and Ross, 1990). In contrast, length increases less rapidly by 57%, 15.2%, 3.7%, 4% and 5.5% (Cockcroft and Ross, 1990). Similarly, the growth rate of bottlenose dolphins *T. truncatus* from the western North Atlantic is high in the first year with an increase in length of 53%, an average of 10% during the second year and a considerable slowing down of the growth rate after

three GLGs (Hohn, 1980b).

The data for either *Kogia* species from the present study also show some variation of length with age, which, considering the above data for other odontocetes, appears common among cetaceans. High variability in total lengths of individuals in any age class is also observed for *T. truncatus* from the western North Atlantic, which indicates that total length alone is not a reliable indicator of the age of the animals (Hohn, 1980b). Juvenile *T. truncatus* from Sarasota, Florida, also show considerable variation in size-at-age (Read *et al.*, 1993). For example, a 200cm long female could be either one, two, or three years old. As these data are derived from known age animals, error due to age estimation from GLGs in the teeth can be excluded.

Both sexes of both species of *Kogia* continued growing past their ASM, which is not necessarily common among odontocetes of similar size. Although among larger mammals females usually start breeding before they have reached adult body weight (Clutton-Brock and Iason, 1986), in bottlenose dolphins *T. truncatus* sexual maturity in the females coincides with physical maturity (Read *et al.*, 1993). Males continue to grow past their attainment of sexual maturity, at which stage they have attained only 70% of their asymptotic mass (Read *et al.*, 1993). In captive populations older males are known to sire more offspring than do young males, and recent genetic evidence suggests that this is also true for the Sarasota population (Duffield and Wells, 2002). This continued growth in males suggests that size may be an important factor in the mating system (see also Chapter 4). Size at ASM is discussed in more detail below (see section on sexual dimorphism).

#### **3.4.3.1 Length and age at physical maturity**

In contrast to Ross' study (1979) it was possible in the present study to calculate physical maturity for females and males separately using the von Bertalanffy growth equation. While Ross estimates physical maturity based on the fusion of epiphyses to occur between 305cm and 330cm for both sexes of *K. breviceps* (Ross, 1979), the results from the present study indicate that for males this is quite a bit smaller (286cm). However, the estimate of the occurrence of physical maturity at 306cm for female *K. breviceps* is in agreement with results from the previous study. An increase in sample size may be accountable for these differences between the two studies. The age at physical maturity appeared to be similar in both sexes of *K. breviceps* and occurred

around 15 years.

For *K. sima* the asymptotic length was calculated as 249.1cm for females and 263.8cm for males. In contrast, Ross (1979) could only calculate the onset of physical maturity for the two sexes combined. The shortest physically mature animal measured 247cm and was a male (Ross, 1979). The data obtained here for *K. sima* may be best compared to those for a similar sized odontocete like the bottlenose dolphin *T. truncatus*. Asymptotic length for these animals off South Africa occurs at 238cm for females and 243cm for males (Cockcroft and Ross, 1990). The age at physical maturity occurred around 13 years in female *K. sima*, while it appeared to be slightly later in males, corresponding to 16 years. Again these data are comparable to data obtained from bottlenose dolphins off South Africa, where both males and females reach physical maturity between 12 and 15 years (Cockcroft and Ross, 1990).

#### 3.4.3.2 Maximum length and age

Data from the present study on the maximum length recorded for female and male *K. breviceps* (327.6cm and 330.5cm, respectively) exceed the previous records reported by Ross for South African animals (Ross, 1979). He states 309.5cm and 325cm as maximum lengths for female and male *K. breviceps*, respectively. Thus the present study presents a substantially greater maximum length for female *K. breviceps* than previous studies, which can again be accredited to the increased sample size available. In comparison, Odell *et al.* (1984) report the mean adult length of females as 303cm and that of males as 307cm based on strandings along the Florida coastline. These data differ somewhat from South Africa and geographical variation in body length is observed quite frequently among odontocetes (Cockcroft and Ross, 1990).

In the present study the longest female *K. sima* measured 274.3cm and the longest male 260.4cm. This is a slight increase from the longest specimen reported by Ross, which was a 264cm long female (Ross, 1979). This is most likely a result of an increased sample available.

The maximum age estimates obtained for *K. breviceps* of 22 years for females and 13 years for males (16 for a male animal from Australia) are in agreement with previous work on the same species. For specimens from New Zealand the maximum age estimates are 12.5 and 16+ for females and males, respectively (Tuohy *et al.*, 2001), while a female from New Caledonia was estimated to be 19 years of age (Bustamante *et*

*al.*, 2003). The shorter life expectancy of *K. breviceps* males in comparison with females is possibly a reflection of the biased sample towards immature males and mature females (see Chapter 2). However, it may also be a true reflection of differential life spans in this species and should be taken into consideration in future studies on the life history and social system. In addition, differences in the interpretation of GLGs between observers and between studies cannot be excluded and any comparison of age between studies in *Kogia* should be carried out with caution.

Maximum age estimates in *K. sima* are also higher for females than for males (21.5 and 17, respectively), with the one for males being five years lower than the estimate for females. As the sample for this species is normally distributed (see Chapter 2) this difference may be a true indication of different life expectancies in this species. Male long-finned pilot whales *G. melas* off Newfoundland have a higher mortality throughout life than females and subsequently females attain higher maximum ages than males (Sergeant, 1962; Bloch *et al.*, 1993). However, additional samples for either *Kogia* species would provide more insight into this aspect.

The maximum life span of 16-23 years for *K. breviceps* and 17-22 years for *K. sima* is surprisingly low for odontocetes the size of *Kogia*. Similar life expectancies have to date only been reported from some of the smallest odontocetes such as the vaquita *P. sinus* (21 years) (Hohn *et al.*, 1996). In Hector's dolphins *C. hectori* the maximum age recorded is 19GLGs for females and 20 for males (Slooten, 1991). Although the highest reported age of harbour porpoises *P. phocoena* from the western North Atlantic is 13 (Gaskin *et al.*, 1984; Read, 1990), animals up to the age of 24 were reported from the population off California and from British waters (Hohn and Brownell, 1990; Lockyer, 1995b). This makes a difference of 11 years, and although it was suggested that 24 may represent the age of an outlier (Hohn and Brownell, 1990) it may well be the maximum age these animals can reach if unaffected by incidental mortality in fishing gear or predation (Lockyer, 1995b). In contrast, odontocetes the size of *Kogia* reach maximum ages around 50 to 60 years (Perrin and Reilly, 1984) (see Chapter 9). The bottlenose dolphin *T. truncatus*, for example, which has a similar body length to *K. sima*, reaches maximum ages in excess of 40 years (Cockcroft and Ross, 1990). The implications of such a surprisingly low life expectancy as well as low age at ASM (see Chapters 4 and 5) in the two *Kogia* species compared to other odontocetes of similar body size are discussed in detail in Chapter 9.

### 3.4.3.3 Body weight

Data on body weights for medium to large odontocetes, including the two *Kogia* species, are scarce in the literature, probably as a result of the logistic difficulties involved. Thus the present sample represents the first comprehensive collection of body weight data for the two *Kogia* species. Ross (1979) presents data for three animals, one of which was a foetus and the other rather emaciated. Weights of another cow stranded with its female calf were added in his 1984 publication (Ross, 1984). In his summary of published data on weights of another six animals from the literature, the maximum weight is 417kg for an animal of 298.6cm; no sex is given (Tomilin, 1957 in: Ross, 1979). This is exceeded in the present study by two females each weighing 480kg. Data published by Marten (2000) on a 179cm long male *K. breviceps* weighing 79kg and by Price (1984) on a 173cm long female *K. breviceps* weighing 84kg appear to fit in well with the present data. However, the weight of 450kg reported for a 317cm long male stranded in New Brunswick, Canada, exceeds the maximum weight recorded for a male *K. breviceps* in the present study (374kg) and appears to be the maximum reported for a male *K. breviceps* (McAlpine and Murison, 1997). Weights for sexually mature male and female *K. breviceps* are discussed in Chapters 4 and 5.

Weight at birth was estimated to be around 53kg in *K. breviceps* in the present study. As there appear to be no published data in the literature this is the first estimate of birth weight of this species. In addition, birth weights of odontocetes are scarce in the literature, making a comparison with other species difficult. No relationship between neonatal weight and adult weight like the one between neonatal length and adult length has been established for any cetacean.

For *K. sima* published data on body weights for 11 animals range from 47.3kg for a 136cm long female to 209.1kg for a 235cm long female from South Africa (Ross, 1979). Data for another three animals were added in his 1984 publication (Ross, 1984), ranging from 61.5kg to 156kg. Thus the data from the present study present new record weights for the species. Willis and Baird (1998) report that adult *K. sima* weigh between 136kg and 272kg, but neglect to define whether they refer to sexual or physical maturity. Data on weights for sexually mature animals are presented in Chapter 4 and 5 for males and females, respectively.

Weight at birth was estimated to be between 13kg and 15kg in the present study, with length at birth being around 103cm. This supports previous data on a 105cm long

*K. sima* calf, which weighed 20kg (Carvan III, 1988).

#### 3.4.3.4 Comparison with other species

The data from other odontocetes indicate that the growth rate constants ( $k$ ) obtained for both species of *Kogia* in the present study fit in well with the general trend that smaller odontocetes have higher growth rates than larger ones. The growth rates of most endotherms are at least an order of magnitude greater than the maximum growth rates of ectotherms, and cetaceans are amongst the fastest growing mammals (Case, 1978). It is thought that between species of mammals, the growth rate is an adaptation to the species' environment, infant mortality rate and the available food to adults (Case, 1978). In this respect, it is thought that harbour porpoises grow quickly in order to attain adult size as quickly as possible and facilitate early reproduction in this short-lived species (Read and Tolley, 1997). However, the present comparison indicates that harbour porpoises *P. phocoena* do not grow any quicker than expected for their body size- and neither do the two *Kogia* species. This result is surprising as species with a fast life history strategy would be expected to exhibit higher growth rates than those with a slow life history strategy (see Chapter 9).

#### 3.4.4 Sexual size dimorphism

Males are consistently shorter at sexual maturity than females in all species of baleen whales (Lockyer, 1984). As females are the larger sex in baleen whales (Ralls, 1976), the data for *K. breviceps*, indicating an overall smaller body size for males at ASM as well as at physical maturity, may suggest that females are actually larger than males in this species. Data from the literature would support this, as the largest animal recorded was a female (Caldwell *et al.*, 1971). These results are surprising since reversed sexual size dimorphism is usually only found in the smallest odontocetes and some mysticetes and is absent in medium to large-sized odontocetes. Although sexual size dimorphism is often used as an indicator of the mating system of a species, it may have evolved from differential evolutionary pressures on males and females (Clapham, 1996) as bigger females appear to be better mothers (Ralls, 1976). Thus the large body size in female *K. breviceps* may well be necessitated by the annual reproduction employed in this species (see Chapter 5). Mammals in which females are larger than males have a

variety of social systems ranging from monogamy to harems (Ralls, 1976; Brownell and Ralls, 1986; Clapham, 1996) and the implications of reversed sexual size dimorphism for the mating system of *K. breviceps* are discussed in more detail in Chapter 4.

In contrast, the pattern found for *K. sima*, with males being of similar size to females at sexual maturity, but reaching larger body lengths at physical maturity, is common among odontocetes. In mammals in which males are considerably larger than females, the females typically cease growth at an earlier age than the males (Bryden, 1972; Ralls, 1976). Although sexual maturity appears to occur at the same time in both sexes, age and length at physical maturity occurs at a greater body length and age in males in this species. Similar trends have been reported for bottlenose dolphins *T. truncatus* (Cockcroft and Ross, 1990), long-finned pilot whales *G. melas* (Sergeant, 1962) and the sperm whale *P. macrocephalus* (Best, 1970). Since female *K. sima* show facultative annual reproduction, which is probably heavily dependent on environmental conditions and resources (see Chapter 5), body size may not be as important in females of this species as it is for female *K. breviceps*.

These data, although in need of support from additional measurements, are interesting in that most reports on the two species of *Kogia* state that there is no difference in size between the sexes. Allen (1941) reports that there does not appear to be great sexual dimorphism in the two *Kogia* species, as the literature up until then always reported the sexes to be of equal size with the male being slightly longer when fully grown. Even a recent review on sexual dimorphism in marine mammals comments on the absence of sexual size dimorphism in the two species of *Kogia* (Ralls and Mesnick, 2002).

As already pointed out additional data for either *Kogia* species would be useful as more recent studies have found that sexual size dimorphism is often expressed in weight or girth in odontocetes rather than total body length (Cockcroft and Ross, 1990; Read *et al.*, 1993; Tolley *et al.*, 1995).

### **3.4.5. Morphological differences between *K. breviceps* and *K. sima***

The observed differences in the size of the appendages of the two *Kogia* species are counter intuitive according to the laws of scaling (Peters, 1983) as one would expect the larger species (*K. breviceps*) to have the larger dorsal fin, flukes and pectoral fins and the smaller species (*K. sima*) to have the smaller appendages. Although the data are

scanty they do indicate that the scenario is the opposite in the two species of *Kogia* (Ross, 1979). This may be an indication of the habitat of the two species. Cetaceans live in an aquatic environment, which acts as a heat conductor, continuously removing heat from the body to the surrounding waters. In comparison to the terrestrial environment, water conducts heat away from the body at 25 times the rate of air (Heyning, 2001). The dorsal fin, flukes and pectoral fins contain counter-current heat exchangers, giving off heat when the animals overheats and shutting down the blood flow to these extremities when the animal is cold (Pabst *et al.*, 1995; Rommel *et al.*, 1998). Reducing the size of the extremities would further reduce the surface-area-to-volume ratio in a cold environment, preventing more heat loss. In this respect, the data on the distribution and preferred sea surface temperatures by the two species (see Chapter 7) in addition to information on diving depths (see Chapter 6) support the idea that *K. breviceps* inhabits cooler, more temperate waters than does *K. sima*. Thus the small size of the extremities of *K. breviceps* may be an adaptation to reduce heat loss. In contrast, *K. sima* appears to prefer warmer, subtropical waters, which is reflected in larger appendage size as heat loss is less prominent in that habitat.

A similar separation by preference for a particular water temperature range can be observed in other closely related species such as the harbour porpoise *P. phocoena* and the vaquita *P. sinus* (Read and Hohn, 1995; Hohn *et al.*, 1996) and the long-finned (*G. melas*) and short-finned (*G. macrorhynchus*) pilot whale (Payne and Heinemann, 1993). Even within the latter species the northern and southern form of Japan exhibit preferences for differing water temperatures (Kasuya and Marsh, 1984; Kasuya and Tai, 1993). In all of these cases the larger (in terms of total body length) of the two species or forms is found in cooler waters, but unfortunately no comparative morphometric studies on flipper length and dorsal fin size on these animals have been carried out to date. This observation is discussed in more detail in Chapter 9.

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## *Chapter 4: Male Reproduction*



## **4.1 Theoretical background**

### **4.1.1 General background to reproductive studies in cetaceans**

The majority of studies of cetacean reproduction are based on material obtained from hunted (Best, 1969; Miyazaki, 1984; Desportes *et al.*, 1993) or stranded animals (Ross, 1979; 1984; Calzada *et al.*, 1996) or from animals incidentally caught and killed in fishing nets (Perrin *et al.*, 1976; Perrin *et al.*, 1977; Read, 1990a; 1990b; Slooten, 1991; van Waerebeek and Read, 1994; Hohn *et al.*, 1996) or anti-shark nets (Cockcroft and Ross, 1990). Data on the reproduction of live, wild animals are difficult to obtain and studies of reproduction in captive animals may not be representative of wild populations. Although animals may be approached by boat, most of the reproductive activities occur underwater and thus are inaccessible for boat-based researchers. However, in recent years, a few studies have successfully observed reproductive and other life history events in wild populations of dolphins (Wells *et al.*, 1987; Herzog, 1997).

Major reviews have been written on reproduction in mysticetes (Lockyer, 1984), phocoenids (Gaskin *et al.*, 1984), delphinids (Perrin and Reilly, 1984), the sperm whale *Physeter macrocephalus* (Best *et al.*, 1984), ziphiids (Mead, 1984), monodontidae (Braham, 1984), and platanistids (Brownell, 1984). Most of the recent reproductive studies have been carried out on pilot whales (Genus *Globicephala*), which are still being hunted in Japan (Kasuya and Marsh, 1984; Kasuya and Tai, 1993) and the Faroe Islands (Desportes *et al.*, 1993, 1994; Desportes, 1994), and on small odontocetes incidentally caught in fishing operations (Barlow, 1984; Collet and Saint Girons, 1984; Perrin and Henderson, 1984; Hohn *et al.*, 1985; Read and Gaskin, 1990; Read and Hohn, 1995).

Detailed studies on the reproductive biology of a number of cetaceans have aided in elucidating the life histories of these animals (Ross, 1979; Kasuya and Marsh, 1984; Ross, 1984; Slooten, 1991; Kasuya and Tai, 1993; Hohn *et al.*, 1996). In a number of cases these studies have been used to estimate the level of human impact from directed or incidental catches on the species concerned (Read and Gaskin, 1990; Slooten, 1991; Hohn *et al.*, 1996).

The present chapter examines the reproductive biology of male *Kogia*, while the following chapter (Chapter 5) examines reproduction in female *Kogia*.

### 4.1.2 Male reproduction

Research on the reproduction of cetaceans has in the past focused on females and studies that exclusively examine male reproduction are still rare (Chittleborough, 1954; Best, 1969; Collet and Saint Girons, 1984; Mitchell and Kozicki, 1984; Hohn *et al.*, 1985; Desportes *et al.*, 1993; Desportes, 1994; Desportes *et al.*, 1994). However, in the last two decades the focus has shifted to detailed studies of both sexes (Hohn and Brownell, 1990; Read and Gaskin, 1990; Slooten, 1991; Sørensen and Kinze, 1994; van Waerebeek and Read, 1994; Read and Hohn, 1995; Hohn *et al.*, 1996).

### 4.1.3 Reproductive anatomy

The morphology of the male reproductive organs of cetaceans has been extensively covered (Slijper, 1966; Harrison *et al.*, 1972; de Smet, 1977). Cetaceans differ from most other mammals in that they are testicond, meaning the testes are located inside the abdominal cavity to improve streamlining (Slijper, 1962; de Smet, 1977). There are minor differences in the morphology of the testes between species and the testis volume may change with age and sexual activity (de Smet, 1977) and between species (see section 4.1.6 below). Thermoregulation of the intra-abdominal testes is carried out by a counter-current heat exchange in *Tursiops truncatus* (Pabst *et al.*, 1995) and there are no differences in spermatogenesis between mammals with abdominal and scrotal testes (Setchell, 1978).

Little has been published on the testes of the two *Kogia* species. Roest (1970) reports 40cm long testes, “lying one behind the other along the midventral body wall between the posterior edge of the liver and the urogenital opening” for a 224cm long *Kogia breviceps*.

### 4.1.4 Attainment of sexual maturity (ASM)

Estimates of the size and age at the attainment of sexual maturity (ASM) (Barlow, 1985; Chivers and Myrick, 1993) and data on the reproductive cycle of a species are necessary to understand the reproductive strategy and ecology of the animals and to be able to make inter- or intraspecific comparisons (Hohn *et al.*, 1985). Data for the length at sexual maturity for a given species are especially useful in the field or for animals for which no age estimates are available (Perrin and Reilly, 1984). Furthermore,

these data are needed for the management of species that are subject to mortality by man (Read and Gaskin, 1990; Slooten, 1991; Chivers and Myrick, 1993; Desportes *et al.*, 1993; Hohn *et al.*, 1996). For example, an increase in length at ASM over time is reported for male spotted dolphins *Stenella attenuata* incidentally caught in the tuna purse-seine fishery in the Eastern Tropical Pacific, with no coincidental increase in age at ASM (Hohn *et al.*, 1985). Perrin and Henderson (1984) report that mature testis weight can vary greatly between populations, possibly as a function of the degree of exploitation. Therefore these data may play an important role in stock assessment studies (Perrin and Henderson, 1984) and in determining the degree of exploitation of a stock or population (Read and Gaskin, 1990; Slooten, 1991; Hohn *et al.*, 1996).

The definition of attainment of sexual maturity (ASM) in male cetaceans is complex (Perrin and Reilly, 1984) and there is no single criterion for the onset of sexual maturity (Perrin and Henderson, 1984). Testis histology (i.e. stage of spermatogenesis) and seminiferous tubule diameter, testis weight or length, sperm abundance, the presence of sperm in the epididymis, and serum testosterone levels have all been used to indicate ASM and are described in detail below. Additionally, there is some discrepancy as to how many different stages of maturity can be defined in odontocetes. Whereas the most common practise is to distinguish between immature, pubertal (also called prepubescent or maturing), and mature animals (Best, 1969; Hohn *et al.*, 1985; Sørensen and Kinze, 1994), a few studies define four different stages of maturity, namely immature, early maturing, late maturing, and mature (Kasuya and Marsh, 1984; Desportes *et al.*, 1993; Kasuya and Tai, 1993). In the present study I have recognised three stages of maturity (immature, early spermatogenesis, late spermatogenesis) based on histological studies of the testes. Early and late spermatogenesis can be regarded as equal to the pubertal (also referred to as prepubescent or maturing) and mature stage mentioned in the literature, respectively. The former is defined as the stage when spermatogonia and spermatocytes are present, but spermatozoa are absent (Hohn *et al.*, 1985).

Histological examination of the testes is the most accurate way to determine ASM (Kasuya and Marsh, 1984; Perrin and Donovan, 1984; Hohn *et al.*, 1985; Desportes *et al.*, 1993), although it is a lengthy process, which has to be carried out in the laboratory. Both examination of the state of spermatogenesis (Best, 1969; Kasuya and Marsh, 1984; Desportes *et al.*, 1993; Kasuya and Tai, 1993) and of the seminiferous tubule diameters (Hohn *et al.*, 1985; Cockcroft and Ross, 1990; Desportes *et al.*, 1993) are carried out widely in male cetaceans.

A rapid increase in testis weight is used as an indicator of ASM (Sergeant, 1962; Perrin *et al.*, 1976; Perrin *et al.*, 1977; Kasuya and Marsh, 1984; Hohn *et al.*, 1985; Kasuya and Tai, 1993). However, large individual variation of testis weight among mature males is reported for mysticetes (Chittleborough, 1954) as well as odontocetes (Collet and Saint Girons, 1984; Desportes *et al.*, 1993). Furthermore, differences in testis weight are observed between two different stocks of spinner dolphins with different degrees of exploitation (Perrin and Henderson, 1984). Thus changes in testis mass should be interpreted with care.

Some studies use the abundance of sperm from both testicular, epididymal (Kasuya and Marsh, 1984; Desportes *et al.*, 1993) and vas deferens smears (Chittleborough, 1954; Desportes *et al.*, 1993), as well as from histological preparations of the testes (Chittleborough, 1954; Best, 1969; Mitchell and Kozicki, 1984) as an indication of the stage of maturity of the animal. The determination of the presence or absence of seminal fluid in the epididymis (Fisher and Harrison, 1970; Harrison and Brownell, 1971; Perrin *et al.*, 1977; Cockcroft and Ross, 1990; van Waerebeek and Read, 1994) may be the easiest method to determine sexual maturity in the field, but it occurs at a slightly later stage in ontogeny than the histological detection of spermatozoa (Sergeant, 1962; Kasuya and Marsh, 1984). If the presence of seminal fluid in the epididymis is used as a single indicator of male maturity, it is generally assumed that sperm are produced continuously in the species concerned (Perrin and Reilly, 1984; Desportes *et al.*, 1993). This assumption is not valid as the males of some species may have a resting phase during which testis size decreases and no sperm are produced (Collet and Saint Girons, 1984; Perrin and Reilly, 1984). The value of this tool is questionable unless the presence of sperm in the seminal fluid is confirmed histologically.

Another indicator of sexual maturity is the level of testosterone in the blood, but studies on male odontocetes so far are restricted to a few captive delphinid species (Harrison and Ridgway, 1971; Wells, 1984; Schroeder and Keller, 1989) and wild long-finned pilot whales *Globicephala melas* (Desportes *et al.*, 1993; 1994). In addition, the ranges of serum testosterone vary between different species of odontocetes (Desportes *et al.*, 1994), which makes comparisons between species difficult. Due to these reasons plasma testosterone cannot be used as single indicator of sexual maturity, but provides a good means of monitoring sexual activity over time (Desportes *et al.*, 1994).

The available information indicates that in the majority of species both testes

mature at the same rate (Chittleborough, 1954; Collet and Saint Girons, 1984; Miyazaki, 1984; van Waerebeek and Read, 1994) and therefore usually only one testis is used for examination (Kasuya and Marsh, 1984; Cockcroft and Ross, 1990).

In some species like the sperm whale *P. macrocephalus* (Best, 1969), the long-finned pilot whale *G. melas* (Desportes, 1994), and Baird's beaked whale *Berardius bairdii* (Kasuya *et al.*, 1997) a zonal maturation of the testes occurs. The testes of the sperm whale appear to mature from the centre outwards (Best, 1969), and this has subsequently been used as a guideline for taking samples for reproductive studies.

Most studies use a combination of criteria to determine the onset of sexual maturity in males (Best, 1969; Cockcroft and Ross, 1990; Desportes *et al.*, 1993). This appears to be the best solution in view of the constraints encountered with each factor mentioned above. Perrin and Donovan (1984) suggest that in order to assess the different stages of maturity in male cetaceans testes weights should be recorded, the epididymis should be examined for sperm, and smears from the periphery as well as from the centre of the testis should be examined histologically. Gonadal characteristics like testis weight (Chittleborough, 1954; Hohn *et al.*, 1996), seminiferous tubule diameter (Mitchell and Kozicki, 1984; Hohn *et al.*, 1985), and testis length (Desportes *et al.*, 1993; Hohn *et al.*, 1996) are reliable indicators of maturity, whereas other factors such as age (Hohn *et al.*, 1985; Desportes *et al.*, 1993), body length (Chittleborough, 1954; Hohn *et al.*, 1985; Desportes *et al.*, 1993), body weight (Desportes *et al.*, 1993), and colour phase (Hohn *et al.*, 1985; Kasuya *et al.*, 1988a) are less reliable. Which characteristic presents the most reliable indicator of maturity may vary between species and even between populations of the same species (Perrin and Henderson, 1984; Hohn *et al.*, 1985). The variety of methods used in determining sexual maturity and age and length at ASM in male cetaceans has to be kept in mind and comparisons between species should be carried out with care (DeMaster, 1984; Perrin and Reilly, 1984; Hohn *et al.*, 1985).

It has been suggested that an index of testis development, which defines maturity in terms of unit testis weight (g) per unit of testis length (mm), may remove some of the variability in testis weight among species of different sizes and thus allow comparison between different stocks or species (Hohn *et al.*, 1985).

### 4.1.5 Seasonality

Whether a mammal reproduces seasonally or continuously depends largely on its environment (Bronson, 1989). Seasonal differences in food availability, rainfall, temperature, photoperiod, predation and female condition are all important determinants of the timing and duration of a seasonal cycle in mammals (Bronson, 1989; Urian *et al.*, 1996). Most habitats have at least some seasonal variation in climate and food availability and this is especially pronounced in higher latitudes, where annual variations in temperature can be extreme (Bronson, 1989; Urian *et al.*, 1996). Although reproductive seasonality has been widely researched in terrestrial mammals (Bronson, 1989), the factors influencing seasonality in marine mammals are little understood. This can primarily be attributed to the complex marine environment with its largely unpredictable spatial and temporal variation in biotic and abiotic factors (Sørensen and Kinze, 1994). Seasonality of reproduction has been widely monitored in marine invertebrates and fish, but it is somewhat more difficult to find cues for seasonality in marine mammals. As males have to shape their annual reproductive pattern around the pattern that is most advantageous for the females (Bronson, 1989), reproductive seasonality has largely been examined in view of the timing and duration of the calving period (see Chapter 5).

Changes in testis weight (Hohn *et al.*, 1985; Read, 1990b; Slooten, 1991; van Waerebeek and Read, 1994; Hohn *et al.*, 1996), testis volume (Gaskin *et al.*, 1984), seminiferous tubule diameters (Fisher and Harrison, 1970; Collet and Saint Girons, 1984; Hohn *et al.*, 1985), sperm abundance (Gaskin *et al.*, 1984; Hohn *et al.*, 1985; Desportes *et al.*, 1993), spermatogenic activity (Sergeant, 1962; Fisher and Harrison, 1970; Desportes *et al.*, 1993; Hohn *et al.*, 1996), Leydig cell diameter (Clarke *et al.*, 1994), and serum testosterone levels (Harrison and Ridgway, 1971; Wells, 1984; Desportes *et al.*, 1993) have all been used as indicators of a male seasonal cycle in cetaceans. Furthermore, testis length and index differ significantly between periods of high and low testicular activity in long-finned pilot whales *G. melas* (Desportes *et al.*, 1993). Based on the above criteria seasonality in testicular activity was reported for a number of wild populations of mysticetes (Chittleborough, 1954) and odontocetes (Sergeant, 1962; Read, 1990b; van Waerebeek and Read, 1994; Read and Hohn, 1995). In captive delphinids serum testosterone levels change seasonally, reflecting seasonal testicular activity (Harrison and Ridgway, 1971; Wells, 1984; Schroeder and Keller,

1989).

One would expect a seasonal peak in male testicular activity to occur shortly before or at the same time as the females are receptive. However, few investigators have concentrated on this aspect and evidence has so far only been gathered for few cetacean species, such as the humpback whale *Megaptera novaeangliae* (Chittleborough, 1954), dusky dolphin *Lagenorhynchus obscurus* (van Waerebeek and Read, 1994), long-finned pilot whale *G. melas* (Sergeant, 1962; Desportes *et al.*, 1993; Martin and Rothery, 1993), harbour porpoise *Phocoena phocoena* (Read, 1990b; Sørensen and Kinze, 1994), and captive bottlenose dolphins *Tursiops truncatus* (Harrison and Ridgway, 1971). Times of elevated testes weights coincided with the mating season in the spotted dolphin *S. attenuata*, but although the seasonal peak in testes weight of the northern and southern offshore stock was similar, calving seasons differed between the two stocks (Hohn *et al.*, 1985).

While testes weights vary seasonally in a number of cetaceans, histological evidence for a seasonal complete cessation of spermatogenesis (also termed aspermatogenesis) is rare in both mysticetes and odontocetes (Perrin and Donovan, 1984) and is only reported for the humpback whale *M. novaeangliae* (Chittleborough, 1954), the common dolphin *Delphinus delphis* (Collet and Saint Girons, 1984), and the harbour porpoise *P. phocoena* (Gaskin *et al.*, 1984; Sørensen and Kinze, 1994). In dusky dolphins *L. obscurus* and the vaquita *Phocoena sinus* complete cessation occurs, but is rare (van Waerebeek and Read, 1994; Hohn *et al.*, 1996). In contrast, a number of species show continuous spermatogenesis throughout the year (Best, 1969; Mitchell and Kozicki, 1984; Cockcroft and Ross, 1990).

#### 4.1.6 Male mating strategy

Copulation and other sexual behaviour of cetaceans are frequently observed in captivity (Saayman and Tayler, 1977), but less often in natural environments (Herzing, 1997). However, as dolphins in particular seem to use sexual contact (both homo- and heterosexual) to strengthen the social bonds of a group or school (Kasuya *et al.*, 1993), observations in the wild may often not give unequivocal evidence about a species' reproductive strategy. Numerous factors are involved in shaping a species' mating system and thus multifactorial models are needed to predict mating systems (Sandell and Liberg, 1992). Indicators like testis mass to body mass ratio, sexual dimorphism, and

group size are used to provide information about the mating system of terrestrial mammals (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986; Rose *et al.*, 1997). These parameters together with the degree of scarring resulting from intrasexual fights (McCann, 1974; Heyning, 1984; MacLeod, 1998) are used for cetaceans to provide a starting point for the development of hypotheses about the mating system of a species (Brownell and Ralls, 1986; Slooten, 1991; Aguilar and Monzon, 1992; Cockcroft, 1993; van Waerebeek and Read, 1994). This is especially useful for species for which data from behavioural observations in the wild are either difficult or costly to obtain.

Based on these data a number of different male mating strategies are described for cetaceans, ranging from floating leks in humpback whales *M. novaeangliae* (Clapham, 1996), multimale polygynous breeding systems (or joint harems) in short-finned pilot whales *G. macrorhynchus* (Kasuya *et al.*, 1993; Magnusson and Kasuya, 1997) and Hector's dolphins *Cephalorhynchus hectori* (Slooten, 1991) to a roving male strategy proposed for the sperm whale *P. macrocephalus* (Best and Butterworth, 1980; Whitehead, 1990; Magnusson and Kasuya, 1997) and the bottlenose dolphin *T. truncatus* (Wells *et al.*, 1987) (for a review see Connor *et al.*, 2000). Sperm competition may occur in some mysticetes (Brownell and Ralls, 1986) as well as some odontocetes like the dusky dolphin *L. obscurus* (van Waerebeek and Read, 1994), the vaquita *P. sinus* (Hohn *et al.*, 1996), and the common dolphin *D. delphis* (Cockcroft, 1993). The majority of proposed mating systems for cetaceans appear to be either polygynous or promiscuous (see Evans, 1987 for a summary) and the latter probably occurs in most delphinids (Evans, 1987; Connor *et al.*, 2000). Geographical variation in the mating system of a species is observed in spinner dolphins *S. longirostris* (Perrin and Mesnick, 2003).

Teuthophagous odontocetes in general show a reduction in dentition (Heyning, 1984; MacLeod, 1998) and recent studies suggest that the remaining teeth are not needed in prey capture (Heyning and Mead, 1996) (see Chapter 6). Thus it is assumed that a number of teuthophagous species retain the teeth primarily as weapons for intraspecific fighting (MacLeod, 1998; Connor *et al.*, 2000). Tooth scars are reported for *K. breviceps* and these may have originated from fights between males (Hubbs, 1951). McCann (1974) also reports scars on the head and body of "combatants" in *K. breviceps*, implying intrasexual fighting, although this is not supported by any evidence.

### 4.1.7 Sperm morphology

The sperm morphology of cetaceans was first described by means of light microscopy by Ballowitz (1907). He examined spermatozoa from the harbour porpoise *P. phocoena* and produced excellent drawings of the sperm morphology. However, he interprets the spherical mitochondria of cetacean sperm as indentations of a helix of mitochondria that spirals around the midpiece as seen in other eutherian mammals. Only in 1909, while reanalysing Ballowitz's results with new results from examinations of the long-finned pilot whale *G. melas*, did Retzius conclude that the mitochondria are indeed spherical in shape and arranged in rows and columns along the midpiece (Retzius, 1909).

Since then spermatozoa of only six other cetacean species have been examined (*M. novaengliae*, Chittleborough, 1954; *P. macrocephalus*, Yamane, 1936; *Eubalaena glacialis*, Omura *et al.*, 1969; *T. truncatus*, Ridgway and Green, 1967; Fleming *et al.*, 1981; *D. delphis*, Ridgway and Green, 1967; Reddy, 1996; and *Balaenoptera acutorostrata*, Mogue *et al.*, in prep.).

### 4.1.8 Aim of the present chapter

In the present study different stages of maturity in males were described based on both macroscopic and histological examination of the reproductive organs. After defining sexual maturity, length and age at ASM were calculated. Indicators of a seasonal reproductive cycle in both species were examined and a hypothesis about the possible mating system of the two species was formulated. Sperm morphology in both species of *Kogia* was described.

## **4.2 Materials and Methods**

### 4.2.1 Sample

Reproductive organs from 19 *K. breviceps* and 19 *K. sima* males were examined to determine the reproductive status of the individual animals. Although the original tissue was not available in some cases (see Appendix B), weights and measurements of the gonads were available from data sheets. This explains discrepancies in sample sizes between tables and figures.

### 4.2.2 Determination of maturity

Testes were weighed (to the nearest 0.01 of a gram) and a piece of tissue approximately 1cm<sup>3</sup> was taken from the middle of the testis. The tissue was dehydrated through a standard series of alcohols (30% to 100%) and then embedded in Paraffin wax. 5µm thick sections were cut with a *Leica* microtome, mounted on slides and stained with Mallory's trichrome. Slides of the testis from 19 *K. breviceps* and 19 *K. sima* were examined and the reproductive status was determined for each animal. Twenty randomly selected sections through seminiferous tubules were examined and specimens were defined as either immature (spermatogonia and Sertoli cells in the seminiferous epithelium), in early spermatogenesis (spermatogonia and spermatocytes present in the seminiferous epithelium, but no spermatids), or in late spermatogenesis (spermatids present in the seminiferous epithelium). An animal was placed into a specific category if more than 50% of the tubules were in a particular condition. Animals in late spermatogenesis were considered adults. Seminiferous tubule diameters were measured using an ocular micrometer. Mean diameters were taken as the average of 20 randomly chosen tubules. For two animals from each species these data could not be obtained due to extensive tissue damage, probably as a result of decay prior to sampling, or freezing subsequent to sampling.

Published results from previous studies on the male reproduction of the two *Kogia* species from South Africa (Ross, 1979; 1984) were included in the analysis only if the original material was not available for re-examination. In most cases new slides were prepared and examined and measured independently of the previous results (for more details see Appendix B). For three *K. sima* males, for which no testis tissue was available for histological examination, body length and testis weight were used as indicators of the stage of maturity.

An index of testis development was calculated as the mean testis weight (excluding the epididimides) (in g) divided by the mean testis length (in mm) per testis pair (Hohn *et al.*, 1985; Desportes *et al.*, 1993).

### 4.2.3 Testis size and male mating strategy

The combined testis weight as a percentage of the total body weight was calculated for the animal with the largest testes for each species. Photographs of stranded

animals of both *Kogia* species were examined to determine the degree of intraspecific scarring.

#### **4.2.4 Sperm morphology**

A piece of tissue (1cm<sup>3</sup>) was cut from the centre of the testis from two sexually mature *K. breviceps* (PEM N342, SAM 78/13) and four sexually mature *K. sima* (PEM N2243, N687, N239 and N148). A smear from the tissue was made on a coverslip and then fixed with 2.5% glutaraldehyde in 0.1 molar phosphate buffer for two hours. Subsequently the coverslips were washed twice with phosphate buffer for 10 minutes. The smears were then put through an ethanol series (30% to 100%), treated with increasing concentrations of amyl acetate (25% to 100%) and critical point dried. The preparations were coated with gold (SEM coating unit E5100; Polaron Equipment Ltd.) and observed at 10kV with the scanning electron microscope (JEOL JSM 840). Micrographs were taken of appropriate specimens and from these, measurements of sperm head length, midpiece length, and tail length were obtained.

In order to look at the ultrastructure of the spermatozoon midpiece a small piece of the testis that had been fixed in 2.5% glutaraldehyde in 0.1 molar phosphate buffer was washed with phosphate buffer and placed into osmium tetroxide solution for 90 minutes. The sample was then dehydrated through a graded ethanol series (30% to 100%) and infiltrated with a series of propylene oxide/resin mixtures and finally with an epoxy resin mixture (Cross, 1989). The tissue was subsequently sectioned at 100nm and examined at 80kV with a transmission electron microscope (JEOL 1210). Due to poor prior preservation of the tissue good results could only be obtained for one *K. sima*. Appropriate micrographs were later saved to a computer and analysed using SigmaScan/Image (Jandel Scientific Software, San Rafael, CA 1992) in order to obtain the surface area values for the individual sperm heads.

### **4.3 Results**

#### **4.3.1 Assessment of stages of maturity**

A dependent paired t-test showed no significant difference in either length or weight between the left and the right testis in both *K. breviceps* (testis length: p=0.27302;

testis weight:  $p=0.2717$ ) and *K. sima* (testis length:  $p=0.155025$ ; testis weight:  $p=0.499991$ ). Thus it was concluded that either testis may be examined to establish the stage of maturity of an animal.

Immature testes were observed in 13 *K. breviceps* (Table 4.1) and six *K. sima* (Table 4.3) based on histological examination. Immaturity is characterised by tightly packed, narrow seminiferous tubules with no lumen, surrounded by abundant interstitial tissue (Figure 4.1a). The seminiferous epithelium comprised one cell layer of Sertoli cells with interspersed spermatogonia (Figure 4.1). Seminiferous tubule diameters of immature animals ranged from  $39.2\mu\text{m}$  to  $67.2\mu\text{m}$  for *K. breviceps* ( $\bar{x}$ :  $53.0\mu\text{m} \pm 9.13$ ; Table 4.1) (Figure 4.2) and from  $34.6\mu\text{m}$  to  $52.0\mu\text{m}$  for *K. sima* ( $\bar{x}$ :  $42.9\mu\text{m} \pm 6.98$ ; Table 4.3) (Figure 4.3).

Early spermatogenesis was characterized by two to four cell layers of spermatogonia and spermatocytes in the seminiferous epithelium (Figure 4.1b). No spermatids were present and very little interstitial tissue was present between the seminiferous tubules (Figure 4.1b). Two *K. breviceps* and one *K. sima* were found to be in early spermatogenesis, with seminiferous tubule diameters of  $72.2\mu\text{m}$  to  $77.6\mu\text{m}$  being recorded for the former (Table 4.1, Figure 4.2) and a diameter of  $65.0\mu\text{m}$  for the latter (Table 4.3, Figure 4.3).

Three *K. breviceps* (Table 4.1) and ten *K. sima* were in late spermatogenesis (Table 4.3), which was characterised by large seminiferous tubules with an open lumen (Figure 4.1c,d). A complex seminiferous epithelium was present, which comprised three or more cell layers of spermatogonia, spermatocytes and spermatids, and little interstitial tissue was present (Figure 4.1c,d). The seminiferous tubule diameters ranged from  $89.0\mu\text{m}$  to  $208.5\mu\text{m}$  ( $\bar{x}$ :  $135.5\mu\text{m} \pm 63.99$ ) (Table 4.1, Figure 4.2) and from  $87.1\mu\text{m}$  to  $123.2\mu\text{m}$  (mean:  $100.2\mu\text{m} \pm 12.16$ ) (Table 4.3, Figure 4.3) for *K. breviceps* and *K. sima* in late spermatogenesis, respectively. No animal with testes in a mature but inactive or resting stage was observed and there was no evidence for a seasonal cessation of spermatogenesis.

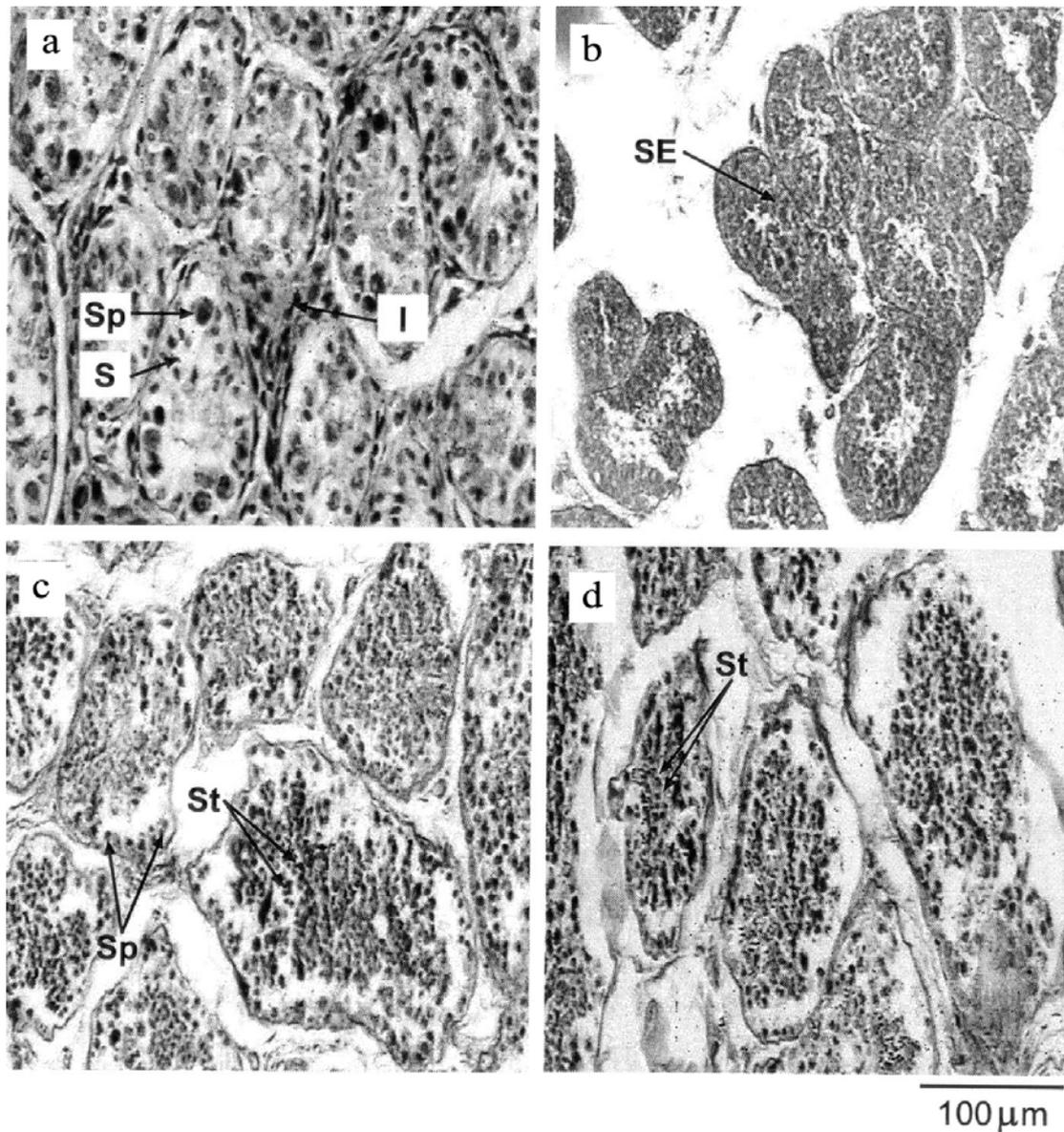


Figure 4.1: Histological preparations of different maturity stages of the testes in *Kogia*. a: Immature testis, characterised by tightly packed, narrow seminiferous tubules with no lumen and abundant surrounding interstitial tissue (I). Sp: Spermatogonia, S: Sertoli cells. b: Early spermatogenesis is characterised by two to four cell layers of spermatogonia and spermatocytes in the seminiferous epithelium (SE). No spermatids are present and only little interstitial tissue is found between the seminiferous tubules. c,d: Late spermatogenesis as indicated by large seminiferous tubules with an open lumen and a complex seminiferous epithelium with spermatogonia, spermatocytes and spermatids (St) present.

Table 4.1: Gonadal characteristics for different maturity stages in *Kogia breviceps*.

Maturity stage	Mean (SD)	Range	Sample size
<b>Single testis weight (g)</b>			
Immature*	42.34 (24.46)	13.8-83.6	13
Early spermatogenesis*	148.7 (69.86)	99.3-198.1	2
Late spermatogenesis	1000.67 (826.64)	457.5-1952.0	3
<b>Mean testis length (mm)</b>			
Immature*	123.8 (25.61)	79.0-158.0	13
Early spermatogenesis*	155.5 (35.71)	130.5-181.0	2
Late spermatogenesis	310.0 (130.77)	220.0-460.0	3
<b>Index of testis development (g/mm)<sup>1</sup></b>			
Immature*	0.33 (0.13)	0.16-0.57	13
Early spermatogenesis*	1.04 (0.69)	0.55-1.52	2
Late spermatogenesis	2.90 (1.17)	2.08-4.24	3
<b>Seminiferous tubule diameter (µm)</b>			
Immature*	53.0 (9.13)	39.2-67.2	12
Early spermatogenesis*	75.2 (3.46)	72.2-77.6	2
Late spermatogenesis	135.5 (63.99)	89.0-208.5	3

<sup>1</sup>=Mean testis weight/mean testis length per testis pair. Rows with an asterisk are not significantly different from each other (p≥0.0001).

Table 4.2: Summary of the size and ages for different maturity stages for *Kogia breviceps* males. Determination of maturity was based on histological examination of the reproductive organs and subsequently only specimens for which the state of maturity could be confirmed were included (i.e. calves were excluded).

	Immature		Early spermatogenesis		Mature	
	n	range	n	Range	n	Range
<b>Age (GLGs)</b>	13	0.57-2.5	2	1.6-2.3	2	5.0-13.33
<b>Length (cm)</b>	14	147.0-241.0	2	218-232.7	3	242.0-276.0
<b>Mass (kg)</b>	12	68.99-210.0	2	182.0-185.97	2	233.6-374.03

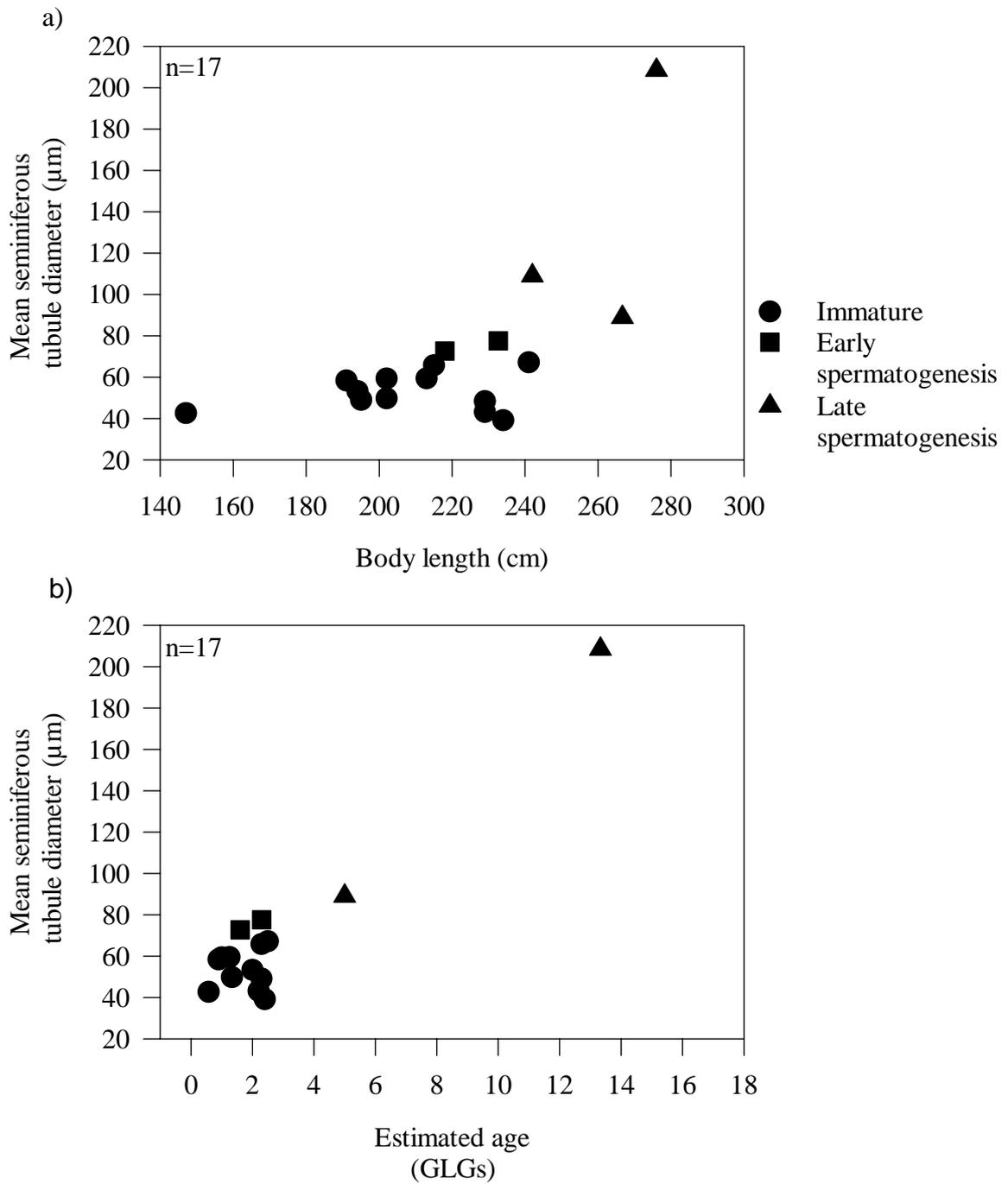


Figure 4.2: Mean seminiferous tubule diameters for male *Kogia breviceps* of different maturity stages in relation to body length (cm) (a) and age (complete GLGs + increment) (b).

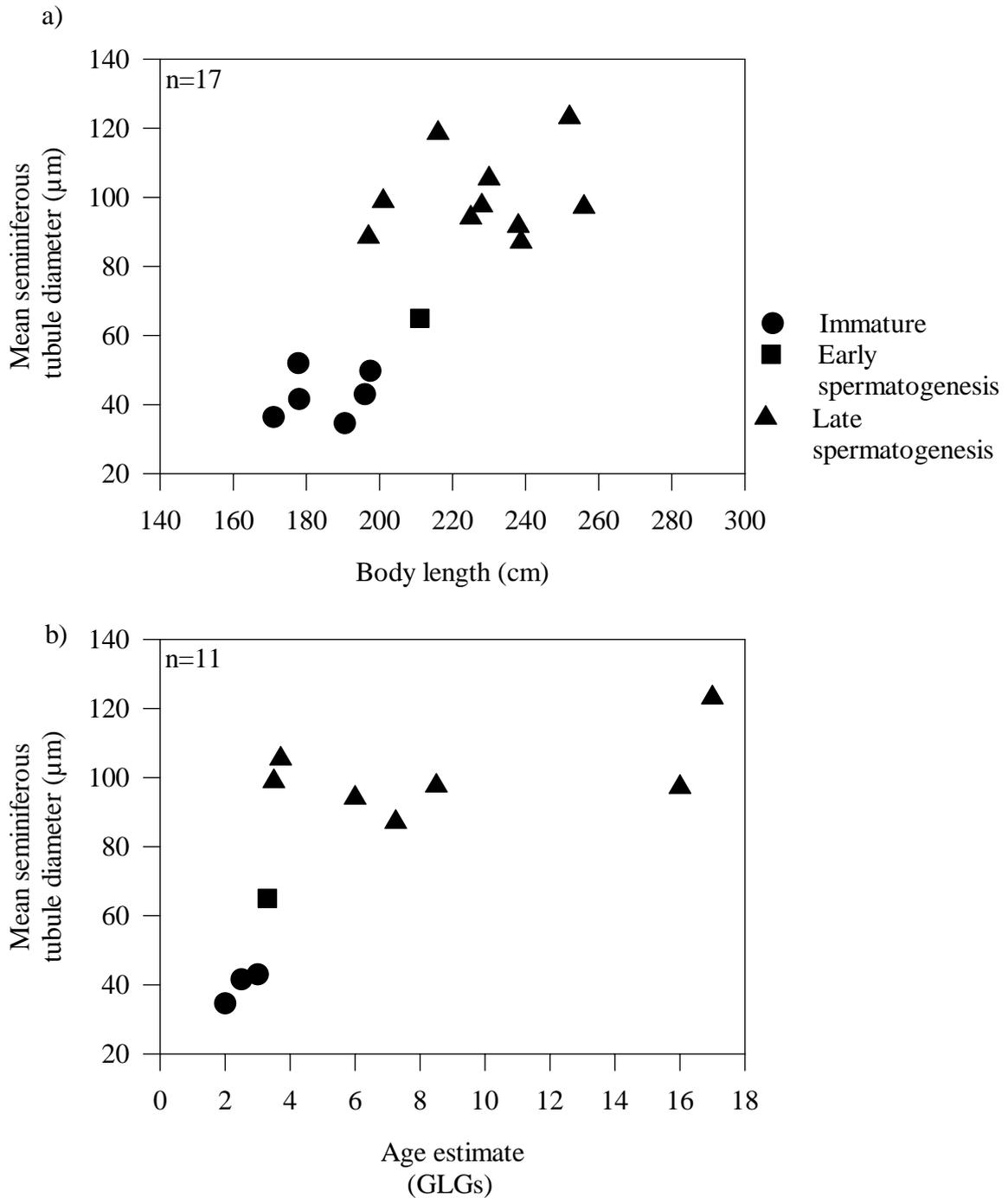


Figure 4.3: Mean seminiferous tubule diameters for male *Kogia sima* of different maturity stages in relation to body length (cm) (a) and age (complete GLGs + increment) (b).

### 4.3.2 Attainment of sexual maturity (ASM)

#### *K. breviceps*

As expected from the length-frequency distribution of the sample (see Chapter 2) the majority of animals for which a tissue sample of the testes could be examined histologically were immature (Table 4.1).

Early spermatogenesis in male *K. breviceps* occurred at a mean testis weight of 148.7g (n=2) and a mean testis length of 155.5mm (n=2) (Table 4.1, Figure 4.4), which corresponds to ages between 1.6 and 2.3 years (Table 4.2, Figure 4.4b), respectively. The three animals in late spermatogenesis had a mean testis weight of 1000.67g ( $\pm 826.64$ ) and a mean testis length of 310mm ( $\pm 130.77$ ) (Table 4.1, Figure 4.4). The age range for these animals was five to 13.33 years (Table 4.2, Figure 4.4). The mean index of testis development was 1.04 for animals in early spermatogenesis and 2.9 for those in late spermatogenesis (Table 4.1). Some overlap of mean testis length occurred between immature animals and animals in early spermatogenesis (Table 4.1).

One-way ANOVA tables showed that there were significant differences between the mean testis weight ( $p=0.0007$ ), mean testis length ( $p=0.0003$ ), mean testis index ( $p<0.0001$ ), and mean seminiferous tubule diameter ( $p=0.0001$ ) of specimens that were immature, in early or in late spermatogenesis. A Tukey's multiple range test yielded significant differences between early and late spermatogenesis, as well as between late spermatogenesis and immature for all four categories, but not between immature and early spermatogenesis (Figure 4.1).

The two male *K. breviceps* that were in early spermatogenesis measured 218cm and 232cm in length with combined testis weights of 198.6g and 396.2g, respectively (Table 4.2, Figure 4.5). The shortest male in late spermatogenesis measured 242cm and had a combined testis weight of 915g (Figure 4.5). Unfortunately, no age estimate was available for this animal. The youngest male in a late spermatogenic state was estimated to be five years old, measured 266.7cm and had a combined testis weight of 1185g (Table 4.2, Figure 4.5). As the sample was too small to calculate a meaningful statistical estimate for the age and length at ASM a range between the oldest/longest immature animal and the youngest/shortest mature animal had to be taken as the onset of sexual maturity. In this sense a summary of the size and age ranges of immature and mature *K. breviceps* shows that ASM occurs between 2.5 and five years and 241-242cm in *K. breviceps* (Table 4.2). However, the oldest male in early spermatogenesis was estimated

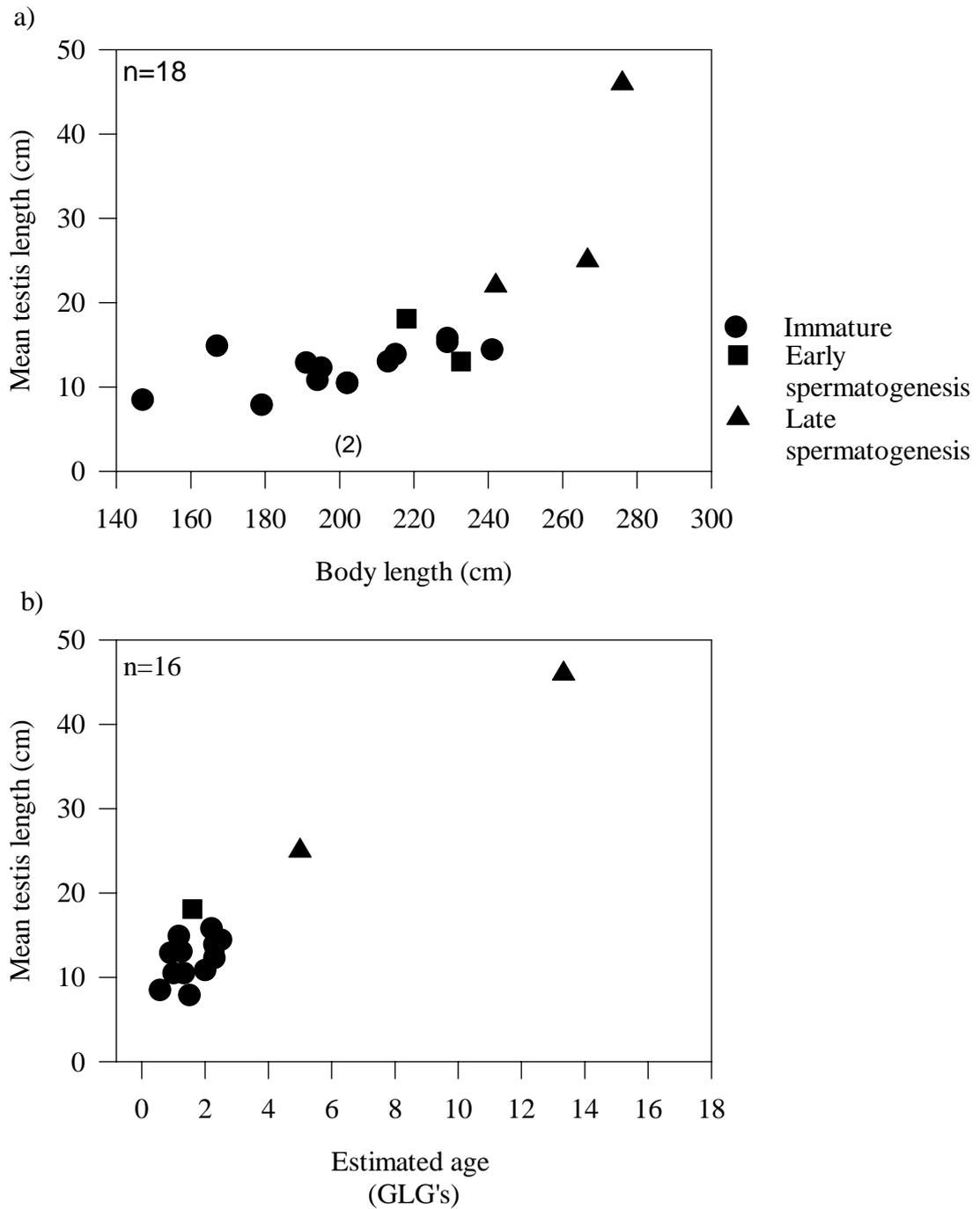


Figure 4.4: Mean testis length (cm) as a function of body length (cm) (a) and estimated age (complete GLG's + increment) (b) in *Kogia breviceps*.

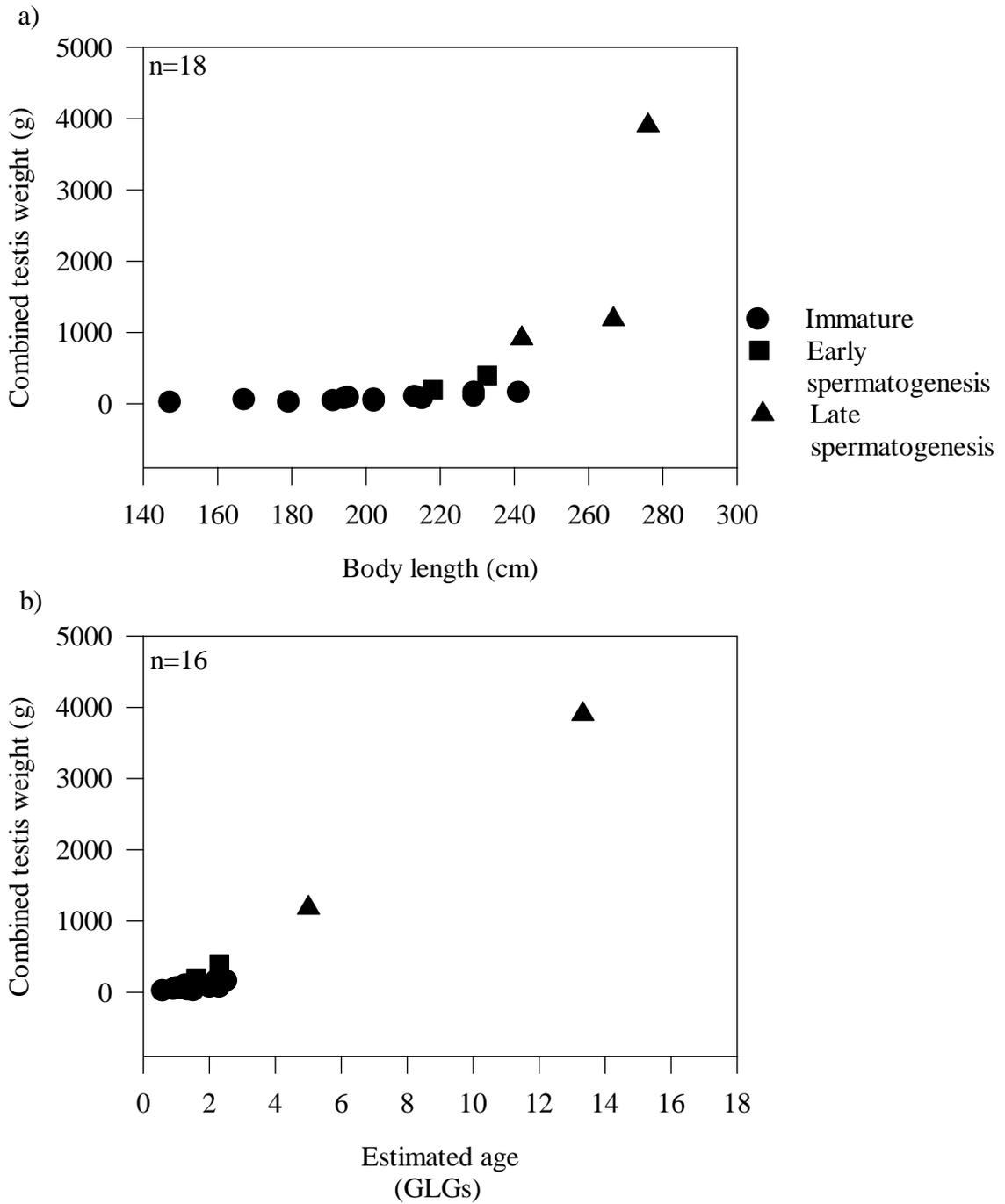


Figure 4.5: Attainment of sexual maturity with body length (cm) (a) and age (complete GLGs + increment) (b) in male *Kogia breviceps*.

to be 2.3 years old. If one takes the conservative approach and defines sexual maturity as the onset of late spermatogenesis this would correspond to five years in male *K. breviceps*.

Compared to age, both body length and body weight appear to better define ASM (Table 4.2). Thus sexual maturity in males was reached between 241-242cm and 210.0- 233.6kg (Table 4.2).

### *K. sima*

The results previously reported for the length-frequency distribution of the sample (see Chapter 2) were reflected in the samples available for histological examination of the testes: immature and mature animals were present in almost equal numbers (Table 4.3).

Only one animal was found to be in early spermatogenesis. It had a mean testis weight of 172.5g and a mean testis length of 225.0mm and an estimated age of 3.3 years (Table 4.3, Table 4.4, Figure 4.6). Late spermatogenesis occurred at a mean testis weight of 1316.99g and a mean testis length of 395.15mm (Table 4.3, Figure 4.6). Animals belonging to this maturity stage ranged from 2.55 to 17 years of age (Table 4.4). The testis development index was 0.77 for the animal in early spermatogenesis and the mean for animals in late spermatogenesis was 2.61 ( $\pm 1.18$ ) (Table 4.3). No overlap between the different stages of maturity was found for any category.

Whether or not the data obtained for the different stages of maturity were significantly different could not be tested because of the low sample size of one animal in early spermatogenesis.

The oldest immature male was estimated to be three years old (Table 4.4) with a body length of 196cm and combined testis weight of 190.93g (Figure 4.7). The youngest male in late spermatogenesis was 2.55GLGs old (Table 4.4), measuring 204.5cm with a combined testis weight of 556g (Figure 4.7). The animal in early spermatogenesis measured 211cm, had an age estimate of 3.3 years and a combined testis weight of 345g (Figure 4.7). The shortest animal in late spermatogenesis measured 197cm and had a combined testis weight of 1454g (Figure 4.7); no age estimate was available. Thus it appears that ASM occurred between 2.55 and three years of age in male *K. sima*.

The body length at ASM can be defined more accurately than in *K. breviceps* at 197cm as the longest immature and the shortest mature male measured 197.5cm and

197cm, respectively (Table 4.4). Furthermore, sexual maturity was reached between body weights of 111.8kg and 124.0kg (Table 4.4).

Table 4.3: Gonadal characteristics for different maturity stages in *Kogia sima*.

<b>Maturity stage</b>	<b>Mean (SD)</b>	<b>Range</b>	<b>Sample size</b>
<b>Single testis weight (g)</b>			
Immature	55.08 (21.67)	32.95-87.5	6
Early spermatogenesis	172.5	172.5	1
Late spermatogenesis	1316.99 (693.80)	210.0-2461.5	12
<b>Mean testis length (mm)</b>			
Immature	145.07 (12.86)	126.0-160.0	7
Early spermatogenesis	225.0	225.0	1
Late spermatogenesis	395.15 (92.56)	255.0-560.0	10
<b>Index of testis development (g/mm)<sup>1</sup></b>			
Immature	0.41 (0.15)	0.26-0.61	7
Early spermatogenesis	0.77	0.77	1
Late spermatogenesis	2.61 (1.18)	0.82-4.19	10
<b>Seminiferous tubule diameter (µm)</b>			
Immature	42.9 (6.98)	34.6-52.0	6
Early spermatogenesis	65.0	65.0	1
Late spermatogenesis	100.2 (12.16)	87.1-123.2	10

<sup>1</sup> Mean testis weight/mean testis length per testes pair.

Table 4.4: Summary of the size and ages for different maturity stages for *Kogia sima* males. Determination of maturity was based on histological examination of the reproductive organs and subsequently only specimens for which the state of maturity could be confirmed were included (i.e. calves were excluded).

	<b>Immature</b>		<b>Early spermatogenesis</b>		<b>Mature</b>	
	<b>n</b>	<b>Range</b>	<b>n</b>	<b>Range</b>	<b>n</b>	<b>Range</b>
<b>Age (GLGs)</b>	4	1.67-3.0	1	3.3	8	2.55-17.0
<b>Length (cm)</b>	7	171.0-197.5	1	211	11	197.0-256.0
<b>Mass (kg)</b>	4	98.5-111.8	1	114.5	9	124.0-303.0

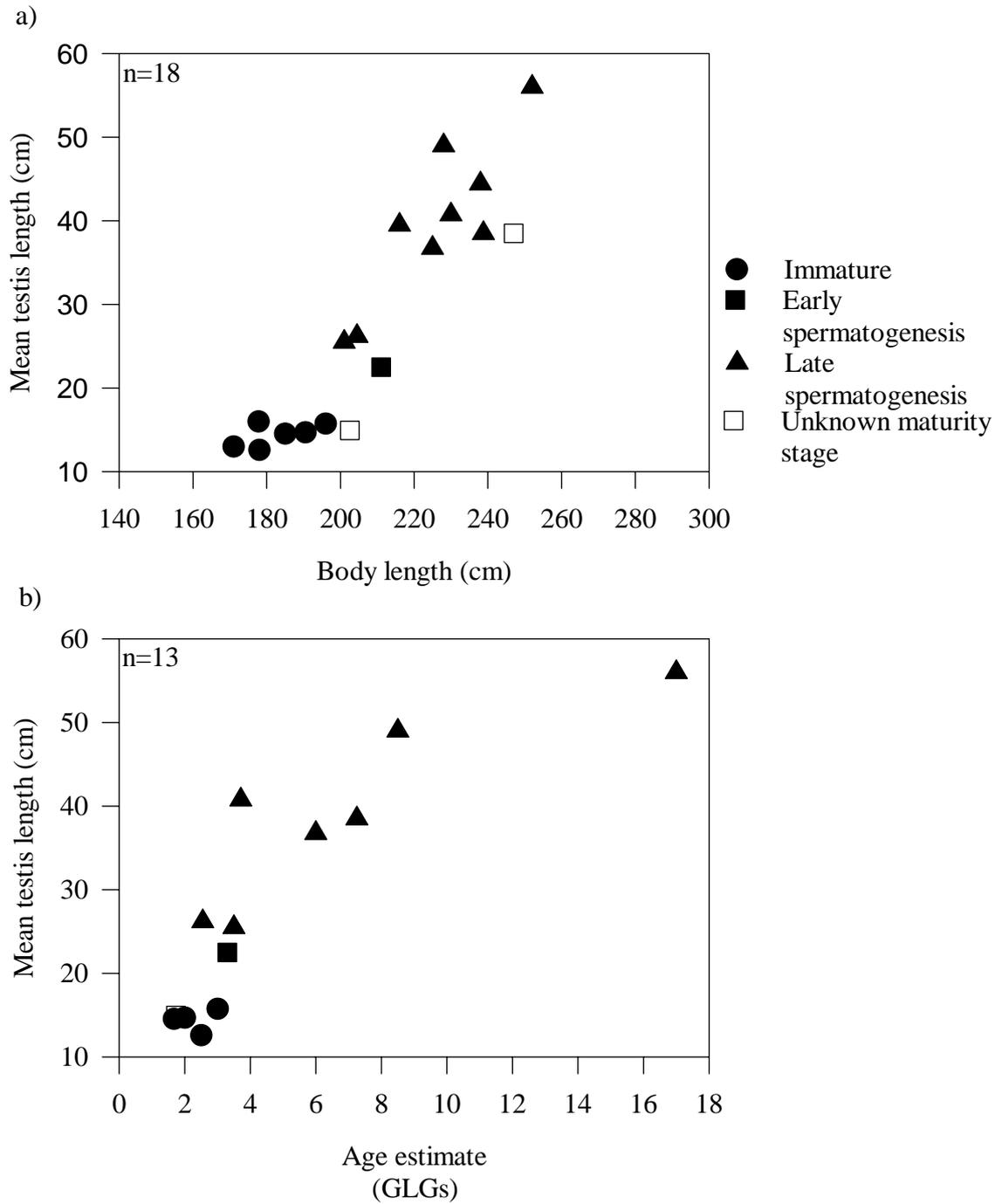


Figure 4.6: Mean testis length (cm) as a function of body length (cm) (a) and estimated age (complete GLGs + increment) (b) in *Kogia sima*.

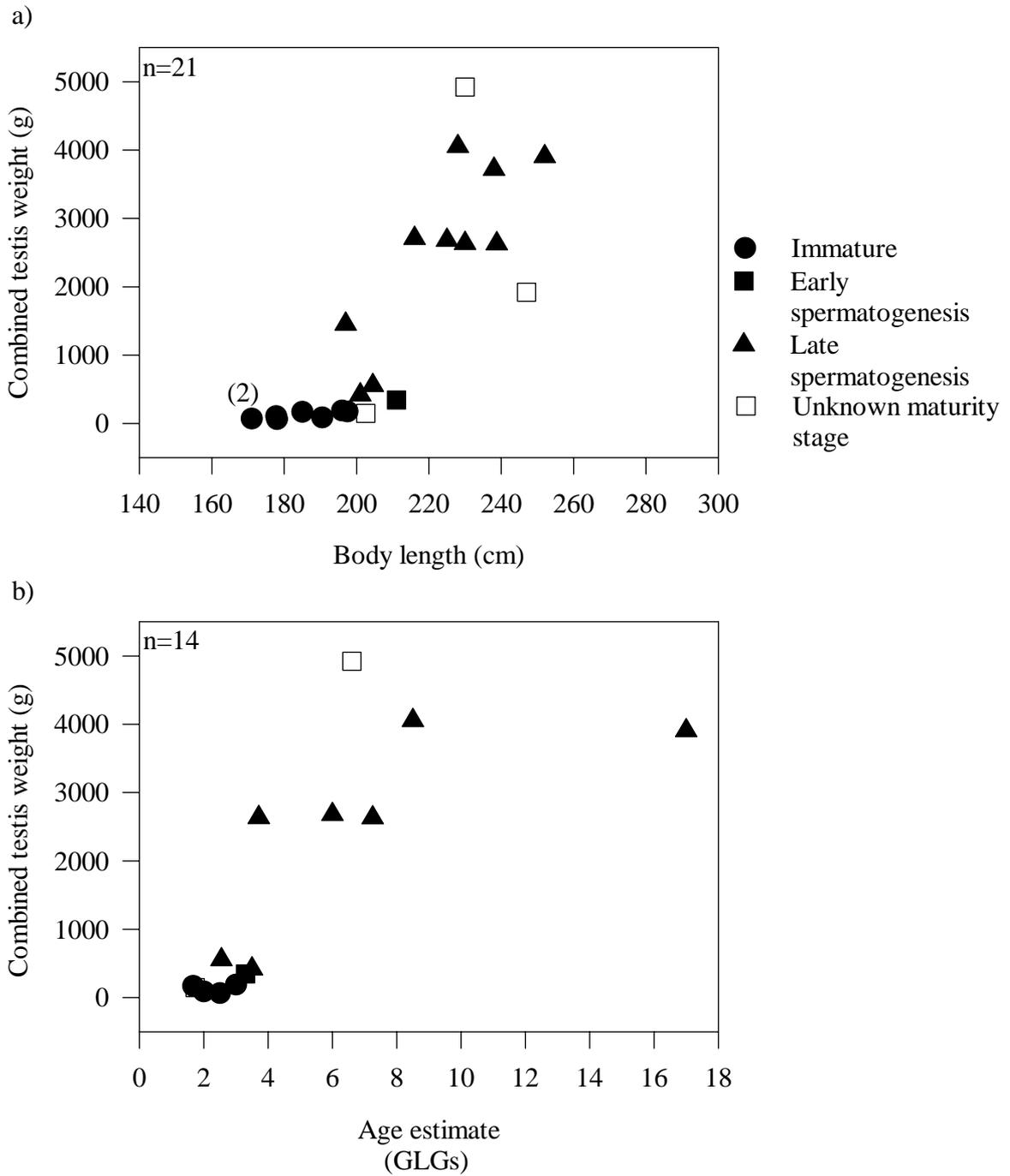


Figure 4.7: Attainment of sexual maturity with body length (cm) (a) and age (complete GLGs + increment) (b) in male *Kogia sima*.

### 4.3.3 Testis weight as a percentage of body weight

The longest mature male *K. breviceps* had a combined testis weight of 3904g or 1.04% of its total body weight. It measured 276cm and the estimated age for this animal was 13.33GLGs, which indicated that it had reached physical maturity (see Chapter 3).

The maximum combined testis weight available for *K. sima* was 4923g for a 230cm long specimen weighing 240kg (GLGs: 9). The combined testis weight made up 2.05% of the total body weight of this animal. However, no testis tissue was available for examination from this specimen to ensure that spermatogenesis was occurring. Another animal that had a combined testes weight of 4053g and was producing sperm, measured 228cm and weighed 202.5kg. The combined testis weight made up 2% of its total body weight. No age estimate was available for the latter specimen, but according to the body lengths of both animals they had reached physical maturity (see Chapter 3).

### 4.3.4 Seasonality

Unfortunately the small sample, which was biased towards immature males in *K. breviceps* (see Chapter 2), prevented a detailed examination of seasonality of spermatogenesis (Figure 4.8 and 4.9). However, the year-round presence of *K. sima* males in late spermatogenesis suggested an absence of seasonal testicular activity in this species (Figure 4.9). All stranded adult *K. breviceps* and *K. sima* males were spermatogenically active.

### 4.3.5 Sperm morphology

The spermatozoa of *K. breviceps* and *K. sima* were similar in shape (Figure 4.10a,b) and size (Table 4.5). While in *K. breviceps* the sperm head was more rounded (Figure 4.10a), it was bullet-shaped in *K. sima* (Figure 4.10b). However, the surface area of the sperm head was the same for both species (*K. breviceps*: n=17 sperm from two animals,  $\bar{x}=5.9\pm 0.72\mu\text{m}^2$ ; *K. sima*: n=13 sperm from four animals,  $\bar{x}=5.9\pm 1.31\mu\text{m}^2$ ). In both species the midpiece was short and comprised of spherical mitochondria arranged in rows and columns (Figure 4.10c). In transverse section it could be seen that the midpiece of the spermatozoon of *K. sima* comprised at least five mitochondria in one row (Figure 4.10d). Unfortunately no results could be obtained from the TEM

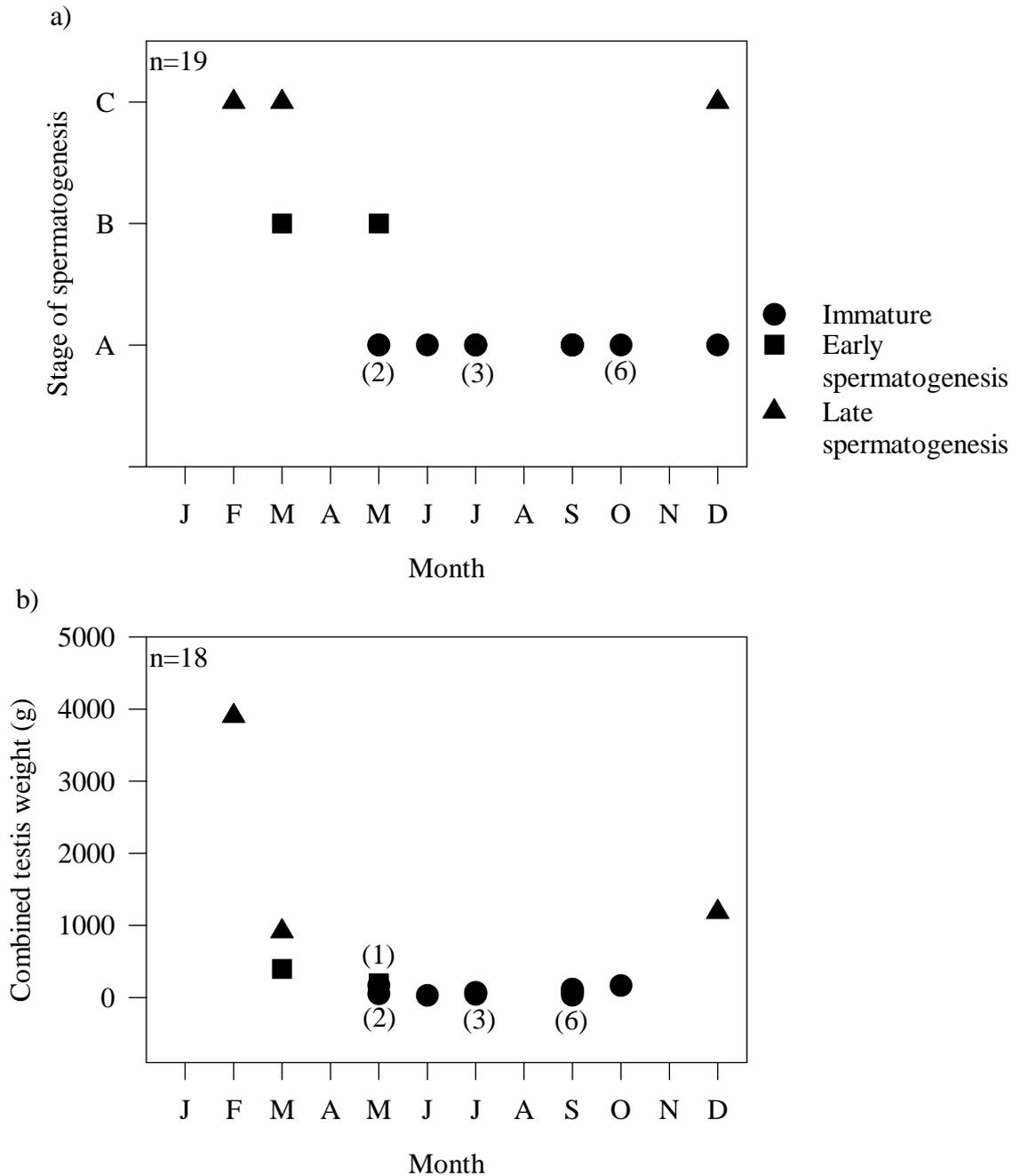


Figure 4.8: Reproductive condition (a) and combined testis weight (b) over the year in male *Kogia breviceps*. Stage of spermatogenesis A: immature; B: early spermatogenesis; C: late spermatogenesis. Numbers in brackets are sample sizes when n>1.

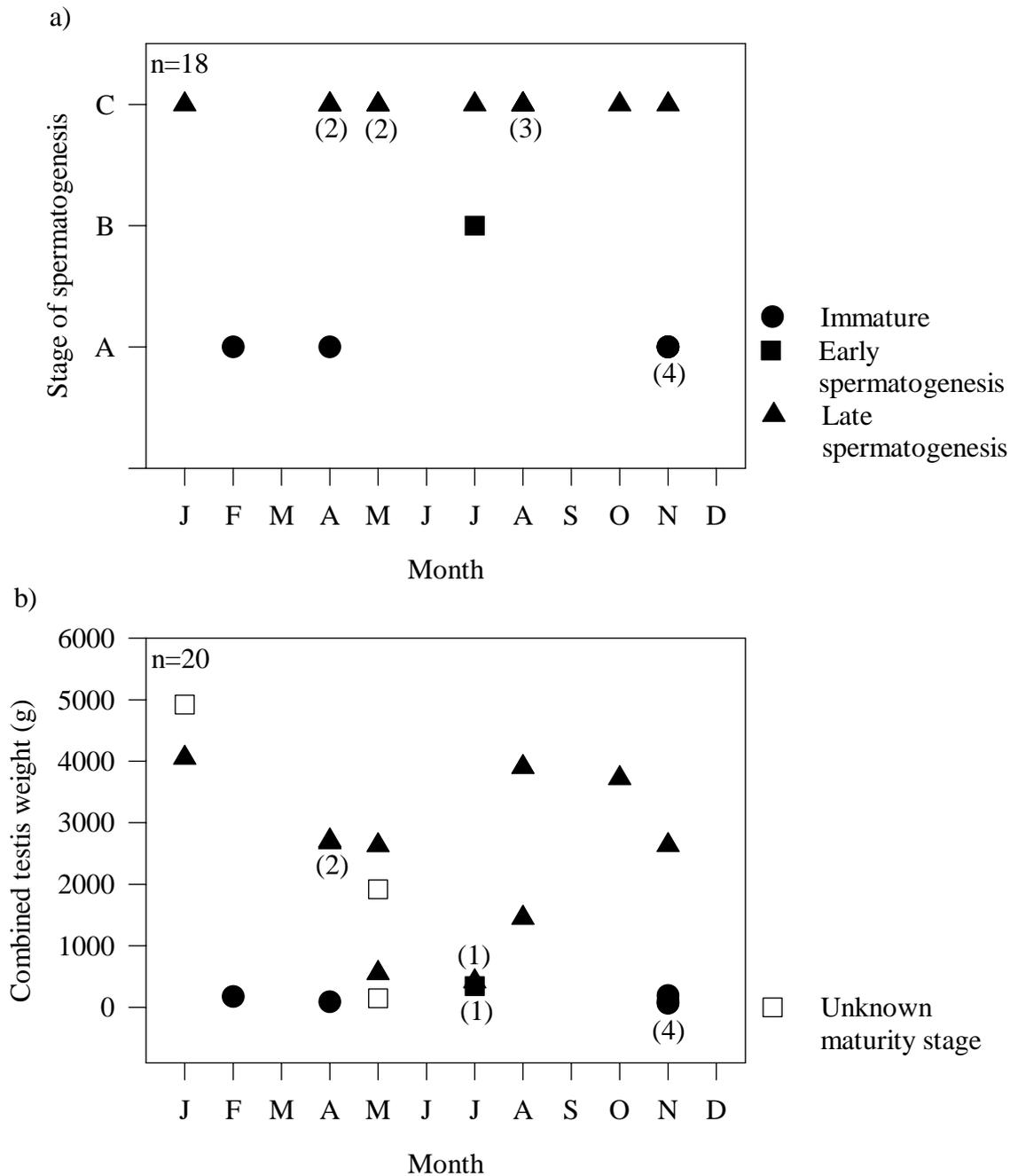


Figure 4.9: Reproductive condition (a) and combined testis weight (b) over the year in male *Kogia sima*. Stage of spermatogenesis A: immature; B: early spermatogenesis; C: late spermatogenesis. Numbers in brackets are sample sizes when  $n > 1$ .

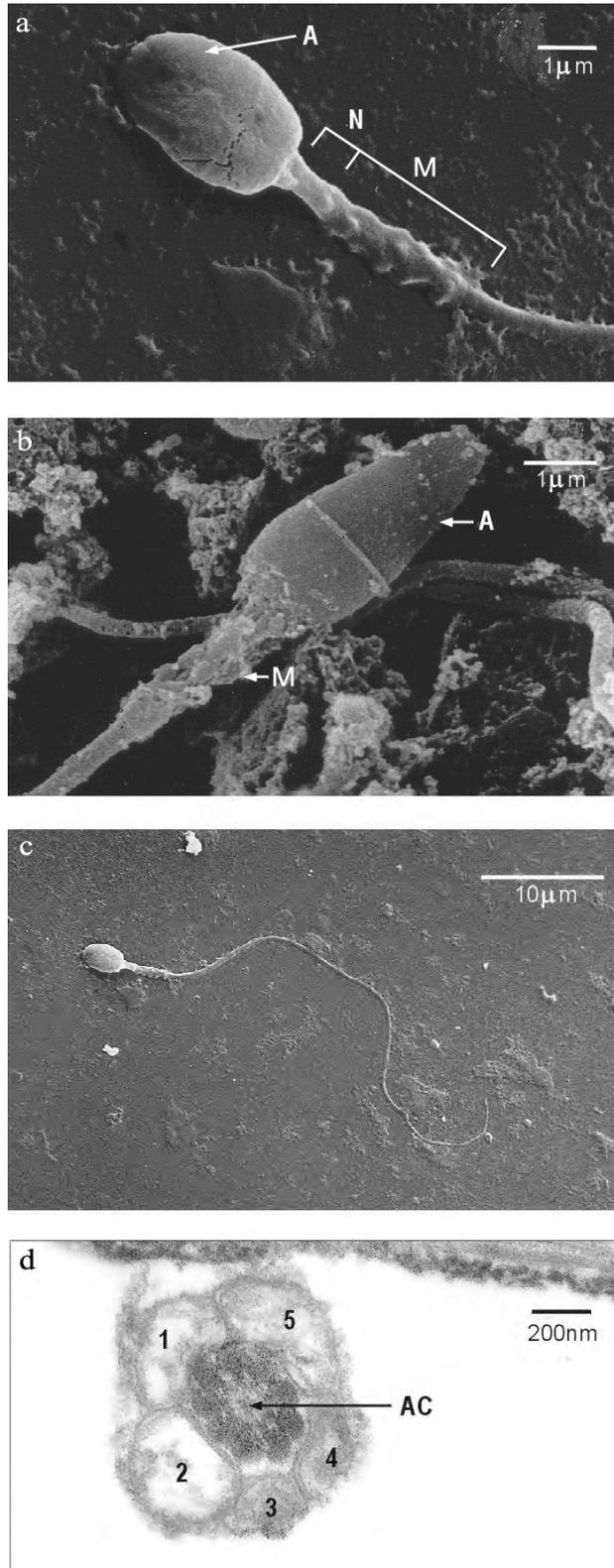


Figure 4.10: Scanning electron micrographs of a *K. breviceps* (a, c) and *K. sima* (b) spermatozoa. A: acrosome; N: neck; M: midpiece. The transmission electron micrograph (d) shows a cross-section through the neck region of a *K. sima* spermatozoon, indicating the number of mitochondria surrounding the midpiece (1-5). AC: axoneme complex.

examination of *K. breviceps* spermatozoa, but SEM pictures indicated that both species had five to six rows of spherical mitochondria. Assuming five mitochondria per row (Figure 4.10d) this would result in 25 to 30 mitochondria.

The mean total length of the sperm was larger in *K. breviceps*, but due to the small sample size of eight spermatozoa from one specimen of *K. breviceps* and one sperm from one specimen of *K. sima* no statistical test was possible. The mean length of the head of the spermatozoon was slightly but significantly larger in *K. sima* than in *K. breviceps* ( $p < 0.001$ ) given the assumption of the equality of means within the samples/species. Although the midpiece of *K. sima* also appeared larger than that of *K. breviceps* there was no significant difference ( $p = 0.136$ ). Consequently, the relative lengths of the head and midpiece (expressed as percentages of total length) were greater in *K. sima*, with the head (6.7%) and midpiece (5.7%) of *K. breviceps* being almost half as long as that of *K. sima* (12.3% and 10.7%, respectively) (Table 4.5).

Table 4.5: Sperm dimensions of *Kogia* from the present study.

	Mean length ( $\mu\text{m}$ )			% of total length	
	Head	Midpiece	Total length	Head	Midpiece
<b>Pygmy sperm whale</b> <i>Kogia breviceps</i>	3.4 ( $\pm 0.24$ ) (n=18/2)	2.9 ( $\pm 0.53$ ) (n=17/2)	50.5 (n=8/2)	6.7	5.7
<b>Dwarf sperm whale</b> <i>Kogia sima</i>	4.0 ( $\pm 0.58$ ) (n=17/4)	3.5 ( $\pm 0.51$ ) (n=8/4)	32.6 (n=1/4)	12.3	10.7

Values in parentheses indicate the number of sperm examined from the given number of specimens.

## **4.4 Discussion**

### **4.4.1 Attainment of sexual maturity**

The onset of sexual maturity, defined here as being late spermatogenesis, has previously been determined to occur between body lengths of 270cm and 300cm for *K. breviceps* and between 210cm and 220cm for *K. sima*, with early spermatogenesis starting at a body length of 200cm in the latter (based on examination of the

epididymides) (Ross, 1979; 1984). The present study, which was based on animals from the same geographical region, showed that the onset of sexual maturity occurred between 241cm and 242cm and 2.5 and five years in *K. breviceps* (Table 4.2) and at about 197cm and between 2.6 and three years in *K. sima* (Table 4.4). Thus this study indicates that both *Kogia* species may actually attain sexual maturity at a somewhat shorter body length than previously reported. There are no previous records for body weight at ASM for either species and thus the present data of 210-233.6kg for *K. breviceps* and 111.8-124kg for *K. sima* present a first report on body weight at the onset of sexual maturity in the two species.

Few records of testis weights and dimensions (Scheffer and Slipp, 1948; Hubbs, 1951; Harrison *et al.*, 1972; Caldwell and Caldwell, 1989) are available for either *Kogia* species. Roest (1970) concludes that a 224cm long *K. sima* was mature based on the size of the testes (each about 40cm long). The only histological studies of ASM in both *Kogia* species have been carried out in South Africa (Ross, 1979; 1984). The data obtained for testis weight and length for the different maturity stages for both species of *Kogia* in the present study concur well with those previously presented in the literature (Roest, 1970; Harrison *et al.*, 1972; Caldwell and Caldwell, 1989). The only data that exceed the ranges presented here are 3090g and 50cm for the left testis and 2840g and 48.5cm for the right testis of a 305cm long mature *K. breviceps* (Caldwell and Caldwell, 1989). Hubbs (1951) reports a 234.5cm long animal with approximately 101.6mm long testes and suggests that it was mature. Although the reported body length could indicate a sexually mature animal, the data for testis length suggest that the animal was immature according to the data gathered in the present study. Testes lengths of 47.5cm and 50cm and testes weights of 910g and 1030g, respectively, presented by Harrison *et al.* (1972) for a 229cm long *K. sima* from Japan are intriguing as body length, testis length, and testis weight indicate a mature animal, but no sperm were present. The only obvious interpretation of this is that the animal may have been producing sperm seasonally, but this would represent the only indication of a male seasonal cycle in the two *Kogia* species in the literature.

The results of the present study reveal that there was no overlap in testis size (both length and weight) in either *K. breviceps* or *K. sima* between early and late spermatogenesis. Thus either measure could be used to indicate the onset of sexual maturity. A small degree of overlap was observed between the mean testis length of immature animals and those in early spermatogenesis in *K. breviceps*; all other

categories showed no overlap. Some overlap has been reported for all categories in spotted dolphins *S. attenuata* (Hohn *et al.*, 1985) and in long finned pilot whales *G. melas* (Desportes *et al.*, 1993), with the exception of testis length in the latter. Thus the little or no overlap in testis size between different maturity stages found for both *Kogia* species in this study may be an artefact of the relatively small sample size and it is difficult to determine which parameter would be the best indicator for sexual maturity in the genus *Kogia*.

As expected the diameter of the seminiferous tubules increased in both species as the testes matured. The seminiferous tubule diameters from the present study as well as the different stages of maturity are in close agreement with the only data available in the literature from a *K. breviceps* from the Californian coast and *K. sima* from Japan (Harrison *et al.*, 1972). The mean seminiferous tubule diameter of adult, spermatogenically active animals is greater in *K. breviceps* ( $135.5 \pm 63.99 \mu\text{m}$ ) than in *K. sima* ( $100.2 \pm 12.16 \mu\text{m}$ ) and similar results have been reported for the two species of *Globicephala* (Kasuya and Marsh, 1984). Since seminiferous tubule diameter is larger in the large cetaceans like the sperm whale *P. macrocephalus* (Best, 1969; Mitchell and Kozicki, 1984) and the humpback whale *M. novaeangliae* (Chittleborough, 1954) it is likely that the differences seen here in the two species of *Kogia* are due to scaling.

An index of testis development was calculated by Collet and Saint Girons (1984), Hohn *et al.* (1985), and Desportes *et al.* (1993) to allow comparison of maturity between stocks and species. But as the above authors have all calculated the testis index in different ways such a comparison is not possible. The mean testis index values obtained for both *K. breviceps* and *K. sima* were roughly half those of Desportes *et al.* (1993) for long-finned pilot whales *G. melas*, using the same formula; the biological significance of these results is unknown.

Attainment of sexual maturity between 2.5 and five years in *K. breviceps* and 2.55 and three years in *K. sima* was surprising, because most other odontocetes of similar size mature at a greater age (Perrin and Reilly, 1984; Evans, 1987). The implications of this are discussed in depth in Chapter 9. Studies on a small number of *K. breviceps* stranded in New Zealand indicate that mature males range in age between three and 16GLGs (Tuohy *et al.*, 2001), which supports the findings of the present study. In general body length and weight are better correlated with the onset of sexual maturity in male *Kogia* than age as different animals which would fall in the same length class showed quite different age estimates (Tables 4.2 and 4.4 and Figures 4.4 and 4.7). This

may partly be a result of the problems encountered with tooth wear and the aging technique (see Chapter 3), or individually differing growth rates.

In both *Kogia* species males attained sexual maturity at a shorter body length and lower body weight than females. The significance of this has already been addressed in Chapter 3. However, age at sexual maturity was similar for both sexes in both *K. breviceps* and *K. sima*, as is commonly found in a number of phocoenid and delphinid species (Miyazaki, 1984; Perrin and Reilly, 1984; Slooten, 1991; Hohn *et al.*, 1996).

#### **4.4.2 Seasonality**

The results for both *K. breviceps* and *K. sima* did not show any conclusive evidence for a seasonal cycle of testicular activity. However, these data must be interpreted with caution due to the small sample size and the bias of samples towards immature males in *K. breviceps* (see Chapter 2). Since the majority of odontocetes appear to exhibit seasonal testicular activity (Sergeant, 1962; Gaskin *et al.*, 1984; Hohn *et al.*, 1985; van Waerebeek and Read, 1994), a similar result would be expected for the two *Kogia* species, especially as the data from the present study indicated that mating does not occur all year round (see Chapter 5).

#### **4.4.3 Testis size and male mating strategy**

Testis size usually increases as body size increases, regardless of the breeding system (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986), but variation in relative testis size within and between species generally reflects variations in the requirements for sperm production (Setchell, 1978; Kenagy and Trombulak, 1986). Therefore testis weight as a percentage of body weight is often used as an indicator of the mating system of a species (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986; Rose *et al.*, 1997). Large testes in relation to body weight are usually associated with a multimale breeding system (or polyandry), in which the males compete with each other in the form of sperm competition (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986). Large testes are apparently a result of the selective pressures of multiple inseminations, sperm competition within the female reproductive tract, spontaneous ovulations, and seasonal reproduction (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986). Sexual dimorphism is usually absent in these species (Aguilar and Monzon, 1992).

Small testes in relation to body weight are indicative of low copulatory frequency and thus of monogamous or extreme polygynous single-male mating systems, the latter involving one male mating with a number of females (i.e. harem) (Harcourt *et al.*, 1981; Kenagy and Trombulak, 1986). Sexual dimorphism is usually great in species where males have to fight over access to a number of females. In cetaceans intraspecific fighting is thought to be reflected in the amount of scarring (MacLeod, 1998). Generally very little sexual dimorphism is found in monogamous species (Harcourt *et al.*, 1981). Intermediate levels of sexual dimorphism, large testes, and thus assumed high copulatory frequency, and low degrees of scarring indicate a multimale breeding system, for example promiscuity or multimale polygyny (Harcourt *et al.*, 1981; van Waerebeek and Read, 1994) (Table 4.6).

Combined testis weights comprise less than 1% of body mass in most terrestrial mammals and cetaceans have slightly, but significantly larger testes relative to body weight (Kenagy and Trombulak, 1986). In addition, there are large differences in testis size between the mysticetes and the odontocetes (Kenagy and Trombulak, 1986; Aguilar and Monzon, 1992). There are a number of possible explanations for cetaceans possessing larger testes than terrestrial mammals. An aquatic mode of life may facilitate larger testes due to the support of body weight in the aquatic medium or it may necessitate larger testes due to a possibly different reproductive physiology involved in internal fertilization in an aquatic medium (Kenagy and Trombulak, 1986). Furthermore, cetaceans as a group may show more frequent copulations than other mammals and thus exhibit larger testes (Kenagy and Trombulak, 1986; Connor *et al.*, 2000). However, marsupials have significantly smaller testes than eutherian mammals, but within their range the testis sizes of the marsupials are still indicative of the different mating systems mentioned above (Rose *et al.*, 1997). Thus relatively small testes in cetaceans probably still indicate a monogamous or extreme polygynous mating system, whereas relatively large testes are assumed to indicate frequent copulations and sperm competition.

In most mysticetes the combined testis weight makes up less than 1% of the total body mass, except in right whales (*Eubalaena* spp.), where it comprises up to 1.31% of the body weight (Brownell and Ralls, 1986). Although a similar percentage has been reported for the humpback dolphin *Sousa chinensis* (0.7%) and the bottlenose dolphin *T.*

Table 4.6: Proposed male mating strategies for different species of odontocetes based on testis size, sexual dimorphism, degree of scarring and group size. Testis size is expressed as a percentage of the total body weight.

Criterion		Species examined											
		Dusky dolphin <sup>1</sup>	Vaquita <sup>2</sup>	Harbour porpoise <sup>3</sup>	Common dolphin <sup>4</sup>	Hector's dolphin <sup>5</sup>	Bottlenose dolphin <sup>6</sup>	Humpback dolphin <sup>7</sup>	Dwarf sperm whale <sup>8</sup>	Pygmy sperm whale <sup>9</sup>	Sperm whale <sup>10</sup>	Pilot whale <sup>11</sup>	Ziphiidae <sup>12</sup>
<b>Testis size</b>	Small testes in relation to body weight						1%	0.7%	2%	1.7%	0.01-0.05%		√
	Medium sized testes in relation to body weight		5%	3-4%	4.2%	2.9%							
	Large testes in relation to body weight	8.5%											
<b>Sexual dimorphism</b>	Males larger than females							√			√	√	√
	Little or no sexual dimorphism				√		√		√	√			
<b>Group size</b>	Females larger than males		√	√									
	Solitary or small groups		√	√		√		√	√	√			
	Medium sized schools	√					√					√	√
<b>Scarring</b>	Large schools				√								
	Little or no scarring	√	√	√	√	√	√	√	√	√		√	
	Extensive scarring										√		√
		Sp	Sp	Sp	Sp	R	R	?	R	R	R	JH	H
		<b>Proposed mating strategy</b>											

Sp= sperm competition; R= roving males; JH= joint harem; H= harem.

<sup>1</sup>van Waerebeek and Read, 1994; Carwardine, 1995; <sup>2</sup>Hohn *et al.*, 1996; <sup>3</sup>Gaskin *et al.*, 1984; Carwardine, 1995; Read and Hohn, 1995; Hohn *et al.*, 1996; <sup>4</sup>Cockcroft, 1993; <sup>5</sup>Slooten, 1991; Carwardine, 1995; Dawson *et al.*, 1993; Slooten and Dawson, 1994; Dawson, pers. com. <sup>6</sup>Wells *et al.*, 1987; Cockcroft, 1993; <sup>7</sup>Cockcroft, 1993; <sup>8</sup>Present study; <sup>9</sup>John Heyning, unpubl. data; <sup>10</sup>Best *et al.*, 1984; Gaskin *et al.*, 1984; Kato, 1984; MacLeod, 1998; <sup>11</sup>Kasuya and Tai, 1993; Magnusson and Kasuya, 1997; MacLeod, 1998; Kasuya, pers. com. <sup>12</sup>Aguilar and Monzon, 1992; MacLeod, 1998

*truncatus* (1%) (Cockcroft, 1993), most odontocetes have a somewhat bigger testis weight to body weight ratio (Table 4.6). In Hector's dolphin *C. hectori* the testes make up 2.9% of the total body weight (Slooten, 1991) (Table 4.6). Furthermore, values of 3.5% and 3-4% have been reported for the harbour porpoise *P. phocoena* (Gaskin *et al.*, 1984; Read, 1990b), 4.2% for the common dolphin *D. delphis* (Cockcroft, 1993), almost 5% in the vaquita *P. sinus* (Hohn *et al.*, 1996), and 5% for the Tucuxi *Sotalia fluviatilis* (Best and da Silva, 1984), respectively (Table 4.6). The dusky dolphin *L. obscurus* has testes weighing up to 8.5% of the total body weight, amongst the highest recorded for mammals (van Waerebeek and Read, 1994) (Table 4.6). Based on testis size it is suggested that the dusky dolphin may have a promiscuous mating system with sperm competition and this is supported by the fact that only little intraspecific scarring is observed on the males (van Waerebeek and Read, 1994) (Table 4.6). A similar scenario is found in the Hector's dolphin *C. hectori* (Slooten, 1991) (Table 4.6). Due to the large testis size in the vaquita *P. sinus*, the small group size and reversed sexual dimorphism, sperm competition is suggested for this species (Hohn *et al.*, 1996) (Table 4.6). A multimale polygynous mating system (or joint harem) is reported for both the southern and northern form of the short-finned pilot whale *G. macrorhynchus* off Japan (Kasuya and Marsh, 1984; Kasuya and Tai, 1993; Magnusson and Kasuya, 1997) (Table 4.6). While this would indicate that mating systems do not vary within a species, the mating systems of bottlenose dolphins *T. truncatus* may vary slightly between populations (Tolley *et al.*, 1995; Connor *et al.*, 2000). The above results support the suggestion that in mammals a polygynous mating system is the dominant strategy (Krebs and Davies, 1981). The one exception to the phenomenon that larger testes are found in cetaceans compared to terrestrial mammals (Aguilar and Monzon, 1992) appears to be the ziphiids, which also show some of the highest degree of intraspecific scarring (MacLeod, 1998). This suggests a mating system where males fight over access to females (Connor *et al.*, 2000).

Although a number of researchers provide combined testes weights for either species of *Kogia* (Harrison *et al.*, 1972; Caldwell and Caldwell, 1989), no body weights are provided for the animals concerned and thus the percentage that the combined testes weight contributes to the total body weight could not be determined. Caldwell and Caldwell (1989) remark on the large testis size of a 305cm long *K. breviceps*, which had a combined testis weight of 5.93kg. Similarly, Maigret and Robineau (1981) estimate the combined testis weight of a 222cm long male *K. sima* stranded in Senegal at around 6kg. Aguilar and Monzon (1992) provide relative testes weights for 54 cetacean species,

including *K. breviceps* and *K. sima*, but unfortunately no reference to the original data is provided. The maximum combined testis weights of 1.04% for *K. breviceps* and 2% for *K. sima* obtained in this study suggest that both *Kogia* species have relatively small testes in comparison with other odontocete species (Table 4.6). Although it is frequently mentioned that both *Kogia* species have large testes (MacLeod, 1998), no indications of bigger testes in relation to body weight could be found in the literature. As yet unpublished data from the Los Angeles County Museum for a 300cm long *K. breviceps* (LACM 88938) weighing 385kg showed a combined testis weight of 6049g (John Heyning, pers. com.), which made up 1.69% of the total body weight. No age estimate was available for the animal. However, none of the South African animals for which relative testis weight could be calculated had reached physical maturity and it is possible that larger specimens may have relatively larger testes.

There is a difference between sexual and social maturity in a number of cetacean species. Social maturity has been defined as the stage when males may gain access to receptive females and successfully fertilise them (*sensu* Best, 1969; Kasuya and Marsh, 1984; Desportes *et al.*, 1993; Kasuya *et al.*, 1997). In some species like the long-finned pilot whale *G. melas*, sexually mature males may be capable of producing sperm, but may not reach social maturity until a later stage (Desportes *et al.*, 1993). In the bottlenose dolphin *T. truncatus* only males older than 21 years appear to sire calves (Duffield and Wells, 2002). An extreme example is the Baird's beaked whale *Berardius bairdii*, in which testis weight continues to increase for almost 20 years after ASM (Kasuya *et al.*, 1997). In other species, such as the short-finned pilot whale *G. macrorhynchus*, full sexual maturity (based on histology) and social maturity occur at the same time (Kasuya and Marsh, 1984). The substantial increase in testes size that occurred after ASM in both *K. breviceps* (4.3 fold) and *K. sima* (11.7 fold) may indicate that social maturity is reached only at a later stage in life. A 7.62 fold increase of combined testis weight after ASM is reported for long-finned pilot whales *G. melas* (Desportes *et al.*, 1993).

Sexual dimorphism is another important indicator as to the mating system (Table 4.6). Cetaceans generally lack secondary sexual characters, with the exception of the narwhal *Monodon monoceros*, where only males possess an up to 2.6m long tusk (Gerson and Hickie, 1985). Sexual dimorphism is most pronounced in the largest odontocete, the sperm whale *P. macrocephalus* (Best *et al.*, 1984), with males being up to five metres longer than females (Leatherwood and Reeves, 1983). Sexual dimorphism in the shape and colour of the melon is reported for the northern bottlenose whale *Hyperoodon ampullatus*

(Bloch *et al.*, 1996) and in the colouration of the patch around the genital area for Hector's dolphins *C. hectori* and Commerson's dolphins *C. commersonii* (Slooten and Dawson, 1994). But in most medium-sized odontocetes sexual dimorphism may be expressed as differences in girth and weight rather than length (Hohn and Brownell, 1990; Cockcroft and Ross, 1990; Cockcroft, 1993; Tolley *et al.*, 1995). Although only slight or no differences in asymptotic length are found between the sexes in bottlenose dolphins *T. truncatus*; (Hohn and Brownell, 1990; Cockcroft and Ross, 1990), males are about 30% heavier (Cockcroft and Ross, 1990; Cockcroft, 1993), more robust and possess larger appendages than females of the same length (Tolley *et al.*, 1995). Thus it appears that robustness rather than length plays a role in male-female (Cockcroft and Ross, 1990) as well as male-male intraspecific interactions (Tolley *et al.*, 1995). This may well be the case for a number of other cetacean species, for example common dolphin *D. delphis* males are about 10% heavier than females (Cockcroft, 1993). In the smallest odontocetes, namely the phocoenids and the delphinid genus *Cephalorhynchus*, and in the large baleen whales sexual dimorphism is reversed, with the females being larger than the males (Brownell and Ralls, 1986; Read and Gaskin, 1990; Slooten, 1991; Connor *et al.*, 2000) (Table 4.6). However, sexual dimorphism in cetacea has not been very well researched in the past and should be the subject of further investigation in order to shed more light on the mating system of cetaceans. In the present study reversed sexual size dimorphism was found for *K. breviceps*, while in *K. sima* the males were larger than the females in body length (see Chapter 3). Mammals in which females are larger than males have a variety of social systems ranging from monogamy to harems (Ralls, 1976; Brownell and Ralls, 1986; Clapham, 1996) and in this respect the reversed sexual size dimorphism found in *K. breviceps* gives no indication as to the mating system of the species. In *K. sima* the fact that males were slightly larger than females may indicate that there is some male-male competition over access to females.

Knowledge about the degree of sexual dimorphism represents a starting point for the exploration of cetacean mating systems as it indicates the degree of male-male competition and the role it plays in determining male reproductive success (Connor *et al.*, 2000). However, the extent of body scarring resulting from intrasexual fights is thought to present a further clue (Table 4.6). Depending on the type of scarring, they are indicators of intraspecific fighting in a number of odontocetes (Heyning, 1984; Kato, 1984; Gerson and Hickie, 1985; MacLeod, 1998) (Table 4.6). In some instances body scars are an indicator of the male maturity status (Kato, 1984) and "quality" (Gerson and Hickie, 1985;

MacLeod, 1998) and thus indirectly add information about the breeding system of a species (Kato, 1984; MacLeod, 1998). A number of odontocete species show a clear reduction in the number of teeth (Gaskin, 1982; MacLeod, 1998) and this is especially obvious in teuthophagous species, such as *Physeter* (Kato, 1984) and both *Kogia* species (see Chapters 3 and 6), and reaches an extreme in the ziphiids (Mead, 1984; Heyning and Mead, 1996; MacLeod, 1998). Recent studies suggest that the ziphiids employ suction-feeding in which the prey is sucked into the mouth in a hoover-like fashion without the need for teeth to grasp or even chew the prey (Heyning and Mead, 1996) (see also Chapter 6). A similar mechanism is considered likely in both genera of the sperm whales (Heyning and Mead, 1996) and a number of other odontocete species (Norris and Møhl, 1983). Thus in species that feed by suction the retained teeth might play a role in social interaction (Heyning, 1984; Kato, 1984; MacLeod, 1998), since in some species the remaining teeth show an adaptation for use as weapons (Gerson and Hickie, 1985). Body scarring is reported for a number of odontocete species (McCann, 1974; MacLeod, 1998) and even for one mysticete (Chu and Nieuwkerk, 1988).

Examination of photographs of stranded specimens of *Kogia* from South Africa did not show any tooth scars. This may be due to the bias in the stranding record since adult males may be under-represented (see Chapter 2). However, no indications of intraspecific scarring were found on animals (both male and female) of both *Kogia* species stranded along the coast of Florida (Nelio Barros, pers. com.). Thus it appears that male animals of either *Kogia* species may not fight over females and this may be due to the small group size, averaging one to two animals for *K. breviceps* and one to six animals for *K. sima* (Ross, 1979; Barlow and Sexton, 1996) (Table 4.6) (see Chapter 1 and Chapter 7). Group size influences the mating system of cetaceans (Evans, 1987; Cockcroft, 1993) as do social structure and association patterns (Evans, 1987; Wells *et al.*, 1987). Large testes and little sexual dimorphism in conjunction with large schools, as found in the common dolphin *D. delphis*, are attributed to sperm competition, whereas small testes, great sexual dimorphism and small group sizes, as found in humpback dolphins *S. chinensis*, are thought to indicate that larger males dominate smaller males and deny access to females (Cockcroft, 1993) (Table 4.6). The stranding data for *Kogia* specimens from South Africa suggested that groups are comprised of females with their calves, small groups of juveniles (up to four animals in *K. sima*) and solitary males (both immature and mature animals) (see Chapter 7). Consequently encounters between males would be rare and thus there may not be a need for intraspecific fights. However, Connor *et al.* (2000) point out that it is

likely that most serious fighting in cetaceans may occur by means of strikes with the peduncle, flukes or other body parts. This would not result in any obvious wounds and thus, in the absence of any direct behavioural observations, the examination of body scars may lead to an underestimation of the frequency and severity of intra- and interspecific aggression (Connor *et al.*, 2000). In this respect one male *K. breviceps* (PEM N2115; L: 275cm) was reported to have stranded with broken mandibles and ribs and specimens stranded in the Western Cape region are often found with broken mandibles (Peter Best, pers. com.). These occurrences are also reported in the literature (McAlpine and Murison, 1997) and may be indications of intraspecific aggression, but could just as easily result from the carcass being washed over rocks. However, this circumstantial evidence can only be clarified with further data from direct observations.

MacLeod (1998) states that the vast majority of 32 species of odontocetes, for which there was no evidence that intraspecific scarring acted as an indicator for male quality, were primarily non-teuthophagous. The four exceptions are the two *Kogia* species, the long-finned pilot whale *G. melas* and the Ginkgo-toothed beaked whale *Mesoplodon ginkgodens*. He suggests sperm competition as an alternative to direct male-male aggressive competition in the genus *Kogia*, but gives no direct indication of testis weights for either *Kogia* species. As the length (Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997) and synchrony (Best and Butterworth, 1980) of female oestrus, as well as the group size, density and dispersion of the females (Best and Butterworth, 1980; Krebs and Davies, 1981; Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997; Connor *et al.*, 2000) have a profound effect on the mating strategy of a species and as these data are lacking for both *Kogia* species, no definite model for the mating strategy of either *Kogia* species can be established. However, based on the comparatively small testis size, indicating moderate copulation frequency (as opposed to high copulation frequency in sperm competition), reversed or small sexual size dimorphism, little scarring and small group size, a promiscuous or polygynous mating system, with more than one male gaining access to females, is suggested for either *Kogia* species (Table 4.6). The density and dispersion of the females largely determines the difference between a harem strategy and a roving male strategy (Best and Butterworth, 1980; Krebs and Davies, 1981; Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997). Where females range widely and are solitary or occur in small groups, as is the case in *Kogia*, males may employ a roving strategy in search of receptive females (Connor *et al.*, 2000). However, observational data are needed to show whether females

aggregate during the breeding season or not, but comparisons with other odontocetes favour the roving male theory (Table 4.6). The roving male strategy is also suggested for the sperm whale *P. macrocephalus* (Whitehead, 1990; Magnusson and Kasuya, 1997) (Table 4.6), although there is evidence for male-male aggressive interaction in this species (Kato, 1984). Bottlenose dolphins *T. truncatus* also show little sexual dimorphism (Wells *et al.*, 1987; Tolley *et al.*, 1995) and have relatively small testes, which make up 1% of the total body weight (Cockcroft, 1993). Extensive studies on bottlenose dolphins in Sarasota, Florida, show that male pairs may adopt a roving strategy in which one male may dominate the other, but both mate with receptive females without showing any aggressive interaction (Wells *et al.*, 1987) (Table 4.6). Alliance formation between males is only observed in habitats where males encounter each other frequently (Connor *et al.*, 2000). Thus if a male has a low probability of encountering a rival male while with a female he would be better off alone (Connor *et al.*, 2000). Although it appears unlikely that males of either *Kogia* species form pairs, as males seem to be solitary based on the stranding data, they may rove between females in order to maximize their reproductive opportunities rather than monopolize and fight over a number of females. Postmortem examinations of stranded specimens of either *Kogia* species along the coast of the United States showed that the epididymis is almost always full of sperm (Nelio Barros, pers. com., John Heyning, pers. com., Dan Odell, pers. com.), which would further support an opportunistic mating strategy. By contrast ziphiids have some of the smallest testes sizes recorded for odontocetes (Aguilar and Monzon, 1992) and this together with their extensive scarring may indicate a harem system (Table 4.6).

Although it has been assumed, based on morphology and field observations, that cetaceans in general have some form of polygynous or promiscuous mating system (Slooten, 1991; van Waerebeek and Read, 1994; Hohn *et al.*, 1996; Connor *et al.*, 2000) like most mammals (Krebs and Davies, 1981), the use of techniques like molecular analysis have, in recent years, provided hard evidence to support these observations (Amos *et al.*, 1993; Clapham and Palsbøll, 1997; Debbie Duffield, pers. com.). Although the analysis of testes size, group size and sexual dimorphism may give a good first indication as to the mating system of a species, it remains widely speculative and only behavioural observations in the wild (Slooten *et al.*, 1993) and genetic analysis will eventually give unequivocal evidence as to which males dominate the matings (Amos *et al.*, 1993; Duffield and Wells, 2002). In these cases, genetic analysis of paternity may lead to interesting results.

#### 4.4.4 Sperm morphology

The sperm of either *Kogia* species were similar in size and shape to those described for other marine mammals (Table 4.7). The only apparent difference was the relatively small total length observed for the sperm of *K. sima*, which resulted in the head and midpiece being longer in relation to the total length than in most other cetaceans (Table 4.7). However, as the total sperm length for *K. sima* was calculated from a single spermatozoon, the above results may be an artefact of an unusually short or damaged sperm. Similarly, the sperm dimensions for the sperm whale *P. macrocephalus* should be treated cautiously as the two sets of measurements that are available from the literature (Yamane, 1936) differ quite substantially from each other as indicated by the large standard deviations (Table 4.7). The results obtained for both *Kogia* species were from material fixed in buffered formalin for a considerable amount of time and it should be noted that some shrinkage would have occurred, leading to underestimations of the measurements.

Within the Cetacea the sperm head is generally bullet-shaped or oval and dorso-ventrally flattened and shows little variation. In this respect the head shapes found in the two *Kogia* species concur with previous results from other species (Ballowitz, 1907; Retzius, 1909; Yamane, 1936). In some cases the acrosome may taper at the tip or even curve slightly over to one side as seen in the pilot whale *G. melas* (Retzius, 1909), but this was not observed in either *Kogia* species.

Table 4.7: Sperm dimensions in marine mammals.

	Mean length ( $\mu\text{m}$ )			% of total length	
	Head	Midpiece	Total length	Head	Midpiece
<b>Balaenopteridae</b>					
Humpback Whale <i>Megaptera nodosa</i> (= <i>Megaptera novaengliae</i> <sup>1</sup> )	3-5	-	52.5	-	-
Minke Whale <i>Balaenoptera acutorostrata</i> <sup>2</sup>	5.2( $\pm$ 0.1)	-	56.7( $\pm$ 0.5)	9.2	-
<b>Physeteridae</b>					
Sperm Whale <i>Physeter catodon</i> <sup>3</sup>	6.9( $\pm$ 1.63)	2.1	41.3( $\pm$ 19.16)	16.7	5.1
Pygmy Sperm Whale <i>Kogia breviceps</i> <sup>4</sup>	3.4( $\pm$ 0.24)	2.9( $\pm$ 0.53)	50.5	6.7	5.7
Dwarf Sperm Whale <i>Kogia sima</i> <sup>4</sup>	4.0( $\pm$ 0.58)	3.5( $\pm$ 0.51)	32.6	12.3	10.7
<b>Delphinidae</b>					
Long-finned Pilot Whale <i>Globicephalus melas</i> (= <i>Globicephala melaena</i> <sup>5</sup> )	-	-	67 <sup>*</sup>	-	-
Atlantic Bottlenose Dolphin <i>Tursiops truncatus</i> <sup>6</sup>	4.5	4.0	65	6.9	6.2
Common Dolphin <i>Delphinus delphis</i> <sup>7</sup>	4.4	2.4	-	-	-
<b>Phocoenidae</b>					
Harbour Porpoise <i>Phocaena communis</i> (= <i>Phocoena phocoena</i> <sup>8</sup> )	5.4-6.3 <sup>**</sup>	2.7-3.6	73.8	7.3-8.5	3.7-4.9
<b>Pinnipedia, Phocidae</b>					
Southern Elephant Seal <i>Mirounga leonina</i> <sup>9</sup>	4.8	5.3	73.7	6.5	7.2

\* Measurements were taken from the published drawings. \*\* The data for this species were only presented as ranges by the author, except for the mean total length. Data in brackets are standard deviations. <sup>1</sup>Chittleborough, 1955, LM; <sup>2</sup>Mogoe *et al.*, *in prep.*, SEM; <sup>3</sup>Yamane, 1936 (LM) and Matano *et al.*, 1976 (measurements from SEM micrographs). The values are means from the two studies. <sup>4</sup>Present study, SEM; <sup>5</sup>Measurements from LM drawings in Retzius, 1909; <sup>6</sup>Fleming *et al.*, 1981, SEM and

TEM; <sup>7</sup>Reddy, 1996, SEM; <sup>8</sup>Ballowitz, 1907, Drawings from LM; <sup>9</sup>Cummins, *pers. obs.*, LM, in: Cummins and Woodall, 1985. LM: light microscopy; SEM: scanning electron microscopy.

In comparison with other orders of mammals such as rodents and artiodactyls the midpiece of cetacean spermatozoa is relatively short (Table 4.8). The general arrangement in mammalian spermatozoa is a number of small, elongate mitochondria arranged end-to-end and helically wrapped around the midpiece to form a tight coil (Fawcett, 1970; 1975; Gould *et al.*, 1975; Phillips, 1975; Eddy, 1988). The latter scenario is more commonly found, but there is a lot of variation in the length of the midpiece and subsequently the number of mitochondria among the different mammalian orders (Fawcett, 1975; Phillips, 1975; Eddy, 1988), ranging from a short midpiece with as few as 15 gyres of fused mitochondria in man to a long midpiece with up to 300 gyres in rodents (Fawcett, 1970; 1975; Gould *et al.*, 1975).

Table 4.8: Sperm dimensions from different orders of mammals.

	Mean length (µm)				% of total length	
	Number of species	Head	Midpiece	Total length	Head	Midpiece
<b>All Mammalia</b>	171	7.9	18.7	96.9	8.4	19.3
<b>Rodentia</b>	92	7.9	25.3	108.9	7.4	23.2
<b>Artiodactyla</b>	14	6.9	9.9	52.2	13.1	19.0
<b>Cetacea</b>	9	4.7(±1.22)	3.0(±0.78)	54.9(±13.71)	8.6	5.5

Data for all Mammalia, rodents and artiodactyls are taken from Cummins and Woodall, 1985. Standard deviations were not provided for those data. For the overall analysis for the Cetacea, species for which only ranges were provided have been omitted.

A short midpiece is only reported for a few rodent species, namely the coypu *Myocastor coypus*, the chinchilla *Chinchilla laniger* and the casiragua *Proechimys guairae*, and man (Cummins and Woodall, 1985). Retzius (1909) reports a short midpiece in the gibbon *Hylobates*, the porcupine *Hystrix*, the sloth *Bradypus* and in monotremes and remarks that the mitochondria are spherical in shape in the gibbon and the sloth.

Unfortunately, there are no recent data to support these observations. As it is assumed that the conditions in the females' reproductive tract, encountered by the spermatozoa, do not vary a great deal between species no explanation for this diversity in midpiece length in mammalian sperm has been put forward to date (Fawcett, 1975). Thus the arrangement of separate, spherical mitochondria along a short midpiece, as found in the cetacea, is unique among mammals. The only other vertebrate for which spherical mitochondria are reported is the tuatara *Sphenodon punctatus* (Healy and Jamieson, 1992).

The shape and arrangement of the mitochondria found in the two *Kogia* species agrees well with previous findings on cetacean sperm morphology (Retzius, 1909; Reddy, 1996). While Ballowitz reports four rows of mitochondria and shows three or four mitochondria per row in his drawings of the harbour porpoise *P. phocoena* spermatozoa (Ballowitz, 1907), Retzius reports four mitochondria per row and three to four rows for long-finned pilot whale *G. melas* sperm (Retzius, 1909). Three rows and three columns of mitochondria are suggested for the common dolphin *D. delphis* (Reddy, 1996). The estimated total number of mitochondria in cetacean spermatozoa ranges from nine reported for the common dolphin *D. delphis* (Reddy, 1996), 12 for the bottlenose dolphin *T. truncatus* (Fleming *et al.*, 1981), to 12-16 for the long-finned pilot whale *G. melas* (Retzius, 1909) as well as for the harbour porpoise *P. phocoena*. From the SEM and TEM examination the number of mitochondria for either *Kogia* species could range between 20 and 30. These data are in contrast to that of other eutherian mammals, in which the estimated number of mitochondria is much higher (Fawcett, 1965).

While one would think that a short midpiece as well as a low number of mitochondria means a lower potential energy output, it appears that spermatozoa can switch between glycolysis and oxidative phosphorylation in order to obtain energy for motility. As human sperm also have small mitochondrial sheaths and rely heavily on glycolysis rather than respiration, the small number of mitochondria in Cetacea suggests a similar scenario (Jim Cummins, pers. com.). The midpiece of aquatic invertebrates usually comprises one ring-like mitochondrion or a cluster of four spherical mitochondria (Fawcett, 1970). Therefore it may be speculated that, in the Cetacea, the spherical mitochondria present a character that has reverted to the primitive condition (reversal) rather than a pleisiomorphic character.

Total lengths of spermatozoa in mammals range from 39.96 $\mu$ m reported for the pig *Scus scrofa* to 258.32 $\mu$ m for the Chinese hamster *Cricetulus griseus* (Cummins and Woodall, 1985). The inverse relationship between body size and total sperm length in

mammals has been mentioned before (Yamane, 1936) and the cetacea are no exception in this respect (Table 4.8).

The morphology of spermatozoa correlates far better with the environment in which fertilization takes place than it does with systematic characters or phylogenetic rank (Fawcett, 1970). As spermatozoon morphology is thought to be an adaptation to the specific conditions under which fertilization occurs, it is interesting to note that another marine mammal, namely the Southern elephant seal *Mirounga leonina* (Cummins and Woodall, 1985), shows a relatively short midpiece as well. This information is unfortunately based on only one other species, but it would be interesting to examine and compare spermatozoa of other animals with an aquatic lifestyle such as Sirenia, Lutrinae and Pinnipeds.

In conclusion the main features of cetacean sperm, namely a short midpiece with few, spherical mitochondria, are unique within the Mammalia. Unfortunately the physiological processes involved in internal fertilization in an aquatic environment are poorly understood and the implications of these results are not clear.

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## *Chapter 5: Female Reproduction*



## **5.1. Theoretical Background**

The continued survival of a number of cetacean species depends on adequate management plans based on knowledge of the reproductive potential and other basic life history parameters of the species concerned (Read and Gaskin, 1990; Read, 1990a; 1990b; Slooten, 1991; Hohn *et al.*, 1996). In particular, knowledge of female reproductive parameters is important for forming an understanding of the impacts that exploitation, habitat degradation, pollution and other factors may have on a population (Perrin *et al.*, 1976; 1977; Perrin and Henderson, 1984; Perrin and Reilly, 1984; Barlow, 1985; Kasuya, 1985; Myrick *et al.*, 1986; Chivers and Myrick, 1993).

But even for species that are unlikely to be exploited knowledge of the reproductive parameters is essential to facilitate a complete understanding of their life history. This would enable an assessment of possible future impacts on a population from factors like pollution and habitat degradation.

### **5.1.1 Reproductive anatomy**

Cetacean ovaries are situated on the dorso-lateral side of the abdominal cavity just behind the kidneys, placing them roughly in the same position as the testes in the male (Slijper, 1966). The literature on the ovaries of odontocetes has been extensively reviewed by Slijper (1966), Harrison (1969; 1972) and Harrison and McBrearty (1977). These works dealt mainly with the macroscopic examination of the ovaries and the different types of corpora, while others described the histology of the corpora in more detail (Sergeant, 1962; Slijper, 1966; Best, 1967; Fisher and Harrison, 1970; Harrison, 1977; Collet and Harrison, 1981; Ivashin, 1984; Collet and Robineau, 1988; Claver *et al.*, 1992). The histology of corpora found in the ovaries of a *Kogia breviceps* female is described by Harrison *et al.* (1972), and Ross (1979; 1984) briefly describes the macroscopic histology of the ovaries of both *K. breviceps* and *K. sima* from South Africa. Ultrastructural studies of cetacean corpora have been carried out by Bryden *et al.* (1984) and Harrison (1977).

Ovary weights have been provided for a number of species and generally increase with increasing length and age of the animal (Best, 1967; Harrison and Brownell, 1971; Marsh and Kasuya, 1984; Cockcroft and Ross, 1990a; Hohn *et al.*, 1996). Ross (1979; 1984) provides ovary weights and dimensions for seven *K. breviceps*

and 13 *K. sima*. Harrison *et al.* (1972) give ovary weights for one mature *K. breviceps* female.

Probably the most comprehensive work to date on the anatomy, both gross and microscopic, of the female reproductive organs of pygmy and dwarf sperm whales was carried out by Beckmen (1986). She examined nine *K. breviceps* and seven *K. sima* stranded along the Florida coastline and concluded that the reproductive tract of the two *Kogia* species is anatomically similar to that of other odontocetes. Immature ovaries of either *Kogia* species are ellipsoid in shape (Beckmen, 1986), which is common for immature odontocetes (Harrison, 1949). The ovaries become less flattened in mature odontocetes and progressively darker, from a light beige in immature animals to a brownish grey with increasing age (Harrison, 1949; Beckmen, 1986). The ovaries of adult animals of either *Kogia* species are ovoid in shape, although slightly deformed due to the *corpora lutea* (CL's) and *corpora albicantia* (CA's) (Beckmen, 1986). In contrast the ovaries of other adult odontocetes are spherical (Harrison *et al.*, 1972). *Corpora albicantia* in the two *Kogia* species are visible macroscopically in the majority of cases due to conspicuous pigmentation as a result of varying amounts of lipochromes present (Beckmen, 1986). Sectioning of the ovary revealed the CA's to be usually spherical with or without a core and trabeculations, or button mushroom or crescent shaped (Beckmen, 1986). The *corpora lutea* (CL's) were typically mammalian (Beckmen, 1986). Although not observed by Beckmen (1986), Harrison *et al.*, (1972) report a female *K. breviceps* with a pedunculate CL.

The accumulation of ovarian scars in a number of species suggests that, unlike other mammals, the corpora of ovulation persist throughout life in cetaceans (Slijper, 1966; Best, 1967; Kasuya, 1972; Harrison, 1977; Collet and Harrison, 1981; Marsh and Kasuya, 1984; Perrin and Donovan, 1984; Sooten, 1991) and therefore present a reliable record of a females' reproductive history (Perrin and Reilly, 1984). One exception is the Franciscana *Pontoporia blainvillei*, in which the corpora are completely reabsorbed after four years (Harrison *et al.*, 1981). Evidence for the persistence of corpora in the ovaries of the two species of *Kogia* is presented by Ross (1979) and Harrison *et al.* (1972). Although some authors claim to be able to distinguish between the scars of ovulations which were infertile and the scars of ovulations that resulted in a pregnancy (Harrison, 1969; Harrison and Brownell, 1971; Collet and Harrison, 1981; Ivashin, 1984), the majority of investigators were not able to reliably differentiate two different types of scars (Perrin *et al.*, 1976; Benirschke *et al.*, 1980; Lockyer, 1984; Perrin and Donovan,

1984; Beckmen, 1986; Slooten, 1991). It has, however, been suggested that the state of the endometrial histology would be a better guide to distinguish between a current or recent pregnancy and an infertile ovulation (Benirschke *et al.*, 1980). The number of scars present in the ovary of a specimen reflects the number of ovulations the animal has had during the course of its life and is therefore an indication of the ovulation rate. It may not, however, accurately represent the number of past pregnancies as a few cetacean species exhibit a number of infertile ovulations at the onset of sexual maturity (Sergeant, 1962; Perrin *et al.*, 1976; Collet and Harrison, 1981; Miyazaki, 1984; Perrin and Reilly, 1984; Cockcroft and Ross, 1990a; Read, 1990a). Furthermore, CL's have been recorded in animals, which, upon closer examination, were not pregnant (Benirschke *et al.*, 1980). Thus ovulation can occur without a subsequent pregnancy as was reported for a number of delphinids (Harrison and McBrearty, 1977; Benirschke *et al.*, 1980; Benirschke and Marsh, 1984). Size ranges for CL's as well as CA's in the two *Kogia* species were provided by Beckmen (1986) and Ross (1979; 1984).

Although accessory corpora (defined as more than one CL occurring per fetus in a pair of ovaries) have occasionally been reported for other cetaceans (Sergeant, 1962; Harrison and McBrearty, 1977), including the sperm whale *Physeter macrocephalus* (Best, 1967), and occur frequently in belugas *Delphinapterus leucas* (Sergeant, 1973; Braham, 1984) and narwhals *Monodon monoceros* (Perrin and Donovan, 1984), there have been no reports for such a phenomenon in either species of *Kogia* (Beckmen, 1986).

The CL of pregnancy persists throughout gestation in cetaceans (Matthews, 1938; Best, 1967; Marsh and Kasuya, 1984; Perrin and Donovan, 1984) and rapidly regresses after birth (Sergeant, 1962; Harrison *et al.*, 1969; Fisher and Harrison, 1970; Harrison *et al.*, 1981; Marsh and Kasuya, 1984; Perrin and Donovan, 1984). The rate of regression of CL's and CA's has been covered in detail by Best (1968), Perrin *et al.* (1976) and Kasuya and Marsh (1984), and briefly by Kasuya *et al.* (1974), Cockcroft and Ross (1990a) and Read (1990b).

Harrison (1949) remarks on transverse vaginal folds found in the pilot whale *Globicephala melas* and gives a short overview of this phenomenon. The number of folds varies between different species of cetaceans, but also within a species. It is thought that the penis probably penetrates these folds during intercourse and that their function is to promote the emission of seminal fluid. The seminal fluid would collect in the chambers formed by the vaginal folds, which will prevent seawater from entering the

uterus (Harrison, 1949; Slijper, 1966), and probably be transported towards the uterus by means of muscular contraction. Beckmen (1986) found a lot of individual variation in size, location and configuration of these folds in both *Kogia* species and the number of folds varied from one to five or more (Beckmen, 1986).

### 5.1.2 Spontaneous and induced ovulations, and ovarian symmetry

The question of whether cetaceans have copulation-induced ovulations or ovulate spontaneously remains unresolved, although it is important in the interpretation of ovarian corpora and ovulation rates (Perrin and Reilly, 1984). Some mammals have either exclusively or predominantly copulation-induced ovulation, while the vast majority exhibits spontaneous ovulation. There is some evidence for copulation-induced ovulation in the bottlenose dolphin *Tursiops truncatus* (Harrison *et al.*, 1969; Harrison, 1977; Harrison and McBrearty, 1977), although evidence for spontaneous ovulation was also presented for the species (Kirby, 1984; Kirby and Ridgway, 1984; Ozharovskaya, 1990; Cockcroft and Ross, 1990a). Spontaneous ovulation has been reported for a number of other delphinids (Harrison *et al.*, 1969; Benirschke *et al.*, 1980; Collet and Harrison, 1981; Kirby, 1984).

Some mammals ovulate almost exclusively from one ovary, whereas in other species both ovaries seem to be functional and therefore either exhibit equal ovulation rates or one ovary being more active than the other (Asdell, 1946; Ohsumi, 1964). Ohsumi (1964) collected ovaries from mature females of 23 species of Cetacea containing representatives of all families except those comprising the river dolphins. From the examination of the number of corpora present in the left and the right ovary, he described three different types of accumulation rates. Species belonging to the same genus show the same type of corpora accumulation. All species of mysticetes have an equal accumulation rate in the left and right ovary (Type I). Although only one specimen of *Kogia* (unidentified to species level) was available to him, which had six corpora in the left ovary and seven in the right, he included the family in the Type I ovulation pattern; the animal was not identified to species level. The sperm whale *P. macrocephalus* was also included in the Type I pattern. It is interesting to note that another family of the odontocetes, the Ziphiidae, are also reported to have a Type I ovulation pattern, whereas all the other families in the odontocetes fall in the Type II or III category (Ohsumi, 1964). Both Type II and III categories are characterised by the

right ovary maturing somewhat later than the left one, resulting in a higher accumulation rate in the left ovary in younger animals, which is exceeded by the number of ovulations from the right ovary in older animals (Ohsumi, 1964). The main difference between the Type II and Type III ovulation pattern is that the difference in accumulation rate between the left and right ovary is only slight in the Type II pattern, but quite pronounced in the Type III pattern (Ohsumi, 1964).

Subsequent examinations support Ohsumi's findings that odontocetes ovulate predominantly or exclusively from the left ovary (Best, 1967; Fisher and Harrison, 1970; Harrison and Ridgway, 1971; Perrin *et al.*, 1977; Benirschke *et al.*, 1980; Collet and Harrison, 1981; Cockcroft and Ross, 1990a; Read, 1990b; Claver *et al.*, 1992; Sørensen and Kinze, 1994; Read and Hohn, 1995; Hohn *et al.*, 1996; Dans *et al.*, 1997) and a Type III accumulation pattern has been described for the Franciscana *P. blainvillei*, in contrast to a Type I pattern in the other river dolphins (*Inia geoffrensis*, *Platanista minor* and *P. gagentica* and *Lipotes vexilifer*) (Brownell, 1984). Harrison, Brownell and Boice (Harrison *et al.*, 1972) state that a 303cm female *K. breviceps* stranded at Jekyll Island, Georgia, had seven corpora in the left ovary and eight in the right ovary, which would support Ohsumi's (1964) findings. Beckmen (1986) also reports an equal accumulation rate in both ovaries as well as an equal implantation rate in both uterine horns for both *Kogia* species, but her sample size did not allow any statistical examination of the data.

### 5.1.3 Attainment of sexual maturity (ASM)

Unlike the gradual process of sexual maturation in male cetaceans, female maturation is rapid and the onset of sexual maturity is generally defined as the age at which a female has ovulated at least once as evidenced by the presence of at least one corpus in her ovaries (Perrin and Donovan, 1984). The corpora, reflecting the females' past reproductive history (Perrin and Donovan, 1984), can be related to the age of the animal in order to determine the age of first ovulation, the birth interval, and the female's reproductive lifespan. This in turn, can lead to further indications as to the reproductive ability of the whole population. Histological examination of the uterus can give further information on the females' reproductive status (Benirschke *et al.*, 1980; Slooten, 1991).

There have been conflicting results on the effects of exploitation on the attainment of sexual maturity (ASM) in small cetaceans (Read and Gaskin, 1990). Sexual maturity was reached at a shorter body length and a younger age in the more

exploited stock of spinner dolphins *Stenella longirostris* in the eastern tropical Pacific than in the less exploited stock (Perrin *et al.*, 1977; Perrin and Henderson, 1984), while no change in age at ASM was found for exploited spotted dolphins *S. attenuata* in the same area (Myrick *et al.*, 1986). But ASM can vary between different parts of the same population as seen in the northern form of short-finned pilot whales *G. macrorhynchus* that reached sexual maturity at a longer length, but at approximately the same age as the southern form (Kasuya and Marsh, 1984; Kasuya and Tai, 1993). Length is usually a better indicator than age for the attainment of sexual maturity (Hohn *et al.*, 1985). This is not least due to errors involved in the age estimation of cetaceans (see Chapter 3).

The attainment of sexual maturity often occurs at a younger age and shorter body length in females than in males of the same species (Laws, 1956; Sergeant, 1962; Perrin and Reilly, 1984; Evans, 1987; Cockcroft and Ross, 1990a; Kasuya and Tai, 1993) and the length at ASM was found to be remarkably constant in female cetaceans, occurring on average at 85.1% (range 80.0-88.5%) of asymptotic length (Laws, 1956).

The slow-fast continuum found in other mammals can also be observed in cetaceans (see Chapter 9). The smaller odontocetes like the phocoenids attain sexual maturity at an early age between three and six years (Read, 1990a; Read and Hohn, 1995; Hohn *et al.*, 1996), while the smaller delphinids reach sexual maturity around six to seven years (Perrin and Henderson, 1984; Perrin and Reilly, 1984; Slooten, 1991; Dans *et al.*, 1997). Larger delphinids reach sexual maturity between eight and 16 years (Perrin and Reilly, 1984; Cockcroft and Ross, 1990a; Kasuya and Tai, 1993) and mysticetes between eight and 12 years (Lockyer, 1984; Evans, 1987). In contrast, the largest mammal on earth, the blue whale *Balaenoptera musculus*, matures at five to six years of age (Evans, 1987). Age at ASM is not available for either *Kogia* species, but Ross (1979; 1984) estimated the length at ASM to be between 270 and 280cm for female *K. breviceps* and between 210 and 220cm for female *K. sima* (Ross, 1979). Larger delphinids appear to have longer life spans (between 25-50 years) than the smaller dolphins (up to 20 years) (Perrin and Reilly, 1984; Slooten, 1991) or the porpoises (up to 24 years) (Hohn and Brownell, 1990; Lockyer, 1995a), while age estimates of mysticetes indicate lifespans in excess of 100 years (George *et al.*, 1997).

The biases and degrees of precision resulting from different ways of estimating age at ASM in cetaceans have been reviewed by Perrin and Reilly (1984) and in more detail by DeMaster (1984), who found the mean age of first time ovulators the best estimate. However, most of these estimates require large sample sizes and will thus not

be applicable to the present study.

## 5.1.4 Ovulation rate and reproductive cycle

### 5.1.4.1 Ovulation rate

The number of ovulations a female has per year is termed the annual ovulation rate and is usually obtained from the slope of the regression equation of the ages of all mature females versus the total number of corpora (Myrick *et al.*, 1986; Cockcroft and Ross, 1990a). If the maximum longevity of a species is known, the ovulation rate can provide an estimate about the maximum lifetime productivity (i.e. the maximum number of offspring in a lifetime) per female, which in turn is important for population management.

The occurrence of a number of infertile ovulations at the onset of sexual maturity in some odontocetes and the decline in ovulation rate with age as well as female senescence have already been discussed. Age-specific ovulation rates can be calculated when the sample is large enough to be divided into age classes (Best, 1980; Marsh and Kasuya, 1984; Perrin and Donovan, 1984; Marsh and Kasuya, 1986), while observations on smaller samples can only indicate a trend in the number of ovulations in relation to age. For example, young female harbour porpoises *Phocoena phocoena* up to the age of four years ovulate more than once per year without becoming pregnant, whereas older females usually ovulate only once per year and achieve conception (Read, 1990a). In contrast, ovulations in older female short-finned pilot whales *G. macrorhynchus* result less often in pregnancy than in younger females (Kasuya and Marsh, 1984; Kasuya and Tai, 1993). Furthermore, fecundity can vary even between different populations of the same species and consequently the comparatively shorter reproductive cycles (defined as the timespan between births) and higher fecundity rates of dusky dolphins *Lagenorhynchus obscurus* off Peru have been attributed to exploitation or to an adaptive strategy to deal with food shortage due to El Niño events (van Waerebeek and Read, 1994).

It is unlikely that all females of a population reach sexual maturity at the same age and subsequently have the same ovulation rate (Collet and Robineau, 1988). Great variation occurs in ovulation rates among odontocetes (Sergeant, 1962; Perrin and Donovan, 1984; Myrick *et al.*, 1986) and there is usually a high variability in the number

of corpora between individual females of the same age for a given population (Perrin *et al.*, 1976; Marsh and Kasuya, 1984; Cockcroft and Ross, 1990a). The factors that contribute to this variation include unreliability of age estimates, variation in the age at ASM, and change in ovulation rate during the reproductive life span (Perrin *et al.*, 1976; Perrin *et al.*, 1977; Marsh and Kasuya, 1984). As the relationship between estimated age and the number of corpora cannot always be satisfactorily described by a straight line, some researchers have fitted a curve instead (Perrin *et al.*, 1976; Marsh and Kasuya, 1984). Those data suggested that the ovulation rate decreases continuously throughout life in short-finned pilot whales *G. macrorhynchus* (Marsh and Kasuya, 1984).

The occurrence of reproductively “senescent” females has been reported for a number of odontocetes (Sergeant, 1962; Best, 1967; Perrin *et al.*, 1976; Perrin *et al.*, 1977; Best, 1980; Kasuya and Marsh, 1984; Myrick *et al.*, 1986; Kasuya and Tai, 1993; Sørensen and Kinze, 1994), while no evidence for this is present in other species and populations of odontocetes (Cockcroft and Ross, 1990a; Read, 1990a). Several criteria have been used to identify post-reproductive females in cetacea. These include a decline in the pregnancy rate with age (Best, 1967; Perrin *et al.*, 1976; Best, 1980), a decline in the lactation rate (Perrin *et al.*, 1976) and in the ovulation rate with age (Marsh and Kasuya, 1984; Myrick *et al.*, 1986), absence of young CA’s (indicating no recent ovulations) in the ovaries of older females (Sergeant, 1962; Perrin *et al.*, 1977; Sørensen and Kinze, 1994), regressed mammary glands (Sergeant, 1962), withered or atrophied ovaries (Perrin *et al.*, 1977), lowered mean ovary weights (Myrick *et al.*, 1986), absence of large follicles in the ovaries (Perrin *et al.*, 1977; Myrick *et al.*, 1986; Sørensen and Kinze, 1994), a decrease in follicle abundance (Marsh and Kasuya, 1984), follicular degeneration or atresia with age (Sergeant, 1962; Best, 1967; Marsh and Kasuya, 1984), and other histological changes of the ovary (Marsh and Kasuya, 1984; Sørensen and Kinze, 1994). However, not all these criteria reliably indicate senescence in female cetaceans and this subject has been reviewed thoroughly by Marsh and Kasuya (1986). In all female mammals the entire number of oocytes is produced prior to birth and follicle production is always in excess of the number that ovulate. Thus the two major factors influencing the age at senescence are the depletion of oocytes and age-related, degenerative changes of the uterus (Marsh and Kasuya, 1986). These have also been reported in long-finned pilot whales *G. melas* (Sergeant, 1962). Post-reproductive female short-finned pilot whales *G. macrorhynchus* have an average life expectancy of another 14 years (Marsh and Kasuya, 1984; 1986), whereas the ages of two senescent harbour

porpoises were 18 and 19 years, respectively (Sørensen and Kinze, 1994). This is close to the maximum age of 24 years reported for the species (Hohn and Brownell, 1990; Lockyer, 1995a). Post reproductive females are observed less frequently in long-finned pilot whales *G. melas* (Sergeant, 1962) and spotted (*S. attenuata*) and spinner dolphins (*S. longirostris*) (Perrin *et al.*, 1976; Perrin *et al.*, 1977) than in short-finned pilot whales *G. macrorhynchus* (Marsh and Kasuya, 1984) and evidence for non-reproductive matings in the latter species suggests that the social system may be the determining factor for these differences (Myrick *et al.*, 1986; Kasuya *et al.*, 1993).

#### 5.1.4.2 Gestation

While gestation lengths in baleen whales range from 10 months in right whales (*Eubalaena australia* and *E. glacialis*) and minke whales (*B. acutorostrata*) to 12 or 13 months in the bowhead whale *Balaena mysticetus*, sei whale *B. borealis* and pygmy right whale *Carporea marginata* (Lockyer, 1984; Evans, 1987), the range of gestation lengths is much broader in odontocetes. The river dolphins exhibit gestation lengths around 10 months (Brownell, 1984; Evans, 1987) and the porpoises around 11 months (Gaskin *et al.*, 1984; Evans, 1987). In the dolphins, pregnancy can last between 10 and 12 months in the smaller species and 11 to 16 months in the larger pilot whales (genus *Globicephala*) and the killer whale *Orcinus orca* (Perrin and Reilly, 1984; Evans, 1987). Monodontidae have gestation lengths of 14 and 15 months (Braham, 1984; Evans, 1987) and the longest gestation reported for odontocetes and in fact for any cetacean is that of the sperm whale *Physeter macrocephalus*, which can last 15 to 17 months on average and up to 19 months maximum (Best, 1968; Best *et al.*, 1984; Evans, 1987). However, within a species of delphinid gestation length is one of the least variable reproductive parameters (Perrin and Reilly, 1984). The length at birth for either *Kogia* species has been discussed in detail in Chapter 3 and estimates of birth size have been used to estimate the length of gestation in delphinids (Kasuya, 1977). These data will be used to verify the length of gestation in the two species of *Kogia*.

Observations of cetacean parturitions both in the wild and captivity are rare. The only account published on a parturition in a *Kogia* species is by Hückstädt and Antezana (2001) on a 277cm long female *K. breviceps*, which gave birth to a male foetus and was accompanied by a 153cm long male calf. Unfortunately, no data were available on the length of the newborn.

#### 5.1.4.3 Lactation and weaning

Only few studies have been carried out on lactation in cetacea and even less information is available on its energetic demands on the mother. Data on the composition of whale milk in general and *K. breviceps* milk in particular are presented by Slijper (1966) and Jenness and Odell (1978), respectively. Cetacean milk is much richer in fat than that of most terrestrial mammals (Gaskin, 1982), possibly because the offspring needs to grow at a fast rate after birth to reach a smaller surface area to volume ratio, which is more advantageous in the cool aquatic environment. Although the energetic demands increase exponentially in the second half of pregnancy in baleen whales (Evans, 1987), the overall costs of lactation were higher than the costs of gestation in fin whales *B. physalus* and probably most other whales (Evans, 1987; Lockyer, 1987). Cockcroft and Ross (1990b) came to the same conclusion when estimating the energy required for lactation in a bottlenose dolphin *T. truncatus*. Furthermore, body condition, food abundance and fertility are intimately linked in a number of marine mammals (Lockyer, 1987; Stewart *et al.*, 1989). The costs of lactation are greater in recently matured females as they are still actively growing to reach physical maturity (Evans, 1987). The length of lactation ranges from five to six months in bowhead whales *B. mysticetus* and pygmy right whales *C. marginata* to 10-12 months in humpback whales *Megaptera novaeangliae* (Lockyer, 1984; Evans, 1987). While mysticetes appear to invest more energy in calf bearing, as reflected by the longer gestation lengths in relation to duration of lactation, odontocetes seem to invest more in calf rearing (Evans, 1987). As already observed with gestation length, the duration of lactation varies greatly among the odontocetes and is the most variable component of the reproductive cycle (Gaskin *et al.*, 1984; Perrin and Reilly, 1984; Evans, 1987; Read, 1990b). For the majority of odontocetes the lactation period lasts between 18 and 20 months, although some solid food will be taken on average from six months onwards (Sergeant, 1962; Evans, 1987; Cockcroft and Ross, 1990b). In the sperm whale *P. macrocephalus* the length of lactation is on average 24 to 25 months (Best, 1968; Evans, 1987), but some male sperm whales may suckle for up to 13 years, females up to 7.5 years (Best *et al.*, 1984). This is thought to have a social function rather than a nutritional one (Best *et al.*, 1984). One reason why the length of lactation appears so varied in odontocetes may be that the lactation period is more difficult to estimate than the length of gestation (Evans, 1987).

Weaning is a response to increased energy requirements resulting from growth and possibly also increased activity of the young (Cockcroft and Ross, 1990b). Solids are taken on average from six months onwards, although in some species calves appear to feed independently from as early as three months of age (Perrin and Reilly, 1984). In calves of the bottlenose dolphin *T. truncatus* solids first appear in the stomach at six months of age, although milk remains are still present until three years of age (Cockcroft and Ross, 1990a). Lactation in species inhabiting inshore waters may last longer as calves may need a greater amount of maternal care and a longer learning period in order to master the more complex inshore environment (Cockcroft and Ross, 1990b). Weaning may coincide with a peak in food availability as reported for the northern form of short-finned pilot whales *G. macrorhynchus* off Japan (Kasuya and Tai, 1993). Usually the age at weaning is estimated from the oldest suckling calf in the sample, but the result may be biased by individual variation in growth rate (Evans, 1987). Another method determines the presence of lactose in the stomachs of calves (Best *et al.*, 1984). Although an estimate of the age at weaning can be obtained by either method, some species may continue suckling for long periods of time to maintain the social bond (“social suckling”) as seen in the sperm whale *P. macrocephalus*, and therefore this estimate may be biased (Evans, 1987).

In *K. breviceps* the calf usually stays with the cow during the first year (Allen, 1941). Evidence from South Africa suggests that calves stop suckling between 171cm and 202cm of body length (Ross, 1979). A 189cm calf from Australia was still reported to be suckling (Hale, 1962). Data from the south-eastern United States suggest that the young may take solid food from 160cm onwards (Caldwell and Golley, 1965). The close association between mother and calf probably ends shortly after weaning in *K. breviceps* (Ross, 1979). *K. sima* from South Africa may suckle until over 150cm in length, but a 136cm long calf already showed indications of taking solid food (Ross, 1979).

#### **5.1.4.4 Simultaneous lactation and pregnancy**

Simultaneous lactation and pregnancy is not uncommon in cetaceans and has been reported for a number of species (Best, 1968; Perrin *et al.*, 1976; Perrin *et al.*, 1977; Marsh and Kasuya, 1984; Miyazaki, 1984), but is usually only found in a very low percentage of the total sample of adult females.

The phenomenon of simultaneously lactating and pregnant females indicates that

the females can conceive during lactation (Best, 1968; Perrin *et al.*, 1976; Kasuya and Tai, 1993). A detailed investigation of this phenomenon in short-finned pilot whales *G. macrorhynchus* showed that females conceive either towards the end of lactation and/or that once lactating females become pregnant they cease lactation soon afterwards (Kasuya and Tai, 1993). In sperm whales *P. macrocephalus* post-partum, mid-lactation and post-lactation ovulations are rare, but about 39% of mature females show at least one ovulation in late lactation and almost all females ovulate after the resting period (Best, 1968). Based on the occurrence of Graafian follicles in lactating female spotted dolphins *S. attenuata* Perrin *et al.* (1976) suggest that oestrus occurs sometime after parturition as opposed to immediately after parturition. A true postpartum oestrus followed by a pre-implantation pregnancy was described for harbour porpoises *P. phocoena* (Read, 1990b).

Among the mysticetes, humpback whales *M. novaeangliae* are often observed with calves in successive years, although the most common reproductive cycle lasts two to three years (Straley *et al.*, 1994). This implies that the females are capable of conceiving at postpartum ovulation. Evidence has emerged that these postpartum pregnancies are successful and that older females appear better in achieving annual reproduction (Straley *et al.*, 1994). Annual reproduction in this species may be a common event, but only a small percentage of mature females may be able to maintain it and deal with the constraints involved (Straley *et al.*, 1994). The maintenance of a postpartum pregnancy could be dependent on the physiological and metabolic condition of the mother and is probably intimately linked to sufficient prey resources (Straley *et al.*, 1994).

Simultaneously pregnant and lactating *Kogia* are reported frequently (Allen, 1941; Hale, 1947; Ross, 1979; Odell *et al.*, 1984; Price *et al.*, 1984; Ross, 1984; Beckmen, 1986; Credle, 1988; Hückstädt and Antezana, 2001), which led to speculations that some females may breed annually (Ross, 1979; Baird *et al.*, 1996). However, to date there are no data on ovulation rates to support this suggestion.

#### 5.1.4.5 Resting period

Female cetaceans that are neither pregnant nor lactating are usually classified as resting (Perrin and Reilly, 1984) and the resting period is a stable part of the reproductive cycle of many cetaceans (Best, 1968; Lockyer, 1984; Perrin and Reilly, 1984). The

resting period is thought to aid in refilling the energy reserves of the female exhausted by the high costs of lactation discussed above (Gaskin, 1982). This resting phase can range between two and fifteen months in odontocetes (Best, 1968; Perrin and Reilly, 1984; Cockcroft and Ross, 1990a), but on average lasts four to five months (Perrin and Reilly, 1984; Evans, 1987). Lactation and resting phase may lengthen with age in the striped dolphin *S. coeruleoalba* and as a result the reproductive cycle becomes longer in older females (Miyazaki, 1984). The resting period may be absent in species that exhibit annual ovulations such as the harbour porpoise *P. phocoena* (Read and Hohn, 1995) and Dall's porpoise *Phocoenoides dalli* (Ferrero and Walker, 1999).

### 5.1.5 Seasonality

The concepts underlying seasonal reproduction in mammals have already been introduced in Chapter 4 and the most accessible data describing the seasonal reproduction of a species in marine mammals are derived from the calving period (Barlow, 1984).

Seasonal reproduction has been observed widely in cetaceans. Mysticetes typically show a definite, highly synchronised annual reproductive season, whereas in odontocetes a variety of patterns are observed (see Kasuya, 1995 for a review of parturition season and calving peaks). Some odontocetes exhibit a definite calving season, which is often protracted over a few months (Best, 1968; Sergeant, 1973; Braham, 1984; Aguilar, 1991; van Waerebeek and Read, 1994; Dans *et al.*, 1997). In contrast, the seasonal frequency of ovulations in long-finned pilot whales *G. melas* showed that ovulations probably occur throughout the year and thus the observed calving peak must be due to the reported seasonal trend in the male reproductive activity (Sergeant, 1962). An extremely high degree of reproductive synchrony is found in the harbour porpoise *P. phocoena* from the North Atlantic (Fisher and Harrison, 1970; Gaskin *et al.*, 1984; Read, 1990b; Read and Hohn, 1995), with the vast majority of births occurring over a one month period (Read, 1990b; Read and Hohn, 1995). Possibly a similar scenario is found in the vaquita *P. sinus* (Hohn *et al.*, 1996). The obvious implications of synchronized reproduction are that a female that either fails to mate, fails to fall pregnant, aborts her foetus or loses her calf, will have to wait for the next mating season (which may be as long as 12 months away) in order to mate again (Barlow, 1984; Read, 1990b) (see Chapter 4). A short breeding season is a reflection of the limited time

span in which conditions are suitable for calving (Kasuya, 1995). Some odontocete species show births all year round, but exhibit a calving peak over part of the year, a phenomenon that is termed “diffusely seasonal” (Sergeant, 1962; Harrison and Ridgway, 1971; Wells *et al.*, 1987; Cockcroft and Ross, 1990a; Martin and Rothery, 1993; Thayer *et al.*, 2003).

Synchrony and seasonality of reproduction vary with latitude in many terrestrial mammals. At high latitudes, where the seasons are more pronounced, births occur over a well-defined short period and are timed in such a way that the elevated energy demands of females and their offspring coincide with times of maximum food availability (Bronson, 1989). In the tropics the birthing period is much less pronounced with reproduction often occurring year-round (Bronson, 1989). This general latitudinal pattern of reproductive seasonality can also be observed in odontocetes (Barlow, 1984; Read, 1990b), but it appears that populations of the same species at similar latitudes can exhibit distinctly different patterns of reproduction (Urian *et al.*, 1996). Geographical differences in reproductive seasonality, which supported differentiation into different populations, have been observed within stocks of spotted and spinner dolphins (*Stenella* spp.) in the eastern tropical Pacific (Barlow, 1984).

Most cases of seasonal reproduction in terrestrial mammals reflect variation of interacting dietary and climatic factors: namely food, rainfall and temperature (Bronson, 1989). Photoperiod, which changes with latitude, influences the length of the pupping season in captive California sea lions *Zalophus californianus* (Temte and Temte, 1993), although latitude does not affect reproductive seasonality in bottlenose dolphins *T. truncatus* (Urian *et al.*, 1996). More likely the seasonal availability of local resources like primary prey species may play a role in the seasonal timing of reproduction in this species (Urian *et al.*, 1996). In Atlantic harp seals *Phoca groenlandica* environmental factors like storms and lack of suitable ice conditions in addition to female body condition have an influence on the timing of reproduction (Stewart *et al.*, 1989). Lactational demands often bring about a change in dietary requirements (Bernard and Hohn, 1989; Young and Cockcroft, 1994) (see Chapter 6), which results in the timing of reproduction being closely related to seasonal peaks in food availability and abundance (Wells *et al.*, 1987; Bernard and Hohn, 1989; Aguilar, 1991; Young and Cockcroft, 1994) as well as prey quality (Read, 1990b). Another factor that may determine seasonal reproduction in cetaceans is water temperature, which in turn may affect prey availability (Urian *et al.*, 1996), but may also be important for the thermoregulatory

requirements of the calf (Wells *et al.*, 1987; Aguilar, 1991).

Differences in seasonality between different populations of the same species were reported in striped dolphins *S. coeruleoalba* (Kasuya, 1972; Miyazaki, 1984; Aguilar, 1991), short-finned pilot whales *G. macrorhynchus* (Kasuya and Marsh, 1984; Kasuya and Tai, 1993) and the harbour porpoise *P. phocoena* (Read, 1990b; Sørensen and Kinze, 1994) and were attributed to differences in climate (Sørensen and Kinze, 1994), food availability (Barlow, 1984; Aguilar, 1991; Kasuya and Tai, 1993) and food quality (Read, 1990b; Sørensen and Kinze, 1994), variation in water temperatures (Aguilar, 1991; Kasuya and Tai, 1993) and degree of exploitation (Barlow, 1984).

Allen (1941) suggests that mating in *K. breviceps* takes place in late summer in the Northern Hemisphere and birth in the following spring after about nine months of gestation. The possibility of food availability as well as temperature playing a role in the reproductive seasonality of the two *Kogia* species will be further explored in Chapters 6 and 7. Other, perhaps less major, factors influencing seasonality are competition between different populations or species for similar types of resources (see Chapter 6) and avoidance of predation by either concentrating or spacing out of births (Rutberg, 1987; Wells *et al.*, 1987; Bronson, 1989).

### 5.1.6 Reproductive strategy

As seen from the data on length of gestation, lactation, and resting period, the majority of mysticetes and odontocetes exhibit a reproductive cycle that lasts between two and three years (Sergeant, 1962; Gaskin, 1982; Brownell, 1984; Gaskin *et al.*, 1984; Lockyer, 1984; Perrin and Reilly, 1984; Evans, 1987; Cockcroft and Ross, 1990a). Exceptions already mentioned include some populations of the harbour porpoise *P. phocoena* (Gaskin *et al.*, 1984; Read, 1990a; Read and Hohn, 1995), the Dall's porpoise *P. dalli* (Kasuya, 1978; Ferrero and Walker, 1999), minke whales *B. acutorostrata* (Masaki, 1979 in: Lockyer, 1984; Lockyer, 1984) and individual humpback whales *M. novaeangliae* (Straley *et al.*, 1994), which all show annual reproductive cycles. Another exception is the sperm whale *P. macrocephalus*, which has a calving interval of four to six years (Best, 1968; Best *et al.*, 1984).

Larger odontocetes appear to have a longer lifespan, but do not necessarily produce a substantially larger number of offspring as they become sexually mature at a later stage and have longer inter-calf intervals (Slooten, 1991). Consequently the number

of calves produced per lifetime in long-finned pilot whales *G. melas* was estimated to be nine (although no estimate for lifespan was given) (Sergeant, 1962), while that for the Hector's dolphin *Cephalorhynchus hectori* (lifespan: 19yrs; Slooten, 1991) and other small odontocetes like the Commerson's dolphin *C. commersonii* (lifespan: 18yrs; Collet and Robineau, 1988; Lockyer *et al.*, 1988), harbour porpoise *P. phocoena* (lifespan: 15yrs; Gaskin *et al.*, 1984; Read, 1990a) and the Franciscana *P. blainvillei* (lifespan: 16yrs; Kasuya and Brownell, 1979; Brownell, 1984) was estimated at four to seven (Slooten, 1991).

### 5.1.7 Foetal and juvenile sex ratio

Biased foetal and juvenile sex ratios are commonly observed in mammals (Clutton-Brock and Iason, 1986) and are also reported for a few cetacean species (Aguilar, 1991; Read and Hohn, 1995; Lockyer, 1995a; Clapham, 1996). The theory that under certain conditions natural selection favours parental ability to adjust the sex ratio of their offspring was first put forward by Trivers and Willard (1973). Maternal condition as well as parental investment is reflected in the fitness of their offspring and males in good condition may gain access to more females and thus pass on their genes to more offspring than females in similar condition (Trivers and Willard, 1973). Breeding success of males of polygynous species generally depends on their fighting ability (male-male competition over females) and therefore body size (Clutton-Brock *et al.*, 1984; Clutton-Brock and Iason, 1986) (see Chapter 4). This in turn is a result of growth and nutrition during the first months and years of their lives (Clutton-Brock *et al.*, 1984; 1985). Nutrition has a weaker influence on growth in females than in males and there is no evidence that this trend is reversed in species where females are larger than males (Clutton-Brock *et al.*, 1984; 1985). Clutton-Brock *et al.* (1985) and Clapham (1996) suggest that different selection pressures operate on males and females concerning body size and larger female size may have evolved to ensure reproductive success, as bigger females are better mothers (Ralls, 1976). Accordingly a female in good condition should invest in male offspring in order to leave more surviving offspring, while a female in poor condition should invest in female offspring (Trivers and Willard, 1973). Existing data from mammals and subsequent research support this theory (Clutton-Brock *et al.*, 1984; 1985; Clutton-Brock and Iason, 1986; Wiley and Clapham, 1993). Other factors that may lead to a biased sex ratio include competition between parents and offspring,

the age, fecundity and nutrition of the mother, stress, habitat quality, population demographics and climatic variation (Clutton-Brock and Iason, 1986).

Data about the effects of parental investment on the fitness of the offspring and the costs of producing and rearing the two sexes is still scanty. In red deer, for example, nutrition may affect the fitness of sons more, whereas social assistance may be more important for the fitness of daughters (Clutton-Brock and Iason, 1986). In many sexually dimorphic species food shortage may have a greater effect on male than on female offspring as they have faster growth rates associated with higher metabolic rates (Ralls *et al.*, 1980; Clutton-Brock and Iason, 1986). The trends found in mammal populations will almost certainly not conform to any single adaptive hypothesis, but will be the result of a number of factors.

### **5.1.8 Aim of the present chapter**

In the present study, length and age at ASM were determined based on the examination of ovarian corpora. Using these results annual ovulation rates and maximum lifetime reproductive output were calculated. Ovarian symmetry and indicators of a seasonal reproductive cycle in both species were examined. The lengths of the gestation and lactation periods were determined and conclusions were drawn about the reproductive strategies employed by females of either species of *Kogia*.

## **5.2 Materials and Methods**

### **5.2.1 Sample**

Reproductive organs from 25 female *K. breviceps* and 26 female *K. sima* from South Africa were examined to determine the reproductive status of the individual animals.

### **5.2.2 Determination of past reproductive history**

Ovaries were weighed, sectioned at 1mm intervals and examined macroscopically to determine the total number of CL's and CA's for each animal. Since corpora atretica result from non-ovulatory events (Best, 1967; Perrin and Donovan, 1984) these were not included in the corpora count. Although CA's in *Kogia* are easily

visible macroscopically, *corpora atretica* can apparently be confused with old shrunken CA's in this genus (Beckmen, 1986), although Ross (1979; 1984) did not report this. Since the fixation of the material was too poor to allow detailed histological examination and, as CA's are relatively larger than *corpora atretica* (Beckmen, 1986), I am confident that *corpora atretica* were not mistaken for CA's. Where possible the total number of corpora in the left ovary versus the total number of corpora in the right ovary was also recorded. The length, height and width of the CL's and the largest CA were measured using vernier callipers and a corpus index ( $\text{mm}^3$ ) was calculated for each (after Cockcroft and Ross, 1990a).

The reproductive condition of the females (i.e. lactating and/or pregnant) at the time of stranding was recorded as was the total length, weight and sex of the foetuses. Lactating females and calves that stranded together were considered cow/calf pairs (sensu Cockcroft and Ross, 1990a). If the larger female was not lactating, but both animals stranded in the same location on the same date or a few days apart, they were considered possible cow/calf pairs. The same was assumed in the case of some refloated animals where definite relationships could not be established.

### 5.2.3 Examination of seasonality

To examine the seasonality of mating and calving in *K. breviceps* three foetuses and 11 juveniles from Australia were included in the sample as they originate from the same hemisphere and may thus reflect the same seasonality (see Appendix C). Although age estimates were only available for eight of the 11 juveniles the other three were included as their lengths fell within the range for animals up to and including two years of age as indicated by the growth curve (i.e. 210cm) (see Chapter 3). Similarly four South African juveniles with no age estimate were included. For *K. sima* no Australian foetuses or juveniles were included and age estimates were only available for three South African juveniles. However, the total lengths of the remaining four juveniles fell within the range for animals up to and including two years (i.e. 160cm) and were thus included in the analysis.

## **5.3 Results**

### **5.3.1 Female Reproduction**

The colour of the ovaries of both species changed from beige or white in immature ovaries (i.e. ovaries without Graafian follicles or corpora) to dark grey, dark brown or black in mature ovaries (Figure 5.1).

#### ***K. breviceps***

To test whether or not ovulations occurred equally in both ovaries a paired t-test was carried out on data available for 13 *K. breviceps* females stranded along the South African coastline and for two taken from the literature (Harrison *et al.*, 1972; Jenness and Odell, 1978) (Table 5.1). No significant difference was found between the accumulation rate of the left (total: 79 corpora) and of the right (total: 66 corpora) ovary at the 5% level ( $p=0.29$ ), which indicates that ovulations occur equally in both ovaries.

On the basis of corpora present in the ovaries, 17 females out of 23 examined were mature and six females were immature (Figure 5.2, Table 5.2). A marked increase in the number of corpora present in the ovaries occurred at a body length of around 260cm and about seven GLGs (Figure 5.2). No female had only one corpus present in her ovaries, but three females measuring 262cm, 263cm and 266cm with seven GLGs, 7.73GLGs and seven GLGs, respectively, all had two corpora (Figure 5.2). The onset of sexual maturity in female *K. breviceps* is therefore estimated to be at about 262cm and seven GLGs. However, considering that the ovulation rate is one per year in this species (see below) and both females already had two corpora present in the ovaries, sexual maturity occurs most likely at around five years. The youngest female with corpora in her ovaries was estimated to be 6.29 years and had 4 corpora present. The maximum number of corpora recorded was 16 for two females (SAM 81/22 and SAM 86/17), which measured 301cm and 321cm and had GLG counts of 22 and 19, respectively.

A concurrent increase in combined ovarian weight was observed at a total body length of about 260cm and at about six GLGs (Figure 5.3). The highest combined ovary weight in an immature female was 12.2g (L: 256.5cm, GLGs: 3.4) and the lowest

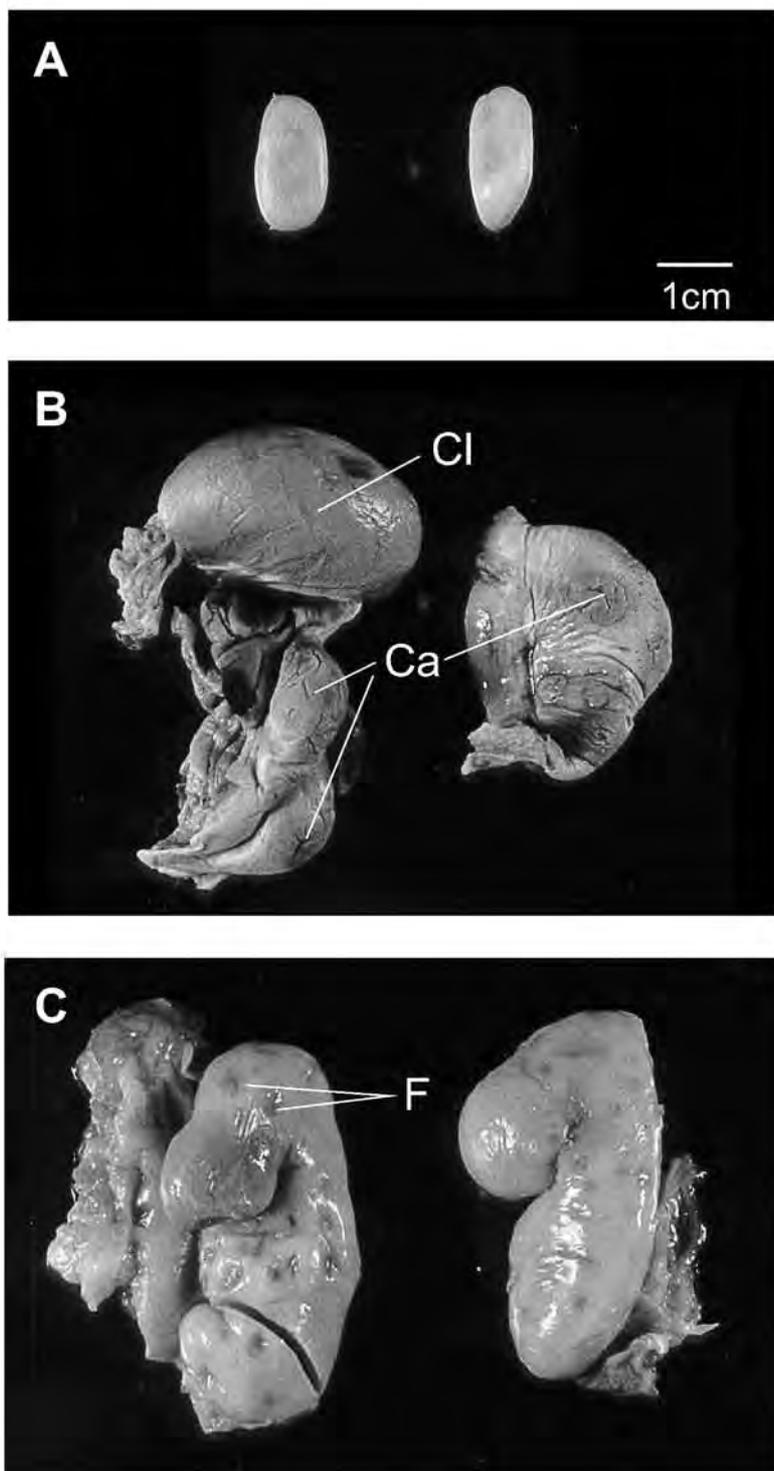


Figure 5.1: Ovaries of *Kogia*. A) Immature ovaries. B) Mature ovaries. CL: *Corpus luteum*. CA: *Corpus albicans*. C) Mature ovaries. F: Follicles.

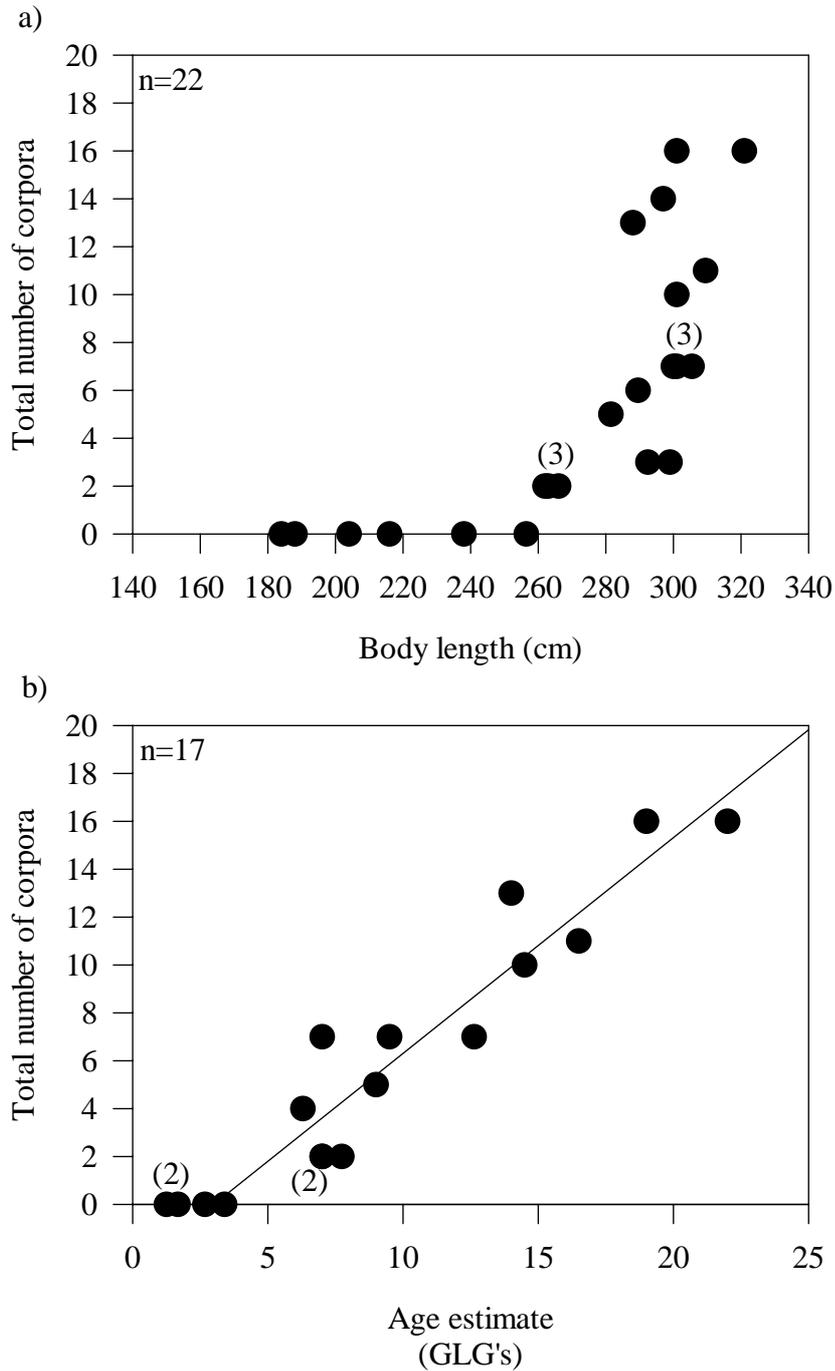


Figure 5.2: Attainment of sexual maturity, in relation to (a) length and (b) estimated age, and ovulation rate in female *Kogia breviceps*. The solid line (b) represents the regression ( $y = -2.7 + 0.9x$ ) between the number of corpora and the age for mature females ( $r^2 = 0.86$ ).

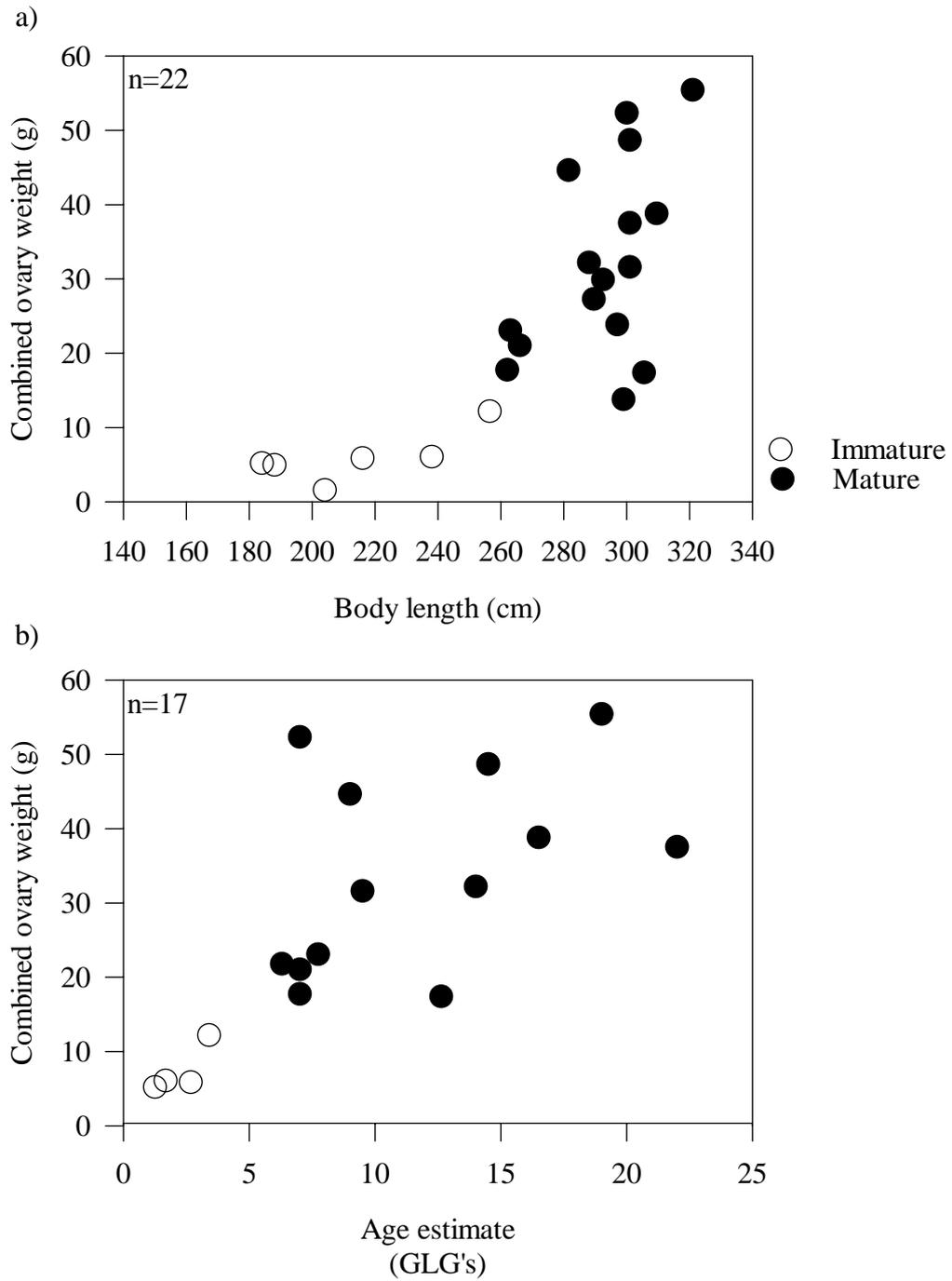


Figure 5.3: Increase of combined ovary weight with (a) body length and (b) estimated age in female *Kogia breviceps*.

combined ovary weight for a mature female with seven corpora was 17.42g (L: 305.5cm, GLGs: 12.63), which indicates that sexual maturity occurs between 12g and 17g of combined ovary weight. One female (SAM 82/20), although mature (with three corpora in her ovaries), had a combined ovary weight of only 13.8g, but one of the ovaries was much smaller than the other one.

Table 5.1: Accumulation of corpora in the left and the right ovary of female *Kogia breviceps*. No significant difference was found between the accumulation rate of the left and of the right ovary at the 5% level ( $p = 0.29$ ), indicating ovulations occur equally in both ovaries.

Animal No.	Number of corpora in the left ovary	Number of corpora in the right ovary
94/09	1	1
92/14	4	3
86/17	9	7
84/24	3	4
83/20	8	2
82/20	0	3
82/04	7	6
81/22	10	6
78/25	2	2
78/19	2	1
N1078	0	2
N178	8	3
N176	2	5
Jenness and Odell, 1978	16	13
Harrison <i>et al.</i> , 1972	7	8
n=15	total=79	total=66
$\bar{x} \pm SE$	5.3 ( $\pm 4.5$ )	4.4 ( $\pm 3.22$ )

The heaviest immature *K. breviceps* female weighed 272.16kg (L: 256.5cm, GLGs: 3.4) (Table 5.2). The lightest mature female was 301kg (L: 266cm, GLGs: 7) (Table 5.2). Therefore the weight at the onset of sexual maturity was between 272.2kg and 301kg for female *K. breviceps* (Table 5.2).

Table 5.2: Summary of the size and ages for different maturity stages for *Kogia breviceps* females. Determination of maturity was based on histological examination of the reproductive organs and only specimens for which the state of maturity could be confirmed histologically were included here (i.e. calves were excluded).

	Immature		Mature	
	n	range	n	range
<b>Age (GLGs)</b>	4	1.25-3.4	13	6.29-22.0
<b>Length (cm)</b>	6	184.0-256.6	17	262.0-321.0
<b>Mass (kg)</b>	4	83.5-272.16	7	301.0-480.0

A regression for all mature females of estimated age against total number of corpora is described by the regression equation  $y = -2.7 + 0.9x$  (where  $y$  is the total number of corpora and  $x$  is the age estimate (GLGs)) and yields an ovulation rate of 0.9 per year (Figure 5.2). This indicates that, on average, ovulations occur about every 13.3 months.

No post-reproductive females were observed based on macroscopic examination of the ovaries. The two oldest females both had 16 corpora in their ovaries and were 19 and 22 years old, respectively (Figure 5.2b), indicating that both females probably ovulated annually after reaching sexual maturity. The oldest female that was pregnant (PEM N178) had an estimated age of 16.5GLGs (Table 5.3).

Data on the length at birth in this species were examined in Chapter 3. Using Kasuya's (1977) formula ( $t_g - t_0 = x / (0.001802x + 0.1234)$ ); where  $x$  = mean neonatal length in cm, and  $t_g - t_0$ : the linear foetal growth period (i.e. a minimum estimate of gestation) the gestation length calculated based on a neonate length of 120cm is 353.3 days or 11.8 months.

The monthly occurrence of foetuses and juveniles up to and including the age of two GLGs suggests a reproductive season with conceptions occurring from April to September and births possibly occurring from March to August (Figure 5.4). The Australian specimens included in this analysis showed the same trend. These results would suggest a gestation period of approximately 11 months. This in combination with a high percentage of simultaneously pregnant and lactating females (24.1%) and the ovulation rate suggests annual reproduction for *K. breviceps*.

The results for the largest corpus (CL or CA) plotted versus month did not support the trend in seasonality seen in Figure 5.4, although the largest corpus still fell into the mating season (September) (Figure 5.5a). When the CL index was plotted

against the length of the foetus or calf it appeared to decrease with increasing length of the offspring. However, a range of CL indices was observed for foetuses between 17.9cm and 49cm (Figure 5.5b).

The longest calf that stranded with a lactating cow measured 211cm (Table 5.3), which would coincide with about two GLGs if extrapolated from the growth curve (see Chapter 3). A 202cm long calf, which also stranded with a lactating female, had an age estimate of two GLGs (Table 5.3), which indicates that lactation can last up to two years. However, the shortest calf that stranded with a cow that was not lactating measured 180cm (Table 5.3). This would indicate that it was around one year old (extrapolated from the growth curve) (see Chapter 3). Another cow, which only showed traces of milk, was accompanied by a 191cm long calf that had an age estimate of just under one GLG (Table 5.3). These data indicate that weaning may start after a year of lactation, but that lactation may continue for two years.

The foetal sex ratio of the 12 *K. breviceps* foetuses present was 1:1.4 for females (n=5) to males (n=7), respectively. The juvenile sex ratio for 19 calves up to and including two years of age ( $\leq 210$ cm) was 1:2.2 for females (n=6) to males (n=13), respectively. However, neither the foetal nor the juvenile sex ratio were significantly different from parity ( $\chi^2=0.33$  and 2.58, respectively;  $p>0.05$ ).

Table 5.3: Records of female *Kogia breviceps* stranded along the Southern African coastline with a foetus or calf. Information on the animals' length, age and sex was included whenever available.

a) Assumed cow/calf pairs

No. of cow/calf	Length of cow/calf (cm)	Age of cow/Calf	Sex of calf	Length of foetus (cm)	Sex of foetus	Comments
N41 N40	269.5 211	- -	- -	19.5	F	cow lactating
N138 -	305 -	9 -	- -	113.5	M	-
N277 N278	266 204	7 -	- F	31	-	-
78/25 -	- -	6.29 -	- -	27	F	-
82/04 *	288 ca 150	14 -	- -	49	F	cow lactating

N853	297	-				cow lactating
N854	202	-	M	-	-	
82/27	300	4.4				
-	-	-	-	65		-
83/20	301	14.5				traces of milk
83/21	191	-	M	21	F	
N1078	262	7				cow lactating
N1079	194	-	M	48	M	
N1707	286	-				
-	-	-	-	27.5	M?	-
92/14	300	7				cow lact., with
*	-	-	-	38	F	2 smaller indiv.

b) Possible cow/calf pairs

No. of cow/calf	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Length of foetus (cm)	Sex of foetus	Comments
-	*	-				
68/13	194.3	0.71	M	-	-	with much larger indiv.(cow?)
N178	309.5	16.5				
N179	197	-	M	17.9	M	-
N176	305.5	12.63				
177	202	1.33	M	23	M	-
82/20	299	-				
82/21	215+	2.29	M	-	-	-
N1174	290	-				
*	-	-	-	-	-	-
N1862	320	-				
N1863	213	1.25	M	-	-	-
94/09	263	7.73				
*	180	-	-	28.6	M	-
96/16	281.5	9				
96/17	184	1.25	F	23	M	-

\* = animal refloated; age of calf = complete GLGs plus increment.

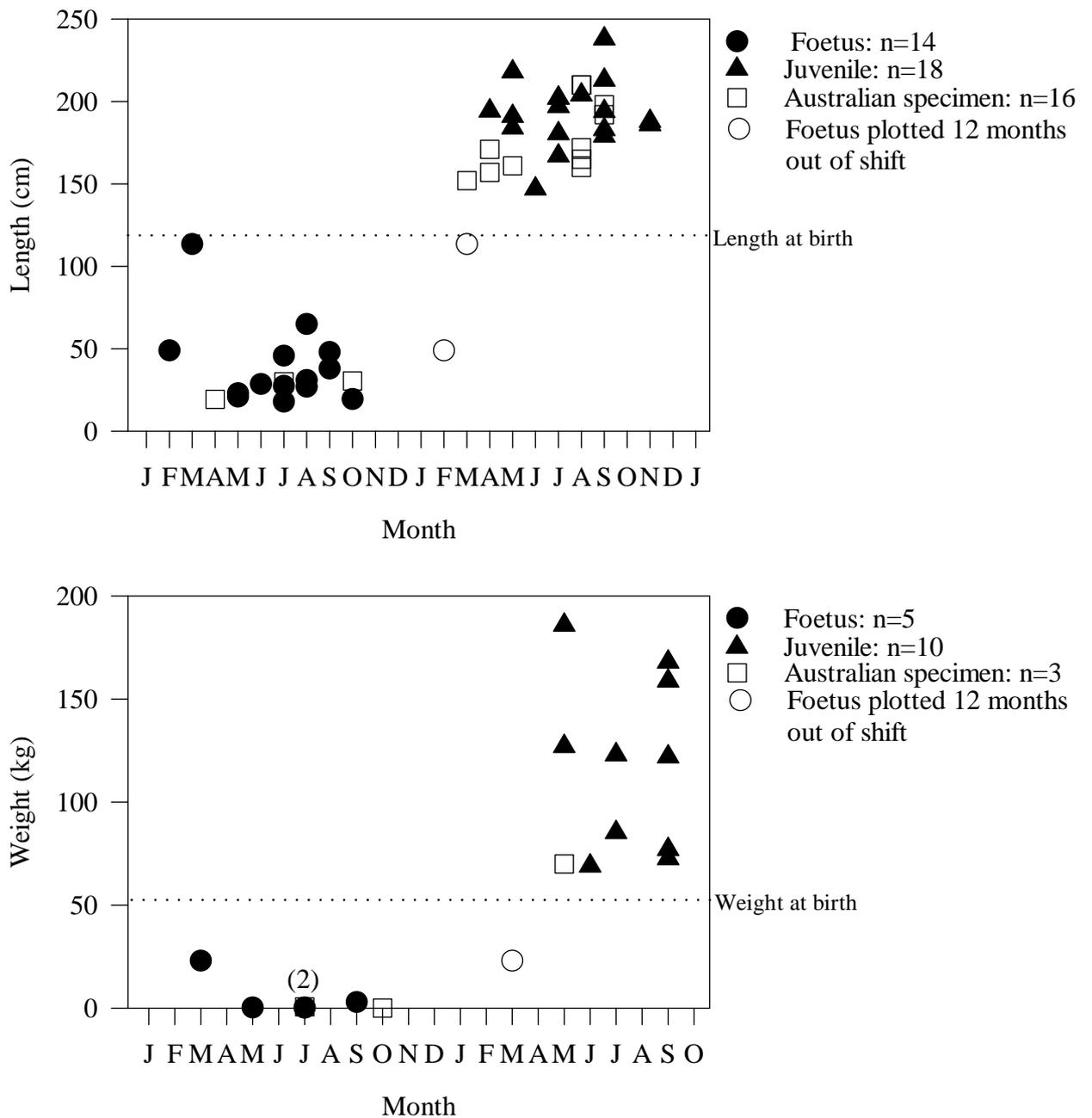


Figure 5.4: Occurrence of *Kogia breviceps* foetuses (filled circles) and juveniles (up to and including the age of two)(filled triangles) throughout the year. Open circles are original data plotted 12 months out of shift. All juveniles were plotted 12 months out of shift. Three of the Australian specimens included (indicated as squares) were foetuses and 11 were juveniles, although weights were only available for two Australian foetuses and one juvenile.

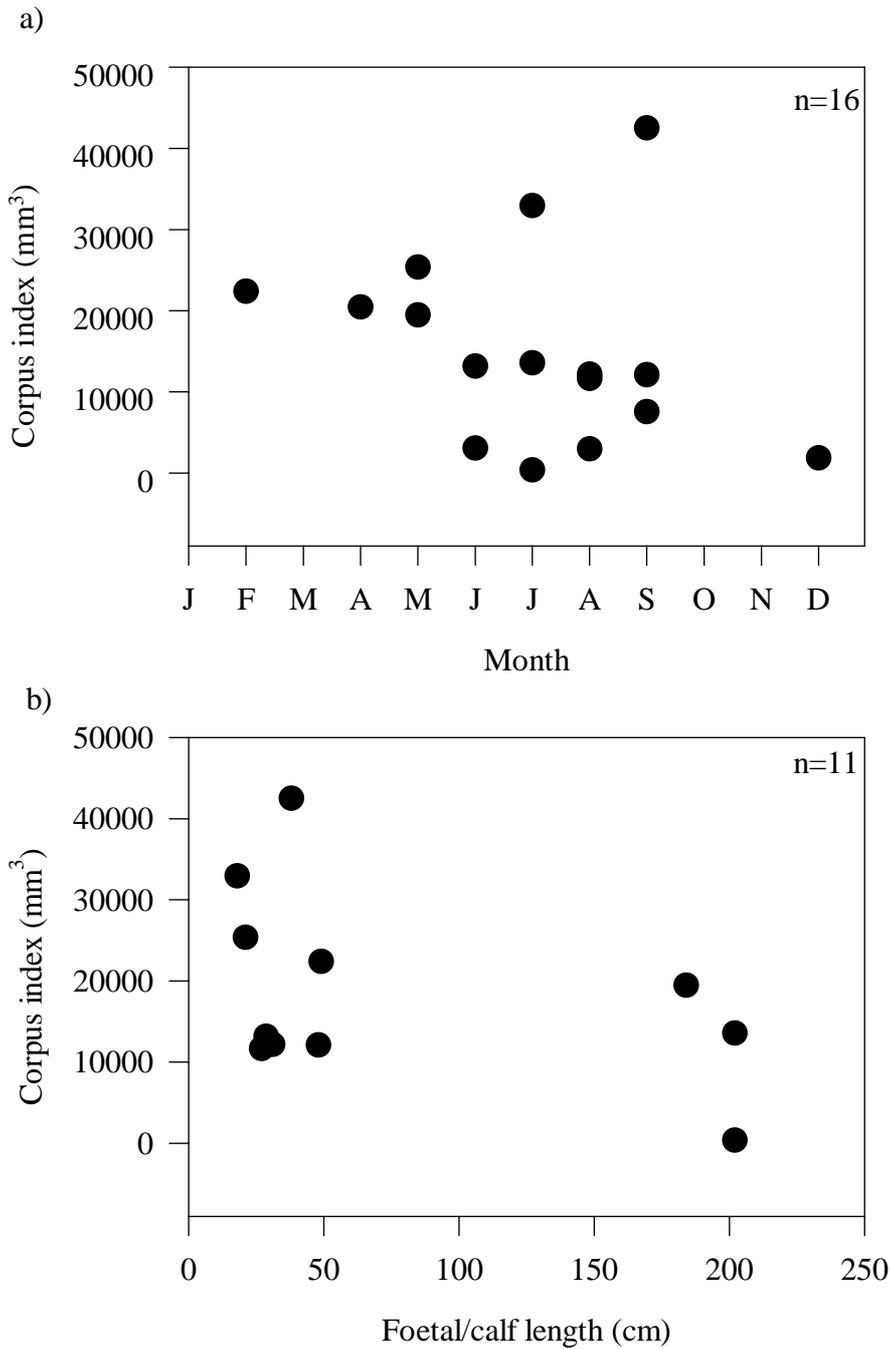


Figure 5.5: Corpus index (in mm<sup>3</sup>) of the largest corpus (CL or CA) in relation to month (a) and foetal or calf length (b) in *Kogia breviceps*.

*K. sima*

There was a significant difference at the 5% level in the rate at which corpora accumulated in the ovaries of nine female *K. sima* from South Africa ( $p=0.0159$ ), with the left ovary (total: 22 corpora) being significantly more active than the right one (total: 9 corpora) (Table 5.4).

Table 5.4: Accumulation of corpora in the left and the right ovary in female *Kogia sima*.

Animal No.	Number of corpora in the left ovary	Number of corpora in the right ovary
88/20	1	0
88/02	1	2
81/03	1	0
76/03	4	1
N832	3	0
N829	3	3
N678	4	1
N243	2	1
N145	3	1
n=9	total=22	total=9
$\bar{x} \pm SE$	2.4 ( $\pm 1.2$ )	1.0 ( $\pm 1.0$ )

Based on examination of the ovaries, 15 females were mature and 10 immature (Figure 5.6, Table 5.5). The onset of sexual maturity in *K. sima* females is somewhat clearer than in *K. breviceps*. A marked increase in the total number of corpora occurred just below a total body length of 220cm and around five GLGs (Figure 5.6). The shortest female with only one corpus was 215cm long (GLGs: 4.5) (Figure 5.6). Two other females with one corpus in the ovaries measured 231cm and 255cm and had 6.12 and five GLGs, respectively. No age estimate was available for a 220cm long female with one corpus. Therefore the onset of sexual maturity for *K. sima* females seems to occur at about 215cm and around five GLGs (Figure 5.6). The youngest mature female had a GLG reading of 4.25, but already three corpora present in her ovaries. The highest number of corpora recorded for *K. sima* was nine in a 236cm long female (PEM N1322, GLGs: 14).

Two outliers were observed: a 265cm long female (PEM N682) with no corpora in her ovaries, for which no age estimate was available, and a 250cm long female (PEM

N440) with one corpus and an age estimate of 8.56GLGs (Figure 5.6a,b, respectively). As these two females seem to have an unusually low corpora count for their length and age it is suggested that they possibly suffered from some impairment of reproductive ability.

The increase in combined ovarian weight with the onset of maturity was not as clear as previously observed for *K. breviceps*, although there was a general trend of increasing combined ovary weight with increasing length and age (Figure 5.7). The highest combined ovary weight for an immature female was 11.63g (L: 189cm, no age estimate available) and the lowest combined ovary weight for a mature female with one corpus was 3.52g (L: 255cm, GLGs: 5), although in the latter case one ovary appeared extremely small and was possibly infertile. There were a number of outliers that should be mentioned. Two mature females (SAM 78/17 and PEM N829), based on the presence of corpora in their ovaries, showed very low combined ovary weights of 3.52g and 4.57g, respectively for their length (L: 255cm and 238cm, GLGs: five and no age estimate available, respectively). In contrast, one immature female (PEM N207) had a remarkably high combined ovary weight of 11.63g for her length (L: 189cm, GLG: no age estimate available) (Figure 5.7a). Another female (PEM N682), which was immature based on ovarian examination, should have been mature according to her combined ovary weight of 11.35g and length of 265cm, no age estimate was available for this female (Figure 5.7a). Furthermore, a range of combined ovary weights was observed for four animals aged around five GLGs (Figure 5.7b). These ranged from 6.63g to 14.85g for animals between 4.25 and 5GLGs. However, the two higher combined ovary weights can be attributed to a large CL present in each case, which resulted in the ovary with the CL being about twice as heavy as the ovary without the CL. The mature female (SAM 78/17) already mentioned as having a relatively low combined ovary weight (3.52g) for her length also had a relatively low combined ovary weight for her age (GLGs: 5) (Figure 5.7b). From Figures 5.6 and 5.7 it appears that at least two females (PEM N682 and PEM N440) may have had a somewhat impaired reproductive ability.

The heaviest immature *K. sima* female weighed 155.58kg (L: 206cm, GLGs: 3.27), whereas the lightest mature female weighed 176.9kg (L: 215cm, GLGs: 4.5) (Table 5.5). There were, however, two mature females for which no age estimate was available, which weighed 169kg and 175kg and measured 236cm and 238cm, respectively. Thus maturity probably occurs between 155.6kg and 169kg in female *K. sima* (Table 5.5) (see Chapter 3).

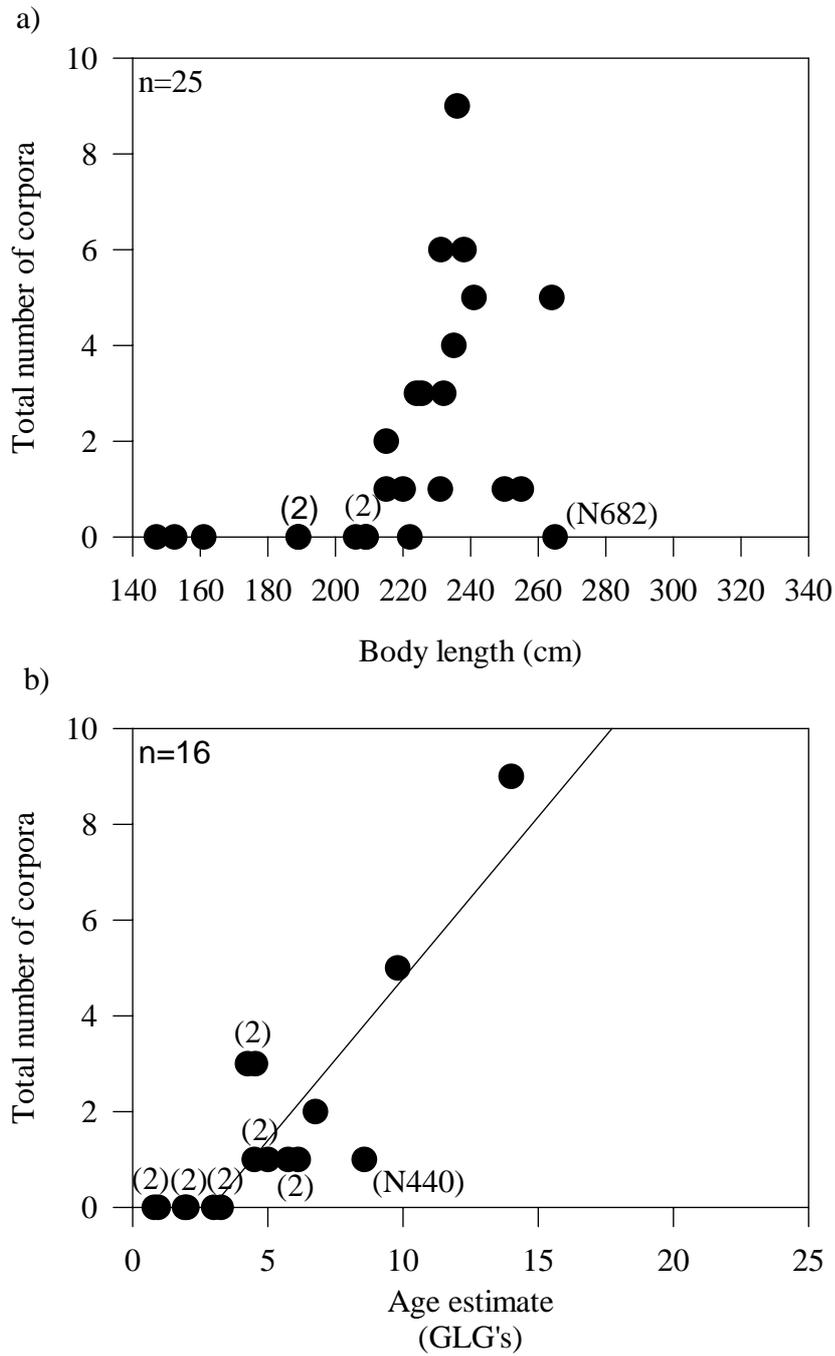


Figure 5.6: Attainment of sexual maturity, in relation to (a) length and (b) estimated age, and ovulation rate in female *Kogia sima*. The solid line (b) represents the regression ( $y=-2.0+0.7x$ ) between the number of corpora and the age for mature females ( $r^2=0.65$ ).

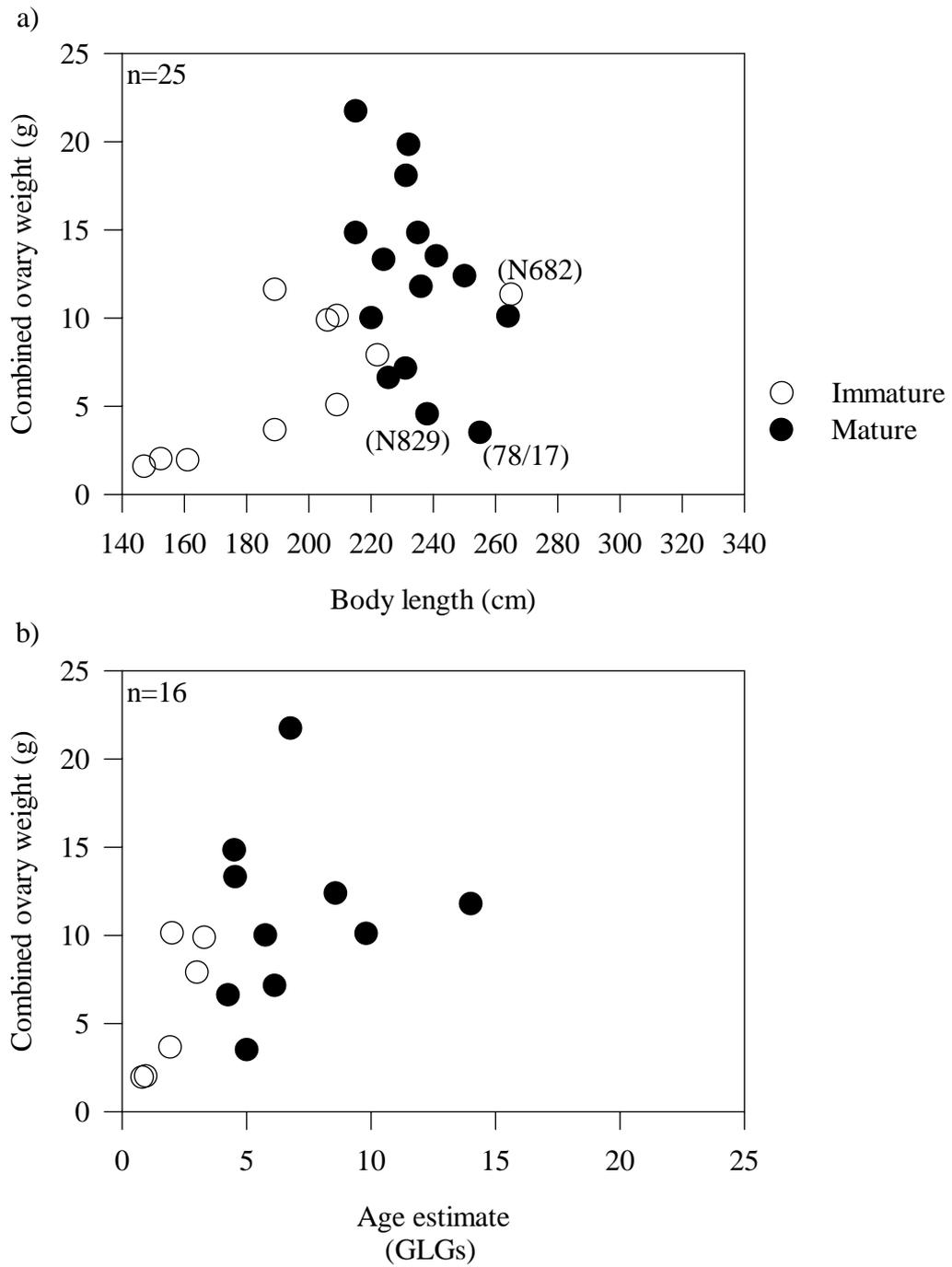


Figure 5.7: Increase of combined ovary weight with (a) body length and (b) estimated age in female *Kogia sima*.

Table 5.5: Summary of the size and ages for different maturity stages for *Kogia sima* females. Determination of maturity was based on histological examination of the reproductive organs and only specimens for which the state of maturity could be confirmed were included (i.e. calves were excluded).

	Immature		Mature	
	n	Range	n	range
Age (GLGs)	6	0.8-3.27	10	4.25-14.0
Length (cm)	10	147.0-222.0*	15	215.0-264.0
Mass (kg)	8	59.42-155.58	9	169.0-264.0

\* One outlier, a 265 cm long female, was omitted here as she appeared to be reproductively abnormal.

A regression of estimated age against total number of corpora described by the equation  $y = -2.0 + 0.7x$  (where y: total number of corpora and x: age estimate (GLGs)) was fitted to all mature *K. sima* females and yielded an ovulation rate of 0.7 per year, which means that ovulations occur about every 17.1 months (or roughly one and a half years) (Figure 5.6).

As in *K. breviceps* no post-reproductive females were observed. The oldest pregnant female was also the oldest female in the sample (PEM N1322) and had an age estimate of 14GLGs (Table 5.5). This may indicate that in *K. sima* females usually do not enter a long post-reproductive period, but reproduce throughout their lives.

Using Kasuya's (1977) formula the estimated gestation length, based on a neonate length of 103cm (see Chapter 3) is 333.3 days or 11.1 months.

For *K. sima* a clearer picture of the reproductive seasonality emerged as both conceptions and births occurred between December and March (Figure 5.8a), although the data set is smaller than for *K. breviceps*. This would indicate a gestation length of 12 months. Although the ovulation rate suggests that ovulations occur roughly every one and a half years, 11.5% of mature females that stranded along the Southern African coast were found to be simultaneously lactating and pregnant (see Chapter 7). These data indicate that *K. sima* may also show annual reproduction, if the conditions are right, although that may be facultative and some animals may only reproduce every two years. This is further supported by one foetus, which was apparently conceived in December, suggesting that in *K. sima* a post-partum oestrus may occur in some animals, some of the time.

As found for *K. breviceps* the results for the largest corpus plotted versus month did not support the trend in seasonality seen in Figure 5.8, and the largest corpus just fell

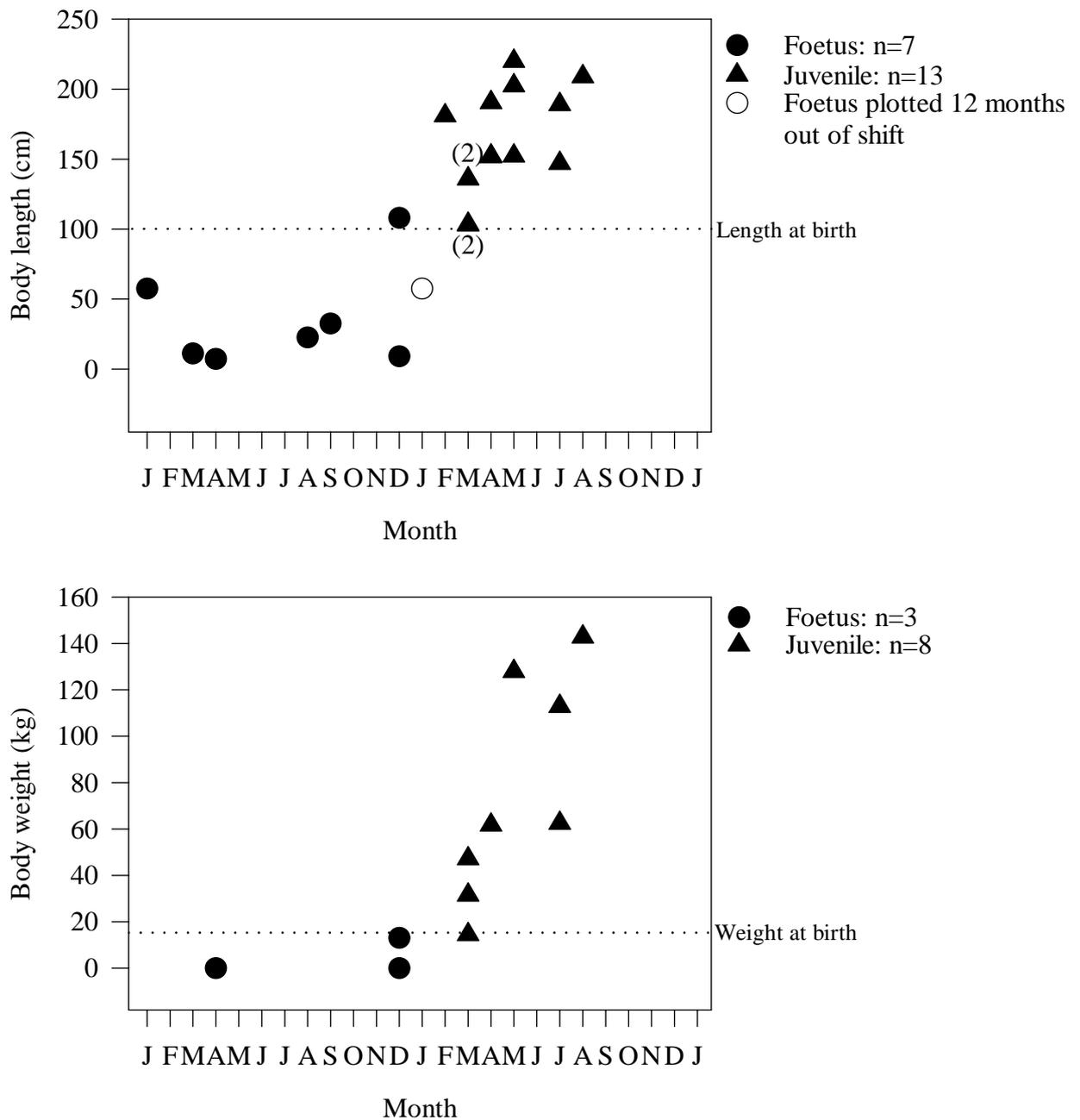


Figure 5.8: Occurrence of *Kogia sima* foetuses (filled circles) and juveniles (up to and including the age of one)(filled triangles) throughout the year. Open circles are original data plotted 12 months out of shift. All juveniles were plotted 12 months out of shift.

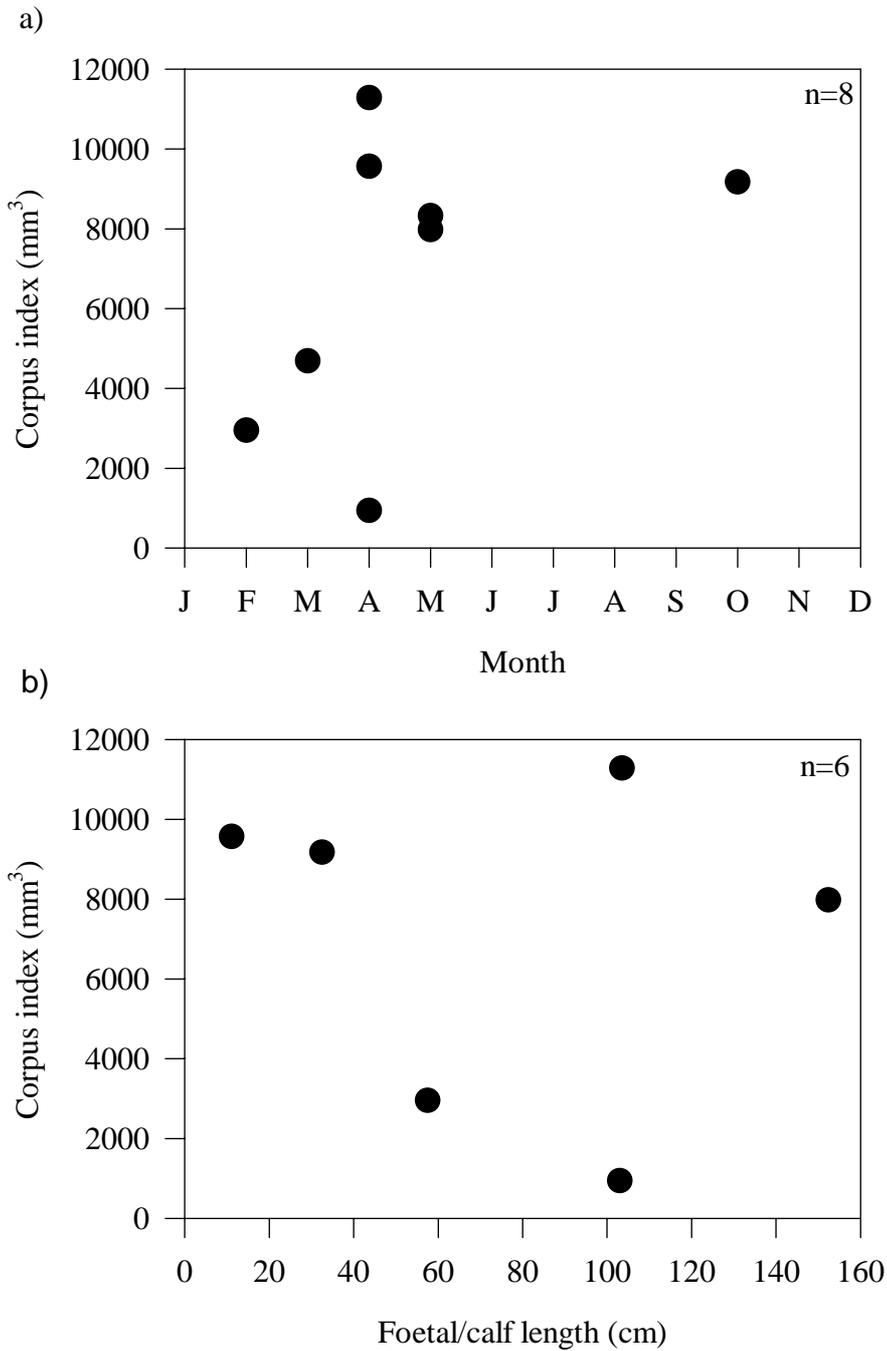


Figure 5.9: Corpus index (in mm<sup>3</sup>) of the largest corpus (CL or CA) in relation to month (a) and foetal or calf length (b) in *Kogia sima*.

outside the mating season (April) (Figure 5.9a). Similarly when the corpus index was plotted against the length of the foetus or calf no real trend could be determined (Figure 5.9b).

The longest calf that stranded with a lactating female measured 152.4cm and had a GLG reading of 0.94 (Table 5.6), which suggests that lactation can last at least one year. Another calf, measuring approximately 130cm (no age estimate was available) stranded with a non-lactating female (Table 5.6), suggesting that weaning can start as early as six months, as extrapolated from the growth curve (see Chapter 3).

The sex ratio for the five *K. sima* foetuses present was 1:1.5 for females (n=2) to males (n=3), respectively. For seven juveniles up to and including two years of age ( $\leq 160$ ) the ratio was 1.33:1 for females (n=4) to males (n=3), respectively. However, neither the foetal nor the juvenile sex ratio were significantly different from parity ( $\chi^2=0.2$  and 0.14, respectively;  $p>0.05$ ).

Table 5.6: Records of female *Kogia sima* stranded along the Southern African coastline with a foetus or calf. Information on the animals length, age and sex was included whenever available.

a) Assumed cow/calf pairs

No. of cow/calf	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Sex of foetus	Length of foetus	Comments
N101	231.2	-				
N102	151.9	-	M	-	-	cow lactating
N103	230.5	-				
N104	152.4	-	M	-	-	cow lactating
N139	ca244	-				
N140	135.9	0.24	F	-	-	cow lactating
N145	235	-				
N146	152.4	0.94	F	F	7.2	cow lactating
N440	250/	8.56				
-	-	-	-	M	108	-
N317	220/	5.75				
N318	147+	-	F	-	-	cow lactating
81/03	215	4.5				
-	-	-	-	M	11.1	-
N678	241	-				
N679	103.5	-	M	-	-	cow lactating
N829	238	-				
N830	103	0	F	-	-	cow lactating

N832 *	232 -	- -	- -	- -	- -	cow lactating
N1322 -	236 -	14 -	- -	- -	9.1	-
88/02 -	225.5 -	4.25 -	- -	M	57.5	-

## b) Possible cow/calf pairs

No. of cow	Length of cow/calf (cm)	Age of cow/calf	Sex of calf	Sex of foetus	Length of foetus (cm)	Comments
N185	240	-	-	-	-	-
N185a	ca130	-	-	-	22.5	-
N243	224	4.53	-	-	-	-
N244	161	0.8	F	F	32.5	-

\* = refloated; age of calf = complete GLG's plus increment

## **5.4 Discussion**

### **5.4.1 Reproductive anatomy**

The morphological characteristics of the ovaries and corpora of the two *Kogia* species as described by Beckmen (1986) and Ross (1979) were in agreement with the findings for the present study. In addition, the ovaries of both *K. breviceps* and *K. sima* get darker in colour with age from a beige-pink over dark-brown to black as reported by Beckmen (1986). There are conflicting results in the literature concerning whether the CL's of the two *Kogia* species are pedunculate (Harrison *et al.*, 1972; Ross, 1979) or not (Beckmen, 1986). Re-examination of Ross' (1979) material with additional material revealed that although the CL's protrude from the surface of the ovary, they are not truly pedunculate.

In general the CL of pregnancy does not change size throughout gestation (Matthews, 1938; Kasuya *et al.*, 1974; Harrison *et al.*, 1981; Marsh and Kasuya, 1984; Perrin and Donovan, 1984; Dans *et al.*, 1997), but may increase slightly in early pregnancy until the foetus has reached a certain length and then regresses again slightly (Sergeant, 1962; Best, 1967; Miyazaki, 1984). However, Harrison *et al.* (1981) observe wide individual variation in the CL volume (or index) against foetal length and similar results are reported in the present study for both species of *Kogia*.

## 5.4.2 Ovarian symmetry

Both ovaries are equally functional in *K. breviceps*, but in *K. sima* the left ovary is more active than the right one. This is an interesting result in view of the recent controversy surrounding the phylogeny of Cetacea (see Chapter 1). Ohsumi (1964) suggests that one criterion for the classification of cetacea could be the type of accumulation of corpora in the ovaries. Accordingly, the results from the present study show that *K. breviceps* would be classed as having a Type I accumulation rate like the sperm whale *P. macrocephalus* and the mysticetes, which is in agreement with previous findings (Ohsumi, 1964; Harrison *et al.*, 1972). However, *K. sima*, although ovulating from both ovaries, would be classed as having a Type II or III accumulation rate. An equal accumulation pattern between the two ovaries is generally regarded as more “primitive” and accumulation predominantly in one ovary as more derived (J. E. Heyning, pers. com.). A similar trend was found in the evolution of the nasal passages of cetaceans from the primitive condition in mysticetes (double nares, nasal passage not confluent) to the intermediate condition in *Physeteridae* and *Kogiidae* (single blowhole, nasal passages not confluent) (Schenkkan and Purves, 1973; Heyning and Mead, 1990) to the most derived state in all other odontocetes (single blowhole, nasal passages confluent) (Heyning, 1997). Thus the results for ovarian symmetry in the two species of *Kogia* may reflect a possible evolutionary history from the mysticetes to the odontocetes as mysticetes, *Physeter* and *K. breviceps* ovulate from both ovaries equally and *K. sima* and delphinids ovulate predominantly from the left ovary (Ohsumi, 1964). In addition, it is interesting to note that the Ziphiids also show a Type I accumulation rate like the mysticetes, and *K. breviceps* and *Physeter* (Ohsumi, 1964). However, sample sizes in the present study are still small and additional samples would help clarify this issue.

## 5.4.3 Attainment of sexual maturity (ASM)

### 5.4.3.1 Ovarian weight

The onset of sexual maturity in *K. breviceps* occurred between combined ovary weights of 12.2g and 17.4g. Ovarian weight was not a good indicator of ASM in *K. sima* as it varied substantially depending on the condition of the latest CL. It is unlikely that inaccuracies in age estimation played a role here since a good relationship between increasing age and increasing number of corpora was found and the age determination

proved to be reliable (see Chapter 3). The lowest combined ovary weight of 3.52g for a female with one seemingly infertile ovary or 4.57g for a mature female with two functional ovaries and six CA's in *K. sima* is surprising. However, combined ovary weights as low as 2.0g, 3.0g, 3.3g and 4.2g for mature females of spotted dolphin *S. attenuata*, Hector's dolphin *C. hectorii* (Slooten, 1991), Tucuxi *Sotalia fluviatilis* (Harrison and Brownell, 1971), and the vaquita *P. sinus* (Hohn *et al.*, 1996) have been reported. The abovementioned species are all smaller in body size than *K. sima* and scaling almost certainly has an affect on ovary weight as well. Marsh and Kasuya (1984) found an overall increase of ovarian weights with increasing length and age in short-finned pilot whales *G. macrorhynchus*, but observed a considerable variation of ovary weights for animals of the same age or length. A large overlap in ovarian weights between immature and mature animals was also reported for sperm whales *P. macrocephalus* (Best, 1967), although the effects a large CL may have on the weight of the ovary were removed by placing pregnant females in a different category. The macroscopic (or histological) examination of the ovaries for corpora remains the most reliable indicator for the onset of sexual maturity in cetaceans.

#### 5.4.3.2 Body length

The length at ASM of 262cm for *K. breviceps* and 215cm for *K. sima* agrees well with the results of 270-280cm and 210-220cm, respectively, reported previously for the South African population (Ross, 1979). Furthermore, they indicate that sexual maturity occurs at 85.62% and 86% of asymptotic body length in *K. breviceps* and *K. sima*, respectively, which is in good agreement with the mean of 85.1% proposed by Laws (1956) for all female cetaceans. Odell *et al.* (1984) report that the smallest adult *K. breviceps* female examined measured 260cm, but subsequent data presented by Credle (1988) include a 252cm long lactating female. The shortest mature *K. sima* female in her dataset was a 218cm long lactating female. The fact that both these females were lactating suggests that the actual length at first ovulation for animals from the southeastern United States may be somewhat shorter than that from South Africa. Similarly, Reyes and van Waerebeek (1992) report on a 260.5cm long female *K. breviceps* from Peru, which was sexually mature. For striped dolphins *S. coeruleoalba* factors affecting size differences between parts of the population inhabiting different areas of the Mediterranean include stronger seasonality and lower population density, leading to

larger individuals (Calzada and Aguilar, 1995). As already mentioned in Chapter 3 differences in body sizes between different populations of the same species have also been attributed to food quality and quantity (Bryden, 1972; Read and Gaskin, 1990; Bloch *et al.*, 1993; Di-Méglio *et al.*, 1996; Read and Tolley, 1997).

#### 5.4.3.3 Age

The estimate of age at ASM from the present study may be somewhat imprecise due to the small number of first time ovulators available (DeMaster, 1984; Read, 1990a). However, estimates for age at ASM have not been attempted before for any population of either species of *Kogia*. The relatively low age estimate at ASM of five GLGs for both *K. breviceps* and *K. sima* is somewhat surprising for odontocetes of a comparatively large body size. Subsequent studies on a small sample of *K. breviceps* females stranded in New Zealand, however, have determined that animals between five and seven GLGs were mature (Tuohy *et al.*, 2001), which would support the present findings. Among the odontocetes, similarly low ages at sexual maturity are usually only found in the porpoises (Perrin and Reilly, 1984). Mean age at sexual maturity in female harbour porpoises *P. phocoena* was estimated to be between 3.15-3.44 years depending on the method used (Read, 1990a). In the vaquita *P. sinus* sexual maturity occurs between three and six years (Hohn *et al.*, 1996). But even among the mysticetes, which reach sexual maturity on average around eight to 10 years (Lockyer, 1984), there are some exceptions to be found. The average age at which the humpback whale *M. novaengliae* reaches sexual maturity is estimated to be five years (Clapham and Mayo, 1990; Clapham, 1992). The implications of these relatively low ages at ASM in both *Kogia* species in relation to other odontocetes will be discussed in detail below and an explanation will be offered in Chapter 9.

#### 5.4.3.4 Body weight

Similarly to male *Kogia*, there are no previous records for body weights at ASM for females of either species. Thus the present data of ASM between 272.16kg and 301kg for female *K. breviceps* and 155.58kg and 169kg for female *K. sima* present the first record for the two species. In addition, these data indicate that sexual maturity occurs at higher body weights in females than in males for both species (see Chapters 3

and 4).

## 5.4.4 Ovulation rate and reproductive cycle

### 5.4.4.1 Ovulation rate

The high correlations ( $r^2=0.86$  for *K. breviceps* and 0.65 for *K. sima*, respectively) of corpora counts with age estimate suggest that in both *Kogia* species corpora *albicantia* persist throughout life as they do in most other cetaceans (Perrin and Reilly, 1984; Read, 1990a), which supports the previous findings for *Kogia* (Harrison *et al.*, 1972; Ross, 1979).

The annual ovulation rate of 0.9 calculated for mature *K. breviceps* in combination with the seasonal birth and mating season observed shows that females ovulate annually. The deviation from parity is probably due to some females failing to conceive in one year and subsequently having to wait until the following year's mating season. Although the majority of cetaceans, both mysticetes and odontocetes, have a reproductive cycle of two to three years (Best *et al.*, 1984; Brownell, 1984; Gaskin *et al.*, 1984; Lockyer, 1984; Perrin and Reilly, 1984), annual reproductive cycles have been reported for other odontocetes like the harbour porpoise *P. phocoena* (Gaskin *et al.*, 1984; Read and Gaskin, 1990; Sørensen and Kinze, 1994; Read and Hohn, 1995), Dall's porpoise *P. dalli* (Kasuya, 1978; Ferrero and Walker, 1999), minke whale *B. acutorostrata* (Masaki, 1979; Lockyer, 1984), and in some humpback whales *M. novaeangliae* (Clapham and Mayo, 1990; Straley *et al.*, 1994). There is also some evidence, although scanty, that the franciscana *P. blainvillei* shows annual reproductive cycles, with a possible post-partum oestrus (Brownell, 1984). A post-partum oestrus and pre-implantation pregnancy has been suggested for the harbour porpoise *P. phocoena* (Gaskin *et al.*, 1984; Read, 1990b; Sørensen and Kinze, 1994). Most adult harbour porpoise females spend much of the year simultaneously pregnant and lactating, nursing the current calf and carrying next years' offspring (Read and Hohn, 1995). Annual ovulation rates reported for other cetaceans with annual reproduction are close to the one reported here for *K. breviceps* and include 0.91 for the Dall's porpoise *P. dalli* (Ferrero and Walker, 1999) and 0.96 (Masaki, 1979) and 0.81 (Best, 1982) for the minke whale *B. acutorostrata*. But even in species that usually exhibit a two-year reproductive cycle, like the fin whale *B. physalus* and the common dolphin *Delphinus delphis*, some females

have been reported to be simultaneously lactating and pregnant (Lockyer, 1987; Mendolia, 1989). Studies of the humpback whale *M. novaengliae* have shown that, although the average reproductive interval is two years, there is considerable individual variability, ranging from one to five years (Clapham and Mayo, 1990) and often individuals show successful annual reproduction (Straley *et al.*, 1994). Although it is likely that postpartum ovulation is common in humpback whales, possibly only a certain percentage of mature females can maintain a pregnancy every year as sufficient prey must be found to sustain it (Wiley and Clapham, 1993; Straley *et al.*, 1994).

The annual ovulation rate for *K. sima* females would indicate that the reproductive cycle lasts roughly one and a half years. However, the data on birth and mating season indicate that reproduction is annual in most females. The annual ovulation rates of 0.66 (Read, 1990a) and 0.68 (Read and Hohn, 1995) reported for harbour porpoises are close to the one reported here for *K. sima* (0.7) and is typical of the annual reproduction of *P. phocoena* (Read, 1990a). As a number of *K. sima* in the present study were also found to be simultaneously pregnant and lactating, *K. sima* may also exhibit annual ovulation, but depending on environmental conditions as well as the constitution of the female, some females probably may only reproduce every other year at least some of the time. This would explain the deviation from an annual ovulation rate of 1. The deviation from unity in the harbour porpoise data may have resulted from younger females ovulating more than once a year (Read, 1990a), but no evidence for that was found for *K. sima* in the present study.

The individual variation of the accumulation rate of corpora in the present study is common in cetaceans and is a reflection of differences in the annual ovulation rate between individuals as well as variation in the attainment of sexual maturity (Perrin *et al.*, 1976; Kasuya and Marsh, 1984; Read and Hohn, 1995). Unfortunately the present sample was too small to attempt to fit a non-linear curve to the data or correct for individual variation in age at ASM (Read and Hohn, 1995).

The two *K. breviceps* females with the highest corpora count of 16 CA had age estimates of 19 and 22GLGs. The highest number of corpora reported for a female *K. breviceps* in the literature was 29 for an animal stranded in Florida; the animal (L: 315cm) was lactating and accompanied by a calf (Jenness and Odell, 1978). As ASM is reached at about five years of age, this female could have been at least 34 years old as there is no evidence for a number of spontaneous, infertile ovulations at the onset of sexual maturity and assuming an annual ovulation rate. Since no post-reproductive

females were observed in the present study, it appears that females remain reproductively active throughout their entire life. If a post-reproductive phase should occur it is unlikely to last very long.

In *K. sima* the oldest female examined (GLGs: 14) was also pregnant and no post-reproductive females were observed in the sample, which would also indicate the absence of a long post-reproductive period. This in turn may reflect certain social structures. Stranding data and observations at sea suggest that females are almost invariably solitary or accompanied by a calf (see Chapters 1 and 7). This would indicate that female *Kogia* do not have cohesive, stable kinship female groups as are observed in species with a high life expectancy for post-reproductive females, like the short-finned pilot whale *G. macrorhynchus* and the sperm whale *P. macrocephalus* (Marsh and Kasuya, 1986). An increased duration of lactation with maternal age and a simultaneous drop in pregnancy rate in these two species (Best, 1968; Kasuya and Marsh, 1984) reflects an increasing investment in calf-rearing and a decreasing investment in calf-bearing with age (Marsh and Kasuya, 1986). A long post-reproductive period for females is thought to have evolved in order to ensure survival of offspring, which is probably closely related to the post-reproductive female (Marsh and Kasuya, 1986). Although no communal nursing, which would provide definite evidence of an important role for older females who spend an increasing proportion of their lives lactating (Marsh and Kasuya, 1986), has yet been observed in any cetacean species, alloparental care in the form of babysitting has been observed in sperm whales *P. macrocephalus* (Whitehead, 1996). Thus the absence of post-reproductive females support the notion that *Kogia* females do not live in stable, closely related female groups. Harbour porpoises *P. phocoena* also show an absence of a long post-reproductive period in old females (Sørensen and Kinze, 1994) and the group size suggests no stable, cohesive female groups in this species (Carwardine, 1995).

The maximum reported ages for a *K. breviceps* and *K. sima* female in the present sample were 22.4GLGs and 21.5GLGs, respectively (see Chapter 3). With age at ASM estimated at around 5GLGs for both *K. breviceps* and *K. sima*, the maximum reproductive lifespan would be 17.4yrs and 16.5yrs, respectively, resulting in 16 and 12 offspring per lifetime using the annual ovulation rates calculated above. However, it is unlikely that each of the ovulations results in a successful pregnancy and rearing of the calf. Even harbour porpoises *P. phocoena* with an annual ovulation have probably not more than a few offspring per lifetime (Read, 1990a). Data presented for the harbour

porpoise in the western North Atlantic indicated a reproductive lifespan of around 13 years and a maximum number of offspring of four to seven (Gaskin *et al.*, 1984; Read, 1990a; 1990b; Read and Hohn, 1995). However, care should be taken when comparing these species, since they have different ovulation rates. The different ovulation rates of *K. breviceps* and *K. sima* reflect the different reproductive strategies employed by the two species, which will be discussed in detail below.

If possible a full histological examination (opposed to a macroscopical one) of the ovaries should be carried out in order to ensure an accurate assessment of the number of corpora. However, considering that samples for either species of *Kogia* will almost invariably originate from stranded animals, which are often decayed to a certain degree, the material may be unsuitable for histological examination. The results obtained in the present study show satisfactory results based on macroscopic examinations.

#### **5.4.4.2 Gestation**

Although the two estimates for length of gestation based on Kasuya's (1977) formula and foetal and calf lengths throughout the year give slightly different results, gestation lengths for both *Kogia* species lie between 11 and 12 months. More data, especially on neonatal length, are needed to define the gestation period more accurately. An estimated gestation length of 11 months for *K. breviceps* based on foetal and calf lengths throughout the year is in agreement with one of Ross' (1979) estimates (using the same method) for the population off South Africa and suggests that his alternative estimate of seven months is not realistic. No previous estimates of gestation length were available for comparison for *K. sima*, but the estimate of 11 to 12 months is in agreement with the general length of gestation in odontocetes (Perrin and Reilly, 1984).

#### **5.4.4.3 Lactation and weaning**

Evidence from the present study indicates that weaning may start after one year of lactation in *K. breviceps*, but as early as six months in *K. sima*. Data for a 136cm long *K. sima* from South Africa (Ross, 1979) and a 131.5cm and 140cm long *K. sima* from Peru (Reyes and Van Waerebeek, 1992) and Sri Lanka (Chantrapornsyl *et al.*, 1991), respectively, all with evidence of solid food in their stomachs support these findings. However, the present data also suggest that lactation can last up to two years in either

species, which supports the suggestion that, although both *Kogia* species may be able to conceive in successive years (Ross, 1979), this may not be the norm (Figure 5.10).

The few estimates available suggest that great energetic demands are placed on the mother during lactation (Evans, 1987; Lockyer, 1987; 1995b). Cockcroft and Ross (1990b) estimated that a female bottlenose dolphin *T. truncatus* required 8.3% of her body mass in food per day (the equivalent of 37000kJ) during lactation, while only needing 5.2% after weaning of the calf. Thus a lactating female needs sufficient fat reserves and must decrease her own energy requirements or increase food consumption to meet these demands (Cockcroft and Ross, 1990b). Lockyer's results (1987) from a study on fin whales *B. physalus* support the idea that fat deposits play an important role as lactating females are the leanest females, while pregnant females are very fat. Similarly body fat decreases in lactating harbour porpoises (Lockyer, 1995b). Thus body condition, food abundance, and fertility are intimately linked. It is possible that the prevailing food conditions from consecutive seasons combined could ensure successful reproduction even in a year when food abundance is low (Lockyer, 1987). The energetic requirements resulting from annual reproduction and thus simultaneous lactation and pregnancy will be discussed in more detail as part of the reproductive strategy of the two *Kogia* species below.

Slijper (1966) remarks that the milk of belugas *D. leucas* is unusually high in water content (66%) and low in fat (22%), which he put down to experimental error as both the fat and water content in other species ranged between 40-50%. Jenness and Odell (1978) present data for the composition of *K. breviceps* milk, which is also unusually low in fat (almost 50% that of other cetacean species). Although individual variation of milk composition is great (Jenness and Odell, 1978), another possible explanation in view of the annual ovulation rate may be that these differences are real and were selected for to compensate for the energetic demands of simultaneous pregnancy and lactation. Further comparative investigation, especially with other odontocetes with an annual ovulation rate like the harbour porpoise *P. phocoena*, is needed to clarify this. Different diets almost certainly account for some of the differences seen in the fat content of cetacean milk as another teuthophagous species, the sperm whale *P. macrocephalus*, also showed a lower milk fat content than other cetaceans (Best *et al.*, 1984). Cockcroft and Ross (1990b) also report an unusually low fat content in bottlenose dolphin *T. truncatus* milk of 14 to 19% compared to over 29% for other dolphin species and suggest that this may be a result of the longer lactation time

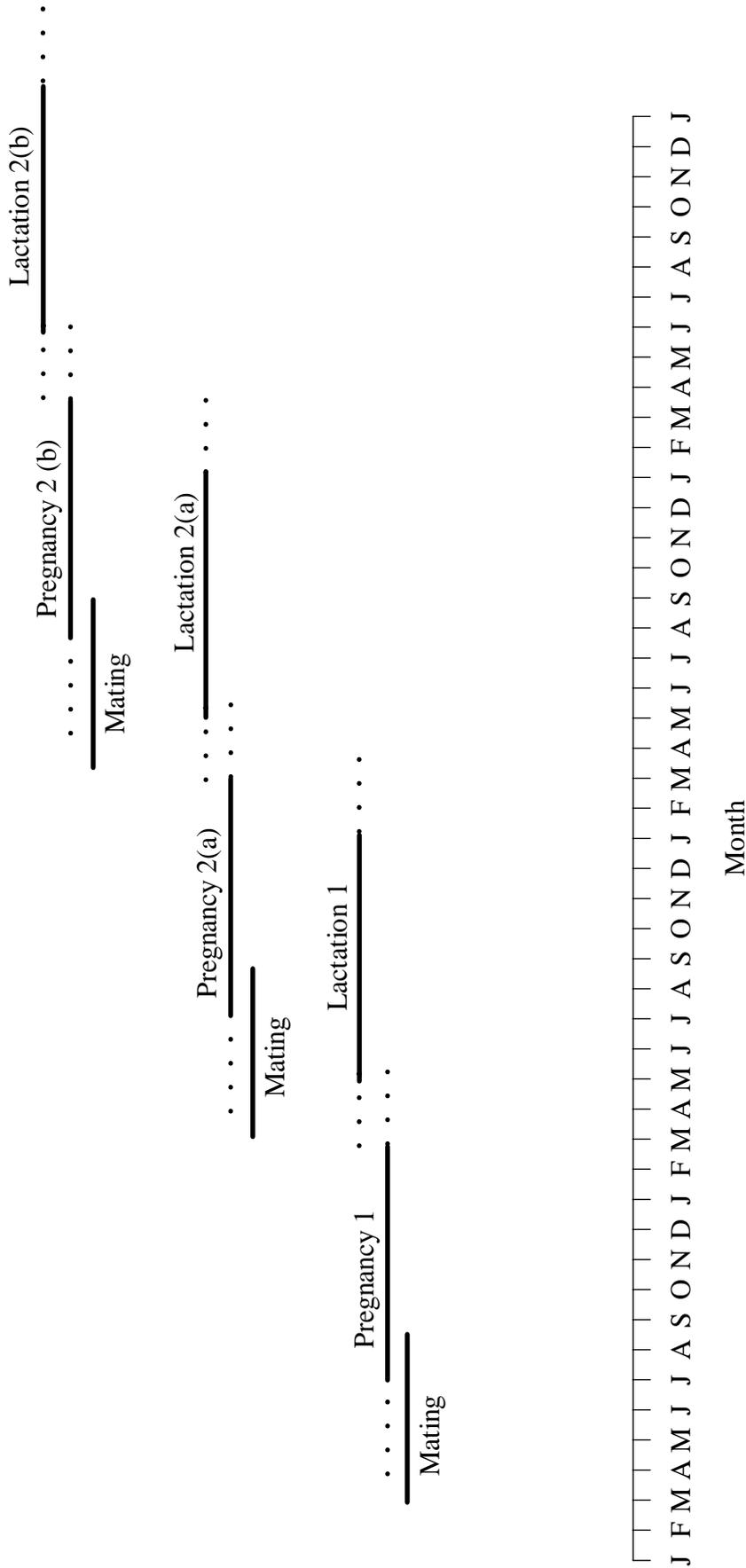


Figure 5.10: Proposed reproductive chronology in *Kogia*. In pregnancy 2a mating occurs in the month post partum. Some animals may miss this pregnancy and only mate in the next season (=pregnancy 2b). The seasonality of the reproductive events is modelled on the data for *Kogia breviceps*. While *Kogia breviceps* may enter more often into pregnancy 2a, *Kogia sima* may enter more often into pregnancy 2b.

of 18 to 24 months (Cockcroft and Ross, 1990a).

In contrast to the two *Kogia* species, the closest relative, the sperm whale *P. macrocephalus*, has a long lactation period that takes up about 40% of the females' reproductive cycle (Gaskin, 1982). Consequently the annual number of receptive females is low and males have to compete for access to females (Gaskin, 1982). Again this is almost the opposite scenario to *K. breviceps* where lactation seems surprisingly short and most females appear to ovulate every year.

The separation of a calf from its mother is not necessarily triggered by the onset of a new pregnancy. In bottlenose dolphins *T. truncatus*, the siblings even remained with the mother after the birth of the new calf in some instances (Wells *et al.*, 1987). There is also some evidence from sightings of mother/calf/juvenile groups that the young of harbour porpoises *P. phocoena* stay with the mother until the next calf is born, and possibly for another month or so after that (Gaskin *et al.*, 1984). However, based on the stranding record there is no evidence of that in either species of *Kogia*, which may be a result of the sufficient independence of the calf to not follow a stranding cow inshore. Alternatively, it may indicate that calves leave the mother when the next offspring is born. The available data do not allow any further conclusions to be drawn.

#### 5.4.4.4 Simultaneous lactation and pregnancy

The high percentage of mature females of *K. breviceps* (24.1%) and *K. sima* (11.5%) simultaneously lactating and pregnant indicates that a large percentage of females may fall pregnant in consecutive years. However, the lower percentage of this condition for *K. sima* suggests that it may not present the normal reproductive strategy employed by this species (Figure 5.10) and this is supported by the ovulation rate. Simultaneous lactation and pregnancy is commonly found only in a small percentage of the total sample of adult females. For example, out of all adult females examined (n=536) of Eastern Tropical Pacific (ETP) spinner dolphins *S. longirostris* 0.75% were simultaneously lactating and pregnant (calculated from Perrin *et al.*, 1977), in striped dolphins *S. coeruleoalba* the percentage was 1.9 (n=699) (Miyazaki, 1984), in ETP spotted dolphins *S. attenuata* the percentage was 4.13 (n=1114) (calculated from Perrin *et al.*, 1976), in dusky dolphins *L. obscurus* the percentage was 9.8 (calculated from van Waerebeek and Read, 1994), and in the northern form of short-finned pilot whales *G. macrorhynchus* the percentage was 9.6 (Kasuya and Tai, 1993). In contrast, only three

mature females of the southern form were found simultaneously lactating and pregnant (Marsh and Kasuya, 1984) and only one female showed that condition in bottlenose dolphins *T. truncatus* from South Africa (Cockcroft and Ross, 1990a). No simultaneously lactating and pregnant females were reported for Hector's dolphins *C. hectori* (Slooten, 1991) or for the vaquita *P. sinus* (Hohn *et al.*, 1996), while the relatively high percentage of 15.5 (n=57; calculated from Sørensen and Kinze, 1994) of simultaneously lactating and pregnant female harbour porpoises *P. phocoena* reflects the annual reproduction found in this species (Read, 1990b; Read and Hohn, 1995). Simultaneous lactation and pregnancy, suggesting reproduction in successive years, has been reported before for *Kogia* (Hale, 1947; 1962; Ross, 1979; 1984; Odell *et al.*, 1984; Beckmen, 1986). Although this is unusual for marine mammals it has also been suggested for the harbour porpoise *P. phocoena* (Gaskin *et al.*, 1984; Read, 1990b), Dall's porpoise *P. dalli* (Kasuya *et al.*, 1974; Ferrero and Walker, 1999) and the harp seal *Pagophilus groenlandicus* (Sergeant, 1966; Bowen *et al.*, 1981). It implies that a post-partum oestrus may occur (Gaskin *et al.*, 1984; Read, 1990b), although no supporting evidence for that was found in either species of *Kogia*. Most adult female harbour porpoises spend much of the year simultaneously lactating and pregnant (Read, 1990b) and as a response to these elevated energy requirements consume larger amounts of prey (Recchia and Read, 1989) (see Chapter 6).

In comparison to the South African data the percentage of *K. breviceps* that stranded on the south-eastern coast of the United States simultaneously lactating and pregnant was only 8.05% and no *K. sima* females were found in this condition (data from (Credle, 1988)). The different oceanographic conditions experienced by the two populations could explain the observed differences in reproduction.

The percentages of *Kogia* females simultaneously lactating and pregnant may not be a true representation of the whole population as females accompanied by a calf may come closer inshore to feed (see Chapter 6) and thus may be more likely to strand (Ross, 1979). Therefore the possibility that this result is an artefact of the sample cannot be excluded.

In the present study 6.9% of mature *K. breviceps* females were lactating and 24% were pregnant, in comparison to 39.1% and 16.1% females, respectively, stranded along the south-eastern United States. For *K. sima* 23% of South African animals were in either condition, compared to adult females stranded on the south-eastern United States coast, of which 40% were lactating and 30% were pregnant. These data suggest a longer

period of lactation and possibly a longer reproductive cycle for the *Kogia* populations off the south-eastern United States and would support the earlier statement that different oceanographic conditions could result in different *Kogia* populations exhibiting differing reproductive strategies.

The occurrence of mother/calf pair strandings is similar in South Africa and the south-eastern United States: for *K. breviceps* it was 51.7% and 41.6%, respectively, and for *K. sima* it was 38.5% and 50%, respectively. In these calculations both assumed cow/calf pairs (the animals stranded together and the cow was lactating) and possible cow/calf pairs (the animals stranded together, but no definite relationship could be established as the mother was not reported to be lactating and no uteri were available for examination) were included. In the latter case researchers commonly assume that the stranded couples have a cow-calf relationship and these data were therefore included in the calculation.

#### 5.4.4.5 Resting phase

The fact that a high percentage of females of both *Kogia* species were found simultaneously pregnant and lactating suggests that a resting period, which is part of the reproductive cycle of many mysticetes and odontocetes (Best, 1968; Lockyer, 1984; Perrin and Reilly, 1984), may be rare. However, females that fail to fall pregnant in the mating season of one year will have to wait 12 months for the next mating season as will females that fail to maintain a foetus. Consequently, if conditions are such that females can not maintain pregnancies in successive years an interval of up to 12 months will occur and it is then likely that the female will be in good condition for the following mating season (Figure 5.10). This interval may be regarded as equal to the resting period of other cetaceans, although somewhat more flexible. Similar data have been reported for the harbour porpoise *P. phocoena* (Read and Gaskin, 1990). Based on the data on ovulation rate from either *Kogia* species this scenario is more often observed in *K. sima* than in *K. breviceps*.

#### 5.4.5 Seasonality

Seasonality is the most obvious effect of the environment on reproduction (Bronson, 1989) and the mating season and gestation time of mammals have probably

evolved to place parturition in a season that maximises the survival of the offspring (Kasuya, 1995). All physiological processes in mammals, including reproduction, are limited by the amount of food available (Bronson, 1989), and in an environment that is characterised by seasonal variation in climate and food availability natural selection will favour reproduction during the season that maximises the potential for success (Barlow, 1984; Bronson, 1989; Kasuya, 1995). Early and late lactation are the energetically most demanding periods for the cow and thus should coincide with a time when levels of resources are optimal (Bronson, 1989; Urian *et al.*, 1996).

The only available reference to seasonal reproduction in *Kogia* stems from Sylvestre (1983), who concludes that calving and mating off Florida may take place in winter to early spring for *K. breviceps* based on one cow-calf pair stranded in mid-March. Additional unpublished data of neonates and calves of the two *Kogia* species stranded in the south-eastern United States (Credle, 1988) suggest that the seasonality of births may be different in the Florida populations of *K. breviceps* and *K. sima* than in the populations off South Africa, but further investigations are needed in this respect. Ross (1979) suggests a mating and calving season of seven months each for *K. breviceps* off South Africa, both lasting from autumn to spring. This is supported by the results from the present study.

The gestation period of *K. breviceps* in the present study was estimated at about 11 months and the data indicate that the mating season would follow immediately after the calving season. In contrast, both the mating and calving period occur at the same time in *K. sima*. The calving seasons of the two species show a small overlap in March. While *K. breviceps* gives birth in autumn and winter and over a longer period of six months, *K. sima* appears to be restricted to a shorter period of four months during summer, although the data for the latter are rather scanty. The shorter, more restricted mating and calving period, which occurs at a time when water temperatures are the highest, may indicate that *K. sima* needs higher water temperatures to meet the thermoregulatory requirements of the newborn calf, whereas *K. breviceps* may be able to cope with slightly lower temperatures as reflected by the general temperature requirements of the two species (see Chapter 7). An annual peak of births appeared to be associated with high water temperatures in bottlenose dolphins *T. truncatus* (Wells *et al.*, 1987). Although the two *Kogia* species appear to occupy a similar habitat over the continental shelf edge and slope (Ross, 1979; 1984; Davis *et al.*, 1998) (see Chapters 1 and 7) and feed on the same prey (Ross, 1979; Candela, 1987) (see Chapter 6) the above

results indicate that the mating seasons overlap only little. Furthermore, the diet of both species indicates that they may partition the same ecological niche (see Chapter 6). If several populations use the same food resource they should evolve mechanisms to reproduce at different times of the year and thus avoid high energetic demands of lactation when the main resource is being heavily utilised (Bronson, 1989; Urian *et al.*, 1996). Food is not the only factor determining the breeding season of a species, but out of the many different environmental factors that interact in complex ways to influence a mammals' reproduction, food availability probably plays the most important role (Bronson, 1989). Therefore the different peaks in the calving season may have evolved to prevent direct competition between the two species at a time when energy requirements are the highest. This correlation of the timing of reproductive seasonality in cetaceans with water temperatures, food availability or other environmental factors has been widely speculated (Wells *et al.*, 1987; Sørensen and Kinze, 1994; Hohn *et al.*, 1996).

The occurrence of neonates of *K. breviceps* in March (124cm), June (120-124cm) and August (122cm) off Florida suggests a calving season from spring to late summer for that population (data from Credle, 1988). Similarly neonates of *K. sima* reported in June (91cm, possibly aborted or early birth), July (100cm), August (105cm) and October (105cm) off Florida suggest a calving season in summer and autumn for this species (data from Credle, 1988). Although further analysis of the reproduction and seasonality of the Florida populations of *Kogia* is necessary, these data show that the calving season differs between species off South Africa and Australia (whose calf lengths revealed a similar seasonal pattern) on the one hand and Florida on the other. Different reproductive seasonalities as well as differing percentages of simultaneously lactating and pregnant females and foetal and calf sex ratios between the South African and Florida populations suggest that the reproductive strategies may differ between different *Kogia* populations.

No clear correlation could be determined between the corpus index and either month or foetal/calf length and thus this analysis did not help in examining the seasonality of reproduction in either species of *Kogia*. Wide individual variation in the volume of the largest corpus has been reported before (Harrison *et al.*, 1981), although Cockcroft and Ross (1990a) found a correlation between corpus volume index and calf length for bottlenose dolphins *T. truncatus* from South Africa. However, the relatively small sample sizes available for either species of *Kogia* for this analysis may explain the

lack of any obvious trend.

#### 5.4.6 Reproductive strategy

The gestation period of *K. breviceps* and *K. sima* was estimated at 11 and 12 months, respectively. Lactation lasts about one year in both species, but may extend to two years. A relatively high percentage of females is simultaneously lactating and pregnant in both species, but the accumulation rate of corpora indicates that although *K. breviceps* may have an annual reproduction, at least some *K. sima* females may only reproduce every two years. Both species exhibit seasonal reproduction, but while *K. breviceps* appears to have a protracted mating and calving season of six months each, *K. sima* exhibits a shorter mating and calving season over the period of three months with births occurring during the warmest part of the year. The mating and calving seasons were found to overlap slightly between the two *Kogia* species off South Africa.

Close similarities in life history strategies have been observed between two species of the same genus before (Hohn *et al.*, 1996). The life history of the vaquita *P. sinus* is very similar to that of the harbour porpoise *P. phocoena* with the exception of an annual ovulation found in the latter (Hohn *et al.*, 1996).

Researchers have had difficulties in explaining how the energetic requirements of annual reproduction in cetaceans could be met (Gaskin, 1982; Straley *et al.*, 1994; Read and Hohn, 1995). As an indicator of body condition blubber mass is thought to be a reflection of a cetaceans energy reserves and thus provide information about an individual's probability of future survival and reproduction (Read, 1990c). Although differing results were obtained, two independent studies that assessed body condition of harbour porpoises *P. phocoena* (Read, 1990c; Lockyer, 1995b) revealed that the variation of blubber parameters (such as thickness, mass and lipid content), and therefore body condition, among different reproductive classes reflect the relative energetic costs of reproduction (Read, 1990c). Accordingly, lactating harbour porpoises had less blubber mass or lipid content than pregnant females (Read, 1990c; Lockyer, 1995b) and Chittleborough's (1965) data from humpback whale *M. novaeangliae* catches indicate that mature females with near term foetuses yielded more oil than other mature females. The current thought is that under good conditions (meaning abundant food resources) reproduction in successive years will be favoured, whereas in poor years the pregnancy will be missed and reproduction may only occur every other year (Gaskin, 1982;

Lockyer, 1987; Straley *et al.*, 1994). Furthermore, female harbour porpoises from the Bay of Fundy population may be able to compensate for the energetic requirements of lactation by an increased energy intake as the annual variation between herring consumption and body condition was found to co-vary (Read, 1990c). In this context the differences in reproductive rates between two populations of harbour porpoises from California and the Bay of Fundy were ascribed to differing prey availabilities (Read and Hohn, 1995). Considering that a truly annual strategy may endanger the survival of the female, Gaskin (1982) proposed that the mean number of calves produced per lifetime in this species is unlikely to exceed four. Apart from the harbour porpoise, annual reproduction has been reported in the Dall's porpoise *P. dalli* (Ferrero and Walker, 1999), the minke whale *B. acutorostrata* (Masaki, 1979; Best, 1982; Lockyer, 1984) and, occasionally, in the humpback whale *M. novaeangliae* (Clapham and Mayo, 1990; Straley *et al.*, 1994). This aspect will be discussed further in Chapter 9 under the aspect of life histories in cetaceans.

A surprising fact in the reproductive strategy of both *Kogia* species is that sexual maturity is attained at a relatively early age. In odontocetes this is usually only found in phocoenids (Gaskin *et al.*, 1984) and small dolphins (Perrin and Reilly, 1984), with a relatively short lifespan of around 15 to 20 years (Gaskin *et al.*, 1984; Perrin and Reilly, 1984; Slooten, 1991; Sørensen and Kinze, 1994; Read and Hohn, 1995; Hohn *et al.*, 1996). In both *Kogia* species the lifespan is similarly short (*K. breviceps*: 22.4yrs; *K. sima*: 21.5yrs; see Chapter 3). It was suggested that although harbour porpoises can live up to 24 years such a high age is rarely found in this species due to a combination of natural and incidental mortality (Hohn and Brownell, 1990; Read and Hohn, 1995; Lockyer, 1995a). The same may be true for either species of *Kogia* as the low age at ASM may have evolved as a result of predation pressure (see Chapter 9). Similarly, a decrease of age at ASM resulting from exploitation has been reported for a number of delphinids (Perrin and Henderson, 1984; Kasuya, 1985) and a higher number of simultaneously lactating and pregnant females was also reported in these populations (Perrin *et al.*, 1976; Perrin *et al.*, 1977). As no data of ovulation rates are available from any other populations of *K. breviceps* and no obvious exploitation of the animals themselves or of their main prey occurs, these data are thought to represent the norm rather than elevated ovulation rates in response to exploitation. This trend will be examined in more detail in Chapter 9.

A high number of ovulations does not necessarily mean that a large number of

offspring is produced per lifetime. Even harbour porpoises with an annual ovulation may only produce between four and seven offspring per lifetime (Gaskin *et al.*, 1984; Read, 1990a). The highest number of corpora recorded for a *K. breviceps* female is 29 reported for a 315cm long animal (Jenness and Odell, 1978). Assuming annual ovulation of 0.9 as observed for *K. breviceps* in the present study and given that the age at ASM is also five this would indicate an estimated age of at least 31.1 years. However, the ovulation rate reported for *K. breviceps* here is not necessarily applicable to animals from the Florida population as differences in the length of the reproductive cycle between two populations of the same species have been reported before for harbour porpoises from the Gulf of Maine (Read and Hohn, 1995) and from California (Hohn and Brownell, 1990). The differences in the length of the reproductive cycle between populations of harbour porpoises at least in part reflect variations in prey resource levels (Gaskin *et al.*, 1984; Read and Hohn, 1995).

#### 5.4.7 Mating system

In Chapter 4 it was suggested that either a roving male strategy or harem strategy may be employed by males of the two *Kogia* species. The difference between the two strategies is largely determined by the dispersal of the females (Best and Butterworth, 1980; Krebs and Davies, 1981; Whitehead, 1990; Sandell and Liberg, 1992; Magnusson and Kasuya, 1997; Whitehead, 1998). Where females range widely or live solitarily or in small groups, males may employ a roving strategy in search of receptive females (Connor *et al.*, 2000). A harem strategy is expected when a male can defend resources (Clapham, 1996) or when females are more gregarious, thus inhabiting fewer, larger groups, which would result in longer travel times between groups for the males and in turn result in residence (Whitehead, 1998). Beckmen (1986) observed that both *Kogia* species show extensive *bursa ovarica* and well developed fimbriae in their reproductive tracts, which is unusual for odontocetes. She theorised that since *Kogia* are solitary and thus may have the need for each mating to be successful these structures may have evolved to ensure that no ova are lost into the body cavity. The small group size in both species (see Chapters 1, 4 and 7) would support such a theory and suggests that males employ a roving strategy rather than are able to defend a harem.

#### 5.4.8 Foetal and juvenile sex ratio

Little research has been carried out on foetal and juvenile sex ratios in cetaceans, but differences in juvenile mortality between odontocetes and mysticetes may reflect differences in the length of the period of maternal care between the two groups (Ralls *et al.*, 1980). Although the foetal sex ratio in *K. breviceps* is slightly skewed towards males and this trend is even stronger in the juvenile sex ratio, neither sex ratio differed significantly from parity. Although a predominance of males in the juvenile sex ratio in *K. breviceps* has been mentioned previously in the literature (Ross, 1979; Brabyn, 1991; Baird *et al.*, 1996), no further possible implications of this were discussed. Since both the foetal as well as the juvenile sex ratio in *K. breviceps* show are slightly skewed towards males this may be a reflection of a higher percentage of males in the population or may indicate that male calves and juveniles are more likely to strand. Possible explanations for this are differential juvenile mortality rates between the sexes as was suggested for the striped dolphin *S. coeruleoalba* (Aguilar, 1991), the sperm whale *P. macrocephalus* (Ralls *et al.*, 1980), and the harbour porpoise *P. phocoena* (Lockyer, 1995b). Greater susceptibility of males to nutritional stress, greater tendencies of males to emigrate, and male-male competition may all contribute to higher mortality rates in males and more than one of these factors may apply to a single species (Ralls *et al.*, 1980). The general mammalian pattern shows more male than female dispersal, and emigration exposes the individual to nutritional stress, high risks of predation, and risks from strange conspecifics (Ralls *et al.*, 1980). Males are more susceptible to nutritional stress than females (Ralls *et al.*, 1980; Clutton-Brock and Iason, 1986) and therefore the inexperience of calves in finding food after separation from the mother may result in increased male juvenile mortality (Read and Hohn, 1995; Lockyer, 1995a, b). Additionally, when home ranges overlap and offspring come into competition with the parents the sex ratio should favour the sex that disperses (Clutton-Brock and Iason, 1986).

In contrast to the data from the present study calves of *K. breviceps* stranded along the south-eastern United States showed a sex ratio of 1.32:1 for females and males, respectively, while it was 1.5:1 for females and males of *K. sima* (data from Credle, 1988), which, in contrast to the South African data, seems to reflect a slight predominance of females. However, it is unclear how old these “calves” were as no age determination was carried out on that sample and it appears that only animals that

stranded with a mature female were classified as calves. Therefore it is possible that a comparison of animals for which age estimates are available may give different results, as only older juvenile males may suffer higher mortality (due to fights or nutritional stress). This example illustrates the potential that comparative studies between geographical regions have, in particular in such interesting species as *Kogia* where sample sizes could be vastly increased by comparative studies. But it also emphasizes the downfalls if methods are not standardized between studies or made sufficiently clear.

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## *Chapter 6: Diet*



## **6.1 Theoretical background**

Knowledge of the diet of a species is relevant to many different aspects of a species' ecology. Aside from demonstrating what an animal depends on as its major food source, it also gives an indication about the animal's distribution, foraging behaviour and, in the case of marine mammals, diving depth. In addition, it contributes to knowledge about the ecology, seasonal fluctuation, and distribution of the food source. Extensions of such analyses in the case of marine top predators can potentially provide information on the biomass of the prey populations, competition between different predators, and the interactions of predators with other species such as commercial fish species (Santos *et al.*, 2001). Ultimately, qualitative and quantitative data on the diet of such species may be used in dynamic models on trophic relationships in communities and ecosystems (Payne *et al.*, 1992; Santos *et al.*, 2001). As different types of marine predators provide different opportunities and problems, the extent to which diet analysis can answer specific questions very much depends on the species under examination (Santos *et al.*, 2001). Piecing together results from different analyses and different species contributes towards an understanding of some of the factors affecting the ecology of both predator and prey (Santos *et al.*, 2001).

A variety of methods have been used to study the diet of marine mammals. Limitations on observations are presented by the aquatic life style of these animals, except where the water is clear (Barros and Clarke, 2002). The traditional method to study the diet of marine mammals has been the analysis of food remains present in the stomachs of stranded animals or, to a lesser extent, the vomit and faeces of live animals (Barros and Clarke, 2002). A review of these methods is given below, with the emphasis on stomach content analysis. For a recent review on the diet and dietary studies of marine mammals see Barros and Clarke (2002).

### **6.1.1 Stomach content analysis**

Stomach content analysis has traditionally been the main method to study the diet of marine mammals. This method relies on finding and identifying hard structures representing the prey. These are fish bones, mainly otoliths (or ear stones) and jaws of cephalopods, also referred to as "beaks" due to their resemblance to parrot beaks (Barros and Clarke, 2002). Both the shape and size of otoliths and cephalopod beaks are species-

specific and thus represent good material for the identification of prey items.

Stranded animals are a good source of data, especially as many stranded cetaceans present rarer and little known species for which information on diet may be otherwise unobtainable (Ross, 1984). Initially it was thought that data from stranded animals may be biased towards inshore prey species due to the fact that the cetaceans must have passed through shallow water to reach the beach (Ross, 1984; Clarke, 1986a). However, Ross (1979b) compared data from stranded animals with those from animals caught offshore and concluded that there was no bias, and thus stranded animals gave a correct indication of the normal diet of the species. Similarly, Gannon (1997a) reports a similar prey assemblage in the stomach of both stranded and by-caught long-finned pilot whales *Globicephala melas* in the western North Atlantic. Although differences in the amount of fish consumed are found between stomach contents from stranded versus stomach contents from caught odontocetes, there are no differences for the percentage of cephalopods in the diet (Sekiguchi *et al.*, 1992). This indicates that the dietary importance of cephalopods may be overestimated, as their beaks are retained and identifiable for longer periods than fish otoliths (Clarke and MacLeod, 1982). However, if stranded animals are sick, which is often the case, their stomachs may either be empty or the diet may not be representative of the normal diet of the species (Ross, 1984). Few studies have had the opportunity to obtain quantitative data from more than a few specimens of any species (Clarke, 1996b) or from more than just a small area of the species' range (Pauly *et al.*, 1998). Therefore such data may not be applicable to their entire distribution range (Pauly *et al.*, 1998).

The second source of data is animals by-caught in fishing gear (Gannon *et al.*, 1997a;b), caught in commercial operations (Desportes and Mouritsen, 1993), or those that were historically commercially hunted, such as sperm whales (Clarke, 1980). As a result of commercial exploitation and the large quantities of beaks that accumulate in their stomachs, more is known about the diet of sperm whales than of any other teuthophagous cetacean species (Clarke, 1980; 1986a; Clarke and MacLeod, 1982).

Few prey items, in particular cephalopods, are found in a sufficiently undigested state to be identified. The digestion process affects fish bones, eye lenses and squid pens less than the flesh of the food, but not much research has been done into identifying these remains to species level, or how to use them in diet analysis (Clarke, 1980). Digestion has even less of an effect on the beaks of cephalopods and otoliths of fish (Clarke, 1980). Cephalopod flesh is digested more rapidly than fish muscle (Santos *et*

*al.*, 2001), and thus the identification of prey items relies on the remaining beaks that accumulate in stomachs. Cephalopod beaks are generally more resistant to erosion from digestion than are fish otoliths (Tollit *et al.*, 1997), and for studies on mainly piscivorous species otolith erosion is one of the most important sources of error in quantifying diet (Bowen, 2000). However, there is wide interspecific variation in the susceptibility of fish otoliths to erosion, depending on fish size and the robustness of the otoliths (Tollit *et al.*, 1997; Bowen, 2000). To some extent these biases can be taken into consideration using data from captive feeding experiments on pinnipeds (Tollit *et al.*, 1997; Bowen, 2000). However, digestive processes depend on a variety of factors: meal size, condition at which the animal is held (including the amount of exercise the animal gets), prey size, predator species, and the effectiveness of hard part recovery (Bowen, 2000). In addition, many otoliths and bones of fish are digested and/or expelled from the stomach before the beaks, either by vomiting or defecating (Clarke, 1980). Retention times have been calculated for the sperm whale (Clarke, 1980) and captive bottlenose dolphins (Ross, 1979b). In the latter, experiments on captive animals indicate that beaks can be retained for three days or more without showing signs of erosion and different sized beaks do not appear to be egested differentially (Ross, 1979b). Due to the fact that food organisms dissolve at different rates and may have been ingested at different times prior to collection, stomach contents will rarely reflect the true proportion of the taxa, unless only samples showing little signs of digestion are used (Ross, 1979b).

Some of the earliest works to identify cephalopod beaks from the stomach contents of cetaceans were carried out by Clarke (1962). The identification of prey remains from stomachs is facilitated by various reference works (Clarke, 1986b; Smale *et al.*, 1995), but usually only certain geographic areas are covered. Thus access to good reference material is essential for the identification of prey remains. Although some beaks of cephalopods remain unidentified in almost any oceanic region, they are often those of rarer species, and the difficulties reflect taxonomic problems due to the inadequacy of sampling cephalopods from oceanic waters (Santos *et al.*, 2001).

Regression equations developed for both fish and cephalopod species allow back calculation from otolith or beak size to determine the weight and length of prey and thus allow an estimation of both the number and size of prey consumed (Ross, 1979b; Clarke, 1986b). It is generally assumed that the relative frequency and size of prey estimated from the otoliths and cephalopod beaks found in the stomach are an accurate representation of the prey consumed. However, there are three types of bias: a) not all

prey are likely to be identified, b) not all individuals in a prey category may be detected (i.e. only parts of the prey may be consumed), and c) size-reduction in hard parts (particularly otoliths) as a result of digestion may lead to underestimation of prey body size (Santos *et al.*, 2001). Additional prey items found in the stomachs of animals, such as crustaceans, may be difficult to incorporate into quantitative analyses and thus may only provide qualitative information (Santos *et al.*, 2001). For a review on the sources of error in estimating the importance of cephalopods in the diet of marine mammals see Santos *et al.* (2001).

### 6.1.2 Alternative methods to study diet in marine mammals

Aside from stomach contents, faeces are often used as a source of data on the diet of marine mammals (Klages and Bester, 1998; Smith and Whitehead, 2000). In pinnipeds this method is increasingly used as faeces are easier to collect for this group of marine mammals than for cetaceans, are less expensive to collect, and are less affected by differential rates of digestion than are estimates from stomach contents (Bowen, 2000).

In contrast to direct methods on the analysis of diet in cetaceans such as scat and stomach content analysis, indirect methods such as stable isotope analysis and fatty acid analysis from blubber samples have been explored (Ostrom *et al.*, 1993; Pauly *et al.*, 1998; Walker and Macko, 1999; Hooker *et al.*, 2001). These methods are a good source of information in the absence of stomach contents and when feeding is difficult to observe, and are less invasive in nature (Ostrom *et al.*, 1993; Hooker *et al.*, 2001). In addition, stable isotope analysis can provide historic data, which may be otherwise unobtainable (Walker *et al.*, 1999) or aid in tracing migration patterns (Best and Schell, 1996). However, while stomach content analysis often provides more of a “snapshot” of the diet of a species at that moment in time, stable isotope analysis and fatty acid analysis provide a record of diet over longer time periods and can only be used to assess differences in diet between species (Hooker *et al.*, 2001). In addition, both methods can only allow diet to be interpreted through a comparison in pattern with their prey (Hooker *et al.*, 2001). Differences in feeding patterns (i.e. at different trophic levels) between adults and juveniles can be detected (Lawson and Hobson, 2000), and temporal changes in diet throughout an animal’s life can be traced in this way (Hobson and Sease, 1998). In stable isotope analysis the carbon isotope signatures can be used to study the energy

transfer between a consumer and its food, while the nitrogen signatures reflect diet and trophic level of the animal studied (Walker and Macko, 1999). Studies indicate that the pygmy sperm whale *K. breviceps* is on the same trophic level as the common dolphin *Delphinus delphis* (both with a mean  $\delta^{15}\text{N}$  signature of 12.4 ‰), with the manatee *Trichechus manatus* showing levels below that (7.8‰) and the sea otter *Enhydra lutris* being above that (14.5‰) (Walker and Macko, 1999). A separate study indicates the highest level in the white-beaked dolphin *Lagenorhynchus albirostris* (16.2‰; trophic level=3.4) and the lowest in the blue whale *Balaenoptera musculus* (9.6‰; trophic level=1.2) (Ostrom *et al.*, 1993). The value for *K. breviceps* (11.9‰; trophic level=2.0) is intermediate between that of the minke whale *Balaenoptera acutorostrata* (12.3‰; trophic level=2.1) and the sperm whale *Physeter macrocephalus* (11.1‰; trophic level=1.7) (Ostrom *et al.*, 1993), and is similar to the result obtained by Walker and Macko (1999). In contrast, trophic levels calculated for marine mammals by Pauly *et al.* (Pauly *et al.*, 1998) range from 3.2-3.4 in baleen whales, over 3.8- 4.4 in most species of odontocetes, to 4.5-4.6 in killer whales *Orcinus orca*. The trophic level of *K. breviceps* is with 4.4 slightly higher than that of *K. sima* (4.3) (Pauly *et al.*, 1998). Both species are thus located near the upper trophic levels for odontocetes and only True's beaked whale *Mesoplodon mirus* and the killer whale have higher trophic levels (Pauly *et al.*, 1998). However, it is unclear why the levels from the former study are so much lower than that from the latter (Pauly *et al.*, 1998).

### 6.1.3 Cephalopods as prey

Cephalopods are an important part of the diet of many odontocetes, but have been less well studied than fish and crustaceans. As a result many remains in stomachs have not been identified properly. At least 50 species of odontocetes include cephalopods in their diet and they form the main food in at least 28 odontocetes (Clarke, 1986a; 1996b). The Ziphiidae, Physeteridae and Kogiidae include the main cephalopod eaters (Clarke, 1986a; 1996b), while all but two species of the family Delphinidae include cephalopods in their diet (Clarke, 1996b). No Balaenidae eat cephalopods, two species of balaenopterids eat squid intentionally at times, namely the minke whale *B. acutorostrata* and the sei whale *B. borealis*, while blue whales *B. musculus* and fin whales *B. physalus* probably only include them in their diet accidentally (Clarke, 1986a; 1996b).

Although cephalopods form a large part of the marine ecosystem and as such are important in the diets of many marine birds (Randall *et al.*, 1981), fish (Smale, 1996), and seals (Klages and Bester, 1998; de Bruyn *et al.*, 2003), this part of the study will concentrate on cephalopods (and to a lesser extent fish) in the diet of cetaceans that are primarily teuthophagous.

There are almost 1000 species of cephalopods with a great variety of life histories and nutritional values (Clarke, 1986a). There are 28 families of cephalopods represented in the diet of cetaceans, with the most important being the oceanic Ommastrephidae, Histioteuthidae and the Cranchidae (Clarke, 1996b). Over the continental shelf the neritic Loliginidae appear most important (Clarke, 1996b). Members of the other 22 families of cephalopods occur opportunistically in the diet of cetaceans and it is assumed that less than 60 cephalopod species occur regularly in the diet of cetaceans (Clarke, 1996b). Knowledge of life history, distribution and habitat of cephalopods that occur in the diet of cetaceans can increase understanding of cetacean distribution, migration, feeding depths, feeding methods, and functional morphology. Besides increasing the understanding of cetacean biology, such work provides valuable information on cephalopod biology, since many species are rarely caught by nets and other sampling devices (Clarke, 1986a). While the species composition and distribution of the coastal cephalopod fauna along some coastlines is well known due to exploitation by commercial fisheries or surveys from bottom trawls (dos Santos and Haimovici, 2001; Wang *et al.*, 2002), it is not well studied in other parts. Often less is known about the cephalopod species inhabiting the upper continental slope and oceanic waters as no surveys targeting cephalopods are performed there and only long line fishing for large pelagic fish occurs (dos Santos and Haimovici, 2001). Our current knowledge of cephalopods is restricted to shelf-living, muscular, negatively buoyant species such as Loliginidae and Octopodidae, gas-supported species like Sepiidae and Nautilidae, and members of the Ommastrephidae, which move onto the shelf at certain seasons (Clarke, 1996a). However, the species inhabiting the continental shelves comprise only about 15% of all cephalopod genera and live in water less than 300m deep (Clarke, 1996a). The rest of the cephalopod genera are spread in the upper 2000m and across the bottom of the deep ocean (Clarke, 1996a). Over 40% of these species are neutrally buoyant (through oil or chemical means) and thus may have very different lifestyles to the shallow water forms (Clarke, 1996a). Improvement of our knowledge on the ecology of these species is hindered by the poor direct sampling methods and rests largely on

sampling from the stomachs of predators (Clarke, 1996a; 1996b; dos Santos and Haimovici, 2001).

Knowledge of nutritive potential and differences in composition between cephalopods, fish, and crustaceans can also increase our understanding of trophic relationships (Clarke, 1986a). However, the natural diet of many species of cetacean is not yet known. Most cephalopods are easy to catch as they cannot sustain high swimming speeds for long and many of the families favoured by cetaceans (e.g. histioteuthids and cranchiids) are neutrally buoyant and sluggish (Clarke, 1996b). In sperm whales, ammoniacal squid comprise 53 to 78% of the cephalopods consumed (Clarke, 1980; 1986a; 1996b). Although these species have a lower energy content (Clarke, 1996b), they also require less energy expenditure during the hunt than fast-swimming species. Data obtained from a few squid species suggest that cephalopods school and congregate to spawn (Augustyn *et al.*, 1994), which presents a concentrated food source for predators and many cetaceans are thought to feed on the spawning grounds (Clarke, 1996b). Cephalopods have short life spans of less than two years and reproduce rapidly, thus compensating for heavy predation (Clarke, 1996b).

The sizes of cephalopods found in the diet of cetaceans ranges from three centimetres mantle length and a few grams in weight to over 20m mantle length and probably over 500kg in weight (Clarke, 1996b). The weight of the cephalopods consumed by sperm whales varies with region, with the greatest weights occurring in the Antarctic (Clarke, 1980; 1986a). Species composition of cephalopods in the diet of cetaceans varies regionally, seasonally and annually, with the greatest difference found between cetaceans that inhabit oceanic waters compared to those living over the continental shelf (Clarke, 1996b; dos Santos and Haimovici, 2001). In addition, there is a positive correlation between both the size of the cetacean and the growth stage within a cetacean species and the size of the cephalopod prey (Clarke, 1996b). As a result some partitioning of resources has been observed, leading to reduced competition among and within species for the food available (Clarke, 1996b). Clarke (1996b) presents an overview of the preferred cephalopod prey by family and species of cetacean.

#### **6.1.4 Teuthophagous odontocetes**

As mentioned above many cetaceans include cephalopods in their diet (Jones,

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1981; Sekiguchi *et al.*, 1992; González *et al.*, 1994), but few odontocetes seem to feed predominantly on cephalopods. The most important squid-eating odontocetes are the Ziphiidae and the two genera of the sperm whales (Clarke, 1980; 1986a; Sekiguchi *et al.*, 1996; MacLeod *et al.*, 2003). In addition, Risso's dolphins *Grampus griseus* (Würtz *et al.*, 1992; Cockcroft *et al.*, 1993) and pilot whales (genus *Globicephala*) (Desportes and Mouritsen, 1993; Gannon *et al.*, 1997a; 1997b) feed on cephalopods to a large extent. These species can be termed teuthophagous, although the diet may be supplemented with fish, crustaceans and other prey to some degree. Both *Kogia* species are primarily teuthophagous and a review of the knowledge of the diet of odontocetes will be restricted to other teuthophagous species for comparative purposes.

#### 6.1.4.1 Dentition

The reduced dentition of *Kogia* and other teuthophagous species has been mentioned briefly in Chapters 1, 3 and 4 with respect to morphological distinction between the two species and as an indicator of the mating system. Here it will be discussed in relation to diet.

Most species of odontocetes have a large number of conical shaped teeth, which they use to hold their prey (Norris and Møhl, 1983). The reduction in dentition can be observed in 27 out of 67 modern odontocetes (or 43%) and consequently it has been suggested that some species, including the sperm whale, may debilitate their prey with sound rather than catch it with their teeth (Norris and Møhl, 1983). Norris and Møhl (1983) in reviewing this idea state that there is no evidence that the lower jaw of the sperm whale plays a big role in catching prey and suggest that it rather immobilizes the prey before using a sucking motion to draw the squid into the mouth. More recently it has been suggested that a number of odontocetes acquire food by means of suction feeding (Heyning and Mead, 1996). However, little real supporting evidence has been presented for that to date, with the exception of a recent study on Ziphiids (Heyning and Mead, 1996). The presence of throat grooves, a small gape, and a reduction in the number of teeth in these species may all present adaptations for suction feeding. The throat grooves aid in creating suction by increasing the intraoral cavity when distended and the small gape found in Ziphiids facilitates the intake of water more efficiently (Heyning and Mead, 1996). Throat gooves are present in the sperm whale *P. macrocephalus* and have been reported for *K. sima* (see Chapter 1) and a small gape is

found in both genera of sperm whales, supporting evidence for suction feeding in these species.

Allen (1941) remarks that the overshot jaw and the almost complete loss of teeth in the maxilla in *Kogia* indicate a diet other than fish, rather like crabs and cephalopods. Gaskin (1982) interprets the small mouth and receding lower jaw as indicators that *Kogia* feed near or on the ocean floor. He also comments on the reduction in the number of teeth in primarily teuthophagous species, and a number of authors subsequently suggest that the teeth retained in these species might serve for social interaction rather than feeding (Heyning, 1984; MacCleod, 1998). Reduction of dentition is also suggested to be advantageous for suction feeders (Heyning and Mead, 1996).

Echolocation coupled with suction feeding may be advantageous for foraging in the aphotic zone and additionally suction feeding would explain the presence of intact squid (without teeth marks) found in the stomachs of ziphiids and the big sperm whale *P. macrocephalus* (Heyning and Mead, 1996).

#### 6.1.4.2 Diet

The diets of teuthophagous odontocetes are to a large extent determined by their geographical location, as well as the seasonal and topographical changes in the abundance of their prey (Clarke, 1986a). Furthermore, preferences of prey species vary depending on age and sex of the animal (Clarke, 1980; Kawakami, 1980).

Risso's dolphins *G. griseus* feed mainly over the continental shelf and in oceanic waters (Clarke, 1986b; Clarke and Pascoe, 1985; Würtz *et al.*, 1992). Some of the cephalopods found occur at daytime depths of over 300m, which indicates that the species probably also feeds over steep slopes of the shelf (Clarke, 1986b; Würtz *et al.*, 1992). In addition, a cephalopod species found near the bottom on sea mounts in oceanic waters has been recorded (Würtz *et al.*, 1992). No fish remains are found in the diet (Ross, 1984; Clarke and Pascoe, 1985; Würtz *et al.*, 1992) and the main prey are cephalopods of the families Ommastrephidae, Sepiidae, Histioteuthidae, Loliginidae and Octopodidae (Evans, 1987). At least 17 species of cephalopods were identified from stomachs of Risso's dolphins from South Africa (Cockcroft *et al.*, 1993). This relatively small number of exclusively cephalopod prey species indicates that the species has a rather specialized diet of a small variety of locally abundant cephalopods and there is a significant difference in the prey consumed by males and females (Cockcroft *et al.*,

1993). Odontocetes which occur in small groups like the Risso's dolphin, are known to feed on cephalopods that are ammoniacal, buoyant, solitary species, which are evenly and widely distributed (Ross, 1984; Clarke, 1986a).

Studies on long-finned pilot whales *G. melas* in the North Atlantic indicate that the species feeds almost exclusively on cephalopods (Sergeant, 1962; Gannon *et al.*, 1997a), mainly those belonging to the Loliginidae, Ommastrephidae, Histioteuthidae, Onychoteuthidae, Gonatidae, Cranchiidae, Brachioteuthidae, Chiroteuthidae and Sepidae as well as octopus (Evans, 1987). However, the diet may be supplemented with some fish (Kasuya and Tai, 1993). Prey items of animals from the North Atlantic include 12 genera of cephalopods, distributed within at least 10 families, and 15 genera of fish, representing at least eight families (Desportes and Mouritsen, 1993). Although the authors thought prey diversity to be large, with at least 30 taxa of fish or cephalopods in the stomachs, the diversity in each individual stomach was low, with 48% of them containing the remains of a single species (Desportes and Mouritsen, 1993). Feeding was estimated to occur at a variety of water depths between 100 and 500m (Desportes and Mouritsen, 1993).

Comparatively little information exists on the diet of short-finned pilot whales *G. macrorhynchus*, which feed mainly on Loliginidae, Cranchiidae, Enoploteuthidae and Octopoteuthidae (Evans, 1987). Animals stranded along the South African coastline feed mainly on *Loligo reynaudi* (Ross, 1984).

A recent review of the diet of beaked whales worldwide shows that all beaked whales predominantly feed on prey, which occur between 200 and 2000m water depth, indicating that beaked whales in general feed off the continental shelf (MacLeod *et al.*, 2003). Beaked whales feed on a high number of different prey species and families, in particular cephalopods (MacLeod *et al.*, 2003). Northern bottlenose whales *Hyperoodon ampullatus* feed at depths of over 800m (Hooker and Baird, 1999), and off the Faroe Islands the prey consists mainly of squid from at least 13 different species, but is also supplemented with fish, decapod crustaceans, starfish and sea cucumbers (Evans, 1987; Bloch *et al.*, 1996). The main families of squid represented in the diet are Gonatidae, Sepiidae, Loliginidae, Enoploteuthidae, Cranchiidae, Myopsidae and Oegopsidae (Evans, 1987). In contrast southern bottlenose whales *Hyperoodon planifrons* feed mainly on cranchiids and neoteuthids (Evans, 1987), but all the species found in the diet live in deep water, extending to depths over 500m and in some cases over 1000m (Clarke and Goodall, 1994). Baird's beaked whales *Berardius bairdii* feed to a large

extent on fish and have squid of the families Gonatidae, Onychoteuthidae and Octopoteuthidae present in their diet (Evans, 1987). Cuvier's beaked whales *Ziphius cavirostris* from both hemispheres feed predominantly on cephalopods of the families Cranchiidae, Onychoteuthidae, Brachioteuthidae, Enoploteuthidae, Octopoteuthidae, and Histioteuthidae (Evans, 1987). *Mesoplodon* species from both hemispheres feed predominantly on cephalopods from the families Ommastrephidae, Octopoteuthidae, Enoploteuthidae and Neoteuthidae (Evans, 1987). Strap-toothed whales *Mesoplodon layardii* stranded on South African and New Zealand coasts feed mainly on oceanic squid, most of them inhabitants of the mesopelagic zone and some of them of the bathypelagic zone (Sekiguchi *et al.*, 1996). In South African animals *Histioteuthis* sp. and *Taonius pavo* were the predominant prey items, while for the New Zealand specimens Chiroteuthidae were dominant by number and *Histioteuthis miranda* by mass (Sekiguchi *et al.*, 1996). No predominance of bioluminescent cephalopods or those with specific buoyancy control mechanisms was observed in any species of beaked whale (MacLeod *et al.*, 2003).

The diet of sperm whales has been well studied due to the long commercial exploitation of the species and its teuthophagous diet has played a major part in advancing the knowledge of cephalopod biology and distribution in many areas of the world (Clarke, 1980; Clarke and MacLeod, 1982; Pascoe *et al.*, 1990). However, in early years the identification of squid beaks had not been developed, thus only flesh remains were identified (Gaskin and Cawthorn, 1967; Kawakami, 1976). Sperm whales feed on medium to large mesopelagic squid, which are usually found in high concentrations over the continental slope and ridges and preferred sperm whale habitats in the western North Atlantic coincide with areas influenced by cooler shelf or slope water, which provides a suitable habitat for squid (Griffin, 1999). A review of sperm whale food worldwide was given by Kawakami in 1980, and more recently for the eastern Pacific Ocean by Smith and Whitehead (2000). Worldwide this species feeds on about 56 species from 36 different genera of cephalopods, belonging to 19 families (Kawakami, 1980). The main prey are cephalopods of the families Histioteuthidae, Onychoteuthidae, Octopoteuthidae, Gonatidae, Cranchiidae, Ommastrephidae, Architeuthidae as well as octopus (Kawakami, 1980; Evans, 1987). Although numerically the main prey items are histioteuthids, followed by gonatids and onychoteuthids, in terms of weight octopoteuthid and histioteuthid squid were most important in most regions of the world (Kawakami, 1980). In terms of mass onychoteuthids, architeuthids and ommastrephids

are important only regionally (Kawakami, 1980). A few studies demonstrate the movements of animals due to the presence of particular cephalopod species in their diet (Clarke, 1980; Clarke and MacLeod, 1982; Clarke and Roper, 1998; Pascoe *et al.*, 1990).

Although diet studies in cetaceans appear largely descriptive rather than comparative, probably due to large gaps in the knowledge of distribution and abundance of both predator and prey, a few general observations can be made.

Studies on diet in odontocetes show that the size of prey (both in length and mass) is positively correlated with predator size, which led Ross (1979b) to the conclusion that odontocete species of different sizes are unlikely to compete for the same food resources. In contrast, species, which are similar in size and particular those that are closely related are quite likely to compete for food resources (Ross, 1979b). Consequently, in *Kogia*, undue competition for food resources was thought to be diminished as *K. breviceps* feeds on larger prey than *K. sima*. In addition, there is some evidence of intraspecific change in prey size with growth, as the size of prey taken by adults is bigger than that taken by juveniles in both *Kogia* species (Ross, 1979b). The smaller gape size in juveniles, inexperience in hunting techniques, and a change in feeding behaviour which occurs at sexual maturity in these species all contribute to the difference in prey size taken (Ross, 1979b). In contrast, only a poor correlation between the length of the dolphin and both mean length of prey and mass of prey is seen in Risso's dolphins *G. griseus* off South Africa (Cockcroft *et al.*, 1993). However, in general the prey length increased with dolphin length and larger cephalopod species are important for larger dolphins (Cockcroft *et al.*, 1993). In addition, the mean prey length of males is greater than that of females (Cockcroft *et al.*, 1993). Curiously strap-toothed whales eat squid of a similar size to those eaten by smaller odontocete species, such as spotted dolphins *Stenella attenuata* and dwarf sperm whales *K. sima* (Sekiguchi *et al.*, 1996).

Different groups within a cetacean species also exhibit differing prey preferences (Desportes and Mouritsen, 1993). Energy requirements in female cetaceans are the highest in lactating females and as a result dietary differences between these and other members of a population are reported for a number of cetacean species (Bernard and Hohn, 1989; Recchia and Read, 1989; Young and Cockcroft, 1994). While these are all piscivorous species, similar results are found in teuthophagous odontocetes. Lactating females of long-finned pilot whales *G. melas* consume more fish and more fish species than any other group of mature females (Desportes and Mouritsen, 1993).

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If the preferred prey item is unavailable due to seasonal environmental changes, including El Niño events, teuthophagous whales appear to diversify their diet and feed at a different depth as was observed for long-finned pilot whales *G. melas* (Desportes and Mouritsen, 1993) and sperm whales *P. macrorhynchus* (Smith and Whitehead, 2000). Some correlation between the distribution and seasonal movement of long-finned pilot whales and their main prey is reported for the populations off the Faroe Islands (Hoydal and Lastein, 1993) and off the north-eastern United States (Payne and Heinemann, 1993), while no seasonal changes could be determined in the diet of Risso's dolphins off South Africa (Cockcroft *et al.*, 1993).

Recent studies on sperm whales *P. macrocephalus* describe a difference between the diet of commercially caught specimens and stranded ones in that commercially caught specimens have more fish present in their diet (Santos *et al.*, 1999). In the North Atlantic the main prey species of both stranded long-finned pilot whales *G. melas* and those caught in the drive fishery were *Todarodes sagittatus* (Desportes and Mouritsen, 1993; Sigurjónsson *et al.*, 1993), but animals caught in the drive fishery also feed on two fish species (blue whiting *Micromesistius poutassou* and greater argentine *Argentina silus*) (Desportes and Mouritsen, 1993). Little difference is reported between the stomach contents of stranded and by-caught specimens of long-finned pilot whales *G. melas* in the western North Atlantic (Gannon *et al.*, 1997b). However, as the animals were found to opportunistically feed on mackerel around the fishing nets at the time of death, the authors concluded that the whales might switch opportunistically to different prey (i.e. fish) when their main prey *Loligo pealei* becomes temporarily unavailable (Gannon *et al.*, 1997a).

Few diet studies on teuthophagous odontocetes have compared the diet between species. In southern Brazil loliginids are the most important cephalopods in the diet of coastal marine mammals, and ommastrephids were most important in the diet of offshore odontocetes (dos Santos and Haimovici, 2001). The diversity of prey in the stomachs is low in coastal marine mammals, but increases in offshore species, where both the fast moving muscular squid and the less mobile mesopelagic and epipelagic neutrally buoyant families are represented in the diet (dos Santos and Haimovici, 2001). Clarke and Kristensen (1980) observe that the squid eaten by northern bottlenose whales *H. ampullatus* are smaller and younger than those consumed by sperm whales *P. macrocephalus* in the same region. Whitehead *et al.* (2003) conclude that out four species of teuthophagous, mesopelagic marine mammals those with larger ranges will

encounter more types of prey and thus exhibit larger niche breadths. Consequently the differences in niche breadth observed between species are closely related to their movement patterns (Whitehead *et al.*, 2003). A recent review of the diet of beaked whales showed that they are generalist feeders of deepwater squid, fish and crustaceans with a possible preference for benthic or benthopelagic species (MacLeod *et al.*, 2003). *Mesoplodon* species are frequently sympatric and a great deal of variation of types of prey items is found in this genus (MacLeod *et al.*, 2003). In addition, the sizes of the prey (measured as mass) vary between genera (MacLeod *et al.*, 2003). These data led MacLeod *et al.* (2003) to the conclusion that a segregation of the ecological niche exists in *Mesoplodon* spp. in order to reduce competition. In contrast, the genera *Hyperoodon* and *Ziphius* feed on the same size prey and probably occupy the same niche, but geographical and/or temporal segregation probably appears to prevent direct competition (MacLeod *et al.*, 2003). As *Mesoplodon* occupies a separate niche from *Ziphius* and *Hyperoodon* they can locally co-exist (MacLeod *et al.*, 2003).

### 6.1.5 Previous studies on diet in *Kogia*

In contrast to other aspects of *Kogia* biology the diet of the two species has been studied in some detail in different geographical areas. Early accounts on the stomach contents of *Kogia* are sparse as many of the identification procedures for the remains of prey items had not been developed.

Clarke (1996b) reviews previous studies on the diet of *Kogia* and reports that 11 families of cephalopods have been represented in the diet of the two species: Histioteuthidae, Lycoteuthidae, Chiroteuthidae, Cranchiidae, Loliginidae, Ommastrephidae, Octopoteuthidae, Onychoteuthidae, Enoploteuthidae, Sepiidae and Octopodidae. While the histioteuthids appear most important in both species, *K. breviceps* also consume inshore loliginids, at least off South Africa, while *K. sima* feeds on inshore sepiids (Clarke, 1996b). In addition, Lycoteuthidae form an important component of the diet of *Kogia* off South Africa and Brazil (Ommastrephidae also being important in the latter), and the Chiroteuthidae off the Azores (Clarke, 1996b). Sepiids are reported in both species from Europe (Allen, 1941) and Australia (Hale, 1947; 1962; 1963). Off New Caledonia the diet of *K. breviceps* consists of *Histioteuthis* sp., *Enoploteuthis* sp., *Taonius* sp. and Octopoteuthidae (Bustamante *et al.*, 2003).

Nagorsen (1985) provides a summary on the diet of *K. sima*, which includes

cephalopods, some fish, and crustaceans, pelagic crabs and shrimp. 13 families of cephalopod have been described from *K. sima* stomachs: Octopoteuthidae, Chiroteuthidae, Onychoteuthidae, Ommastrephidae, Loliginidae, Vampyroteuthidae, Lycoteuthidae, Cranchiidae, Sepiidae, Octopodidae, Gonatidae, Enoploteuthidae, and Histioteuthidae (Nagorsen, 1985). Mastigoteuthidae were added to that list by Willis and Baird (1998). In addition, Pinedo reports Brachioteuthidae from the stomach of an animal from southern Brazil (1987).

A brief summary of crustaceans in the diet of *Kogia* is presented by Debrot and Barros (1994). Amongst the more bizarre stomach contents found in *Kogia* are sargassum seaweed (Raun *et al.*, 1970) and the ligaments from a kangaroo found in an animal from South Australia, apparently constituting the remains of bait used by crayfish- or big-game fishermen (Hale, 1962).

One of the earliest detailed studies of *Kogia* diet was carried out by Fitch and Brownell (1968), who provide a review of otoliths recovered from the stomachs of three animals caught off Japan, but it is unclear whether they examined *K. breviceps* or *K. sima*. Surprisingly they report 153 otoliths originating from a minimum of 92 fish representing 18 species. For the primarily teuthophagous *Kogia* this is an unusually high number of fish consumed, but may be due to the fact that these animals were caught rather than stranded. The otoliths in the stomachs of the *Kogia* caught off Japan are from representatives of seven families of fish: Argentinidae, Gonostomatidae, Macrouridae, Myctophidae, Sternoptychidae, Congridae and Moridae; Myctophids (or lanternfishes) comprise the greatest number of otoliths found in the stomachs of these animals. Cephalopod beaks and crustacean remains are also reported, but not identified (Fitch and Brownell, 1968). The analysis of the otoliths present in the stomachs suggests that these animals dive to 300m and deeper to forage. As these data are in contradiction to other data on the diet of *Kogia*, which show that they are mainly teuthophagous, these results might mean that *Kogia* off Japan have a higher fish content in their diet than elsewhere. Alternatively the possibility that a higher amount of fish can be found in the diet of commercially caught and by-caught whales in comparison to stranded animals has been mentioned above.

While the vast majority of reports on stomach contents of *Kogia* is based on the results from a few stranded animals (Allen, 1941; Hale, 1947; 1962; 1963; Raun *et al.*, 1970; Jones, 1981; Martins *et al.*, 1985; Pinedo, 1987; McAlpine and Murison, 1997; Cardona-Maldonado and Mignucci-Giannoni, 1999; Hückstädt and Antezana, 2001;

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Bustamante *et al.*, 2003), only few studies have had a larger sample size for systematic analysis.

One of the more extensive studies on the diet of *Kogia* is the analysis of 53 *K. breviceps* and eight *K. sima* stomachs from animals stranded in the south-eastern United States and it reports that histioteuthids and ommastrephids together account for the majority of the beaks found in *K. breviceps*, followed by enoploteuthids and cranchiids (Candela, 1987). While these families are found over the deep shelf and slope, oceanic species make up the remainder of the sample. Neritic species such as loliginids are found in one third of all the animals, but contribute only 1.5% to all the beaks (Candela, 1987). Enoploteuthids are most abundant in *K. sima*, making up 33% of all beaks, followed by histioteuthids, ommastrephids and loliginids (15% each) and to a lesser extent, cranchiids (4%) (Candela, 1987). Small numbers of salps and deepwater shrimp are also reported from the stomachs of the two specimens (Candela, 1987).

The analysis of six *K. breviceps* and five *K. sima* from Taiwanese waters indicates that both species feed exclusively on oceanic cephalopods, with both species having *Enoploteuthis chunii* and *Taonius pavo* as their main prey items (Wang *et al.*, 2002). *K. breviceps* feeds on eighteen species, representing nine families of cephalopods. In *K. sima* thirteen species from seven families of cephalopods are represented in the diet.

Although there have been reports that both *Kogia* species feed on the same main prey items (Wang *et al.*, 2002) and no differences in the families of prey eaten are discovered between the two species (dos Santos and Haimovici, 2001), a number of studies conclude that *K. sima* has a more coastal habitat than *K. breviceps* and that *K. breviceps* lives seaward of the continental shelf and dives deeper than *K. sima* based on the results of the diet analysis (Ross, 1979a; Candela, 1987; Klages *et al.*, 1989; Wang *et al.*, 2002). Maigret and Robineau (1981) speculate that *K. sima* may be capable of diving to between 500 and 1300m depth due to the presence of a deepwater crustacean in the stomach of a stranded animal from Senegal. McAlpine and Murison (1997) conclude that feeding by a *K. breviceps* stranded in New Brunswick, Canada, had occurred in the deep zones of the continental shelf and slope or in the open ocean at mesopelagic depths. Pygmy and dwarf sperm whales in the Gulf of Mexico are found in waters with the steepest sea-surface temperature (SST) gradient (Davis *et al.*, 1998). As the two species are known to feed on squid they are thought to be foraging along thermal fronts where their prey aggregates (Davis *et al.*, 1998).

As already mentioned in Chapter 1, it is remarkable that most studies on diet in *Kogia* report a high number of nematodes in the digestive tract (Johnston and Mawson, 1939; Allen, 1941; Hale, 1947; Scheffer and Slipp, 1948; Hale, 1962; 1963; Raun *et al.*, 1970; Roest, 1970; Ross, 1979a; Martins *et al.*, 1985; Hückstädt and Antezana, 2001). An overview of this topic is given in Chapter 1.

### 6.1.5.1 Studies off southern Africa

Ross (1979a) provides data on the frequencies of occurrence of various families of cephalopods in the stomachs of both *Kogia* species off Southern Africa. Sepiids, which are commonly found over the continental shelf, are more common in *K. sima*, while oceanic cephalopods such as histioteuthids, cranchids, octopoteuthids and chiroteuthids are more prevalent in the diet of *K. breviceps*.

Klages *et al.* (1989) present results from stomach content analysis of 35 *K. breviceps* and 33 *K. sima* from South Africa. The majority of the prey is made up of cephalopods (81.6% and 94.9% for *K. breviceps* and *K. sima*, respectively), with some fish (14% and 3.2%, respectively) and crustaceans (4.4% and 1.9%). The most frequently occurring prey species are *Lycoteuthis diadema* and *Histioteuthis* sp. in both whales. Cranchiids like *Teuthowenia pellucida* and *Taonius pavo* are more prominent in *K. sima* than *K. breviceps*, with mesopelagic fish and the mysid *Gnathophausia ingens* making up the rest of the diet (Klages *et al.*, 1989). In addition, *Loligo vulgaris* and *Octopoteuthis* sp. are more important on the east coast, but insignificant on the south and west coast (Klages *et al.*, 1989).

Sekiguchi *et al.* (1992) report that *K. breviceps* off South Africa has the most diverse diet out of 20 odontocete species examined (49 prey species), followed by southern bottlenose whales *H. planifrons* (39 species) and *K. sima* with 27 species. *K. breviceps* also has the third highest dietary diversity index (Sekiguchi *et al.*, 1992). Both *Kogia* species feed on cephalopods that are characteristically found over the continental slope, mainly *Histioteuthis* sp. and *Lycoteuthis diadema* (32.1% and 13.4% for *K. breviceps* and 48.4% and 18% for *K. sima*) (Sekiguchi *et al.*, 1992).

Consequently, the diet of the two *Kogia* species off Southern Africa is well known and previous studies have determined that the two species feed predominantly on the same prey. However, little emphasis has been placed on determining dietary and thus ecological differences between the two *Kogia* species.

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### **6.1.6 The niche concept and resource partitioning**

An ecological niche is defined as the range of physical and biotic conditions within which a species is adapted to survive and reproduce (Wittenberger, 1981; Spellenberg, 1996). Each resource, such as food, space or time, can be considered as a dimension of the niche (Pianka, 1975; Spellenberg, 1996). Species that exhibit a high overlap along one dimension of a niche may be in competition if the common resource is in short supply (Pianka, 1976). However, most resources may be sufficiently abundant for more than one species to exploit, and competition occurs only when the use of a resource by one consumer reduces the amount of the same resource available to another (Wittenberger, 1981), thus information on the abundance of a resource is necessary to determine competition. One of the central concepts in ecology is the competitive exclusion principle, which states that two species cannot coexist if they are in direct competition, therefore two sympatric species must differ in some aspect of their ecological niche (Hardin, 1960; May and MacArthur, 1972). Niche overlap theory thus aims to explore just how similar competing species can be if they are to co-exist (May and MacArthur, 1972; Pianka, 1974; Schoener, 1974).

Niche overlap indices measure the degree of overlap between species in the utilization of a common resource (Pianka, 1975). Early works by Pianka (1973) attempted to measure how various lizard species coexisted with regard to their selection of food size, their location, and their time of foraging. It emerged that two species with similar niche requirements show a high degree of overlap. However, overlap indices are merely based on the relative use of resources without accounting for their relative availability (i.e. it is usually assumed that resources are equally available) (Pianka, 1976). Therefore no measure of significance is available, i.e. what value is sufficiently different from 0 (indicating no overlap) to indicate a significant degree of overlap. As a result studies on resource partitioning remain to some extent descriptive in nature.

A high niche overlap index therefore merely indicates that two or more species utilize the particular niche largely to the same extent. However, overlap is never complete and each species concentrates on a different part of the overall resource spectrum (Wittenberger, 1981). Species vary considerably in their degree of specialization and the resource spectra they exploit often overlap, leading to resource partitioning. It is tempting to equate niche overlap with intensity of interspecific competition, but the relationship between niche overlap and competition is too complex

for that (Pianka, 1976; Wittenberger, 1981). Competition is affected by resource availability as well as the degree of niche overlap and in this respect two species may both obtain much of their food from a single, abundant resource without competing (Pianka, 1976; Wittenberger, 1981).

### **6.1.7 Aim of the present chapter**

The aim of this part of the study was to examine the diet composition of the two species of *Kogia*, and, in particular, to determine whether different parts of the populations feed on differing prey and how the sympatric *Kogia* populations off South Africa partition the dietary resources they both use.

## **6.2 Materials and methods**

Stomach contents of 42 *K. breviceps* (21 females, 20 males and one animal of unknown sex) and 33 *K. sima* (20 females and 13 males) stranded along the South African coastline and accessioned to both the Port Elizabeth Museum (now Bayworld) and the South African Museum marine mammal collections were examined. Stomachs from stranded animals were removed after the oesophagus and intestine had been ligated, transported to the museum and temporarily stored frozen. Stomach contents were subsequently opened, washed out into metal sieves with 1.0mm mesh diameter to isolate hard parts and the remains were preserved in 70% alcohol for long-term storage. Only lower squid beaks and undigested otoliths were taken for prey identification purposes. Where possible the squid beaks and otoliths were identified to species level using the reference collection for prey identification at the Port Elizabeth Museum. The lower rostral length (LRL) of the beaks and total length of the otoliths was measured using Vernier calipers to the nearest 0.1mm. The hood length (HL) was measured in the case of octopods and sepiids (Clarke, 1986b). Prey sizes and masses were estimated from regressions relating dimensions of otoliths and cephalopod beaks with total lengths (TL) or dorsal mantle lengths (DML), respectively. Regression equations are part of the otolith and cephalopod beak reference collections held at the Port Elizabeth Museum and have been obtained from the collection for some species (e.g. *Argonauta argo*). Regressions equations for other species were obtained from the literature (Cooper, 1979; Clarke, 1980; 1986b; Wolff, 1982; Smale, 1983).

Cephalopod classification follows that of Clarke (1986b). Although initially identified separately, *Histioteuthis atlantica* and *Histioteuthis* 'B4' were both grouped into *Histioteuthis atlantica*. Similarly, *Histioteuthis sp.* and *Histioteuthis* 'A5' were assigned to *Histioteuthis sp.* (after Clarke, 1986). *Loligo vulgaris reynaudii* and *Loligo vulgaris* were grouped into *Loligo vulgaris*. In cases where identification to species level was not possible, cephalopod weight and length were estimated by using regressions available for the genus or family (Clarke, 1986b). Unidentified prey and some minor prey items with no available mass data were omitted from the calculations. This was also the case for crustacean remains.

Not all otoliths and cephalopod beaks were measured. Where large numbers of one prey species were present a sub sample of 20-50 was taken for measurement, and the total mass of each prey item was calculated from the average mass of those measured.

The percentage number (%Num), percentage mass (%Mass) and percentage frequency of occurrence (%FO) of the individual prey items were calculated for each animal, each species and for groups of different reproductive and/or developmental status (see below). Proportion of numerical abundance (%Num) is the percentage of the total number of prey items recovered from all stomachs represented by a particular prey category. Similarly, proportion of reconstructed mass (%Mass) is the percentage of the mass of prey recovered from all stomachs represented by a particular prey category. Frequency of occurrence (FO) is the proportion of stomachs that contained a particular prey category, regardless of its mass or abundance. For the determination of the main prey items only prey species that numerically amounted to more than 10 individuals per group were included in the analysis. Similarly, in the presentation of the results only the main prey items that made up over 2% of the total number of prey items were included.

In order to determine whether the diets of the two *Kogia* species were different from each other as well as to detect diet differences within each *Kogia* species the data were analysed separately for the following groups: males and females, immature and mature animals, and sexually mature males and sexually mature females neither lactating, pregnant or accompanied by a calf (group 1) and immature animals of both sexes and females that were lactating and/or pregnant and/or accompanied by a calf (group 2). The classification into group 1 and 2 arose from the observation that certain prey items were only present in animals belonging to either group. In addition, the composition of group 1 and 2 reflects the composition of animals, which are thought to travel and therefore feed together based on sighting and stranding data of the two species

(see Chapters 1 and 7). The state of maturity was determined by histological analysis (see Chapters 4 and 5). In the males, early spermatogenesis was classified as immature; only animals in late spermatogenesis were considered mature. Where no reproductive organs were available for examination body length was used as an indicator for maturity based on length at sexual maturity as established in Chapter 4 and 5. A niche overlap index ( $\alpha$ ) following Pianka's (1975) formula:

$$\alpha = \frac{\sum_i^n P_{ij}P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}$$

(where:  $P_{ij}$  and  $P_{ik}$  are the proportions of the  $i^{\text{th}}$  resource used by the  $j^{\text{th}}$  and  $k^{\text{th}}$  species, respectively)

was calculated for the two species as well as for males and females and mature and immature animals of the same species and for groups 1 and 2 within a species as defined above using the percent numerical data. In order to obtain a more accurate comparison only prey items that could be identified to genus level were included in this analysis. In addition, ANOVA's were performed for the Simpson diversity index ( $H = \sum P_i^2$ ; where:  $P_i$  is the proportion of the  $i^{\text{th}}$  resource) and Shannon-Weaver diversity index ( $H = -\sum P_i \times \ln P_i$ ; where:  $P_i$  is the proportion of the  $i^{\text{th}}$  resource) as well as for species richness (as determined by the number of prey species consumed) between the two *Kogia* species to determine whether the diets of the two species were significantly different.

In order to elucidate the dietary differences between the different groups of *K. breviceps* and *K. sima* further, size-frequency analyses were performed on the cephalopod prey consumed by the individual groups. For this purpose 3150 cephalopod beaks from the stomachs of *K. breviceps* were analysed and 1317 cephalopod beaks from the stomachs of *K. sima*.

In addition to the South African material, previously unstudied stomach contents for four Australian specimens were available from the collections of the Australian Museum (AM; one female) and the South Australian Museum (SAUSM; three males). These are also presented, but were excluded in any calculations regarding the South African material.

### 6.3 Results

#### *K. breviceps*

The diet of *K. breviceps* comprised 50 different cephalopod species from 22 families and 17 other prey species including fish (12 species), crustaceans (five species), and colonial salps (one species) (Table 6.1). Numerically *Histioteuthis* sp. made up the major part of the diet (28.34%), followed by *Lycoteuthis diadema* (14.49%). The next important prey items were *Loligo vulgaris*, *Octopoteuthis* sp. and *Sepia* sp. (8.73%, 4.10% and 3.67%, respectively). Similarly, the most important prey item in terms of mass was *Histioteuthis* sp., making up 29.26% of the total prey, followed by *Lycoteuthis diadema*, which comprised 9.61% of the total prey mass (Table 6.1). The next most important prey species in terms of mass were *Loligo vulgaris*, *Octopoteuthis* sp. and *Ancistrocheirus leseuri* with 13.86%, 6.87% and 5.16%, respectively. In terms of frequency of occurrence *Lycoteuthis diadema* was more abundant than *Histioteuthis* sp. (8.50% and 7.38%, respectively) (Table 6.1). The next most abundant prey species were *Chiroteuthis* sp. (6.04%), *Octopoteuthis* sp. (5.15%) and *Taonius pavo* (3.80%).

Table 6.1: Species list of prey eaten by *Kogia breviceps*.

Prey species	Number	% Number	Mass(g)	% Mass(g)	Relative abundance (Number)	Frequency of Occurrence (%)
<b>CEPHALOPODA</b>						
<b>Bathyteuthidae</b>						
<i>Bathyteuthis</i> sp.	2	0.05	68.69	0.02	1	0.22
<b>Bolitaenidae</b>						
<i>Japetella</i>	1	0.03	-	-	1	0.22
<b>Brachioteuthidae</b>						
<i>Brachioteuthis</i> sp.	12	0.31	96.61	0.02	4	0.89
<b>Cranchiidae</b>						
<i>Leachia</i>	3	0.08	32.81	0.01	1	0.22
<i>Taonius</i> sp.	9	0.23	204.98	0.05	4	0.89
<i>Taonius pavo</i>	136	3.64	4749.64	1.12	17	3.80
<i>Teuthowenia</i> sp.	34	0.87	6830.83	1.61	7	1.57
<i>Teuthowenia megalops</i>	12	0.31	2555.71	0.60	4	0.89
<i>Teuthowenia pellucida</i>	52	1.32	7000.05	1.65	14	3.13
<i>Megalocranchia</i> sp.	19	0.48	1076.62	0.25	4	0.89
<b>Chiroteuthidae</b>						
<i>Chiroteuthis</i> sp.	134	3.41	12891.60	3.04	27	6.04
<b>Cycloteuthidae</b>						
<i>Cycloteuthis</i> sp.	4	0.10	726.28	0.17	4	0.89
<i>Discoteuthis</i> sp.	28	0.71	4166.13	0.98	10	2.24
<i>Discoteuthis laciniosa</i>	4	0.10	269.88	0.06	3	0.67

<b>Enoploteuthidae</b>						
<i>Anchistrocheirus lesueuri</i>	33	0.84	21869.51	5.16	16	3.58
<i>Enoploteuthis</i> sp.	2	0.05	295.59	0.07	1	0.22
<i>Abralia</i>	15	0.38	1271.80	0.30	7	1.57
<b>Gonatidae</b>						
<i>Gonatus antarcticus</i>	24	0.61	2800.88	0.73	11	2.46
<b>Histioteuthidae</b>						
<i>Histioteuthis</i> sp.	1113	28.34	124105.07	29.26	33	7.38
<i>Histioteuthis atlantica</i>	7	0.18	1319.99	0.31	3	0.67
<i>Histioteuthis bonnellii</i>	45	1.15	4420.80	1.04	4	0.89
<i>Histioteuthis dofleini</i>	6	0.15	1825.65	0.43	3	0.67
<i>Histioteuthis macrohista</i>	9	0.23	513.68	0.12	1	0.22
<i>Histioteuthis meleagroteuthis</i>	8	0.20	693.04	0.16	1	0.22
<i>Histioteuthis miranda</i>	20	0.51	2608.75	0.62	3	0.67
<b>Lepidoteuthidae</b>						
<i>Lepidoteuthis grimaldi</i>	2	0.05	335.86	0.08	1	0.22
<b>Loliginidae</b>						
<i>Loligo vulgaris</i>	343	8.73	58803.67	13.86	14	3.13
<b>Lycoteuthidae</b>						
<i>Lycoteuthis diadema</i>	569	14.49	40741.63	9.61	38	8.50
<b>Mastigoteuthidae</b>						
<i>Mastigoteuthis</i> sp.	3	0.08	9.24	0.00	1	0.22
<b>Octopodidae</b>						
<i>Octopus</i> sp.	31	0.79	676.48	0.16	9	2.01
<i>Octopus dofleini</i>	11	0.28	157.22	0.04	1	0.22
<i>Octopus vulgaris</i>	2	0.05	1275.18	0.30	1	0.22
unidentified						
Octopodidae	2	0.05	24.6	0.01	1	0.22
<b>Octopoteuthidae</b>						
<i>Octopoteuthis</i> sp.	161	4.10	29138.99	6.87	23	5.15
<i>Taningia danae</i>	2	0.05	2679.18	0.63	2	0.45
<b>Ommastrephidae</b>						
<i>Ommastrephes bartrami</i>	63	1.60	7435.98	1.75	15	3.36
<i>Ornithoteuthis volatilis</i>	22	0.56	1927.35	0.45	4	0.89
<i>Todarodes</i> sp.	2	0.05	619.02	0.15	1	0.22
<i>Todarodes angolensis</i>	5	0.13	4930.20	1.16	3	0.67
<i>Todarodes sagittatus</i>	25	0.64	18909.48	4.46	8	1.79
<i>Todaropsis eblanae</i>	57	1.45	5004.87	1.18	9	2.01
unidentified						
Ommastrephidae	11	0.28	539.18	0.13	8	1.79
<b>Onychoteuthidae</b>						
<i>Onychoteuthis banksii</i>	7	0.18	1151.31	0.27	5	1.12
<i>Moroteuthis</i> sp.	33	0.84	8273.10	1.95	8	1.79
<i>Moroteuthis ingens</i>	5	0.13	6842.93	1.61	2	0.45
<i>Moroteuthis robsoni</i>	5	0.13	4195.86	0.99	2	0.45
unidentified						
Onychoteuthidae	3	0.08	165.10	0.04	3	0.67
<b>Pholidoteuthidae</b>						
<i>Pholidoteuthis</i> sp.	1	0.03	825.23	0.19	1	0.22

<i>Pholidoteuthis boschmai</i>	15	0.38	9295.41	2.19	7	1.57
<b>Sepiidae</b>						
<i>Sepia</i> sp.	144	3.67	245.27	0.06	13	2.91
<i>Sepia papillata</i>	85	2.16	46.54	0.01	3	0.67
<b>Sepiolidae</b>						
<i>Rossia</i> sp.	10	0.25	1103.25	0.26	2	0.45
<b>Vampyroteuthidae</b>						
<i>Vampyroteuthis infernalis</i>	1	0.03	125.80	0.03	1	0.22
<b>Vitreledonellidae</b>						
<i>Vitreledonella richardi</i>	1	0.03	48.66	0.01	1	0.22
unidentified cephalopods	117	2.98	15896.30	3.75	22	4.92
<b>FISH</b>						
<b>Dirtemidae</b>						
<i>Dirtemus argenteus</i>	1	0.03	-	-	1	0.22
<b>Engraulidae</b>						
<i>Engraulis japonicus</i>	4	0.10	-	-	2	0.45
<b>Evermannellidae</b>						
<i>Evermannella</i>	20	0.51	-	-	1	0.22
<b>Gempylidae</b>						
<i>Diplospinus multistriatus</i>	32	0.81	-	-	2	0.45
<b>Merlucciidae</b>						
<i>Merluccius</i> sp.	32	0.81	-	-	7	1.57
<i>Merluccius capensis</i>	41	1.04	-	-	2	0.45
<i>Merluccius paradoxus</i>	5	0.13	-	-	1	0.22
<b>Moridae</b>						
unidentified Moridae	2	0.05	-	-	1	0.22
<b>Myctophidae</b>						
<i>Lampadena</i>	1	0.03	-	-	1	0.22
<i>Lobianchia</i>	4	0.10	-	-	1	0.22
unidentified Myctophidae	32	0.81	-	-	4	0.89
<b>Paralepididae</b>						
<i>Magnisudis prionosa</i>	4	0.10	-	-	1	0.22
<b>Phosichthyidae</b>						
<i>Phosichthys argenteus</i>	79	2.01	-	-	2	0.45
<b>Trichiuridae</b>						
<i>Benthodesmus elongatus elongatus</i>	9	0.23	-	-	1	0.22
unidentified fish	92	2.34	-	-	6	1.34
<b>CRUSTACEA</b>						
<b>Amphipoda</b>						
unidentified Amphipoda	1	0.03	-	-	1	0.22
<b>Isopoda</b>						
unidentified Isopoda	7	0.18	-	-	2	0.45
<b>Mysidae</b>						
<i>Gnathophausia ingens</i>	44	1.12	-	-	8	1.79
<b>Euphausiid</b>						
unidentified Euphausiid	3	0.08	-	-	3	0.67
<b>Stomatopodidae</b>						
<i>Squilla</i>	38	0.97	-	-	1	0.22
Crab larva	1	0.03	-	-	1	0.22
unidentified crustacea	4	0.10	-	-	4	0.89
<b>OTHER</b>						
<b>Colonial salp</b>						
<i>Pyrosoma</i>	1	0.03	-	-	1	0.22

*K. sima*

In contrast to *K. breviceps* *K. sima* fed on a smaller range of prey species made up of 32 cephalopod species from 17 families and 6 others (three fish and three crustacean species) (Table 6.2). *Lycoteuthis diadema* made up the majority of the diet in terms of numbers (23.63%), followed very closely by *Histioteuthis* sp. (21.50%). The next most important prey items numerically were *Sepia papillata*, *Taonius pavo* and *Chiroteuthis* sp. (12.36%, 7.97% and 7.62%, respectively). In contrast to the numerical results *Histioteuthis* sp. made up the bulk of the diet in terms of mass with 45.31%, followed by *Lycoteuthis diadema* with 16.58% (Table 6.2). These were followed by *Loligo vulgaris* (5.17%), *Todaropsis eblanae* (3.84%) and *Taonius pavo* (3.61%). *Lycoteuthis diadema* and *Histioteuthis* sp. were the most frequently occurring prey species (13.77 and 13.17%, respectively), followed by *Taonius pavo*, *Chiroteuthis* sp. and *Ommastrephes bartrami* (6.59%, 5.99% and 4.19%, respectively) (Table 6.2).

Table 6.2: Species list of prey eaten by *Kogia sima*.

Prey species	Number	% Number	Mass(g)	% Mass(g)	Relative abundance (Number)	Frequency of Occurrence (%)
<b>CEPHALOPODA</b>						
<b>Argonautidae</b>						
<i>Argonauta argo</i>	1	0.07	9.00	0.01	1	0.60
<b>Cranchiidae</b>						
<i>Leachia</i>	1	0.07	-	-	1	0.60
<i>Taonius</i> sp.	50	3.43	2256.45	2.51	2	1.20
<i>Taonius pavo</i>	116	7.97	3239.17	3.61	11	6.59
<i>Teuthowenia</i> sp.	16	1.10	1814.92	2.02	3	1.80
<i>Teuthowenia megalops</i>	2	0.14	505.86	0.56	2	1.20
<i>Teuthowenia pellucida</i>	9	0.62	672.65	0.75	6	3.59
<b>Chiroteuthidae</b>						
<i>Chiroteuthis</i> sp.	111	7.62	2786.067	3.10	10	5.99
<b>Cycloteuthidae</b>						
<i>Discoteuthis</i> sp.	2	0.14	386.49	0.43	1	0.60
<b>Enoploteuthidae</b>						
<i>Anchistrocheirus lesueuri</i>	1	0.07	46.24	0.05	1	0.60
<i>Enoploteuthis</i> sp.	5	0.34	78.53	0.09	2	1.20
<i>Abralia</i>	13	0.89	229.88	0.26	3	1.80
<b>Gonatidae</b>						
<i>Gonatus antarcticus</i>	27	1.85	1292.27	1.44	3	1.80
<b>Histioteuthidae</b>						
<i>Histioteuthis</i> sp.	313	21.50	40671.43	45.31	22	13.17
<i>Histioteuthis atlantica</i>	1	0.07	231.92	0.26	1	0.60

<i>Histioteuthis macrohista</i>	4	0.27	192.97	0.21	1	0.60
<b>Loliginidae</b>						
<i>Loligo vulgaris</i>	28	1.92	4640.62	5.17	4	2.40
<b>Lycoteuthidae</b>						
<i>Lycoteuthis diadema</i>	344	23.63	14886.9	16.58	23	13.77
<b>Mastigoteuthidae</b>						
<i>Mastigoteuthis</i> sp.	1	0.07	10.18	0.01	1	0.60
<b>Octopodidae</b>						
<i>Octopus</i> sp.	3	0.21	22.41	0.02	2	1.20
<i>Octopus dofleini</i>	1	0.07	41.66	0.05	1	0.60
<b>Octopoteuthidae</b>						
<i>Octopoteuthis</i> sp.	4	0.27	445.16	0.50	4	2.40
<b>Ommastrephidae</b>						
<i>Ommastrephes bartrami</i>	24	1.65	2424.29	2.70	7	4.19
<i>Ornithoteuthis volatilis</i>	2	0.14	86.69	0.10	2	1.20
<i>Todaropsis eblanae</i>	27	1.85	3446.13	3.84	4	2.40
unidentified						
Ommastrephidae	1	0.07	23.63	0.03	1	0.60
<b>Onychoteuthidae</b>						
<i>Onychoteuthis banksii</i>	4	0.27	702.64	0.78	3	1.80
<i>Moroteuthis</i> sp.	3	0.21	344.87	0.38	3	1.80
<b>Sepiidae</b>						
<i>Sepia</i> sp.	14	0.96	40.76	0.05	5	2.99
<i>Sepia papillata</i>	180	12.36	44.8	0.05	4	2.40
<b>Sepiolidae</b>						
<i>Rossia</i> sp.	2	0.14	60.99	0.07	1	0.60
<b>Vampyroteuthidae</b>						
<i>Vampyroteuthis infernalis</i>	15	1.03	96.14	0.11	1	0.60
unidentified squid	60	4.12	8036.82	8.95	8	4.79
<b><u>FISH</u></b>						
<b>Engraulidae</b>						
<i>Engraulis capensis</i>	7	0.48	-	-	1	0.60
<b>Merlucciidae</b>						
<i>Merluccius capensis</i>	20	1.37	-	-	1	0.60
<b>Myctophidae</b>						
unidentified	8	0.55	-	-	3	1.80
Myctophidae						
<b>Phosichthyidae</b>						
<i>Phosichthys argenteus</i>	6	0.41	-	-	1	0.60
unidentified fish	9	0.62	-	-	3	1.80
<b><u>CRUSTACEA</u></b>						
<b>Isopoda</b>						
unidentified	1	0.07	-	-	1	0.60
<b>Mysidae</b>						
<i>Gnathophausia ingens</i>	10	0.69	-	-	4	2.40
<b>Euphausiid</b>						
unidentified crustacea	2	0.14	-	-	1	0.60
	8	0.55	-	-	8	4.79

### 6.3.1 Comparison of the diet of *K. breviceps* and *K. sima*

It is evident from Table 6.1 and 6.2 that *K. sima* fed to a larger extent on fish than

*K. sima*. Crustaceans, such as Euphausiids and the deep-water mysid *Gnathophausia ingens*, also appear to a larger extent in the diet of *K. breviceps* than *K. sima*.

Both *Kogia* species fed mainly on *Histioteuthis* sp. and *Lycoteuthis diadema* and the results for these two cephalopod species are listed separately in Table 6.3 for comparative purposes. The data indicate that *Histioteuthis* sp. made up about a quarter of the diet of *K. breviceps*, both numerically and in terms of mass, while *Lycoteuthis diadema* made up about one sixth in terms of numbers and only about one tenth in terms of mass. In contrast *K. sima* fed to almost equal amounts on *Histioteuthis* sp. and *Lycoteuthis diadema* in terms of numbers, but *Histioteuthis* sp. made up almost half of the prey mass consumed, while *Lycoteuthis diadema* comprised only about one sixth of the total prey mass. These data indicate that *K. sima* preyed to a larger extent on both *Histioteuthis* sp. and *Lycoteuthis diadema* in terms of mass than *K. breviceps*. While the two cephalopod species combined numerically made up similar amounts in both *Kogia* species (42.83% and 45.13%, respectively), they comprised only 38.87% of the total prey mass in *K. breviceps*, while they made up 61.89% of the total prey mass in *K. sima* (Table 6.3). This in combination with the wide range of prey items found in the stomachs indicates that *K. breviceps* fed on a greater variety of prey species than *K. sima*, which made up more of the diet in *K. breviceps* than *K. sima*. The data on the frequency of occurrence of *Histioteuthis* sp. and *Lycoteuthis diadema* support this as these prey items occurred only in 15.88% of the stomachs of *K. breviceps*, but in 27.48% in *K. sima* (Table 6.3).

Table 6.3: The two main prey items of *Kogia breviceps* and *Kogia sima* presented in percentage number, percentage mass and percentage frequency of occurrence based on all prey items present.

Prey species	Stomach content (%)					
	<i>Kogia breviceps</i>			<i>Kogia sima</i>		
	No.	Mass	Frequ.	No.	Mass	Frequ.
<i>Histioteuthis</i> sp.	28.34	29.26	7.38	21.5	45.31	13.71
<i>Lycoteuthis diadema</i>	14.49	9.61	8.50	23.63	16.58	13.77
<b>Total</b>	42.83	38.87	15.88	45.13	61.89	27.48

The main stomach contents listed for *K. breviceps* and *K. sima* in Table 6.4

support these findings. For example, both *Loligo vulgaris* and *Octopoteuthis* sp. were more important in the diet of *K. breviceps* in both numbers and mass, than in *K. sima* (Table 6.4). In addition, some species such as *Pholidoteuthis boschmai* and *Moroteuthis* sp., each contributing around 2% to the total prey mass of *K. breviceps*, were absent from the diet of *K. sima*. In *K. sima* *Taonius pavo*, *Taonius* sp. and *Todaropsis eblanae* appeared more important in both numbers and mass than in *K. breviceps*. And while *Sepia papillata* was more pronounced in at least numbers in *K. sima*, *Sepia* sp. were slightly more prevalent in *K. breviceps*. These data support the result that although the main prey items were the same, each whale species fed on a suite of prey species, which differed between the two *Kogia* species.

Table 6.4: Main stomach contents of *Kogia breviceps* and *Kogia sima* presented as numerical percentages and percentage mass based on all prey items present.

Main prey species	Stomach content (%)			
	<i>Kogia breviceps</i>		<i>Kogia sima</i>	
	Number	Mass	Number	Mass
<i>Histioteuthis</i> sp.	28.34	29.26	21.50	45.31
<i>Lycoteuthis diadema</i>	14.49	9.61	23.63	16.58
<i>Sepia papillata</i>	2.16	< 2	12.36	< 2
<i>Taonius pavo</i>	3.64	< 2	7.97	3.61
<i>Chiroteuthis</i> sp.	3.41	3.04	7.62	3.1
<i>Loligo vulgaris</i>	8.73	13.86	< 2	5.17
<i>Octopoteuthis</i> sp.	4.10	6.87	< 2	< 2
<i>Sepia</i> sp.	3.67	< 2	< 2	< 2
<i>Taonius</i> sp.	< 2	< 2	3.43	2.51
<i>Todaropsis eblanae</i>	< 2	< 2	< 2	3.84
<i>Phosichthys argenteus</i>	2.01	-	< 2	-
<i>Ommastephes bartrami</i>	< 2	< 2	< 2	2.7
<i>Pholidoteuthis boschmai</i>	< 2	2.19	n.p.	n.p.
<i>Moroteuthis</i> sp.	< 2	< 2	n.p.	n.p.
<i>Teuthowenia</i> sp.	< 2	< 2	< 2	2.02
Other	24.08	72.56	15.33	14.56

Other = all prey species that comprised less than 2% of the total prey number and mass, respectively. n.p.= not present.

Both analyses of the Simpsons diversity index and the Shannon-Weaver diversity index showed that the diversity of prey species eaten differed significantly between the two *Kogia* species ( $F=13.39$ ,  $df=1$ ,  $p<0.0005$  and  $F=18.81$ ,  $df=1$ ,  $p<0.0001$ , respectively). In addition, the species richness of prey items was significantly different between *K. breviceps* and *K. sima* ( $F=34.72$ ,  $df=1$ ,  $p<0.0001$ ). In contrast, the niche overlap index of 0.86 (where 1.0 indicates complete overlap and 0.0 indicates none) showed that the diet and therefore the foraging areas of the two species overlapped to a great extent (Table 6.5). The data used to calculate the niche overlap index are shown in Figure 6.1 and only include prey items identified to species level. Therefore they differ slightly from those presented above in Tables 6.1, 6.2 and 6.3, but reflect the trend shown in Table 6.4.

Table 6.5: Niche overlap index calculated for different groups of *Kogia breviceps* and *Kogia sima*.

Groups examined	Niche overlap index*
<i>K. breviceps</i> vs <i>K. sima</i>	0.86
<i>K. breviceps</i> males vs <i>K. breviceps</i> females	0.75
<i>K. sima</i> males vs <i>K. sima</i> females	0.92
<i>K. breviceps</i> immatures vs <i>K. breviceps</i> matures	0.86
<i>K. sima</i> immatures vs <i>K. sima</i> matures	0.65
<i>K. breviceps</i> group 1 vs <i>Kogia breviceps</i> group 2	0.81
<i>K. sima</i> group 1 vs <i>K. sima</i> group 2	0.73

\*= after Pianka (1975).

### 6.3.2 Comparison of the diet between different groups within *K. breviceps* and *K. sima* using Pianka's niche overlap index

As most of the niche overlap indices between males and females, immature and mature animals, and animals belonging to group 1 and 2 were quite high in both species of *Kogia*, an effort was made to determine dietary differences between the individual groups.

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***K. breviceps***

In *K. breviceps* the lowest niche overlap index was found between males and females (0.75) (Table 6.5). While female *K. breviceps* consumed about 2.5 times the amount of *Histioteuthis* sp. than males, the consumption of *Lycoteuthis diadema* was similar in both sexes (Figure 6.2). As a result of the lower consumption of *Histioteuthis* sp., males fed on more prey species (12 main species compared to eight in females), each making up a relatively small percentage of the diet. Males consumed more fish, such as *Phosichthys argenteus* and *Merluccius capensis*, than females, as well as *Loligo vulgaris* (8.7% in males, 2.1% in females) (Figure 6.2). In contrast, all the *Gnathophausia ingens* found in *K. breviceps* were consumed by females (Figure 6.2). Similarly, most of the *Sepia* sp. and *Sepia papillata* were consumed by male *K. breviceps* (Figure 6.2). However, the fact that the *K. breviceps* sample had a predominance of immature males and mature females should be kept in mind here and will be examined further below.

The highest niche overlap index for *K. breviceps* was recorded for mature and immature animals (0.86) (Table 6.5). Mature animals preyed to a larger extent on fish and consumed all specimens of *Phosichthys argenteus*, while all specimens of *Merluccius capensis* were found in the stomachs of immature *K. breviceps* (Figure 6.3). Similarly, all of the *Squilla* (crustacean) reported for *K. breviceps* were consumed by immature animals (Figure 6.3). In addition, *Loligo vulgaris* was found to a greater extent in mature animals (12.7%) than immature ones (3.2%) (Figure 6.3). Immature animals also consumed the majority of *Sepia* sp. and *Sepia papillata*, which better explains the differing result between males and females with regard to these two cephalopod species. Overall the number of prey items consumed by mature *K. breviceps* was substantially higher (n=23480) than those consumed by immature animals (n=1366), although the sample sizes for both groups were similar (20 mature *K. breviceps* and 21 immature animals).

The niche overlap index for group 1 and group 2 was 0.81 (Table 6.5). As Figure 6.4 indicates both groups fed to almost equal amounts on *Histioteuthis* sp. and “other”. However, group 1 fed to a smaller degree on *Lycoteuthis diadema* (8.4%) than group 2 (21.2%). Instead, most of the *Loligo vulgaris* consumed by *K. breviceps* were eaten by animals belonging to group 1 (Figure 6.4). In addition, they consumed more fish (all *Phosichthys argenteus* were consumed by group 1), while group 2 ate more *Sepia* sp. and *Sepia papillata* (Figure 6.4).

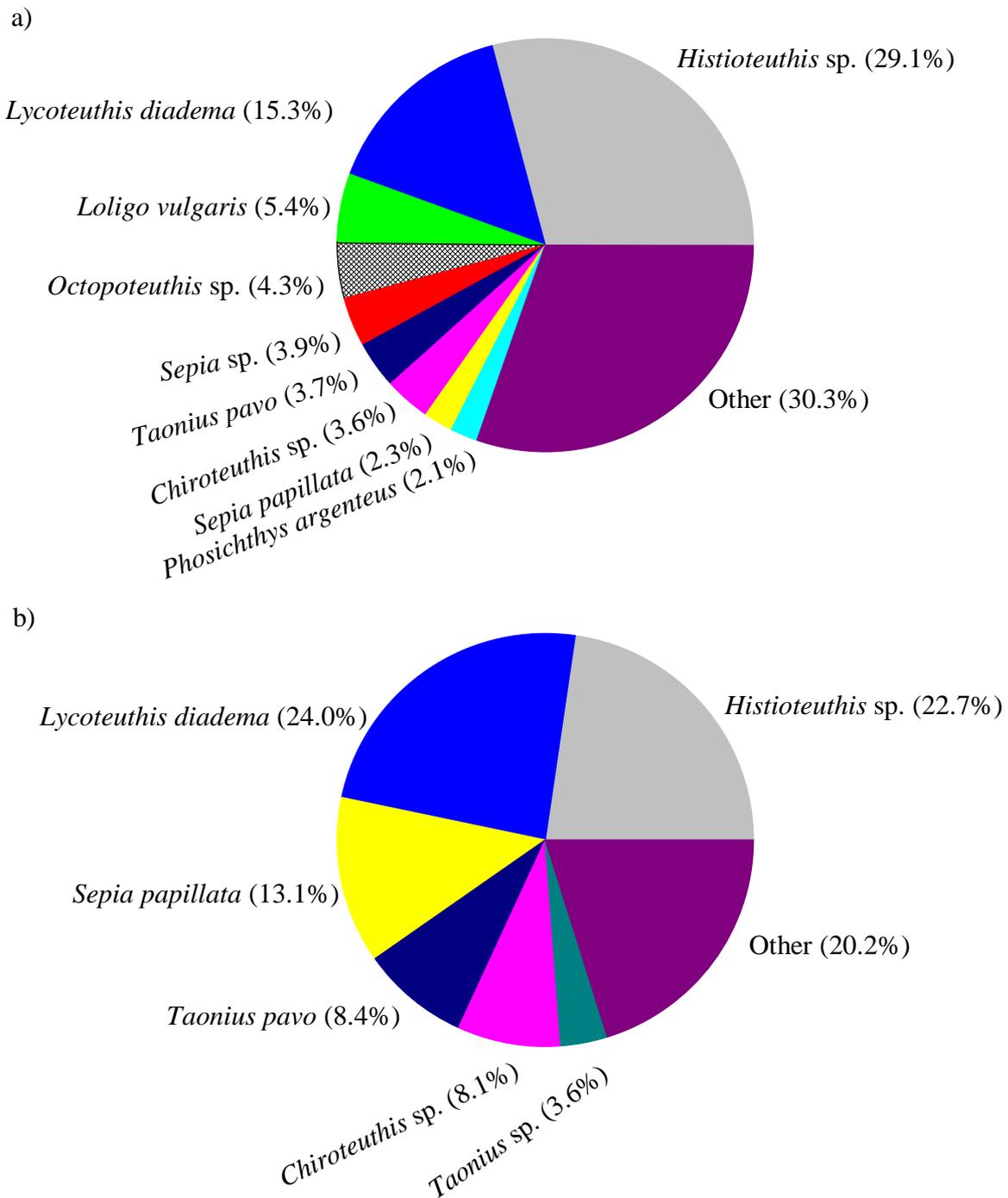


Figure 6.1: Diet composition of *Kogia breviceps* (n=41) (a) and *Kogia sima* (n=31) (b).

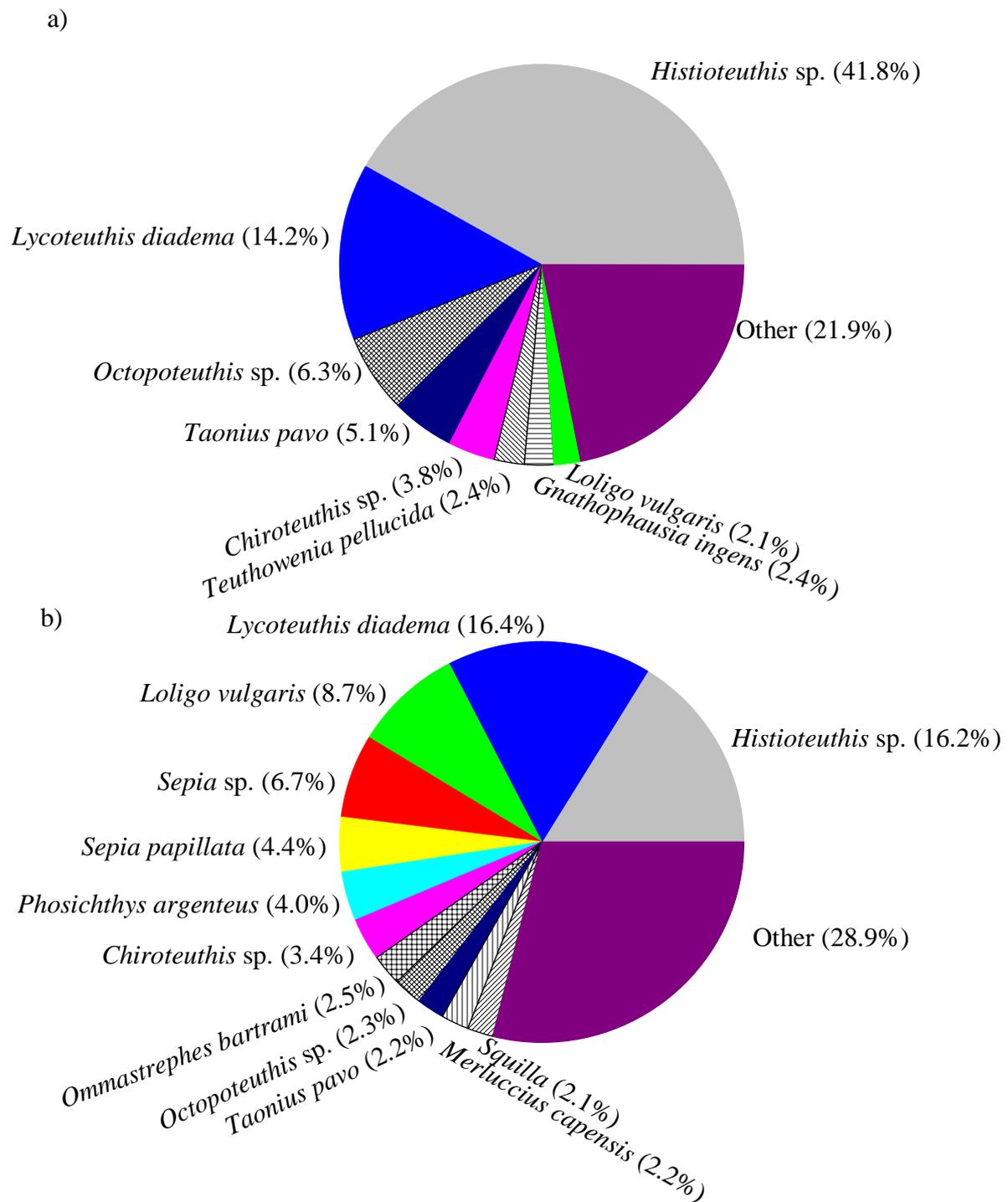


Figure 6.2: Diet composition of female (n=21) (a) and male (n=20) (b) *Kogia breviceps*.

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From the combined data it emerges that mature male *K. breviceps* fed to a greater extent on *Phosichthys argenteus* and *Loligo vulgaris*, while mature females consumed more *Gnathophausia ingens*, and, in addition, females ate more *Histioteuthis* sp. Similarly, immature males consumed more *Merluccius capensis*, as well as *Sepia* and *Sepia papillata*.

### ***K. sima***

In contrast to *K. breviceps* the highest niche overlap index in *K. sima* was recorded for males and females (0.92) (Table 6.5). Indeed most of the main prey items were found in both sexes to almost equal amounts (Figure 6.5). While females consumed slightly more *Histioteuthis* sp. than males, males had a more varied diet in terms of numbers of prey species (7 main prey species in females compared to 10 in males) (Figure 6.5). Although not evident from Figure 6.5 females had more fish in their diet than males and also consumed all of the Euphausiids and *Gnathophausia ingens* found in *K. sima*. In addition, they consumed all *Loligo vulgaris* and more *Sepia papillata* and *Sepia* sp. than males.

The lowest niche overlap index for *K. sima* and overall in the whole analysis was between immature and mature animals (0.65) (Table 6.5). Figure 6.6 shows clearly that immature animals fed to a large extent on *Sepia papillata*, which made up over one third of their diet (35.0%). In contrast, mature animals fed to a larger extent on *Loligo vulgaris* (they consumed all *Loligo vulgaris* reported for *K. sima*) and also consumed more fish (they ate all the *Merluccius capensis* found in *K. sima*) (Figure 6.6).

The niche overlap index calculated between group 1 and group 2 for *K. sima* was 0.73 (Table 6.5). Group 1 consumed almost twice as much *Lycoteuthis diadema* than group 2 (Figure 6.7), while group 2 fed to a much larger extent on *Sepia papillata* (20.4%) than group 1 (3.0%).

Therefore it appears that mature female *K. sima* fed to a larger extent on *Loligo vulgaris* and on fish, while immature females fed predominantly on *Sepia papillata*.

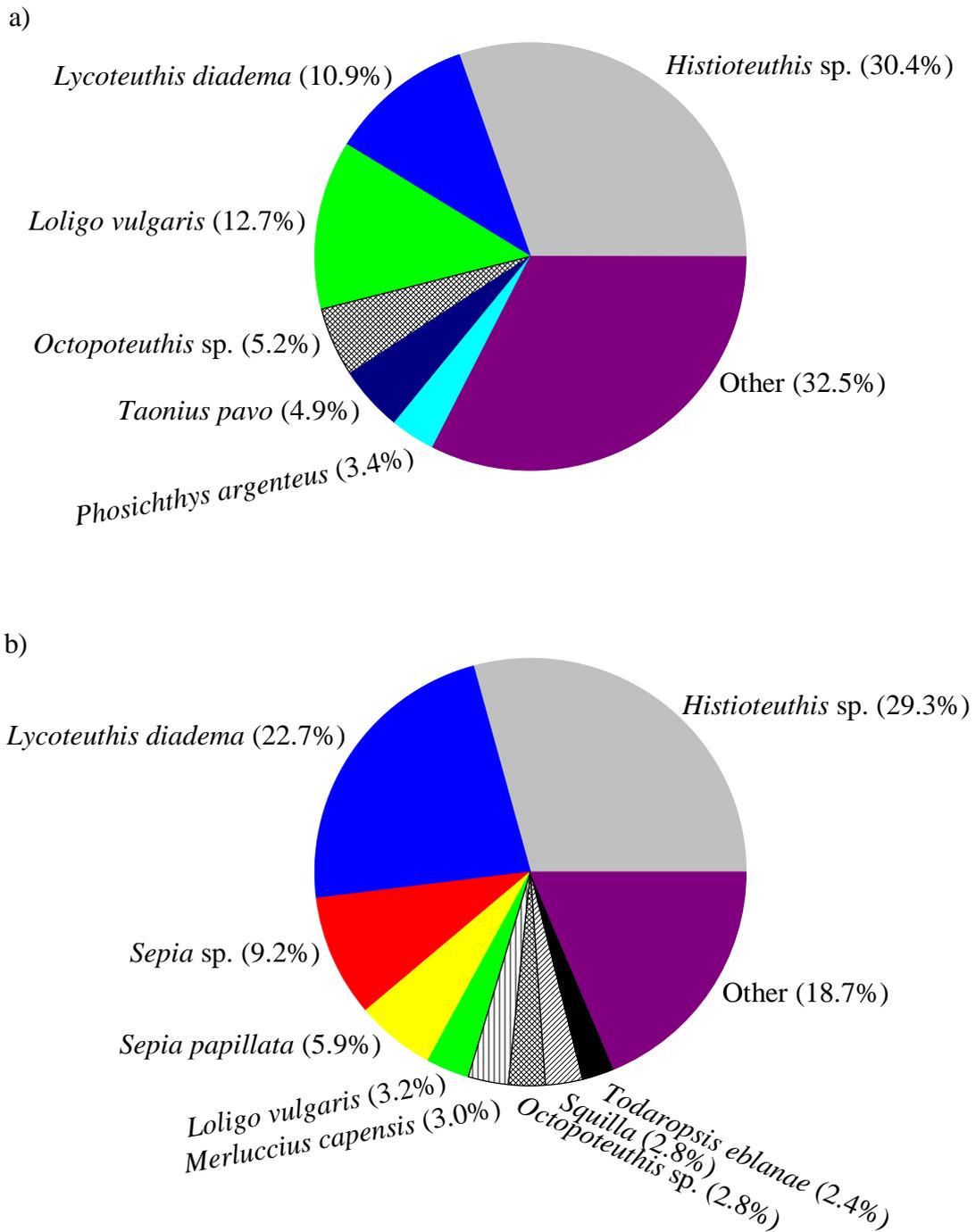
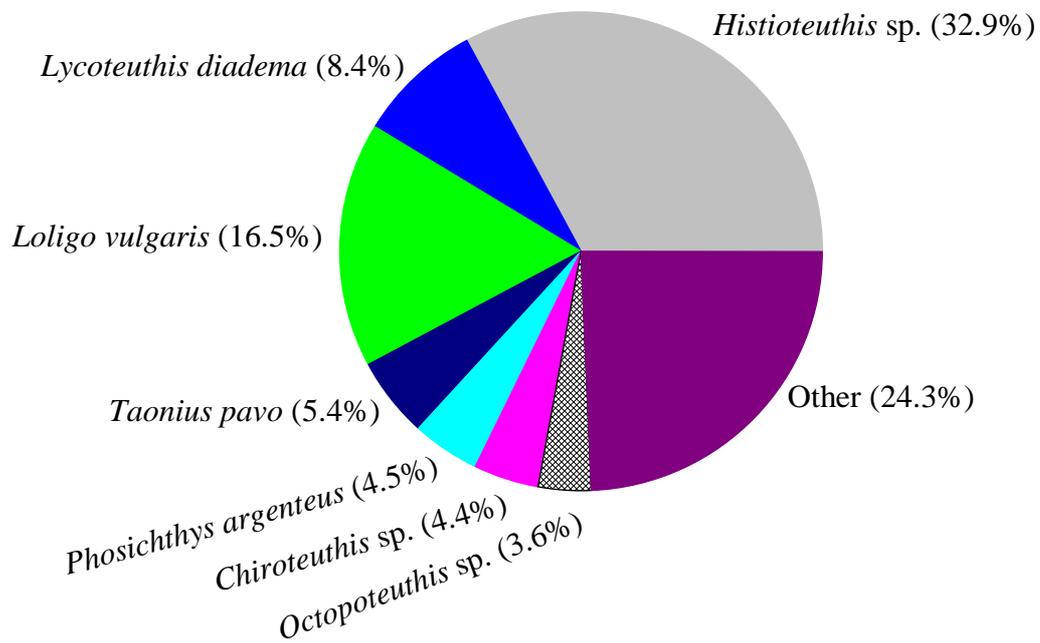


Figure 6.3: Diet composition of mature (n=20) (a) and immature (n=21) (b) *Kogia breviceps*.

a)



b)

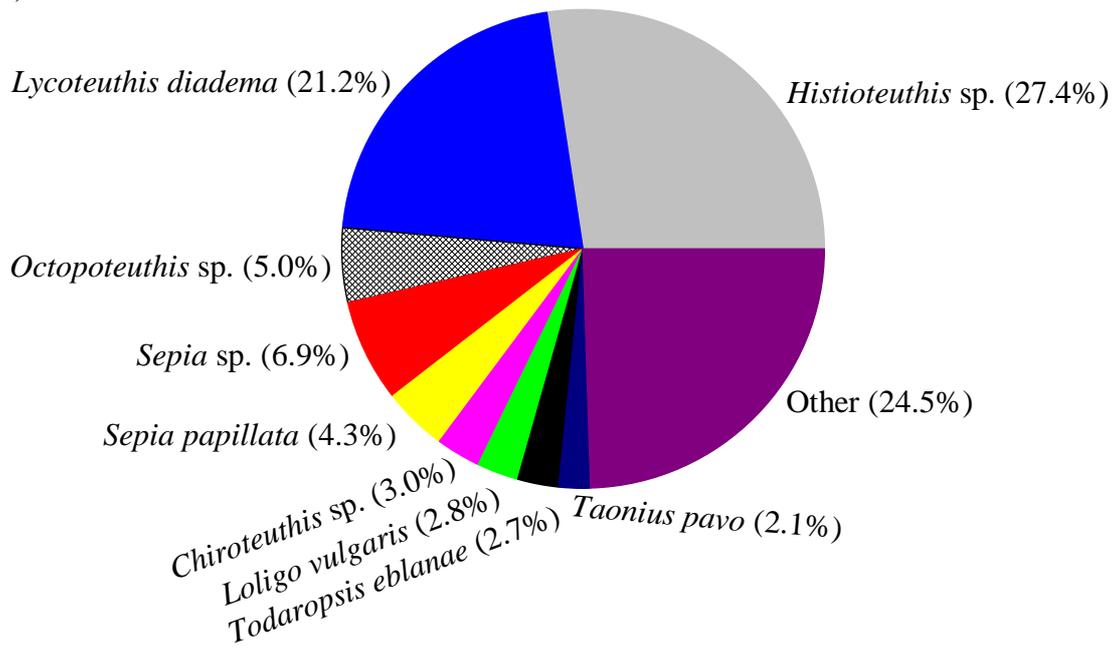


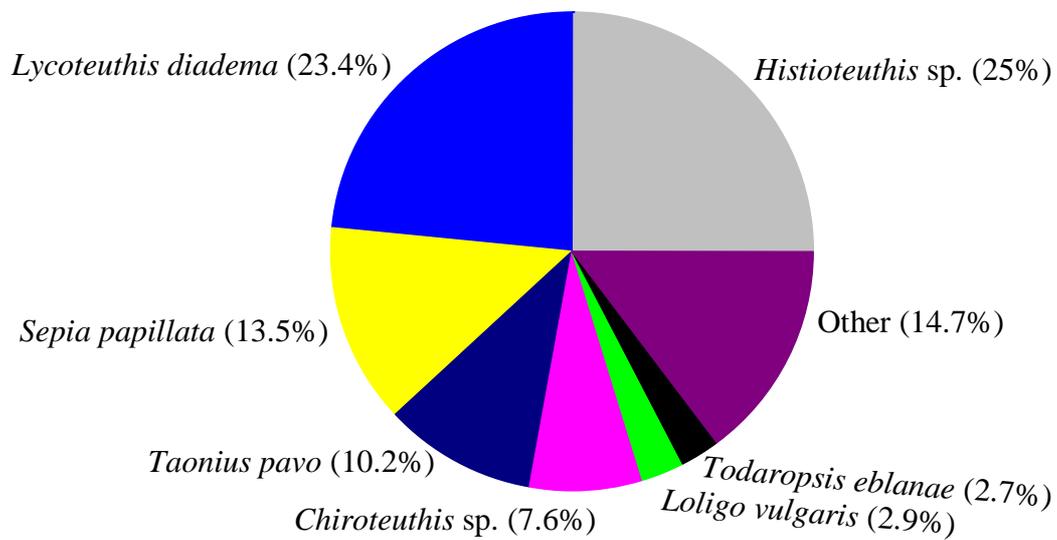
Figure 6.4: Diet composition of group 1 (n=12) (a) and group 2 (n=29) (b) of *Kogia breviceps*.

The examination of the prey items that differed between the groups showed subtle differences in diet composition. Overall mature male *K. breviceps* predominantly consumed *Loligo vulgaris* and also fed to a larger extent on fish, in contrast to *K. sima*, where it was the females that fed on *Loligo vulgaris* and fish. Similarly, immature males of *K. breviceps* fed to a large extent on *Sepia papillata*, while it was immature females in *K. sima*. In addition, immature males of *K. breviceps* predominantly consumed *Merluccius capensis*, while mature animals of *K. sima* fed predominantly on that species. Furthermore, group 1 of *K. breviceps* fed to a larger extent on *Loligo vulgaris*, *Gnathophausia ingens* and Myctophids, while in *K. sima* group 2 fed to a larger extent on those prey items. However, in both species of *Kogia* females consumed more *Histioteuthis* sp. than males.

The data on the niche overlap indices indicated some further differences between the two *Kogia* species in that the biggest dietary differences within *K. breviceps* would be expected between males and females, while the biggest difference occurred between immature and mature animals in *K. sima*. However, all indices are relatively high, indicating extensive niche overlap. The only exception appears to be the result for immature and mature *K. sima*, which, according to the present analysis, showed some real differences in diet.

As the index of niche overlap only compares numerical percentages, differences in diet in terms of mass would not be detected with this method. During the data analysis it was noted that lactating and/or pregnant females and immature animals (group 2) of both *Kogia* species had *Sepia papillata* present in their stomachs, while that species hardly ever appeared in animals of either *Kogia* species belonging to group 1. An examination of the main stomach contents of group 1 and group 2 for either *Kogia* species is presented in Table 6.6. These data indicate clear differences in diet for animals of different reproductive status, with animals belonging to group 2 feeding to a larger extent on inshore cephalopods, like *Sepia papillata* (4.31% in *K. breviceps* and 20.43% in *K. sima*) (Table 6.6). In addition, animals belonging to group 2 in *K. breviceps* fed to a larger extent on *Sepia* sp. (6.94%) than animals belonging to group 1 (< 2%). In contrast, *K. breviceps* belonging to group 1 fed more on *Loligo vulgaris* (16.54%) than those belonging to group 2 (2.79%). In *K. breviceps* the fish *Phosichthys argenteus* was quite pronounced in group 1, while it was represented by less than 10 animals in *K. sima*. In *K. breviceps* *Merluccius capensis* was only present in group 2, while in *K. sima* it was present to a substantial amount in group 1 and absent from group 2 (Table 6.6). In

a)



b)

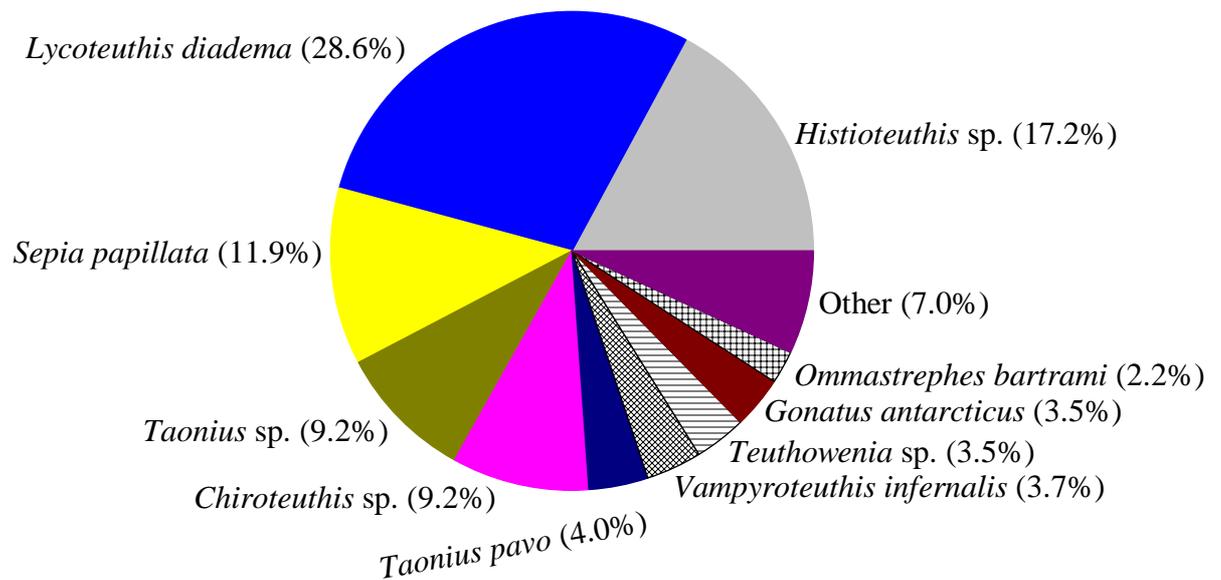
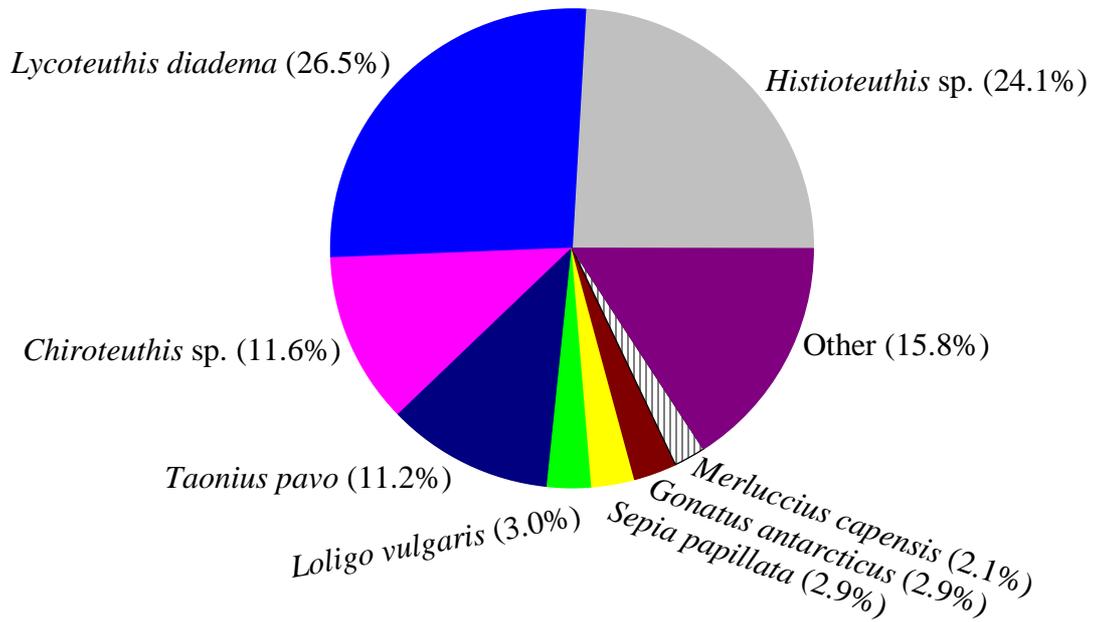


Figure 6.5: Diet composition of female (n=19) (a) and male (n=12) (b) *Kogia sima*.

a)



b)

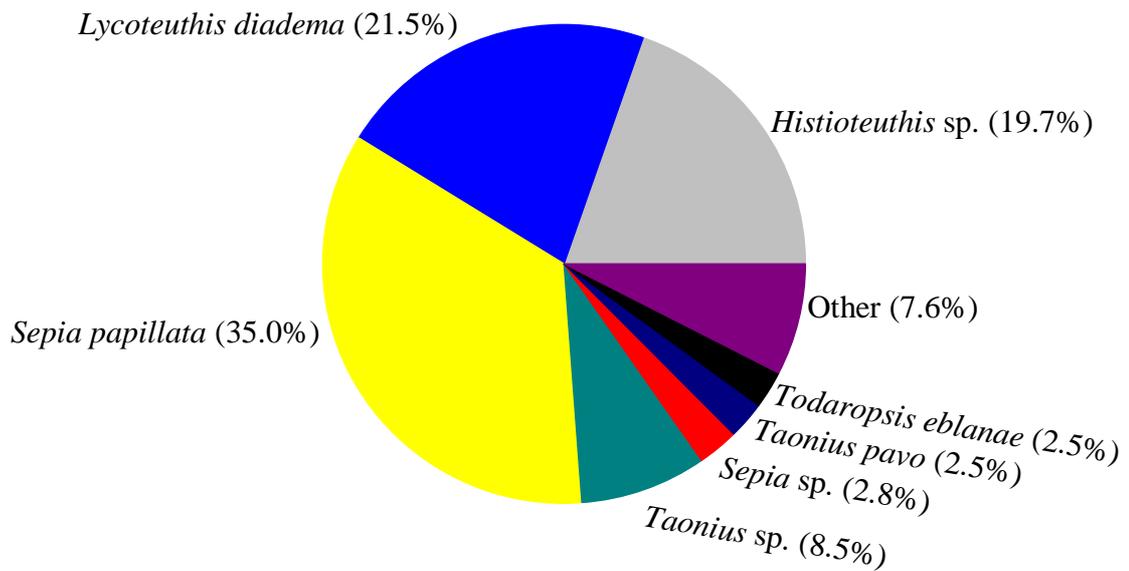
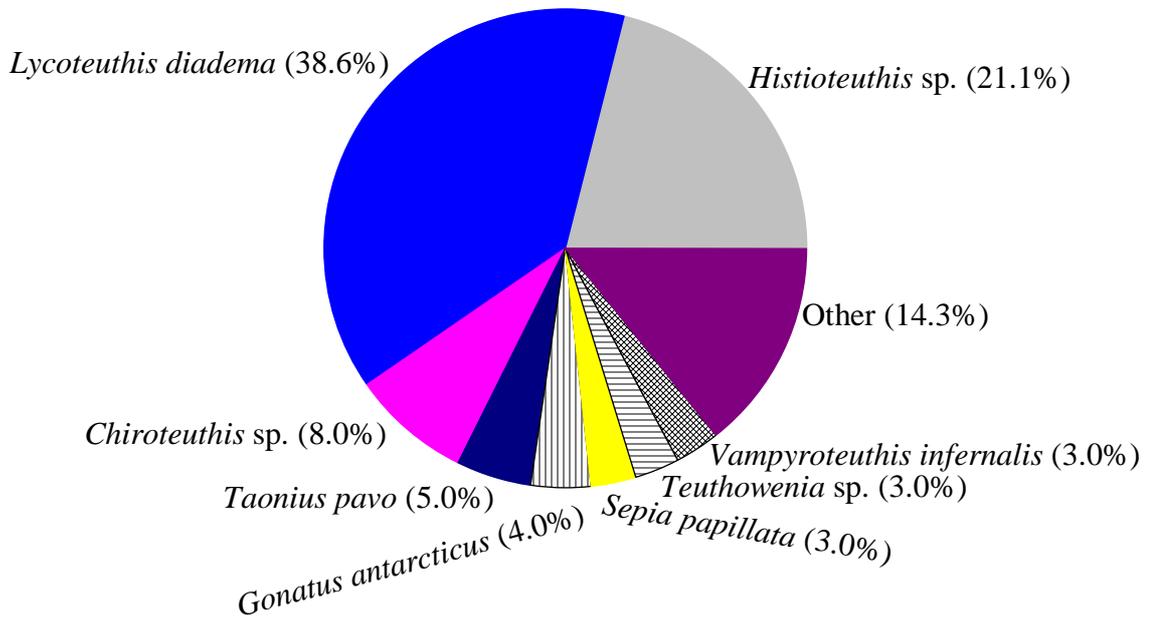


Figure 6.6: Diet composition of mature (n=22) (a) and immature (n=9) (b) *Kogia sima*.

a)



b)

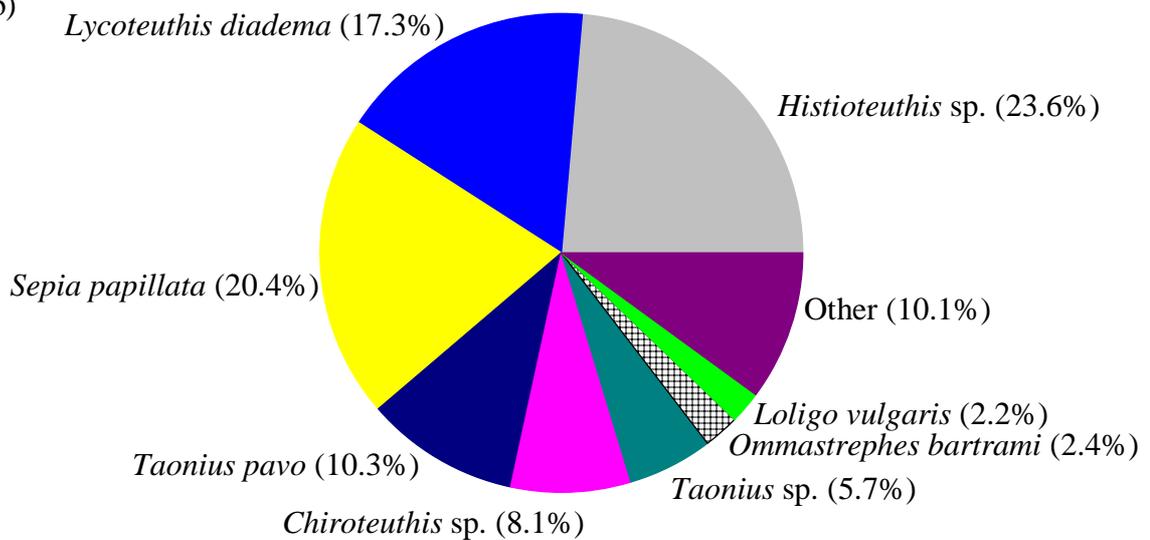


Figure 6.7: Diet composition of group 1 (n=13) (a) and group 2 (n=18) (b) of *Kogia sima*.

*K. sima*, *Vampyroteuthis infernalis* was only found in the diet of group 1.

Table 6.6: Main stomach contents of group 1 and group 2 of *Kogia breviceps* and *Kogia sima* presented as numerical percentages based only on prey items identified to genus level.

Main Prey Species	Stomach Content (Numerical %)			
	<i>Kogia breviceps</i>		<i>Kogia sima</i>	
	Group 1	Group 2	Group 1	Group 2
<i>Histioteuthis sp.</i>	32.85	27.42	21.08	23.61
<i>Lycoteuthis diadema</i>	8.56	21.29	38.55	17.35
<i>Sepia papillata</i>	-	4.31	-	20.43
<i>Taonius sp.</i>	*	*	-	5.68
<i>Chiroteuthis sp.</i>	4.37	2.99	8.03	8.06
<i>Loligo vulgaris</i>	16.54	2.79	< 2	2.16
<i>Sepia sp.</i>	< 2	6.94	< 2	< 2
<i>Taonius pavo</i>	5.40	2.13	5.02	10.33
<i>Phosichthys argenteus</i>	4.54	-	*	*
<i>Octopoteuthis sp.</i>	3.56	5.02	*	*
<i>Merluccius capensis</i>	-	2.08	4.02	-
<i>Teuthowenia sp.</i>	< 2	< 2	3.01	< 2
<i>Vampyroteuthis infernalis</i>	*	*	3.01	-
<i>Gonatus antarcticus</i>	< 2	< 2	3.01	< 2
<i>Todaropsis eblanae</i>	< 2	2.74	2.61	< 2
<i>Ommastrephes bartrami</i>	< 2	< 2	< 2	2.38
<i>Other</i>	14.79	18.65	9.05	5.46

- = prey species was not present.

\* = prey species was represented by less than 10 individuals in both groups combined and thus not considered for calculations of main prey items.

Other = all prey species that comprised less than 2% of the total prey number.

### 6.3.3 Size-frequency analysis of prey

Overall *K. breviceps* fed predominantly on prey between 60 and 80mm in dorsal mantle length (20.29%), which was slightly smaller than the main prey of *K. sima*, which measured between 80 and 100mm in length (23.39%) (Figure 6.8). However, the next predominant size class that *K. breviceps* fed on was cephalopods between 80 and 100mm in length (18.16%) (Figure 6.8).

Both *K. breviceps* females and males fed predominantly on cephalopods between 60 and 80mm in length (21.7% and 18.46%, respectively), although females also fed to a large extent on prey that was between 80 and 100mm long (20.12%) (Figure 6.9a). Similarly, both sexes of *K. sima* fed primarily on prey of similar size, which was somewhat larger than that of *K. breviceps* and measured 80 to 100mm in length (21.86% for females and 26.97% for males, respectively (Figure 6.9b).

In *K. breviceps* immature animals fed primarily on prey between 60 and 80mm in dorsal mantle length (24.56%), while mature animals predominantly fed on cephalopods between 80 and 100mm in length (21.33%) (Figure 6.10a). In *K. sima* immature animals fed to a large extent on very small cephalopods up to 20mm in length (30.17%), while mature animals consumed mainly cephalopods between 80 and 100mm in length (28.15%) (Figure 6.10b). Therefore it appears that immature animals in both *Kogia* species fed on smaller prey than mature animals, but mature animals of both *K. breviceps* and *K. sima* fed primarily on the same sized prey.

When the split into group 1 and group 2 was considered, *K. breviceps* belonging to group 1 fed primarily on cephalopods between 80 and 100mm long (24.02%), while animals belonging to group 2 fed on cephalopods between 60 and 80mm in length (21.9%) (Figure 6.11a). The results for *K. sima* were the same with animals belonging to group 1 feeding mainly on cephalopods between 80 and 100mm in dorsal mantle length (43.49%), while animals from group 2 fed on prey between 60 and 80mm in length (15.39) (Figure 6.11b). However, the latter group also fed to a large extent on small prey up to 20mm in length (14.7%) (Figure 6.11b). Again immature animals and females either pregnant and/or lactating/ and/or accompanied by a calf of both *Kogia* species fed on smaller prey than mature males and females that were temporarily not reproducing. However, there were no differences in size preference between the respective groups of the two *Kogia* species.

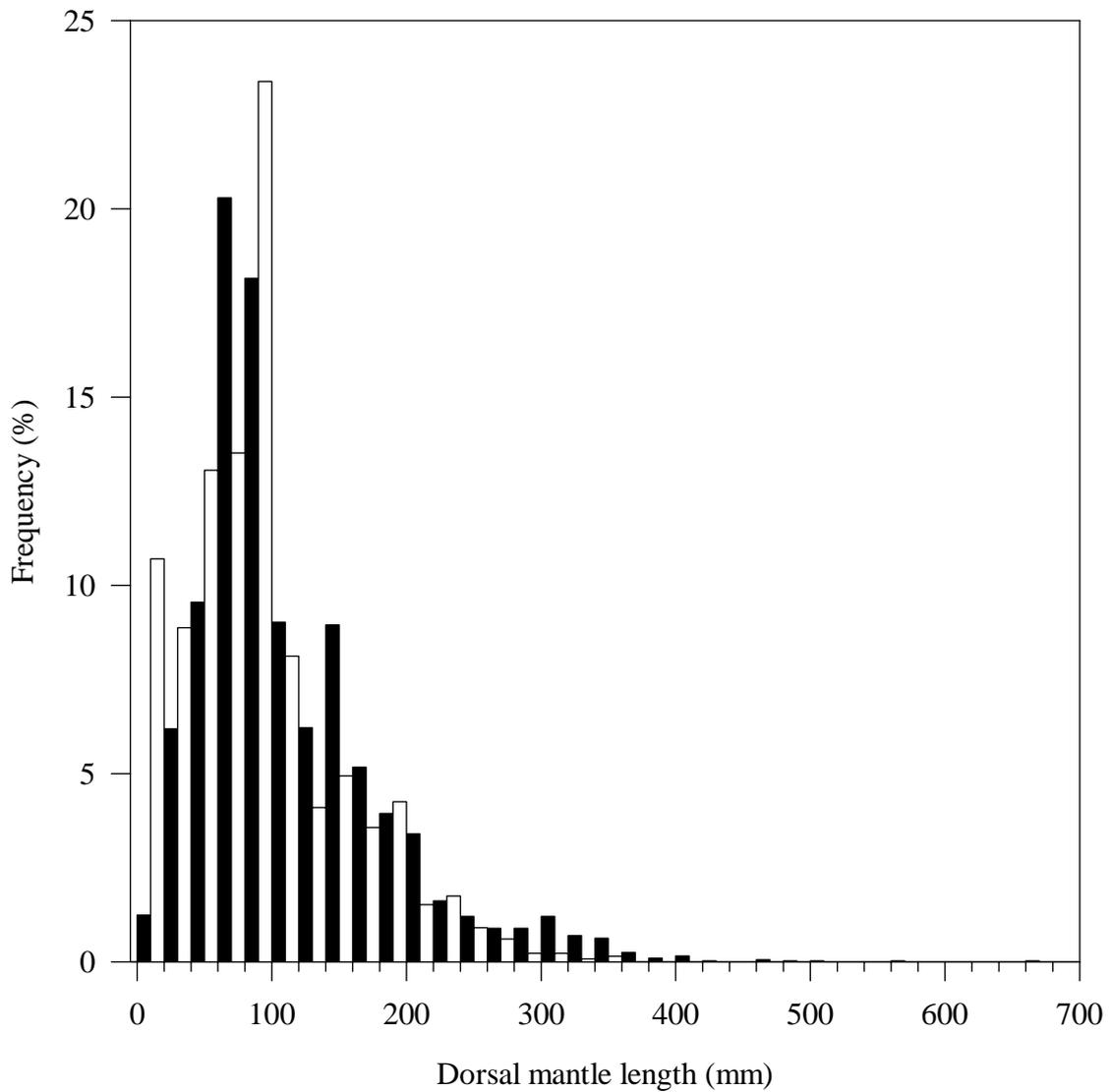


Figure 6.8: Size-frequency distribution of squid eaten by *Kogia breviceps* (n=3150 beaks, n=41 whales) (black) and *Kogia sima* (n=1317 beaks, n=31 whales) (white).

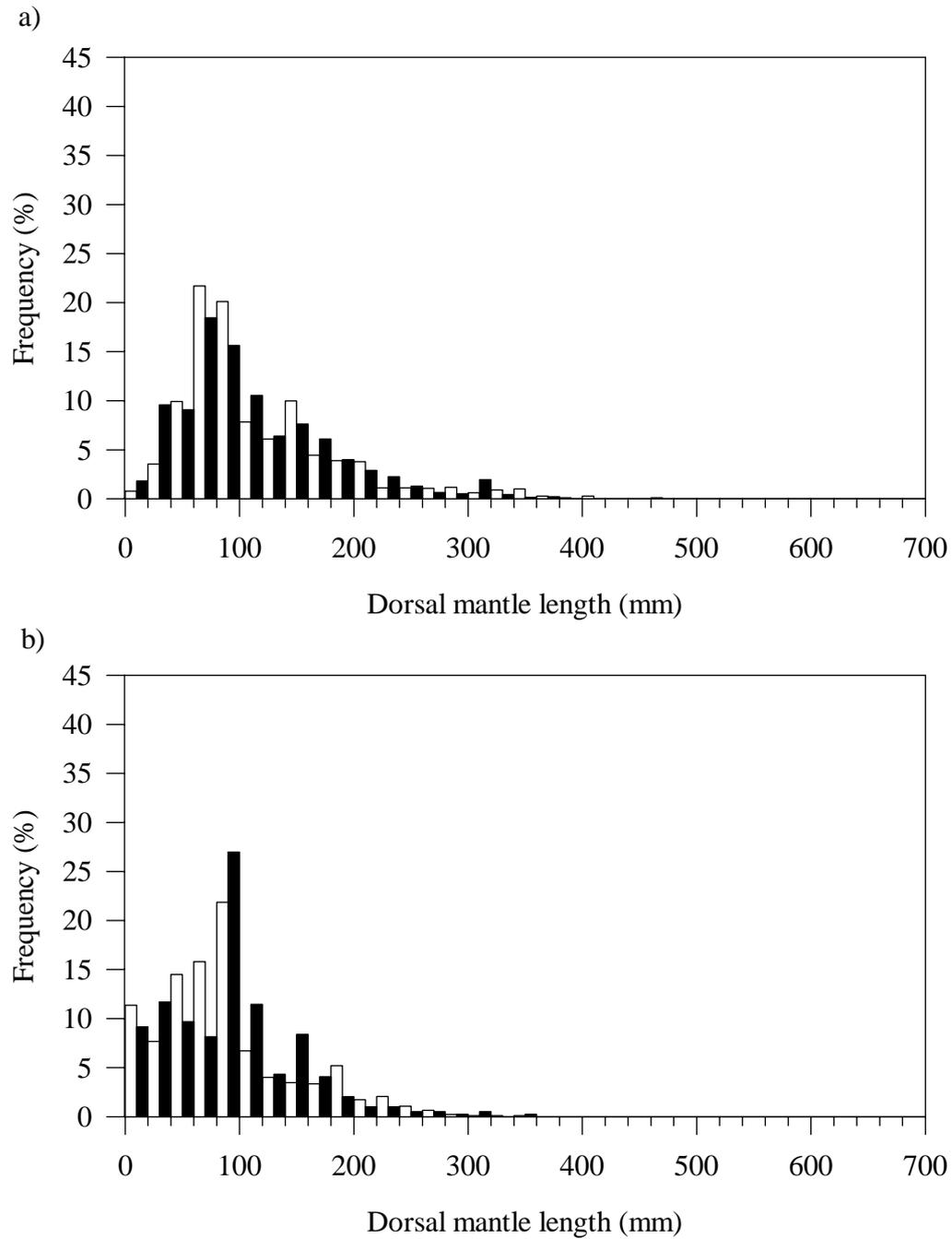


Figure 6.9: Size-frequency distribution of male (n=20) (black) and female (n=21) *Kogia breviceps* (a) and male (n=12) (black) and female (n=19) (white) *Kogia sima* (b).

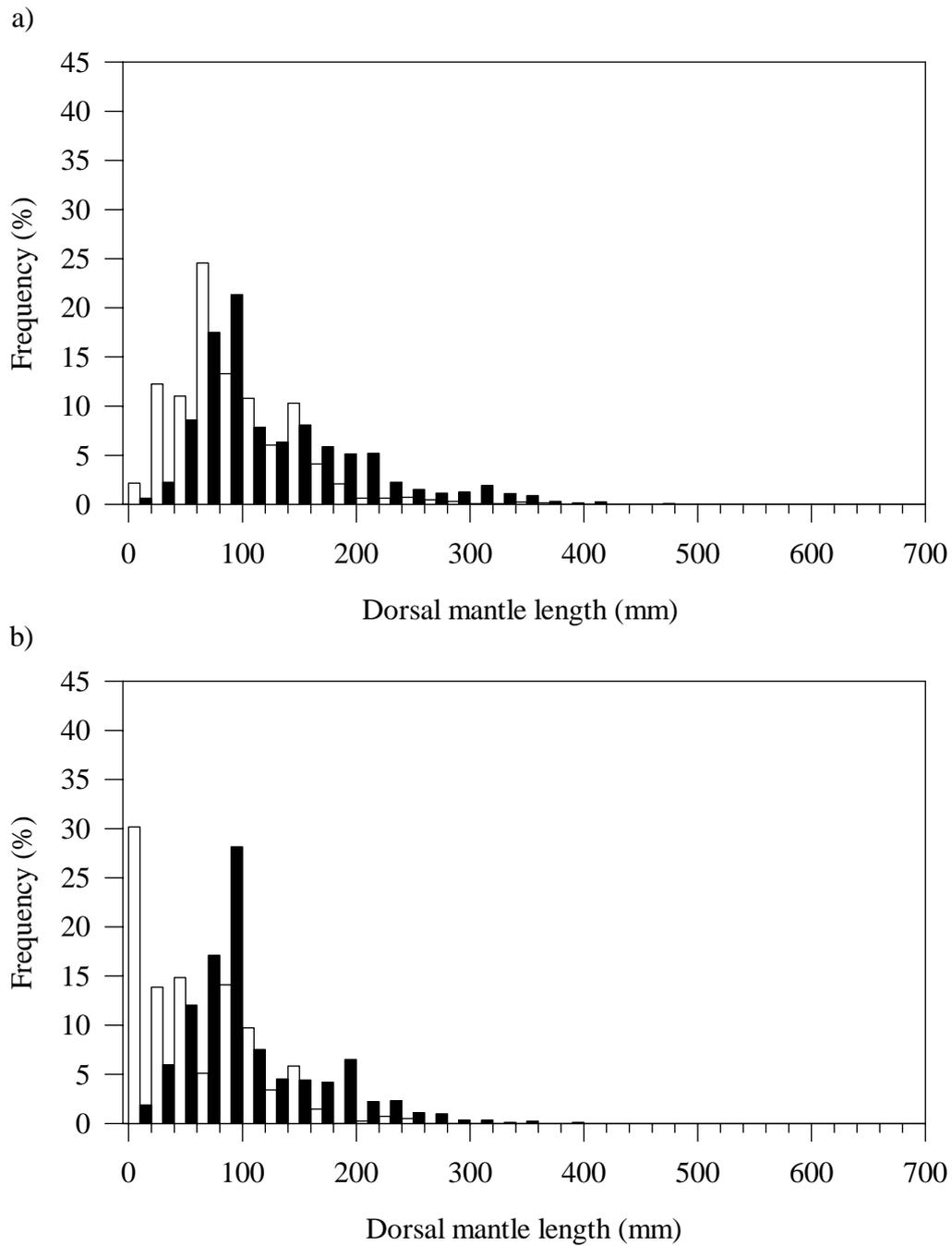


Figure 6.10: Size-frequency distribution of squid eaten by immature (n=20) (white) and sexually mature (n=21) (black) *Kogia breviceps* (a) and immature (n=9) (white) and sexually mature (n=22) (black) *Kogia sima* (b).

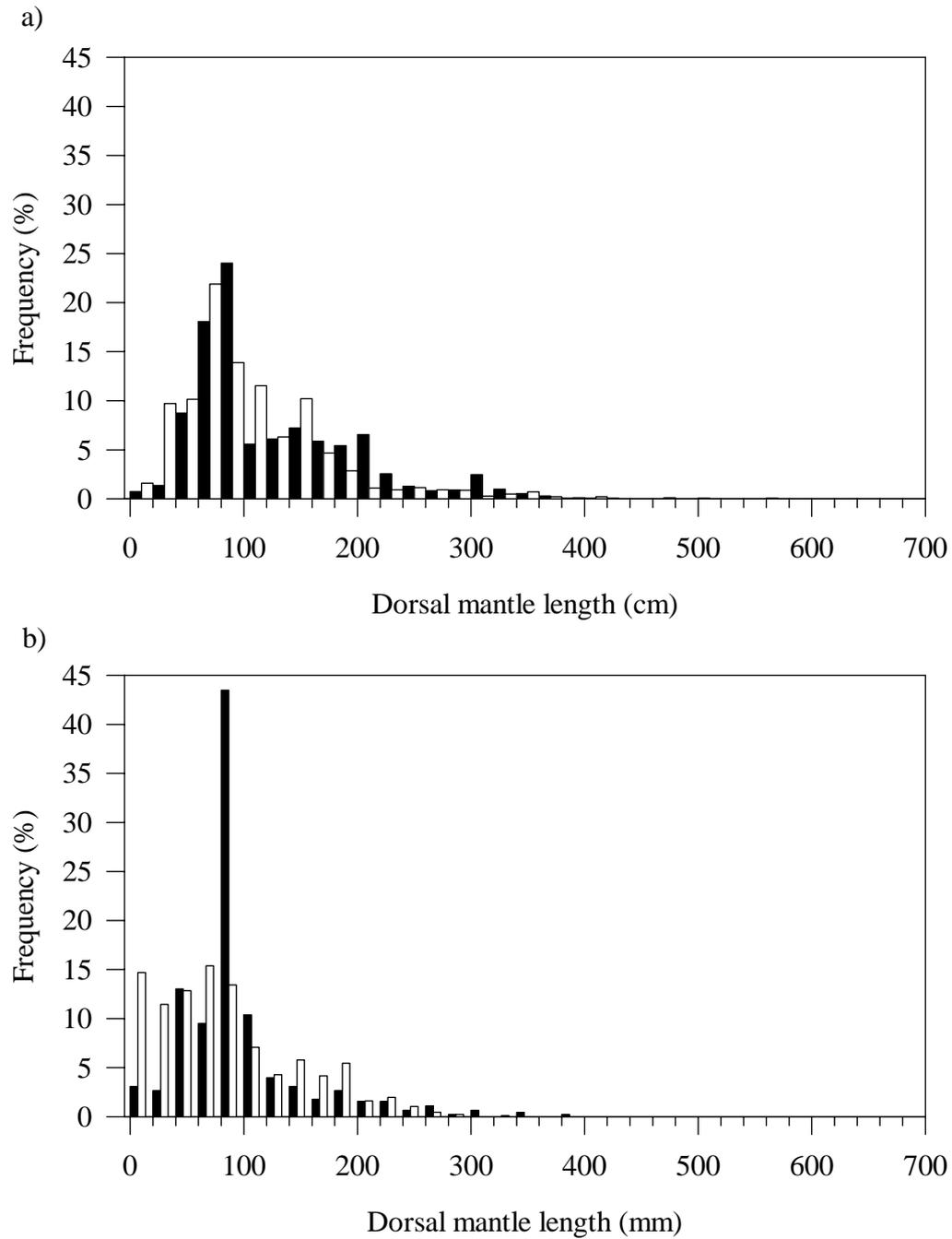


Figure 6.11: Size-frequency distributions of squid eaten by *Kogia breviceps* belonging to group 1 (n=12) (black) and group 2 (n=29) (white) (a) and by *Kogia sima* belonging to group 1 (n=13) (black) and group 2 (n=18) (white) (b).

### 6.3.4 Australian data

The stomach contents of four Australian animals were similar to the South African animals (Table 6.7). Remains of the crustacean *Gnathophausia ingens* were found in two stomachs and could not be quantified further. *Histioteuthis* sp. was again very prevalent in the stomach of one of the Australian animals (SAUSM M15814), although it was surpassed by the presence of *Enoploteuthis* sp. (Table 6.7).

Table 6.7: Stomach contents of four Australian *Kogia breviceps*.

Animal No.	Prey species	No.	% No.	Mass (g)	% Mass (g)
<b>M25869</b> <b>F; L:160cm;</b> <b>A:0.37yrs</b>	Octopodidae <i>Octopus</i> sp.	9	100	1039.63	100
<b>M15814</b> <b>M;</b> <b>L:242cm;</b> <b>A:6.2yrs</b>	Chiroteuthidae <i>Chiroteuthis</i> sp.	2	8	132.00	8.02
	Enoploteuthidae <i>Enoploteuthis</i> sp.	13	52	856.17	52.00
	Histioteuthidae <i>Histioteuthis</i> sp.	7	28	352.87	21.43
	<i>Histioteuthis atlantica</i>	1	4	212.20	12.89
	Octopoteuthidae <i>Octopoteuthis</i> sp.	1	4	27.38	1.66
	Ommastrephidae <i>Martialia hyadesi</i>	1	4	65.86	4.00
	<i>Gnathophausia ingens</i> remains				
<b>M16471</b> <b>M;</b> <b>L:289cm;</b> <b>A:3.67yrs</b>	Mastigoteuthidae <i>Mastigoteuthis</i> sp.	2	66.67	143.48	14.54
	Ommastrephidae <i>Todarodes</i> sp.	1	33.33	843.62	85.46
<b>M16393</b> <b>F; L:210cm;</b> <b>A:-</b>	<i>Gnathophausia ingens</i> remains				

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## **6.4 Discussion**

### **6.4.1 Niche partitioning between *K. breviceps* and *K. sima***

The results of the dietary analysis indicate that both *Kogia* species, which are sympatric off the coast of Southern Africa, share the same ecological niche in terms of prey species. Superficially they appeared to feed on the same main prey items and large niche overlaps existed between the two *Kogia* species as well as between different groups within the two species. In addition, an examination of prey size indicated that little differences exist between the sizes of prey consumed by *K. breviceps* and *K. sima*.

However, species pairs with high overlap along one niche dimension often, but by no means always, overlap little along another (Pianka, 1975). Thus an attempt is made here to tease from the data the areas in which the two species differ.

#### **6.4.1.1 Trophic segregation**

##### **6.4.1.1.1 Generalist vs. specialist**

While dietary differences within each *Kogia* species are explored in more detail below under section 6.4.2, subtle differences in species composition appear to indicate some partitioning of the trophic niche of the two *Kogia* species off South Africa. *K. breviceps* had a wider range of prey species, with 67 species of prey recorded from the stomach contents, while *K. sima* fed on a smaller range of prey items with 49 species of prey found in the stomachs. This indicates that *K. breviceps* is more of a generalist than *K. sima*, which can be considered a specialist feeder. These results support previous findings by Sekiguchi *et al.* (1992), which indicated that out of 20 species of smaller odontocetes *K. breviceps* has the most diverse diet (49 species), followed by southern bottlenose whales *H. planifrons* (39 species) and *K. sima* (27 species). Although in the present study both species fed on the same two cephalopod species as their main prey items, the composition of the additional suite of cephalopod prey differed between the two. In this respect the crudeness of the prey data appears to have obscured real dietary differences between the two *Kogia* species, a phenomenon which has been observed previously when using niche overlap indices (Huey and Pianka, 1983).

Surprisingly, the data on prey size indicated that *K. sima* fed on slightly larger prey than *K. breviceps*, although the latter fed on a larger range of prey sizes. These data are in contrast to previous studies on diet in odontocetes in general, and *Kogia* in

particular, which determined that larger whale species feed on larger prey (Ross, 1979b; Clarke, 1980; Desportes and Mouritsen, 1993; Clarke and Goodall, 1994; dos Santos and Haimovici, 2001). The size of the cephalopods consumed by *K. breviceps* off Taiwan ranges from 48.6 to 490.2mm, while in *K. sima* the size of the prey consumed was smaller, measuring 30.4 to 348.3 mm (Wang *et al.*, 2002). Possibly the large number of immature animals (n=20) in the sample of *K. breviceps* compared to *K. sima* (n=9) may have skewed the results somewhat in the present study.

Although the niche overlap index is high and both *Kogia* species fed on the same prey types and on the same size of prey, thus not indicating any resource partitioning, they may not be in competition if the prey is available in sufficient supply to sustain both populations (Pianka, 1976). In addition, the data indicate that *K. breviceps* has a wider niche breadth, which is defined as the sum total of the variety of different resources exploited by an organism (Pianka, 1976; Whitehead *et al.*, 2003), in terms of diet than *K. sima*. This would allow *K. breviceps* to forage on other prey species and other sizes of prey when those that it shares with *K. sima* are in short supply.

#### 6.4.1.1.2 Nutritional value

No clear preference for either ammoniacal or muscular squid could be observed in either whale species. In the present study *K. breviceps* fed to a larger extent on Octopoteuthidae, which belong to the ammoniacal squid, as well as Loliginids, which are muscular squid, than *K. sima*. However, since these prey species only made up a small part of the diet of each *Kogia* species and no clear preference for either ammoniacal or muscular squid could be detected for either *K. breviceps* or *K. sima*, this difference may just be a reflection of dietary preferences in species rather than indicating a trend for nutritional preferences between the two *Kogia* species. This is in contrast to previous studies on *Kogia* diet elsewhere. While muscular squid make up more than 60% of the diet of both *Kogia* species off Taiwan, *K. sima* consumes more muscular squid than *K. breviceps* (74% and 65.7%, respectively) (Wang *et al.*, 2002). In contrast, the prey of both *Kogia* species off southern Brazil is comprised of small to medium sized cephalopods, with neutrally buoyant species making up 65% of the specimens, while muscular squid make up 31% (dos Santos and Haimovici, 2001). Only few fishes and crustaceans are present in the diet (dos Santos and Haimovici, 2001).

### 6.4.1.2 Spatial segregation

In addition to subtle differences in prey species and prey size between *K. breviceps* and *K. sima* at least some spatial segregation seems to occur.

#### 6.4.1.2.1 Depth

In order to determine the depth distribution of the prey of *K. breviceps* and *K. sima*, which in turn gives an indication about potential differences in foraging depth between the two species, an attempt was made to examine the habitat of the prey species. However, as already stated the knowledge and literature on the habitat and, in particular, diel migrations of most cephalopod species is scarce. In addition, there are no data or indications at what time of the day or night either *Kogia* species forages. In order to determine differences in the diet between the two *Kogia* species, a few observations made during the analysis of the data are examined here.

The primary prey of both *Kogia* species was *Histioteuthis* sp., which are medium to large squids usually found below 200m of water depth (Nesis, 1987; Clarke, 1996a). Some species, such as *Histioteuthis miranda*, which was only found in *K. breviceps*, have been reported from depths between 700 and 900m and are thought to be benthic (Roeleveld *et al.*, 1992).

The other main prey item, *Lycoteuthis diadema*, has been reported from depths between 300 to 900m, some even as deep as 3000m (Roper and Young, 1975). However, it is most abundant at depths between 400 and 500m (Payne and Crawford, 1989), although more recent surveys suggest that its peak abundance is between 500 and 900m off the South African west coast (Roeleveld *et al.*, 1992). It lives at or near the bottom over continental slopes (Nesis, 1987).

A number of prey species found in the diet of *Kogia* appear to be benthic. The cephalopods *Sepia* sp. and *Rossia* sp. are both benthic over the continental shelf (Roper and Young, 1975; Clarke, 1996a), the former even reportedly burying in the sea bottom during the day and only emerging at night (Nesis, 1987). *Octopus* sp., *Octopus dofleini* and *Octopus vulgaris* are to a larger extent found in the diet of *K. breviceps* than *K. sima* and are benthic over the continental shelf (Roper and Young, 1975; Nesis, 1987; Clarke, 1996a). *Histioteuthis macrohista*, which occurred in the stomach contents of both *Kogia* species, is also benthic on the lower continental slope (Roeleveld *et al.*, 1992).

Some cephalopod species, which were more common in *K. breviceps* than *K.*

*sima*, are found at great depths. The Octopoteuthid squid *Taningia danae* is only present in *K. breviceps* and is found below 500m over the continental slope (Clarke, 1996a). Other Octopoteuthidae, like *Octopoteuthis* sp., were to a much larger extent present in the diet of *K. breviceps* than in the diet of *K. sima* and are found below 200m, but most abundantly between 300 and 700m depth (Roper and Young, 1975). *Pholidoteuthis boschmai*, which was found in *K. breviceps*, has only been caught between depths of 998 and 1412m (Nesis, 1987). However, *Taonius pavo*, which was relatively common in the diet of both *Kogia* species, has been reported from depths between 600 and 900m (Roper and Young, 1975; Roeleveld *et al.*, 1992). The ommastrephid *Todaropsis eblanae*, which was more common in the diet of *K. breviceps* than *K. sima*, is also benthic at depths between 300 to 500m (Nesis, 1987; Roeleveld *et al.*, 1992).

In contrast, Onycoteuthidae, which again were more common in *K. breviceps* than *K. sima*, are found around and below the 200m isobath, and are therefore regarded to belong to the more shallow water cephalopods. Similarly, *Gonatus antarcticus* occurs at about the same depth (Clarke, 1996a) and was found at almost equal amounts in both *Kogia* species.

The commercially exploited chokka squid *Loligo vulgaris* was also found to a large extent in the diet of *K. breviceps*, while it was only present in small numbers in *K. sima*. This species is found at all depths between the coast and 300m and two major inshore spawning grounds have been identified off the Eastern Cape coast: Algoa Bay and St. Francis Bay (Roberts and Sauer, 1994).

Some species, such as *Vitreledonella richardi*, are classed as deep-sea animals and are usually found below 1000m water depth. However, this specimen weighed just under 50g and was taken by an immature male *K. breviceps*. Juvenile *Vitreledonella richardi* are found in the upper 300m and this is possibly where the present specimen was taken. These results indicate the care one has to take when interpreting the depth distribution of cephalopod prey. However, the deep-sea mysid shrimp *Gnathophausia ingens* was more commonly found in *K. breviceps* than *K. sima*, possibly indicating that *K. breviceps* dives more frequently to greater depths than *K. sima*.

Most fish species identified were more common in the diet of *K. breviceps* than *K. sima*. Myctophids (or lantern fishes) and hake *Merluccius capensis* was found in greater numbers in *K. breviceps* than *K. sima*. Interestingly, the anchovy *Engraulis japonicus* was only present in *K. breviceps*, while a different species of anchovy, *Engraulis capensis*, was found in *K. sima*, which may be a further indication of resource

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partitioning between the two species.

Thus the diet of both *Kogia* species included benthic prey species, indicating that they can dive to the bottom at least in coastal waters up to 200m in depth. In addition, the diet of both species indicated that they feed over the continental shelf and over the slope. The availability of prey in dense patches has been linked to oceanographic features, including bathymetry, fronts, eddies, and primary productivity (Fiedler, 2002). Teuthivores are most abundant at the continental shelf edge and deep diving species may be found near temperature fronts in deep water, where the squid may aggregate (Kenney and Winn, 1987; Davis *et al.*, 1998; Baumgartner *et al.*, 2000). The presence of species like *Histioteuthis miranda*, *Taningia danae*, and *Pholidoteuthis boschmai* in the diet of *K. breviceps* indicated that this whale species also foraged over the lower slope and slope edge. The depth at which a suitable prey source is available is a limiting factor for marine mammals, which are dependent on returning to the surface to breathe. Shallow, coastal waters are thus frequented by small cetaceans, which feed both benthically and pelagically (Ross, 1979b) and this is reflected here by *K. sima*. In contrast in oceanic waters the use of benthic or benthopelagic zones is limited to those species capable of making deep dives (Ross, 1979b), which is reflected in the diet of *K. breviceps*. Candela (1987) also noted that the foraging ranges of the two *Kogia* species off the south-eastern United States broadly overlap, concentrating on the epi-and mesopelagic zones of the deeper shelf and slope. However, *K. breviceps* forages to a greater extent on larger and deep ranging squid, in contrast to *K. sima*, which takes smaller squid and feeds at lesser depths (Candela, 1987).

#### 6.4.1.2.2 Inshore/offshore

This segregation of the niche along the spatial dimension does not only concentrate on depth, but also results in an inshore/offshore segregation. The waters a certain species is usually found in are characterised by the physical conditions that facilitate the accumulation of their prey (Forcada, 2002). Deep-diving species gain access to prey that is unavailable to the shallower diving species and are thus often found over deep ocean areas (Forcada, 2002). The shallower foraging/diving species i.e. *K. sima* is thus restricted to the shallower inshore waters, while *K. breviceps* is capable of deeper dives and thus able to exploit more offshore areas. This in turn results in preferences in terms of temperature and oceanographic conditions between the two

*Kogia* species due to the characteristic conditions off the South African coastline. While the inshore waters are warmer due to the combined influence of shallow depth and the warm Agulhas current, the offshore waters have prevailing cooler temperatures. This temperature preference between the two *Kogia* species is further explored in Chapter 7.

The affinity of *K. breviceps* for a wider range of prey items, resulting in the species being able to forage in cooler and deeper waters also has implications for the largest spatial scale- distribution. Kenney and Winn (1986) found that the ultimate controlling factor for the distribution of cetaceans is food. Offshore species of cetaceans feed on a higher variety of prey (dos Santos and Haimovici, 2001) and a wide range of prey items allows a predator to be distributed over a wide range (Forcada, 2002). Vice versa a large range results in the animal encountering more types of prey and thus in having a larger niche breadth (Whitehead *et al.*, 2003), thus the causality in this case is unclear. In this respect the generalist diet of *K. breviceps* allows it to have a larger distribution than *K. sima* (see Chapters 1 and 7) and travel more widely (see Chapter 8).

### **6.4.1.3 Temporal segregation**

#### 6.4.1.3.1 Diel

Another segregation of the niche occupied by both *Kogia* species off South Africa appears to occur along the temporal dimension. Sympatric predators are often active at different times of the day (Schoener, 1974; Huey and Pianka, 1983) and a number of cephalopod species rise to the surface at night. Consequently, species feeding on these cephalopods save energy by feeding at night since they do not have to spend as much energy on deep dives (Gaskin, 1982). Unfortunately no data are available on the time of day either *Kogia* forages, but it is possible that the two species may feed at different times in order to avoid direct competition (Huey and Pianka, 1983).

#### 6.4.1.3.2 Seasonal

Different environmental factors influencing reproduction can interact with each other in a complex way to regulate reproduction in a mammal and not only one factor will prime it (Bronson, 1989). Of the many environmental factors food availability plays the most important role and it is particularly important in relation to seasonal variation in reproduction (Bronson, 1989). However, no habitat can provide a continuous supply of

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food for a certain species; food is usually patchily distributed and its availability varies between years as well as between seasons (Bronson, 1989). Feeding strategy (being either generalist or specialist) can affect the pattern of reproduction and the specialists tend to be more seasonal breeders than generalized feeders as the latter can shift easily from one food source to another (Bronson, 1989). This is also reflected in the data for seasonal reproduction in the two *Kogia* species, with *K. breviceps*, being the generalist feeder, having a longer mating and calving period extending over a period of six months, while *K. sima*, which is more of a specialist feeder, has a shorter mating and calving period of four months (see Chapter 5).

An extreme scenario of resource partitioning is if two species exploit the same resource at different times of the year. The most environmentally dependent phase of a female's cycle is late lactation, when the female has to find and consume enough food to nourish both herself and the rapidly growing offspring (Bronson, 1989). A female's reproductive effort would be wasted if there was no chance of success because of adverse environmental conditions and females compete with each other for food in order to maintain pregnancy and lactation (Bronson, 1989). Therefore if several populations use the same food resource they should evolve mechanisms to reproduce at different times of the year and thus avoid high energetic demands when the main resource is being heavily utilised (Dasmann and Mossman, 1962; Bronson, 1989). Differences in reproductive seasonality were observed between the two *Kogia* species off South Africa (see Chapter 5). While *K. sima* showed a calving peak during the austral summer months (December and January), *K. breviceps* showed a peak in the austral autumn (March and April). These differences in reproductive seasonality may have been selected for in order to prevent utilisation of the same resource at a time when energetic demands are the highest.

In addition, the diet analysis has shown that animals of both species belonging to group 2 feed to a large extent on *Sepia* sp. and *Sepia papillata*, an inshore cuttlefish. This trend is more pronounced in *K. sima* than *K. breviceps*. Unfortunately little information is available on the seasonal migration of most cephalopod species off South Africa. However, data on *Sepia australis* (Roeleveld *et al.*, 1993) and *Loligo vulgaris reynaudii* (Augustyn *et al.*, 1994) indicate that late summer (March) and summer, respectively, are peak spawning times for these cephalopod species, resulting in large aggregations of animals. The colder upwelled waters over the Agulhas Bank are closer inshore over the eastern part of the Agulhas Bank in late summer and a preference of at least these two

cephalopod species for colder temperatures results in spawning in that area. Cephalopods are known to undertake seasonal migrations in response to spawning (Brodziak and Hendrickson, 1999) and the seasonal movement of another teuthophagous odontocete, the long-finned pilot whale *G. melas*, has been linked with the seasonal movement of its cephalopod prey (Sergeant, 1962; Hoydal and Lastein, 1993; Payne and Heinemann, 1993). It is possible that other cephalopod species such as *Sepia papillata* may move onto the Agulhas Bank at the same time of the year as *Sepia australis* or *Loligo vulgaris reynaudii* in order to spawn. In this respect a peak in the abundance of the preferred prey item of pregnant and/or lactating females of either *Kogia* species would coincide with the timing of births and onset of lactation when energetic demands are the highest. However, as most cephalopod species are short lived and have a number of spawning events throughout the year (Augustyn *et al.*, 1994; Roberts and Sauer, 1994) the different reproductive seasonalities of the two *Kogia* species may be linked to separate spawning events.

#### 6.4.1.4 Sympatric species

While the above points try to emphasise the segregation of the two *Kogia* species along the trophic, spatial and temporal dimension of their shared niche off South Africa, the global distributions of *K. breviceps* and *K. sima* overlap to a large extent (see Chapter 1). Based on our current knowledge the two species are only truly sympatric off South Africa, Florida, and the coasts of Taiwan and Japan. Little research has been done to study the coexistence of sympatric whale species due to the logistic difficulties involved, the only exception being the well-known dietary differences of two sympatric populations of killer whales in the coastal waters of British Columbia, Canada, and Washington State and southeast Alaska, USA (Ford *et al.*, 1998). The two populations do not mix, show differences in seasonal distributions, social structure, and behaviour. However, the most pronounced difference can be found in the diet: the resident population feeds predominantly on fish and prefers salmon, while the transient population feeds on at least six different species of marine mammals (Ford *et al.*, 1998). In one of the classic studies on niche overlap in sympatric species, the diversity of resources exploited by lizards along various niche dimensions and the extent of niche overlap among them varied widely between three continents, and as a result the relative importance of various niche dimensions in separating niches differs between locations

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(Pianka, 1975). However, in order to define the dietary niches of each *Kogia* species in more detail studies on allopatric populations of *K. breviceps*, for example off New Zealand, and *K. sima*, for example in the Gulf of California, may help elucidate differences. In addition, such research might help to interpret niche shifts between areas where the two species occur allopatrically and where they occur sympatrically. However, the interpretation of data from such investigations are often difficult due to geographical variations in various environmental aspects, such as resource availability.

Finally, it has to be pointed out that competitive interactions can influence a number of parameters of a species' ecology as described above, but it is not the only possible cause of resource partitioning. Consequently, such partitioning is most likely a combination of competition, predation, and environmental or physiological constraints.

#### **6.4.2 Niche partitioning within *Kogia* species**

Aside from the interspecific differences in diet some clear differences in diet were observed between groups within each *Kogia* species. This dietary segregation into separate feeding groups is a common phenomenon among cetaceans (Evans, 1987; Cockcroft and Ross, 1990a; Smith and Read, 1992), and it is thought that the partitioning into subgroups and the use of different foraging ranges, different prey sizes and different prey species reduces intraspecific competition (Cockcroft and Ross, 1990a). However, as the niche overlap indices between different groups were again very high and thus obscured some real dietary differences an attempt is made here to tease them out.

##### **6.4.2.1 Males versus females**

Dietary differences between the sexes are commonly found in many cetacean species and sexual segregation may have evolved in some species due to differing energy demands between adult males and females (Gaskin, 1982). In both *Kogia* species females appeared to feed to a larger extent on *Histioteuthis* sp. than males. This was particularly pronounced in *K. breviceps*, probably leading to the reduced niche overlap index between these two groups. In both *Kogia* species males had a more diverse diet and in *K. breviceps* they fed to a larger extent on fish than female *K. breviceps*, which in turn showed a preference for crustaceans. In odontocetes males appear to often have a higher consumption of fish. In long-finned pilot whales mature males consume more fish than any other group (Desportes and Mouritsen, 1993) and *Priacanthus*, a deep-water

fish species, is only found in the diet of mature male bottlenose dolphins *Tursiops truncatus* (Cockcroft and Ross, 1990a). In contrast, there are no differences between the sexes with regard to the number of prey species consumed by Risso's dolphins *G. griseus* off South Africa (Cockcroft *et al.*, 1993).

Although not evident from the data on prey composition, the sexual dimorphism found in *K. breviceps* (see Chapter 3) is also reflected in the prey size preferences in *K. breviceps*, with females taking same-sized as well as slightly larger prey than males. Sexual dimorphism has been related to different types of food consumed by the two sexes in other animals, including mammals (Ralls, 1976). In some of the mammals that show reversed sexual dimorphism in size intersexual competition for food may be reduced by exploiting a wider range of resources than would be possible if the sexes were of equal size (Ralls, 1976). Differential niche utilization may be accomplished by sexual dimorphism in size, by sexual dimorphism in the feeding apparatus, by a combination of both, or by differences in foraging behaviour (Ralls, 1976). However, exact links between sexual dimorphism and differential niche utilization are as yet unclear (Ralls, 1976), and again the results observed for *K. breviceps* may be a reflection of the skewed sample towards immature males and mature females in this species.

#### 6.4.2.2 Mature versus immature animals

In both species of *Kogia* mature animals consumed more fish than immature animals. In addition, in *K. breviceps* mature animals foraged predominantly on a different species of fish (*Phosichthys argenteus*) to immature animals (*Merluccius capensis*). In *K. sima* there was also some difference in the type of cephalopod consumed: while mature animals consumed mainly *Loligo vulgaris*, immature animals fed predominantly on *Sepia papillata*. It is interesting to note here that the comparison of the diets of mature and immature animals yielded the highest niche overlap index in *K. breviceps* (0.86), but the lowest niche overlap index in the whole study in *K. sima* (0.65).

Some additional differences in the size of prey taken by the two groups were observed between *K. breviceps* and *K. sima*. While in both species mature animals fed mainly on larger prey than immature animals (80-100mm), immature *K. sima* foraged predominantly on much smaller prey (0-20mm) than immature *K. breviceps* (60-80mm). This may present further subtle differences in niche segregation between the two *Kogia* species.

While the dietary comparison between the sexes as well as between mature and immature animals showed some interesting results, the trends in dietary segregation already observed within the two species are even more pronounced in the following analysis.

#### **6.4.2.3 Group 1 (adult males and non-reproductive adult females) versus group 2 (pregnant and/or lactating females and immature animals)**

In *K. breviceps* animals belonging to group 1 showed a clear preference for *Loligo vulgaris reynaudii* and for fish. Animals of both *Kogia* species from group 2 foraged predominantly on *Sepia* sp. and *Sepia papillata*. As these cuttlefish species are usually found in inshore waters between 0 and 200m water depth (Roper and Young, 1975; Nesis, 1987), these results indicate that animals from group 2 feed closer inshore than animals from group 1. It is interesting to note that group 1 in *K. sima* fed almost twice as much on *Lycoteuthis diadema* than group 2, while animals from group 2 in *K. breviceps* consumed more *Lycoteuthis diadema* than those from group 1. This seems to present a further overlap between the two *Kogia* species with *K. breviceps* from group 2 and *K. sima* from group 1 feeding to large extents on *Lycoteuthis diadema*, and may indicate some spatial overlap in foraging area between the two groups of the two *Kogia* species.

Interestingly, the size-frequency analysis of the prey indicated that in both species animals belonging to group 1 fed predominantly on prey that was 80 to 100mm in size, while animals from group 2 fed on prey 60-80 mm in size. In addition, *K. sima* from group 2 also fed on smaller prey 0-20mm in size.

The results indicate that in both *Kogia* species females accompanied by calves and immature young fed on smaller prey and closer inshore than mature males and non-reproducing mature females. This inshore movement may be due to the fact that the cow would not have to dive as deep in search of prey as she would over the edge of the continental shelf. Thus she would not have to leave her calf unattended on the surface too long or reduce her own foraging success, because the calf would not be able to dive for as long or as deep. A similar strategy has been suggested for the spotted dolphin *S. attenuata* (Bernard and Hohn, 1989). The above mentioned restrictions would decrease the females ability to catch prey at a time when her energetic demands are increased and thus the alternative would be to feed at a shallower depth.

The results of dietary segregation between different groups within the two *Kogia* species are in agreement with previous studies on the diet of both *Kogia* species off South Africa. Ross (1979b) reports that a high proportion of the diet of immature *K. sima*, calves and adult females consists of cephalopods that occur over the continental shelf (93% of all prey items), in particular small sepiids (Ross, 1979b). In contrast, adult animals feed to a larger extent on oceanic cephalopods (71% of all prey items). Similarly, only 55% of prey items in the stomachs of immature animals, calves and accompanying adult females of *K. breviceps* are from oceanic species, while it is 85% in adult *K. breviceps* (Ross, 1979b). These data suggest that juvenile and immature *Kogia*, and in particular those of *K. sima*, live closer inshore than adults, probably over the outer part of the shelf and upper part of the slope (Ross, 1979b). In contrast, adult animals are found over deeper water. This conclusion differs from a previous conclusion by Ross (Ross, 1979a), which was based on an analysis of all age groups together and suggested that *K. breviceps* lives further offshore than *K. sima*. Ross concludes that the continental slope is important as a “nursery” area for immature animals of both *Kogia* species (Ross, 1979b).

Similarly, studies on the bottlenose dolphins off northern Natal, South Africa indicate that cow/calf pairs feed inshore, while resting females and adult males feed offshore; adolescent animals feed inbetween (Cockcroft and Ross, 1990b). Young and Cockcroft (1994) also found clear differences in the contribution of particular prey species to the diet of different sex and size groups of common dolphins *D. delphis* off South Africa, with strong evidence of resource partitioning between groups. While male common dolphins concentrate on a single prey species i.e. pilchard, the diet of females is more diverse (Young and Cockcroft, 1994).

In addition to inhabiting shallower waters than other cephalopod species, *Sepia* species contain more calcium than squids and octopods (Clarke, 1986a) and may thus be important in the diet of lactating females (helping in lactation) and growing immature animals (aiding in the growth process and the formation of bones). Dietary preferences depending on reproductive condition have been recorded in other cetaceans. Most female adult harbour porpoises *P. phocoena* spend the year simultaneously lactating and pregnant, which results in high energy requirements. No differences in relative prey importance are present between adult harbour porpoises of different reproductive condition in the Bay of Fundy, but lactating females ingest more fish and have a significantly higher total caloric intake than non-lactating females or mature males

(Recchia and Read, 1989). Similarly, lactating female spotted dolphins *S. attenuata* consume mainly flying fish, while pregnant females feed almost exclusively on squid (Bernard and Hohn, 1989). Lactating common dolphins *D. delphis* off South Africa consume more squid than pregnant females and both lactating and pregnant females are the only groups to feed on flying fish (Young and Cockcroft, 1994). Squid have a high water content and are thus thought to be important in the production of milk and maintenance of lactation (Young and Cockcroft, 1994). An increase in the daily food intake of lactating female bottlenose dolphins *T. truncatus* has been observed both in the wild (Cockcroft and Ross, 1990a) and in captivity (Cheal and Gales, 1991).

### 6.4.3 Comparison with data on *Kogia* diet elsewhere

By far the majority of detailed dietary studies on both *Kogia* species originate from South Africa (Ross, 1979a; 1979b; Klages *et al.*, 1989; Sekiguchi *et al.*, 1992). However, in comparison with dietary studies elsewhere it seems typical for the two *Kogia* species to feed on the same main prey items (dos Santos and Haimovici, 2001; Wang *et al.*, 2002) and to show some degree of spatial segregation in places where they are sympatric (Candela, 1987; Wang *et al.*, 2002).

As found in other teuthophagous odontocetes the preferred prey of a species can vary with geographic location (Candela, 1987). The present data for the four Australian specimens support that. While Histioteuthids appear to be important in the diet of *K. breviceps* throughout the world (Clarke, 1996b), interestingly the diet of *K. breviceps* from New Caledonia also contains a large portion of *Enoploteuthis* sp. (Bustamante *et al.*, 2003) as found in the Australian specimens.

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## *Chapter 7: Stranding patterns*



## **7.1 Theoretical background**

The phenomenon of whale strandings has fascinated scientists and laymen for centuries. During this time a number of theories have been put forward to explain the reasons behind strandings and just as many have been dismissed due to their shortcomings. However, as the biology and taxonomy of the majority of cetacean species remains relatively poorly known, in comparison with our present knowledge of terrestrial mammals, stranding data present a good source of information (Ross, 1984). The best-known species of cetacean are either hunted commercially or by-caught in fishing operations such as the dolphin-tuna fishery in the Eastern Tropical Pacific (ETP). For other cetacean species, in the absence of direct exploitation, data on the biology of a species has to come from stranded animals or sightings at sea (Ross, 1984).

Since no systematic surveys of cetacean distribution and abundance have ever been conducted off the South African coastline, very little is known about the spatial and temporal patterns of the distribution of cetacean species in this area. Although it is widely accepted that stranding data are, due to their bias, a poor source of information about a species' biology (see Chapter 2), in some cases they represent the only information available. In particular life history studies in cetaceans progress slowly and are hindered by low overall sample sizes (Ross, 1984). In addition, long-term stranding records provide a baseline for comparative studies between species and aid in determining distribution and seasonality of strandings.

Although there has been much debate about the usefulness of stranding data in establishing spatial distribution, such data have been widely used as they often represent the sole source of information for a given population, species or geographical area (Silva and Sequeira, 2003). Thus, for those species, for which data are otherwise inaccessible, strandings, in conjunction with information on the local oceanographic conditions, represent a starting point to gather information about a species' distribution and habitat.

### **7.1.1 Oceanographic features off Southern Africa**

To understand the zoogeography of marine flora and fauna the physical characteristics of the area under investigation need to be taken into consideration (Christensen, 1980). Thus in order to analyse the stranding data of *Kogia* from the southern African coastline a detailed knowledge of the oceanographic conditions off the

subcontinent is essential. The following section provides a brief overview of the main features characteristic of the waters off southern Africa.

The marine topography off Southern Africa is characterised by a relatively narrow continental shelf along the east coast, which is less than 10km in width (Figure 7.1) and provides little resistance to the fast, southward flowing Agulhas current (Gründlingh, 1983) (Figure 7.2). At about East London on the Eastern Cape coast the shelf widens rapidly to form the Agulhas Bank, which stretches westward along the southern Cape coast to south of the Cape of Good Hope, where the shelf narrows again to about 40km off the Cape Peninsula (Findlay, 1989) (Figure 7.1). At its widest point the Agulhas Bank is up to 270km wide (Schumann and van Heerden, 1988) (Figure 7.1). The topology of the Bank is characterised by rocky capes and shallow sandy bays, which are usually less than 50 metres in depth (Findlay, 1989). North of the Cape Peninsula the shelf slowly widens again until it reaches a relatively great width of 180km off the Orange River (28° 35'S, 16° 25' E) (Findlay, 1989) (Figure 7.1).

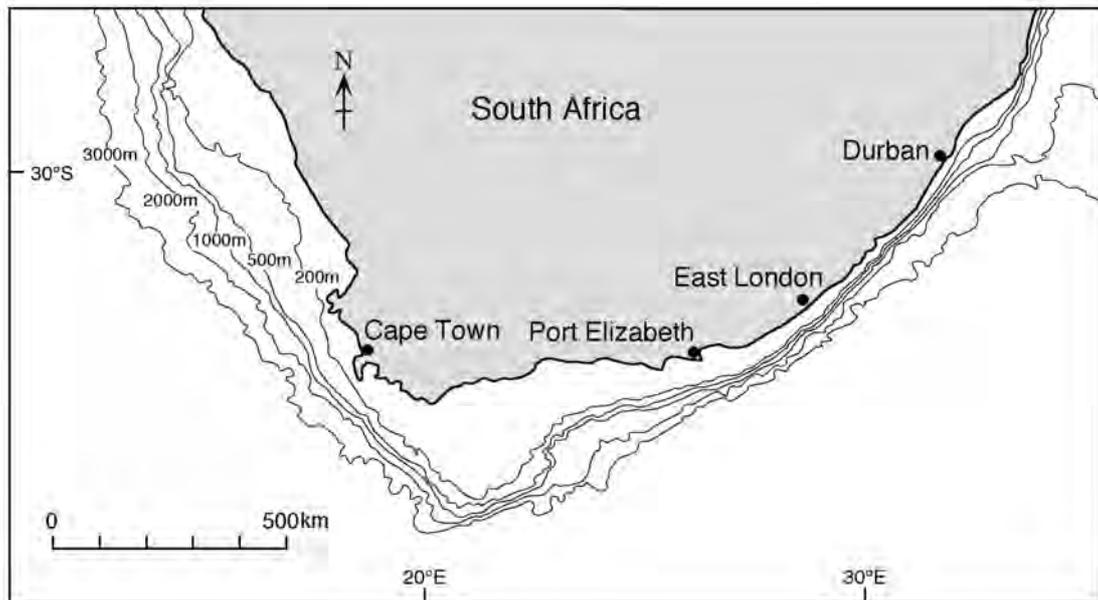


Figure 7.1: Bathymetry off Southern Africa (map by the Department of Geography, Rhodes University, Grahamstown, South Africa).

The oceanography off the subcontinent is dominated by two major current systems: the warm Agulhas Current to the east and south and the cold Benguela system to the west (Figure 7.2). In contrast to the Benguela system, the Agulhas Current, especially the oceanographic features off the Southern Cape coast and the Agulhas Bank,

has not been studied as intensively (Boyd *et al.*, 1992). In particular, the flow patterns over the Agulhas Bank are little understood (Boyd *et al.*, 1992). The Agulhas Current forms the western boundary current of the south Indian Ocean from 27°S to 40°S (Gordon, 1985) and has its counterparts in other major western boundary currents such as the Gulf Stream in the North Atlantic and the Kuroshio in the North Pacific (Goschen and Schumann, 1988). The source water of the Agulhas at the northern end is derived from the East Madagascar Current and the Mozambique Current (Gordon, 1985). The Agulhas Current flows fast and deep along the east coast of South Africa, reaching its maximum velocities and flowing most closely to shore in the area between Port Edward (31°03'S, 30°14'E) and the Bashee River (31°55'S, 28°27'E) (Boyd *et al.*, 1992) (Figure 7.2). Shelf regions east of 24° E are more regularly influenced by the Current than those to the west of that longitude (Boyd *et al.*, 1992). The core of the Agulhas Current lies off the shelf-edge and generally follows the 1000m isobath between Port Elizabeth and Mossel Bay (Boyd *et al.*, 1992) (Figure 7.2). The Current follows the southern coastline of the African continent with separation occurring at the Agulhas Bank near 22°E (Gordon, 1985) (Figure 7.2). After separation the flow makes an abrupt anticyclonic turn to the east in what is referred to as the Agulhas Retroflexion (Gordon, 1985) (Figure 7.2). So-called Agulhas Rings are formed here at intervals of about two months and they are the most intense found anywhere (Cockcroft *et al.*, 1990). Weak cyclonic currents are recorded on the central Agulhas Bank, while the flow is aligned with the bathymetry over the western Agulhas Bank and joins the Benguela system as it flows past the Cape Peninsula (Boyd *et al.*, 1992) (Figure 7.2). At Cape Columbine on the west coast the Agulhas current gains speed again as it diverges into a major offshore arm and a minor northward arm (Boyd *et al.*, 1992) (Figure 7.2).

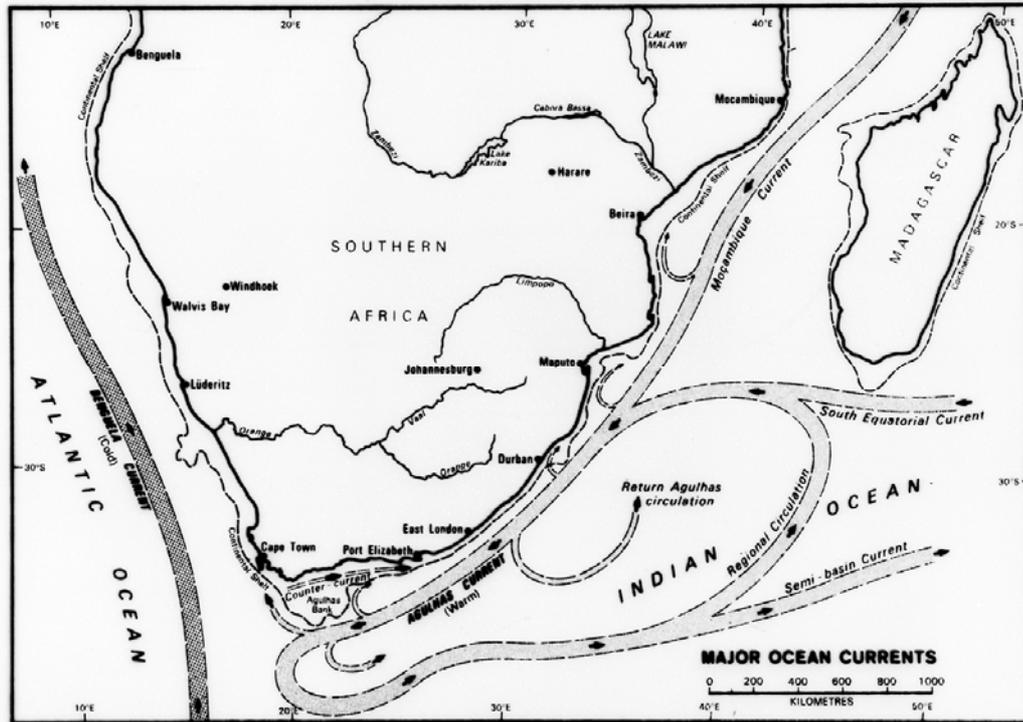


Figure 7.2: Major ocean currents off the South African subcontinent (map by the Department of Geography, Rhodes University, Grahamstown, South Africa).

Swift western boundary currents such as the Agulhas Current and the Gulf Stream govern most of the inshore processes along their contiguous coastlines (Lutjeharms, 1981) and commonly exhibit upwelling along the inshore front of the current (Schumann and van Heerden, 1988). The oceanography of the borders of the Agulhas Current is characterized by a number of mesoscale circulation phenomena (Lutjeharms, 1981; Lutjeharms *et al.*, 1989; Goschen and Schumann, 1988), which include meanders and eddies, and are to a large extent due to the horizontal shear between the current and the relatively quiescent water overlying the adjacent continental shelf (Lutjeharms *et al.*, 1989). Such features are also present in other western boundary currents, such as the Gulf Stream off the east coast of the United States (Lutjeharms *et al.*, 1989). These shear-edge features are a consistent and ever-present part of the northern border of the Agulhas Current (Lutjeharms, 1981). The shape and dimensions of these shear edge features are generally small with strongly defined boundaries near Port Elizabeth, but as they move downstream their lateral dimensions increase markedly (Lutjeharms, 1981). It is unclear to what depth these edge features extend, but the area they cover during their dispersive stages indicates their important influences on

circulation patterns and water masses on both the Agulhas Bank as well as the South Atlantic Ocean (Lutjeharms, 1981).

However, all along the east coast of Southern Africa the northern Agulhas Current follows the continental shelf edge quite closely with no regular meandering or large border eddies (Gründlingh, 1983; Lutjeharms *et al.*, 1989) (Figure 7.2). Occasionally so called Natal pulses are formed in the Natal bight and result in the concurrent deflection of the core of the Agulhas Current offshore as well as having a decided effect on the shear-edge features adjacent to the Agulhas Bank (Lutjeharms, 1981). But only once the current flows past Port Elizabeth on the eastern part of the Southern Cape coast, where it encounters the wide continental shelf, which forms the Agulhas Bank, is significant meandering behaviour, similar to that of the Gulf Stream, frequently observed (Lutjeharms *et al.*, 1989). Upstream of Port Elizabeth the current does not meander noticeably and no significant border features are observed (Lutjeharms *et al.*, 1989). Downstream of Port Elizabeth meanders increase in amplitude and trailing plumes of warm water are associated with each shoreward meander of the Agulhas Current (Lutjeharms *et al.*, 1989). South of Mossel Bay and south-east of Port Elizabeth warm plumes have also been observed (Lutjeharms *et al.*, 1989) and the number of meanders observed between Port Elizabeth and the southern extremity of the Agulhas Bank is far higher than in the areas either side of it as is the occurrence of eddies and plumes in this area (Lutjeharms *et al.*, 1989). However, the core of the current lies well offshore of the shelf break at all times and much of the time the main flow is observed 50km and more from the shelf edge (Schumann and van Heerden, 1988). Plumes associated with meanders offshore from the southern tip of the Agulhas Bank usually drift off in a north-westerly direction into the south-east Atlantic Ocean (Lutjeharms, 1981), but sometimes get advected back onto the Agulhas Bank to reach the shore between Cape Agulhas (the southernmost tip of Africa) and Cape Town (Lutjeharms *et al.*, 1989). In the centre of the Agulhas Bank cooler water temperatures indicate inshore upwelling areas (Schumann and van Heerden, 1988; Lutjeharms *et al.*, 1989). Larger oceanographic features such as the Agulhas Current and Agulhas Rings were shown to extend vertically for a few hundred metres, while other features visible at the sea surface were found to be shallow e.g. warm water plumes probably do not extend further than 50-100m downward (Lutjeharms *et al.*, 1989).

The hydrographic structure of the Agulhas Current is very similar to that of other large western boundary currents (Gründlingh, 1983) and can be identified by high

current velocities and temperatures in the surface structure (Goschen and Schumann, 1988). For most of its course it is characterised by a high-speed central “core” flowing at over 1m/sec, with maximum velocities of 2.5m/sec recorded beyond the shelf break (Gründlingh, 1983; Goschen and Schumann, 1988). The core has a width of some tens of kilometres (Gründlingh, 1983) and is usually located just beyond the shelf break, which in the case of Algoa Bay would be about 70km offshore (Goschen and Schumann, 1988). The associated maximum temperatures are about 26°C in summer and 3-4° less in winter; the temperatures are about 3°C lower than the corresponding values off Kwazulu Natal, indicating a marked cooling downstream (Goschen and Schumann, 1988). A difference of 6°C was recorded between inshore waters in Algoa Bay and the offshore current (Goschen and Schumann, 1988). Strong seasonal thermoclines are found off Algoa Bay and on the Agulhas Bank (Goschen and Schumann, 1988) and a separate study over the Agulhas Bank further to the west just off Mossel Bay indicated the extreme variability of the region in terms of water temperatures (Schumann and van Heerden, 1988). Plumes of warm water may cross the shelf edge and disperse over the continental shelf, thus advecting warmer and more saline tropical and subtropical surface water from the Agulhas Current into the surface layers of the Agulhas Bank (Goschen and Schumann, 1988). Shelf-edge upwelling within these frontal eddies introduces nutrient-rich water to these regions (Goschen and Schumann, 1988). Although no strong seasonal change was found in the flow behaviour of the Agulhas Current (Lutjeharms *et al.*, 1989), the core of the current shows large episodic meanders several times a year, which move Agulhas Current surface water over the shelf and closer inshore as well as creating upwelling in the core of a cyclonic eddy thus bringing cold water to the surface (Goschen and Schumann, 1988). Cold Indian Ocean Central Water can also be brought onto the shelf by current-induced upwelling (Goschen and Schumann, 1988). The Agulhas Current thus plays an intermittent role in determining the current and temperature structures of the adjacent shelf water (Goschen and Schumann, 1988). On the wider shelf areas wind can be expected to be the main forcing mechanism (Goschen and Schumann, 1988). Unfortunately little information is available about the offshore (i.e. southward) extent of the Agulhas Current and its influence on the surrounding waters.

Algoa Bay is the largest and easternmost bay on the south-eastern Cape coast and faces into the South-West Indian Ocean with the dominant oceanographic feature being the Agulhas Current (Goschen and Schumann, 1988). It appears to represent a special

scenario in the course of the Agulhas Current. The prevailing winds in Algoa Bay are generally parallel to the coastline and the surface flow is generally the same (Goschen and Schumann, 1988). During easterly winds a localized upwelling cell has been reported off Cape Recife, Algoa Bay (Beckley, 1983; 1988), similar to that seen in St. Helena Bay north of Cape Town (Goschen and Schumann, 1988). Such wind-induced upwelling is especially conspicuous at headlands and sudden drops in temperature at Humewood Beach, which occur each year during February and/or March suggest that temperature reversals across Algoa Bay are annual oceanographic events (Beckley, 1988). In addition, the presence of cold water at shallow depths i.e. 10° C at 20m has been reported (Beckley, 1988). This is surprising as Algoa Bay is relatively shallow (<50m depth) and one would assume that the water is generally well mixed. The origin of the cold water is unknown, but it has been suggested that it could originate from cold Atlantic Central water (Chapman and Largier, 1989).

In contrast to the Agulhas Current system, the cool, nutrient rich waters off the west coast of the subcontinent have been subject to extensive study and most mechanisms involved in the upwelling phenomena along this coastline are well understood. The dominant mechanisms over the southern Benguela shelf are coastal trapped waves, which organize large-amplitude pulses in upwelling (Jury and Brundrit, 1992). This produces a periodic input of nutrients during active upwelling, followed by enhanced primary production during the quiescent phase (Jury and Brundrit, 1992). North-directed, upwelling-favourable winds associated with low sea levels, northward shelf currents and declining coastal sea surface temperatures coexist in the active upwelling phase (Jury and Brundrit, 1992). Furthermore, a comparison between sites reveals the propagating nature of the pulses, being southwards along the West Coast and continuing eastwards along the South Coast beyond Port Elizabeth (Jury and Brundrit, 1992). A definite seasonal pattern in the movement of surface water off the west and south-west coasts of South Africa was reported by Duncan and Nell (1969). During summer (December- February) a southward flowing current is found inshore and a northward flowing current offshore off the west coast, while in the winter months (June-August) either the summer pattern may prevail or a general southerly trend is found both inshore and offshore (Duncan and Nell, 1969). Off the south-west coast a westward drift from Cape Agulhas often rounds Cape Point during summer, while the flow in winter is consistently eastwards (Duncan and Nell, 1969).

## 7.1.2 Cetacean distribution at sea

### 7.1.2.1 General

A myriad of factors influence the spatial and temporal distribution and abundance of cetaceans and they can be roughly categorised into environmental, biotic and anthropogenic factors (Davis *et al.*, 1998). Environmental factors, including physiochemical, climatological and geomorphological variables, operate on time scales ranging from hours to thousands of years (Davis *et al.*, 1998). Diel, seasonal, interannual and decadal patterns of variability or periodicity may occur for each factor (Davis *et al.*, 1998). Biotic factors are prey distribution, inter- and intraspecific competition, reproductive events and predation pressure, while anthropogenic factors range from historical hunting, pollution, shipping and fishing operations to geochemical and seismic explorations (Davis *et al.*, 1998). The spatial and temporal distribution of marine mammals and their prey may be influenced by a number of these factors, but the relative contribution of each may be difficult to quantify.

The combined interpretation of stranding data and distribution of free ranging animals at sea is vital to get a clear understanding of a species' ecology. While stranding data can contribute to the known distribution range of a certain species, information of its distribution and habitat preference at sea in turn is important for a more sound interpretation of stranding data. The distributions of species are not uniform, but show varying patterns throughout their ranges. Understanding the factors that influence these patterns and the abundance of animals is a central theme in ecology and is critical for the management of long-lived marine animals. Knowledge on preferences in temperature, bathymetry and prey all aids in interpreting stranding data, ultimately contributing to the formation of a clearer picture about a species' distribution and preferred habitat.

In contrast to mysticetes the majority of odontocete species appear to restrict their habitat to a limited oceanographic environment (Kasuya, 1995; Davis *et al.*, 1998). Factors such as temperature, chlorophyll *a* and/or plankton distribution and oceanography, including salinity and bathymetry, all influence the distribution of odontocetes to a greater or lesser extent (Kenney and Winn, 1986, 1987; Smith *et al.*, 1986; Davis *et al.*, 1995; Griffin, 1999; Baumgartner *et al.*, 2000). Temperature is considered to be one of the most important factors limiting the distribution of organisms in the marine environment (Christensen, 1980; Fiedler and Reilly, 1994) and such baseline data are particularly important for abundance estimates (Fiedler and Reilly,

1994). Seasonal changes in distribution in relation to temperature are observed in some species (Reilly, 1990), and some species show a preference for warm current systems (Geraci and Lounsbury, 1993). Although initial studies concentrated on examining the effect a single environmental variable, studies during the last decade have increasingly examined the interactions between a number of factors and cetacean distribution in order to understand mechanisms that produce and maintain the observed patterns. In particular, the use of satellite tracking, remote sensing and GPS systems has increased the collection of data on cetacean distribution in recent years. Strong associations to different habitats are increasingly linked to a number of geographic and oceanographic patterns of co-varying factors such as sea surface temperature, thermocline depth, upwelling, and salinity (Au and Perryman, 1985; Reilly *et al.*, 1996; Griffin, 1999).

In addition, behavioural patterns such as predator avoidance, interspecific competition and reproductive strategies all affect cetacean distribution to some extent, but studies of energy budgets in cetaceans indicate that most species need to feed every day and thus habitat is assumed to be primarily determined by the availability and abundance of prey (Reilly *et al.*, 1996; Baumgartner *et al.*, 2000). Concentrations of whales feeding on plankton were shown to be located in areas with the richest food base (Volkov and Moroz, 1977). However, for teuthophagous species it is not always possible to establish a direct dependence of the observed distribution on the distribution of prey species and hydrological characteristics of the area (see Chapter 6). Kenney and Winn (1986) determined that high-use habitats for teuthophagous whales are found in the shelf edge region. This area usually shows quite a diverse cetacean assemblage, although the individual species may have quite narrow dietary specializations (Kenney and Winn, 1986). In comparison, regions over submarine canyons, although thought to be of major importance in the distribution of cetaceans, are significantly less important than the shelf break region (Kenney and Winn, 1987).

The distribution of oceanic cetaceans is thus presumed to be linked to the oceanographic processes by physical-biological interactions and the trophic relationships between phytoplankton, zooplankton, micronekton and cetacean prey species (Baumgartner *et al.*, 2000); unfortunately, it is to date still extremely difficult to measure the distribution of cetacean prey (Reilly *et al.*, 1996) (see Chapter 6).

### 7.1.2.2 Distribution of cetaceans off southern Africa

There is a general lack of data on the distribution of cetaceans off southern Africa. This is mainly due to the fact that dedicated survey trips are lacking and most data are collected opportunistically onboard other vessels. However, the collection and analysis of stranding data from the southern African coastline gives an insight into the distributions of the species found here (Ross, 1979a,b; 1984; Findlay, 1989; Findlay *et al.*, 1992).

Although cetaceans were thought to be associated with the Agulhas Retroflexion and the Agulhas Rings due to the enhancement of primary productivity in this area, this was not supported by any sightings (Cockcroft *et al.*, 1990). However, 13 out of 15 sightings were made on the edges or within Agulhas Rings, although not associated with increased chlorophyll *a* concentrations (Cockcroft *et al.*, 1990). It was concluded that warm/cold water interfaces determined the distribution of cetaceans in the area (Cockcroft *et al.*, 1990).

### 7.1.2.3. Distribution of *Kogia* at sea

Although the distribution of either *Kogia* species has so far only been studied by indirect means of stomach content analysis (see Chapter 6), for reasons already mentioned in Chapter 1, there have been some opportunistic gatherings of distribution data at sea during survey studies (Davis *et al.*, 1995; 1998; Ballance and Pitman, 1998; Baumgartner *et al.*, 2000). However, in most cases the observers were not able to distinguish between the two *Kogia* species to their similar appearance and sightings could only be classified as *Kogia* spp. (Davis *et al.*, 1995). In the Gulf of Mexico stranding records in the area indicate that the two species are not uncommon, but there was an absence of sightings of these animals, which the observers put down to the “cryptic” behaviour of the species and the difficulties of identifying them at sea (Davis *et al.*, 1995). Similarly, the stranding data indicate that *Kogia breviceps* is more common in the study area than *K. sima*, while the sighting data gained from the survey show the opposite (Davis *et al.*, 1995). There are seasonal differences in the amount of sightings, with animals being seen less frequently in autumn than in summer (Davis *et al.*, 1995). Sightings that could be identified to species level show that *K. breviceps* is absent in autumn and *K. sima* is seen almost exclusively in spring and summer (Davis *et al.*, 1995). In general, *Kogia* sightings are associated with higher sea surface temperatures

(SST) and are typically recorded along the mid-to lower slope in waters over 1000m deep (Davis *et al.*, 1995). In contrast, Baumgartner reports that sightings are restricted to the upper continental slope in regions with high epipelagic zooplankton biomass in the same area (Baumgartner *et al.*, 2000). As there has been some niche overlap documented between the two *Kogia* species (Ross, 1979b) (see Chapter 6), this association may be due to the utilization of zooplankton in the diet of one or more of their common prey species (i.e. cephalopods) (Baumgartner *et al.*, 2000). Like other deep diving species *Kogia* are found in waters with the steepest SST gradients (Davis *et al.*, 1995; 1998) and over the deepest bottom depths, but at intermediate bottom-depth gradients (Davis *et al.*, 1998). Since they are cephalopod feeders they may forage along thermal fronts associated with eddy systems and may be associated with upwelling events, which are more productive than warmer surface water (Davis *et al.*, 1995; 1998; Baumgartner *et al.*, 2000).

In the North Atlantic both *K. breviceps* and *K. sima* are found exclusively in waters associated with the Gulf Stream (Griffin, 1999), which is characterised by a higher mean water temperature (26.6°C) and a significantly greater mean water depth (4421m) (Griffin, 1999). In addition, the area also displays one of the highest zooplankton densities (Griffin, 1999).

In the ETP *K. sima* is found in all waters, but was seen most frequently near the coast (Wade and Gerrodette, 1993). In addition, all *K. breviceps* sightings (n=4) are recorded north of 24°N, while all *K. sima* (n=84) sightings are recorded south of 24°N, indicating that *K. breviceps* has a more northerly distribution range (Wade and Gerrodette, 1993). These data support the fact that *K. sima* may have a more tropical distribution than *K. breviceps*.

In the western tropical Indian Ocean Ballance and Pitman (1998) were able to distinguish between *K. breviceps* and *K. sima* sightings and found that *K. sima* associates with warm, deep and clear (i.e. low chlorophyll levels) water characterised by a deep thermocline (Ballance *et al.*, 1996a). Sightings of 20 specimens of *K. sima* were reported, while only two solitary *K. breviceps* were spotted (Ballance *et al.*, 1996b). The latter were observed at sea states of Beaufort zero and one, while *K. sima* were observed at sea states zero to two (Ballance *et al.*, 1996b), which is similar to other studies (Barlow and Sexton, 1996). Comparisons of abundance estimates for *K. breviceps* indicate that estimates are higher in the western tropical Indian Ocean than in the Gulf of

Mexico (Ballance and Pitman, 1998). In contrast, abundance estimates for *K. sima* are the highest in the ETP and lowest in the Gulf of Mexico (Ballance and Pitman, 1998). The mean school size for both *Kogia* species is the highest in the Gulf of Mexico (Ballance and Pitman, 1998). It appears that the higher number of sighting records for *K. sima* in the wild may be due to the fact that they are easier to observe owing to the larger dorsal fin and larger group size (Wade and Gerrodette, 1993; Ballance *et al.*, 1996a; Ballance and Pitman, 1998). However, this point needs further investigation before it can be determined whether this presents a clear bias in sighting data and, as a result, in abundance estimates.

### 7.1.3 Cetacean strandings

Over the last few decades a number of theories about the causes of cetacean strandings have emerged and these are reviewed here.

#### 7.1.3.1 The analysis of stranding data

Although stranding databases are common in most developed countries and are, for the most part, well maintained, few researchers have utilised this resource. Nevertheless, some useful information has emerged from analyses carried out on the British (Sheldrick, 1979; Klinowska, 1985a,b; 1986a,b), French (Hussenot *et al.*, 1996), Portugal (Silva and Sequeira, 2003), South African (Ross, 1984; Findlay, 1989), New Zealand (Brabyn, 1991), and United States (Mead, 1979; Credle, 1988; Polacheck *et al.*, 1995) stranding records.

Stranding data contain useful information on spatial/seasonal distributions and mortality processes as well as on life history parameters. However, a number of biases are inherent in data from stranded animals and should be kept in mind when utilising such data (Mead, 1979). Klinowska (1985a) presents a good summary on the advantages and downfalls of stranding records, as well as their value to research on cetaceans. A stranded animal will have to be noticed, reported and recorded and it appears that the most commonly reported cetaceans are the large ones i.e. the mysticetes, followed by the rare ones, resulting in the common species being underrepresented (Mead, 1979). There may be problems with identifying specimens, in particular when the species are similar in appearance or when the specimens are incomplete or decomposed (Mead, 1979) (see

also Chapter 8). Most strandings are reported in areas of concentrated effort and species that are usually found in the inshore fauna of that given coastline are likely to strand in that area, while animals, which do not have their usual distribution range along a given coastline, are unlikely to wash ashore due to the large distance involved and scavengers or decomposition breaking up the carcass before it reaches the shore (Mead, 1979). The size of a population and its mortality rate will contribute to the abundance of a species in the stranding record and these factors will change with season (Mead, 1979). In addition, the interaction of these factors may be important in some cases, for instance an offshore species which has relatively low population levels, but has regular inshore movements coincident with increased mortality rates may be represented by more records in the stranding database than a more common species with an opposite pattern of movement or mortality (Mead, 1979). Additional problems in maintaining stranding databases with using data from stranding databases often limit the analysis. These include incomplete reporting of information, inconsistency between different observers and a lack of standardised methods. The most important bias in the longitudinal trend of stranding databases is varying effort (Klinowska, 1986b). In particular, follow-up information such as age determination and examination of reproductive status are not carried out consistently and lack of information on datasheets introduces potential for errors. In addition, strandings only represent a sample of the total population and it is therefore important to closer determine the relationship between strandings and the rest of the population in order to gain a complete understanding of the total population (Klinowska, 1985a).

Strandings are for many areas the only source of information on the local species (Klinowska, 1985a). Very little is known about natural mortality in free-ranging cetacean populations. This is due to the difficulties in obtaining basic information on population size, calf production and survival data as well as accurate age estimates (Perrin and Reilly, 1984; Geraci, 1993). Thus this basic information has to be gathered from stranded animals (Ross, 1979a) or animals taken incidentally in fishing gear (Cockcroft and Ross, 1990a; Geraci, 1993). Natural mortality trends in mammals usually show a high rate in very young animals, decreases markedly in mature animals and increases again with older age (Ralls *et al.*, 1980; Geraci, 1993). Mortality seems higher in males than in females and also in species with polygynous mating systems as opposed to alternative mating systems (Geraci, 1993).

Furthermore, stranding records can be maintained over a long period of time as

well as large geographical areas (Klinowska, 1985a). Over the years the accumulation of such data increases the significance of the stranding database and the possible results of such vast amounts of data gathered can be seen in the present study. And as recent studies indicate (Hussenot *et al.*, 1996; Silva and Sequeira, 2003) the analysis of stranding patterns does still yield important data about the cetacean fauna in a certain area and thus is a valid research tool.

### 7.1.3.2 Stranding patterns

Most stranding events are probably the result of numerous contributing and interacting factors rather than having a simple cause-and-effect relationship (Cordes, 1982). Factors which may contribute to a stranding include the physical environment represented by tides, currents, coastal configuration, weather and man- induced features; low water temperatures; changes in water chemistry; the seasons; feeding conditions; possible feelings of alarm in the affected whales; interference with their echolocation mechanism; presence of disease and behavioural characteristics (Cordes, 1982).

In general, the majority of strandings in a particular geographical region are comprised of single animals (Sheldrick, 1979; Brabyn, 1991; Polacheck *et al.*, 1995), which in some areas are comprised of mainly dead animals (Mead, 1979; Klinowska, 1985a), while in others live strandings are more common (Brabyn, 1991). Stranding implies the beaching of a live animal in contrast to the casting ashore of a dead one, although this distinction can not always be made as a stranded animal often dies on shore before being discovered (Cordes, 1982). In addition, many animals that strand probably die at sea and then drift ashore (McManus *et al.*, 1984; Evans, 1987), although it is assumed that dead animals will rarely be carried for longer distances than 100km (Brabyn, 1991).

Single strandings usually result from accidents or are sick, old, weak, or pregnant individuals (Klinowska, 1985a; Evans, 1987). Other frequent causes for strandings are young animals, which have not been weaned successfully or lost their mothers (Evans, 1987). Cow/calf pair strandings may often occur as a result of difficulties with parturition; however, if both individuals come ashore it may be impossible to determine which animal leads the way to the stranding (Geraci, 1993).

Stranding rates may vary seasonally according to the prevailing weather conditions as sick or struggling animals are more prone to strand during rough weather.

Strandings along the New Zealand coastline are high in summer and lower in winter, with the extent of the seasonality varying between species and between groups (Brabyn, 1991). An in-depth study of harbour porpoise *Phocoena phocoena* strandings along the Atlantic coast of the U.S. shows that some animals are resident year round, while a large part of the population migrates along the shore, or moves inshore/offshore in certain areas (Polacheck *et al.*, 1995). Higher mortality rates are observed seasonally, perhaps reflecting prey shortages (Polacheck *et al.*, 1995). Natural mortality rates vary from year to year, possibly due to environmental factors, and is highest for juveniles between two and three years old (Polacheck *et al.*, 1995).

Inshore species often may have consistent and more or less predictable stranding patterns due to their residency or seasonal migration through the area concerned (Geraci, 1993). However, these more traditional patterns have become less clear and predictable due to human activities (Geraci, 1993). For pelagic species stranding patterns are more confused, but correlations with locations, tides, storms, geomagnetic disturbances and other factors have been suggested (Klinowska, 1985b; Brabyn, 1991; Brabyn and McLean, 1992; Geraci, 1993).

There is evidence that the frequency with which a species strands is related to the local abundance of the food supply and that there is some direct relationship between the incidence of stranding and the abundance of whales in neighbouring waters (Cordes, 1982). Coastal species are more commonly found in single stranding events, perhaps at a frequency related to their population density in neighbouring seas (Cordes, 1982).

One phenomenon, which may play an important role in the occurrence of strandings, but which has been little researched, are El Niño events (G. Ross, pers. com.), which may result in changes of prey quality and quantity, and in turn in increased numbers of stranding events. However, there has been no publication to date that examines the connection between the two.

Parasite infections are very common in cetaceans and some may even be contracted *in utero* (Geraci and St. Aubin, 1987; Geraci, 1993). Some parasites may play an important role in disease and mortality, and some infestations, in particular those affecting the brain, have been linked to stranding events (Geraci, 1979; Hall and Schimpff, 1979; Geraci, 1993).

Human related mortality events include entanglement in both coastal fishing gear (Hohn *et al.*, 1996; Kraus *et al.*, 1997) and pelagic fisheries (Perrin and Henderson, 1984) as well as habitat degradation, oil spills and other forms of pollution, including

noise pollution (Calzada *et al.*, 1994). In recent years evidence has emerged which indicates that noise pollution, resulting from commercial shipping traffic, seismic explorations and oil drilling rigs may be a more important factor in the cause of whale strandings than previously thought (Holmes, 1997). In particular, low-frequency sound emissions used in military tests appear to be linked to an increased frequency of beaked whale strandings both in the Mediterranean (Holmes, 1997; Frantzis, 1998) and the Bahamas. However, the adverse effects of low-frequency sound on whales are poorly understood and the definite results are still pending.

Other forms of pollution, oil spills in particular, contribute to overall habitat degradation, which may have an adverse effect on prey abundance and diversity and may increase stress and susceptibility to infection (Geraci, 1993). Some populations have accumulated high levels of contaminants that possibly result in disease, including tumors and reproductive disorders (Geraci, 1993). Furthermore, unusually high amount of naturally occurring toxins caused by red tides have also been linked to a number of cetacean strandings (Geraci *et al.*, 1989; Aguilar, 1991).

While solitary strandings are strongly influenced by disease, mass-strandings appear largely related to the behaviour of the herd (Cordes, 1982) and occur less commonly (Sheldrick, 1979; Brabyn, 1991). Usually mass strandings are defined as stranding events, which involve two or more animals, excluding cow/calf pairs (Geraci and Lounsbury, 1993). Numerous theories about the reasons for mass strandings of cetaceans have emerged in the past. These include possible escape behaviour, suicide attempts and a means of regulating populations (Sergeant, 1982; Odell *et al.*, 1984). Mass-stranding cetaceans are usually pelagic forms with a strong social cohesion (Sergeant, 1982; Evans, 1987), which causes some animals of the herd to follow stranded animals ashore (Geraci and Lounsbury, 1993). Most of the species involved in such stranding events are pelagic and are thought to follow their prey inshore (Cordes, 1982; Geraci and Lounsbury, 1993). However, it is doubtful that inshore foraging behaviour alone could lead to strandings (Geraci and Lounsbury, 1993). There are too few data available to indicate any cyclic activity in stranding patterns and although some theories appear very plausible the fact remains that stranding events are difficult to link with variations in environmental parameters (Odell, pers. com.). As a result most of these theories have been dismissed by most researchers due to a lack of convincing evidence.

However, a few studies have presented some supporting evidence and are still

thought to explain some of the reasons behind mass strandings. Klinowska (1985b; 1986a) proposes that cetaceans use the earth's magnetic field both as a compass and a map. Magnetite in the form of iron oxide crystals is found in the brains of a number of cetaceans (Klinowska, 1986a) and is thought to aid in navigation, similarly to homing pigeons. Furthermore, it is known that migration routes of cetaceans do follow geomagnetic contours (Klinowska, 1986a). Offshore species strand more frequently and strandings occur where geomagnetic contours run perpendicular to the coastline (Klinowska, 1985b; 1986a). As a result Klinowska (1986b) proposes that cetaceans have an integrated travel system based on features of the geomagnetic field, using the geomagnetic topography as a basic map and monitoring their progress using geomagnetic time cues. Magnetite crystals are reported from the brain of common dolphins (Zoeger *et al.*, 1981) as well as *K. breviceps* (Credle, 1988). However, there are little data indicating just what role these crystals play in cetaceans and whether they actually aid in navigation and magnetic map sense has not been proven for any species of animal (Geraci and Lounsbury, 1993). Subsequently, Brabyn and McLean (1992) fail to provide supporting evidence for Klinowska's hypothesis. Their analysis of herd strandings in New Zealand shows that whales do not strand at random locations, but rather strandings are concentrated in five locations (namely Whangerei, Kaipara, Hawkes Bay, Golden Bay and the Chatham Islands) (Brabyn and McLean, 1992). The topography of the beach is thought to be the determining factor as all these beaches are long, gently sloping beaches, most having some protrusion from the coastline (Brabyn and McLean, 1992). A comparison with other multiple herd-stranding sites around the world shows a similar beach topology (Brabyn and McLean, 1992). This would be in agreement with another hypothesis on the cause of mass-strandings, which is that shallow water or gently sloping beaches distort the animals' sonar, providing it with false information and causing it to strand (Geraci and Lounsbury, 1993). However, cetacean sonar has largely been studied in bottlenose dolphins *Tursiops truncatus*, a predominantly inshore species, and little is known about the ability of pelagic forms to alter signals and compensate for background noise (Geraci and Lounsbury, 1993).

Sometimes animals accidentally get trapped and subsequently grounded by the outgoing tide. Such incidents occur frequently in areas with long meandering channels, broad tidal flats, strong or unusual currents, or extreme tidal flow or volume (Geraci and Lounsbury, 1993). Areas, which are famous for being such "whale traps", include Cape Cod, Massachusetts, and Sable Island, Nova Scotia (Geraci and Lounsbury, 1993).

Many individuals in a group of mass-stranded cetaceans often show signs of illness infestations (Hall and Schimpff, 1979) and it appears that viruses may have been overlooked for some time as possible causes of mass mortality events in cetaceans as recent outbreaks of morbillivirus suggest (Geraci, 1993; Calzada *et al.*, 1994).

Brabyn (1991) suggests that stranding patterns for any given species may be explained by differences in the distribution of prey species, feeding patterns, migration and social organisation. Unfortunately for most species much of these data are either poorly documented or still unknown. However, the increase in the frequency of stranding reports which has been observed in the last two decades is most likely due to easier access to remote stretches of coastline as well as enhanced public and government awareness of cetaceans (McManus *et al.*, 1984). In this way, chances of the discovery of rare species have improved over the years (McManus *et al.*, 1984).

Although strandings are an important source of material for scientific studies, especially those concerned with pathology, anatomy, toxicology and ecology, they do not simply reflect population abundance and distribution and thus great care should be taken when using them to infer such information (Gonçalves *et al.*, 1996).

### 7.1.3.3 Cetacean strandings off southern Africa

Ross (1984) describes the small cetacean fauna of the south-east coast of Southern Africa, using data from 350 specimens originating from strandings since 1968. To this day his analysis serves as a guideline for anyone carrying out research on any species of small odontocete in South Africa as his work was valuable for the re-evaluation of the taxonomic status of a number of species and in a comparatively short period of time provided nearly one third of the world's recorded material for three species of *Mesoplodon*, both species of *Kogia*, as well as *Lagenodelphis hosei* (Ross, 1984). It indicates that Southern Africa is a major source of samples for the cetacean fauna of much of the South Atlantic and Southern Indian Ocean (Ross, 1984).

The number of species of the small cetacean fauna (24) off South Africa is high compared to the number of species recorded for other regions and suggests that this diversity results from the variable oceanographic conditions found off the subcontinent (Ross, 1984). Four components that structure this diversity can be described:

-a tropical/subtropical component, containing species associated with the Agulhas Current;

-a temperate/subantarctic component containing species associated with cool water, which intrudes eastwards inshore of the Agulhas Current;

-a cosmopolitan component, which is represented by species which occur in both warm and cool water off Southern Africa, such as *K. breviceps*; and

-a mixed water component, which includes species like *K. sima*, which have apparently restricted distributions in the region of mixing cool and warm waters over the Agulhas Bank (Ross, 1984). Based on this distribution a probably isolated population contained wholly within the southern African region was suggested for *K. sima* (Ross, 1984).

However, there is still lack of data on the detailed distribution of cetaceans off Southern Africa, in particular on the some of the larger cetaceans, like the mysticetes, for which there is only data originating from the whaling industry. Findlay (1989), in reviewing published and unpublished records, altogether comprising about 60000 animals, of sightings, strandings and specimens from the study area up to the end of June 1986, reports nine species of large cetaceans and 28 species of small ones present in the study area (Findlay, 1989). His analysis of stranding data (1477 specimens) reveals that the majority were live strandings (n=625), compared to 609 animals found dead on shore, 44 dead strandings and 23 dead at sea (Findlay, 1989). Skeletal remains, which were found on beaches made up 79 specimens and nine were either dredged or trawled up at sea (Findlay, 1989). Two animals were found in the gut of a predator (Findlay, 1989). Furthermore, 506 animals were recorded as caught incidentally and 138 as caught directly (Findlay, 1989).

Ekman (1967; in: Findlay, 1989) noted the wide spectrum of zoogeographic components in southern African oceans and stated that faunistic boundaries are complex due to the oceanographic conditions. This zoogeographic pattern can only be understood if the faunistic regions are defined by water characteristics and not by geographical boundaries (Ekman, 1967; in: Findlay, 1989). Findlay (1989) suggests that the high species diversity of cetaceans in southern African waters arises largely from these complex oceanographic conditions. The mixing of the tropical/subtropical waters brought in from the east by the Agulhas current with the cold temperate waters of the west coast results in the formation of a descending cline of surface water temperature from east to west. Certain species appear to be strongly confined to particular temperature ranges and faunistic boundaries seem to coincide with temperature fronts (Findlay, 1989). Within this temperature cline the distribution patterns of certain species are strongly associated with water depth. Therefore the non-migratory cetacean fauna of

the region can be ascribed to 10 different habitats, which are largely characterised by water temperature and depth (Findlay, 1989). According to this system, Findlay (Findlay, 1989) describes the habitat of *K. breviceps* as pelagic cosmopolitan. Strandings of cetacean species on both the west and east coast may suggest that they move around the Cape Peninsula in cells of Agulhas current water into the Benguela system (Findlay, 1989). Similar events during interglacial temperature maxima may have facilitated the east to west dispersal of present pan-tropical species through the Cape cold-water barrier (Findlay, 1989). Findlay considers both species of *Kogia* as sympatric off Southern Africa since the longshore distributions of strandings overlap, but that that may not be the case if the two species were confined to different depths (1989).

#### 7.1.3.4 *Kogia* strandings

As already mentioned in Chapter 1 *Kogia* are primarily known from stranding events (Credle, 1988). The majority of records of the two species of *Kogia* deal with stranded animals, usually single strandings (see Chapter 1). However, few studies have pooled these events together and analysed them.

Early in the last century Allen (1941) reports about 20 or so *Kogia* stranded along the east coast of North America, including Canada. At that stage many *Kogia* records exist from the western Pacific, but only two (namely from Peru and Mexico) in the eastern Pacific (Allen, 1941). This lack of records can partly be put down to a lack of observers in that area, but it may possibly reflect preferences of *Kogia* for certain areas where food and water temperatures are optimal, especially as the regions of strandings are influenced by major ocean currents like the Agulhas, the Gulf Stream and the Japanese (Kuroshio) Current (Allen, 1941).

Almost four decades later Mead (1979) in his 1979 study of the stranding records from the Atlantic and Gulf coast of the U.S. remarks that *K. breviceps* is the third most abundant species to strand in the study area (108 records), making up 33% of all live strandings, which is surprising as it was usually considered a rare as well as an offshore species (Mead, 1979). He speculates that these records may be the result of an inshore movement of part of the population during a period of increased natural mortality, resulting in a disproportionate number of strandings (Mead, 1979). However, studies in the south-eastern United States support a high stranding rate of both *Kogia* species along that coastline (Odell *et al.*, 1984), with *K. breviceps* being the second most commonly

stranding species after *T. truncatus*, with most of the strandings occurring in Florida (Odell, 1991). The majority are live strandings (Bossart *et al.*, 1985). Out of 2381 cetaceans reported to have stranded *K. breviceps* makes up 224 stranded animals, while only 50 specimens of *K. sima* are reported (Odell, 1991). Odell *et al.* (1984), examining over 100 stranding records of *K. breviceps* in Florida, suggest a seasonal pattern with stranding peaks in autumn and winter. While adult males and females strand in approximately equal numbers, the males seem to conform to the bimodal seasonal pattern better than the females do (Odell *et al.*, 1984). Adult, non-pregnant females, pregnant females, and females with calves strand at similar frequencies and most pregnant females are found in January and February (Odell *et al.*, 1984). Juveniles strand in a conspicuously low frequency, which may indicate different distribution patterns for different age classes (Odell *et al.*, 1984). Credle (1988) examines strandings of both species of *Kogia* in the south-eastern United States from Florida and surrounding states, looking for correlations with the earth magnetic field. A total of 384 *Kogia* strandings from 1883 until 1988 are analysed and of these 317 (83%) are *K. breviceps* and 67 (17%) are *K. sima* (Credle, 1988). She confirms the presence of magnetite, a strong magnetic iron oxide ( $\text{Fe}_3\text{O}_4$ ) required for magnetoreceptive ability, in the brain of both *Kogia* species. Contrary to previous findings a correlation exists between live strandings and days of low atmospheric magnetic activity (Credle, 1988). Field strengths are higher and the magnetic field gradient is steeper in areas of live stranding events than in areas with no strandings (Credle, 1988), which is somewhat contradictory to the findings by Klinowska (1985b; 1986a; 1986b) (see above), but overall correlations between stranding events and geomagnetic characteristics are not as strong as those reported for other cetacean species (Credle, 1988). However, since *Kogia* are oceanic and deep diving species the coastal magnetic field may not have any impact on them and these species would be expected to strand in random locations with respect to local magnetic field intensity (Credle, 1988). Furthermore, all stranded adult *Kogia* have cardiomyopathy, a condition that may be linked to a dietary thiamine deficiency (Credle, 1988).

The combined works of Hale (Hale, 1947; 1959; 1962; 1963) give an overview of the *Kogia* strandings along the South Australian coastline. Strandings appear to mainly occur in the austral autumn and winter, namely from late April to late September (Hale, 1962). During this period both calves and adults strand and most strandings happen during calm weather (Hale, 1962). Strandings in New South Wales are restricted

to August and September, whereas strandings in New Zealand are reported to occur from August to July, thus extending into the summer months, which Hale believed suggests some migratory pattern, similarly to that observed for baleen whales (Hale, 1962). Similarly, Sylvestre (1988) suggests a seasonal movement of *Kogia* off the west coast of New Caledonia based on the fact that strandings only occur between June and December.

In New Zealand *K. breviceps* has the highest incidence of stranding (364 individuals represented by 297 stranding events) of any cetacean species, based on records from 1873 to 2001 (Brabyn, 1991; Tuohy *et al.*, 2001). The majority of strandings are single, live events and only few group strandings, the largest group comprising four animals, are reported (Brabyn, 1991). Most strandings occur in May and only few animals strand in October and November/December (Brabyn, 1991). Twice as many females appear to strand as males, approximately half of which are accompanied by a calf (Brabyn, 1991). The majority of the stranding events occur in Hawke's Bay (74%) on the east coast of the North Island, concentrating mainly in two hotspots in the area: Mahia and Opoutama Beach (Tuohy *et al.*, 2001). These two regions alone account for 47% (n=141) of all stranding events (Tuohy *et al.*, 2001). The area is close to the Hikurangi Trough and Poverty Bay Canyon and the East Cape Current, which flows past the east coast of the North Island of New Zealand, passes over the Poverty Canyon and probably causes nutrient-rich upwelling in the Hawke's Bay area (Tuohy *et al.*, 2001). An abundance of methane-rich seeps associated with the subduction zone in the area further enriches the waters and results in great faunal assemblages (Tuohy *et al.*, 2001), which in turn would result in nutrient rich waters with high prey densities. Hawke's Bay appears to have the greatest number of stranded cow-calf pairs as well as pregnant females in New Zealand, leading a number of researchers to conclude that it may present a calving and/or nursery area (Brabyn, 1991; Tuohy *et al.*, 2001). Although the majority of strandings occur between 38°S and 42°S on the east coast of the North Island, suggesting a sizeable population of this species off the coast, the absence of sightings in coastal waters indicates that the species may live beyond the continental shelf, perhaps over the region of deep (3250m) trenches and canyons between Cook Strait and East Cape (Baker and van Helden, 1990).

Amongst the records analysed by Findlay (94 *K. breviceps*, 71 *K. sima*, 17 *Kogia* spp.) (Findlay, 1989) for South Africa only one sighting of a *Kogia* was recorded, which was observed in August 1971 off the south-east coast near East London (30°36'S,

31°08'E) over a water depth of 2000 to 3000 metres and a salinity and temperature of 35.2-35.4‰ and 20°-22° C, respectively (Findlay, 1989). The paucity of sighting records for the two species is thought to reflect small school size, small body size, a deep-water habitat and possibly diving behaviour (Findlay, 1989).

Of the 94 *K. breviceps* strandings the majority (n=47) were dead strandings, while 21 animals stranded alive (Findlay, 1989). Four animals were found dead on the shore, for seven animals only the skeletal remains were recovered and for 15 specimens there was no indication in the records (Findlay, 1989). In *K. sima* the trend was similar with the majority of the 71 specimens being dead strandings (n=42), while only 16 animals stranded alive (Findlay, 1989). One specimen was found dead on the beach and for two others only the skeletal remains were discovered (Findlay, 1989). Two specimens were either dredged up or found in the gut of a predator and eight records showed no details (Findlay, 1989). After examining the abundance pattern for both species by season, Findlay concluded that both species are “resident” in South African waters (1989).

So-called “mass stranding” events are rare in *Kogia* and only two have been found in the literature. One was reported by Ross (1979a) and involved a juvenile male and three juvenile female *K. sima*. These data were included in the present study. The other was described by Caldwell and Caldwell (1989), who report the stranding of three adult-sized *K. breviceps* (one 320cm long male, two females of 300 and 310cm length, respectively) on a Florida beach in 1968.

#### **7.1.4 Aim of the present chapter**

Since the original sample analysed by Ross' (1979a) was relatively small and additional data have emerged since, the aim of this part of the present study was to determine basic stranding patterns, stranding range, and distribution for both species of *Kogia* from southern Africa and to establish whether there are differences between the two species. No attempt was made to explain causes of stranding events. As the misidentification of the two *Kogia* species is often encountered when working with a stranding record (Credle, 1988), this problem has been addressed in Chapter 8.

## **7.2 Materials and methods**

### **7.2.1 Sample**

Appendix A lists all the strandings of *Kogia* from southern Africa used in the present analysis by species in reverse chronological order. Information on the collection number, date, sex, total length, latitude, longitude, locality and type of event is listed for each stranding event. Species identification after 1979 was based on Ross' (1979a) findings on the morphological and external distinguishing characteristics of the two species (see Chapter 1). Since the genus was only recognised to have two distinct species as late as 1966, species identification prior to that date may not always be correct.

### **7.2.2 Analysis of strandings**

Stranding events were either defined as dead or live strandings. It is presumed that live strandings involved animals which were alive when first discovered or at the time of the arrival of a stranding coordinator. The vast majority of the records is based on the stranding records held at the Port Elizabeth Museum (PEM, now Bayworld) or the South African Museum (SAM) and it could not be discerned from the records what criteria were used to assess that. Furthermore, strandings were considered to be either single or, when two or more animals stranded together, multiple. Cow/calf pair strandings were defined as a mature female stranding with an immature, younger animal at the same time and the same beach.

The general distribution of *Kogia* strandings along the South African coastline was plotted by means of a geographical information system (GIS). In order to calculate the mean sea-surface temperature (SST) at the time of a live stranding, SST charts for 10-day periods issued by the Department of Environment Affairs were consulted. These charts are held by the J.L.B. Smith Institute of Ichthyology (now South African Institute for Aquatic Biodiversity (SAIAB)) in Grahamstown and are available for both the east and west coast dating back to 1968.

## **7.3 Results**

### **7.3.1 Composition of stranded animals**

106 strandings of *K. breviceps* and 85 strandings of *K. sima* along the South African coastline between 1880 and 1995 were analysed. Data on the size-frequency distributions of the stranded animals of both species have already been presented in Chapter 2 and will not be discussed any further here.

In both *Kogia* species females were found to strand slightly more frequently than males, with 37.7% (Figure 7.3a) and 44.7% (Figure 7.3b) of strandings being made up by females of *K. breviceps* and *K. sima*, respectively. In comparison, 34% of *K. breviceps* strandings were males (Figure 7.3a), while 38.8% of *K. sima* strandings were males (Figure 7.3b). 28.3% and 16.5% of *K. breviceps* and *K. sima* strandings, respectively, were not determined to sex (Figure 7.3 a,b).

Furthermore, about one third of all strandings comprised immature animals (35.1% in *K. breviceps* and 31.9% in *K. sima*) (Figure 7.4 a,b). Based on the data for length at sexual maturity, which were established for males in Chapter 4 and females in Chapter 5, respectively, roughly two thirds of the stranded animals were mature in both species (64.9% in *K. breviceps* and 68.1% in *K. sima*, respectively) (Figure 7.4 a,b).

Live animals were found to strand considerably less often in both species: in *K. breviceps* 32.6% of all strandings comprised live animals, whereas in *K. sima* only 26.2% stranded alive; the rest were dead strandings (Figure 7.5 a,b).

In addition, the majority of strandings in both species was found to be single, namely 58% in *K. breviceps* and 59.5% in *K. sima* (Figure 7.6 a,b). Multiple strandings, defined as more than one animal stranding at a time and including cow/calf pairs, were found to occur less often, comprising 42% of the *K. breviceps* strandings and 40.5% of the *K. sima* strandings (Figure 7.6 a,b). The majority of these were made up of cow/calf pairs. The highest number of animals stranding at one time was three for *K. breviceps* and four for *K. sima*.

For the following analyses only strandings from 1965 onwards were included as observer effort has been more reliable. Furthermore, additional environmental variables such as sea surface temperatures were historically only available from that date onwards.

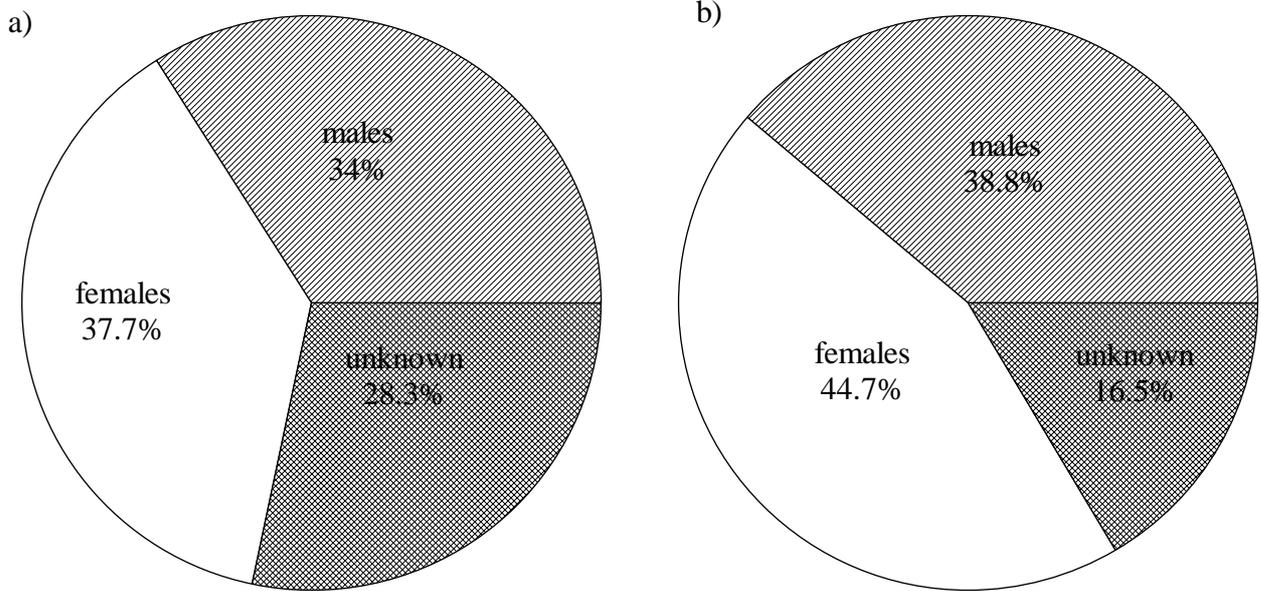


Figure 7.3: Total number of *Kogia breviceps* (a) and *Kogia sima* (b) strandings (in %) between 1880 and 1995 analysed by sex.

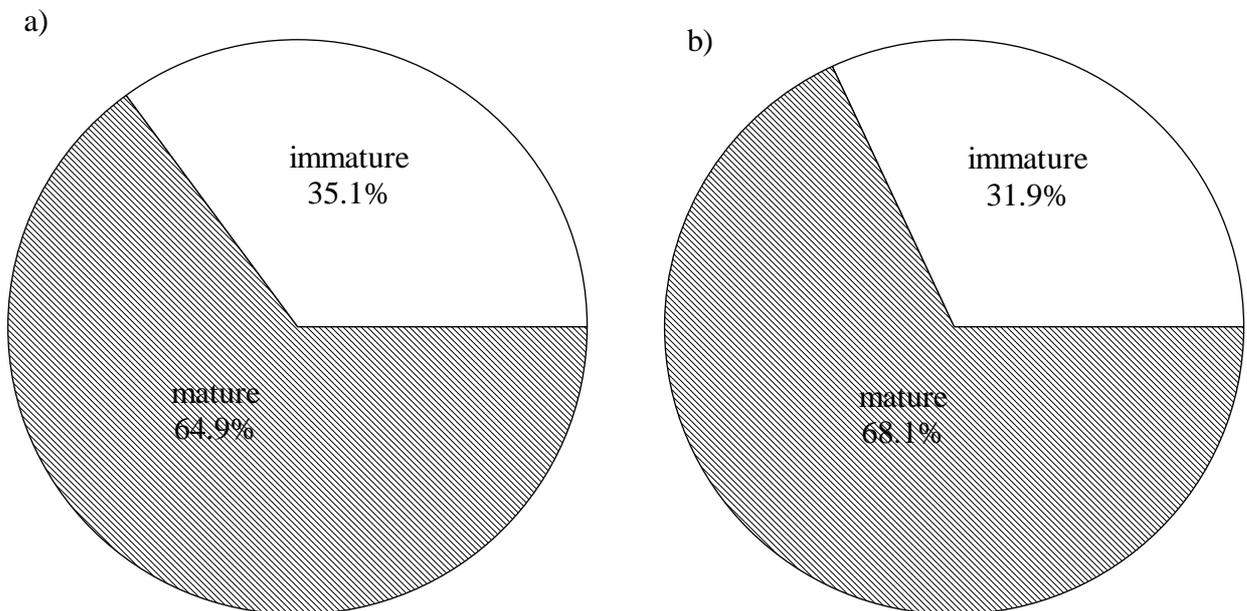


Figure 7.4: Total number of *Kogia breviceps* (a) and *Kogia sima* (b) strandings (in %) between 1880 and 1995 analysed by reproductive status.

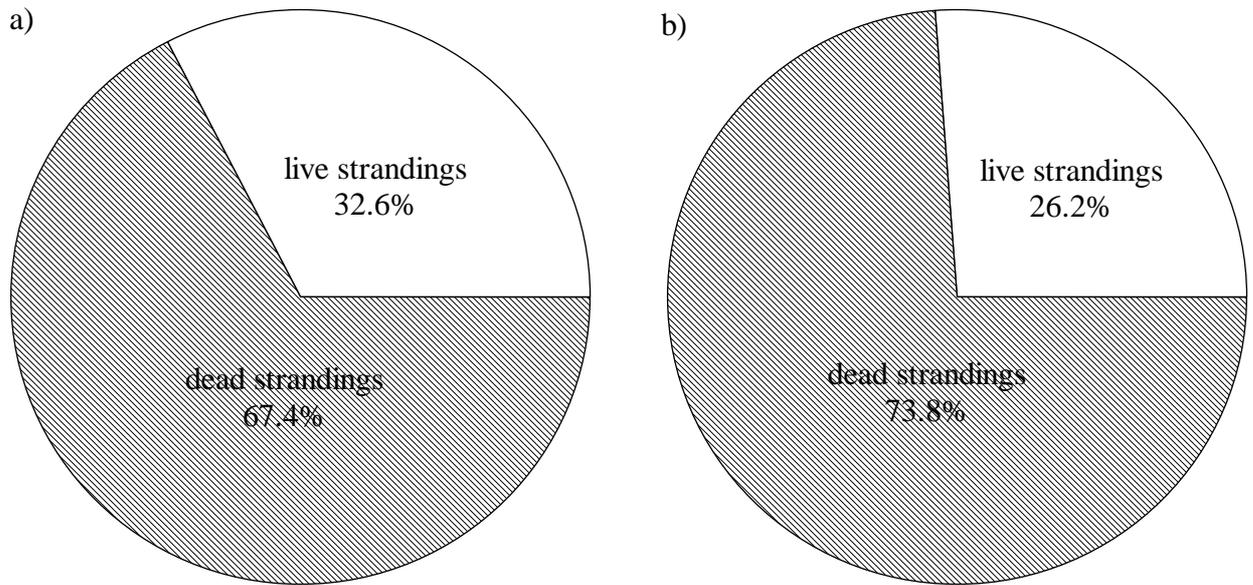


Figure 7.5: Total number of *Kogia breviceps* (a) and *Kogia sima* (b) strandings (in %) between 1880 and 1995 analysed by the condition of the animal.

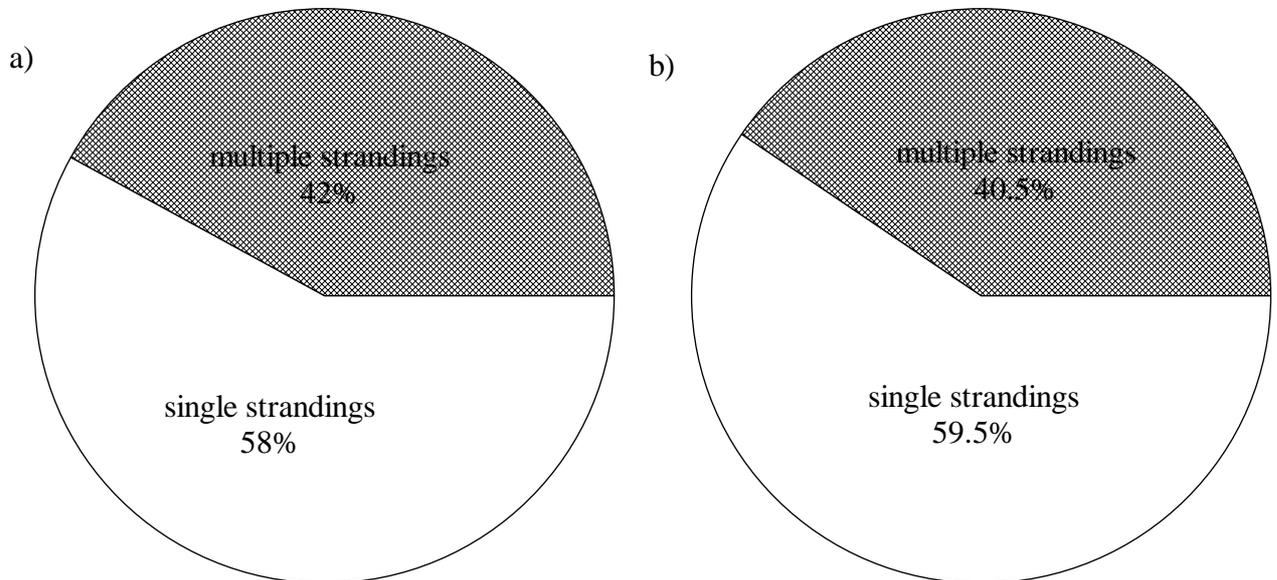


Figure 7.6: Total number of *Kogia breviceps* (a) and *Kogia sima* (b) strandings (in %) between 1880 and 1995 analysed by the type of stranding event. Stranding events in which more than two animals stranded together at the same time were classified as multiple strandings.

### 7.3.2 Stranding trends over time

The occurrence of *Kogia* strandings over the years showed some fluctuation and while in some years no strandings were recorded for either species, in other years there appeared to be unusually high records of stranded animals (Figure 7.7). However, while no strandings of *K. breviceps* occurred in 1974, 1978, 1989 and 1990, these years do not coincide with those in which there were no strandings for *K. sima* (namely 1974, 1984, 1988, 1992 and 1993), except for 1974 (Figure 7.7). It also appears that the record for *K. breviceps* is slightly more consistent, with between one to three strandings occurring in most years (Figure 7.7a), while *K. sima* strandings seem to have more definite peaks (Figure 7.7b).

### 7.3.3 Seasonality of strandings

An analysis of the number of stranded animals in relation to month showed that *K. breviceps* stranded more frequently in the austral winter and spring (July to October) (Figure 7.8a), whereas *K. sima* show a peak in April and July (late summer and winter), although it is not as pronounced as in *K. breviceps* (Figure 7.8b). It is noteworthy that no strandings of *K. sima* occurred during June over a 30-year period (Figure 7.8b).

The analysis of live strandings by month show a definite peak of strandings of *K. breviceps* in September, while they stranded in more or less equal numbers throughout the rest of the year (Figure 7.9a). In contrast, *K. sima* showed a peak in live strandings in March and April, and remarkably no live stranding events at all during June and October (Figure 7.9b).

### 7.3.4 Stranding distribution

In order to analyse the geographical location of both *K. breviceps* and *K. sima* strandings the peak stranding location along the southern Cape coast was determined for each month by determining the location where the greatest number of animals stranded averaged over the years. The peak stranding location (in degrees longitude) was plotted versus the month of the stranding and indicated that *K. breviceps* seems to strand in the Western Cape throughout the whole year, with the exception of July (Figure 7.10 a). Strandings do, however, also occur in the Eastern Cape more or less regularly

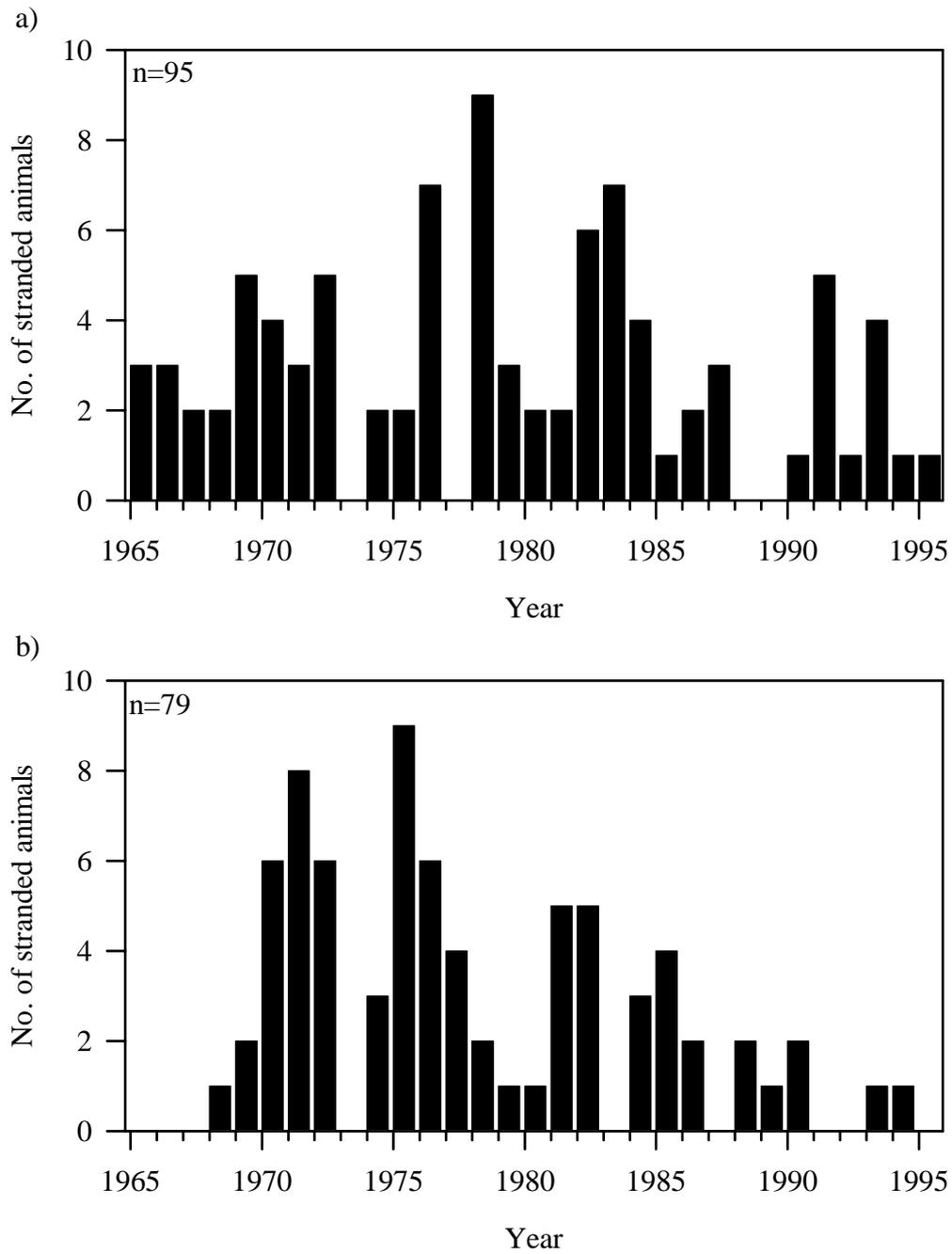


Figure 7.7: Total number of stranded *Kogia breviceps* (a) and *Kogia sima* (b) along the Southern African coastline between 1965 and 1995.

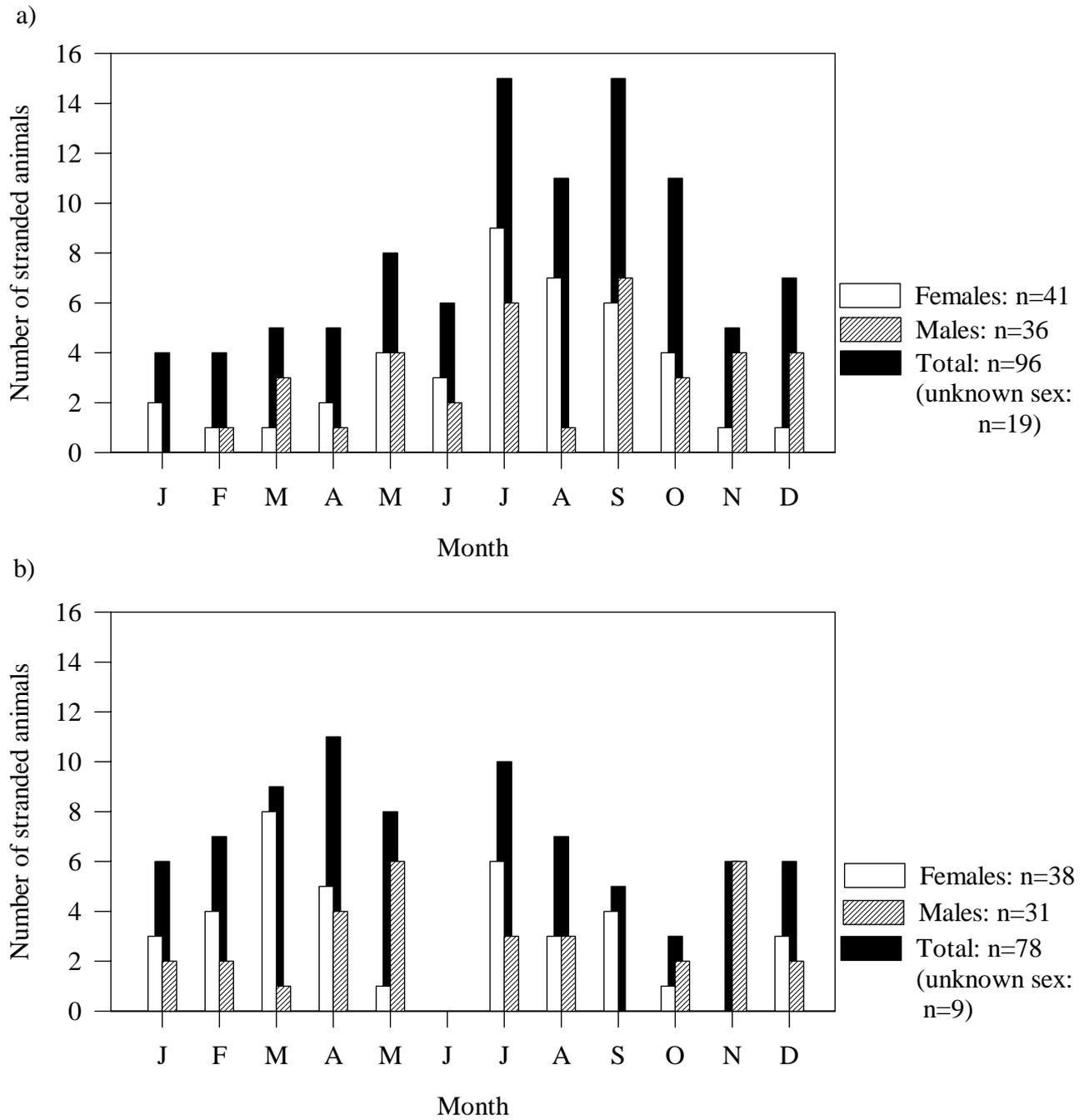


Figure 7.8: Total numbers of stranded *Kogia breviceps* (a) and *Kogia sima* (b) per month.

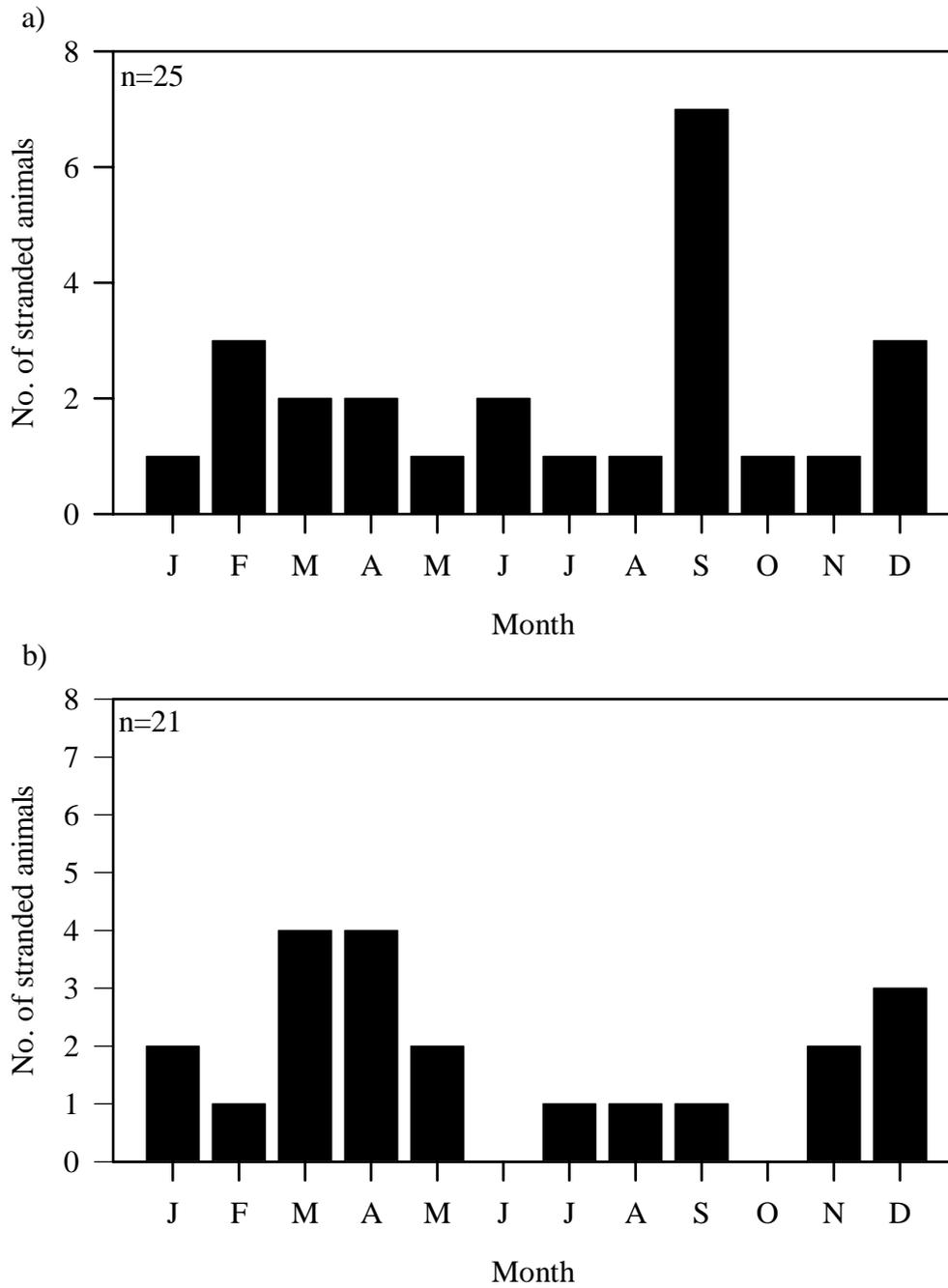


Figure 7.9: Seasonal occurrence of live strandings of *Kogia breviceps* (a) and *Kogia sima* (b) between 1965 and 1995.

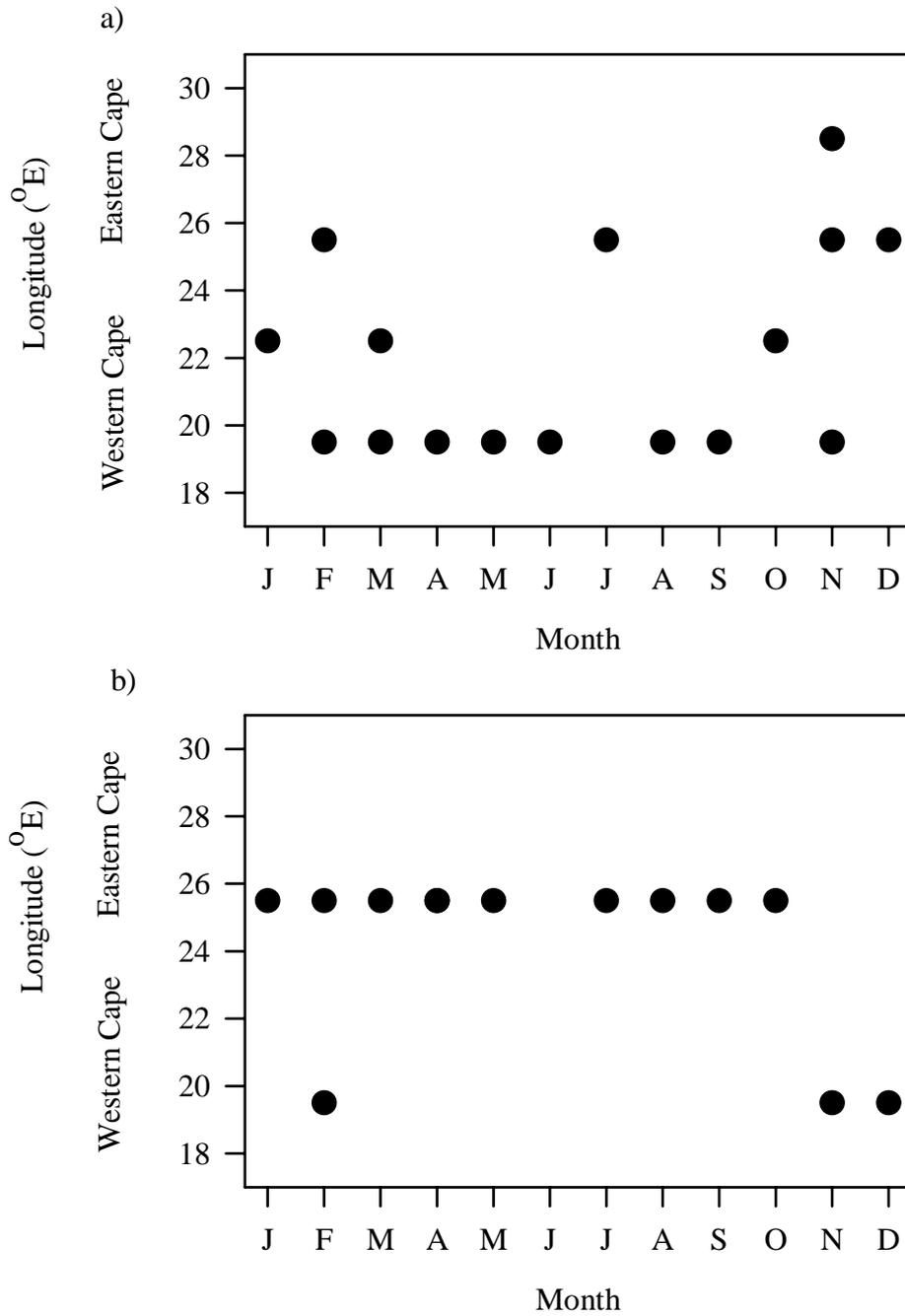


Figure 7.10: Seasonal geographic distribution of *Kogia breviceps* (a) and *Kogia sima* (b) strandings along the Southern Cape coastline between 1965 and 1995.

throughout the year (Figure 7.10a). In contrast, *K. sima* strandings occur predominantly in the Eastern Cape, except in late spring and summer (November, December and February) when peak strandings happened in the Western Cape as well (Figure 7.10b).

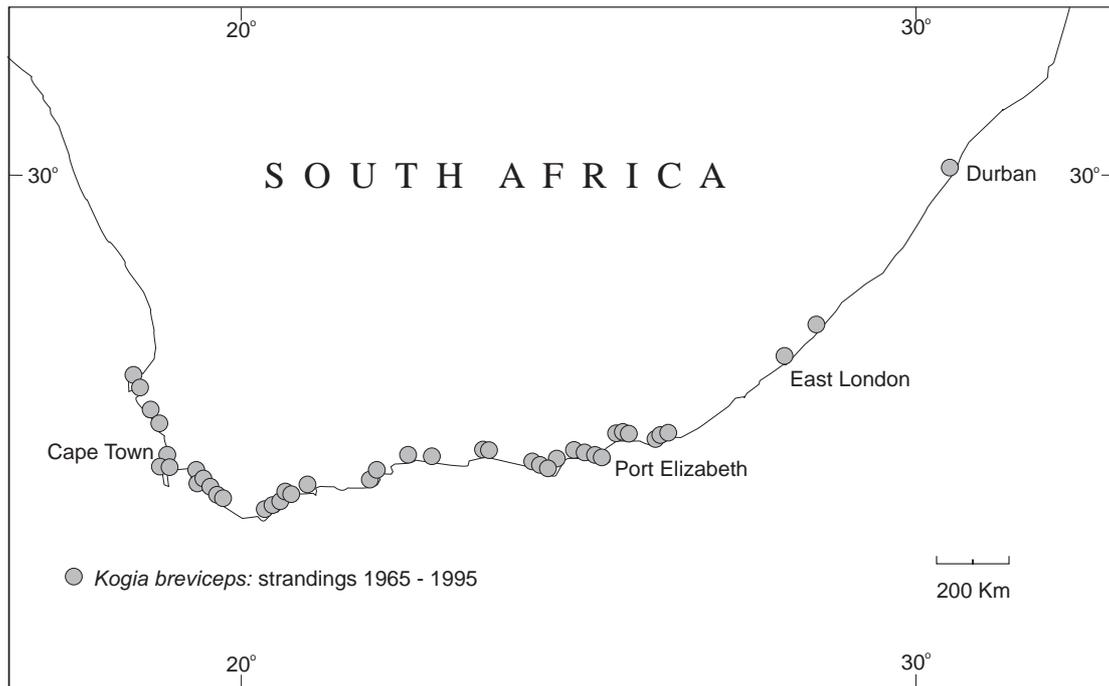
The general distribution of the *Kogia* strandings along the South African coastline showed that *K. breviceps* has a wide range of stranding events, ranging between Saldanha Bay on the West coast (33°03'S, 18°02'E) and St. Lucia in Natal (28°24'S, 32°22'E) on the east coast (Figure 7.11). Strandings of this species have in fact also been reported as far North as Swakopmund in Namibia (22°40'S, 14°34'E), but those were not included in this study.

In contrast *K. sima* strandings occurred only from Rocher Pan (32°36'S, 18°18'E) to Sodwana Bay (27°31'S, 32°42'E) and thus occupied a much shorter stretch of the coastline than those of *K. breviceps* (Figure 7.12).

The distribution of cow/calf pairs of *K. breviceps* along the South African coastline showed that there may be a slight eastward movement throughout the year (Figure 7.12a) as the first stranding events occurred in February on the Atlantic coast of the Western Cape, strandings in April and May happened along the southern coast of the Western Cape, and strandings occurred in the Eastern Cape between July and October (Figure 7.12a). This was supported by a continuous increase in the length of the calves as the strandings occurred further eastward. In contrast, the distribution of *K. sima* cow/calf pair strandings along the coastline was confined to a much narrower stretch of coastline and strandings occurred exclusively to two bays in the Eastern Cape, Jeffrey's Bay and Algoa Bay (Figure 7.12b).

The distribution patterns of stranding events of immature *K. breviceps* and *K. sima* versus mature animals showed a similar trend in both species (Figure 7.13 and 7.14). While the stranding locations of mature animals were spread out along the entire coastline (Figure 7.13b and 7.14b), immature animals had a more localised distribution in stranding events (Figure 7.13a and 7.14a). This phenomenon was particularly pronounced in *K. sima*, where mature animals stranded along the southern Cape coast between Cape Town and Port Elizabeth (Figure 7.14b), while immature animals stranded only in the vicinity of these two locations (Figure 7.14a). However, this may reflect a bias in the stranding records since the majority of the stranding events were comprised of mature animals.

a)



b)

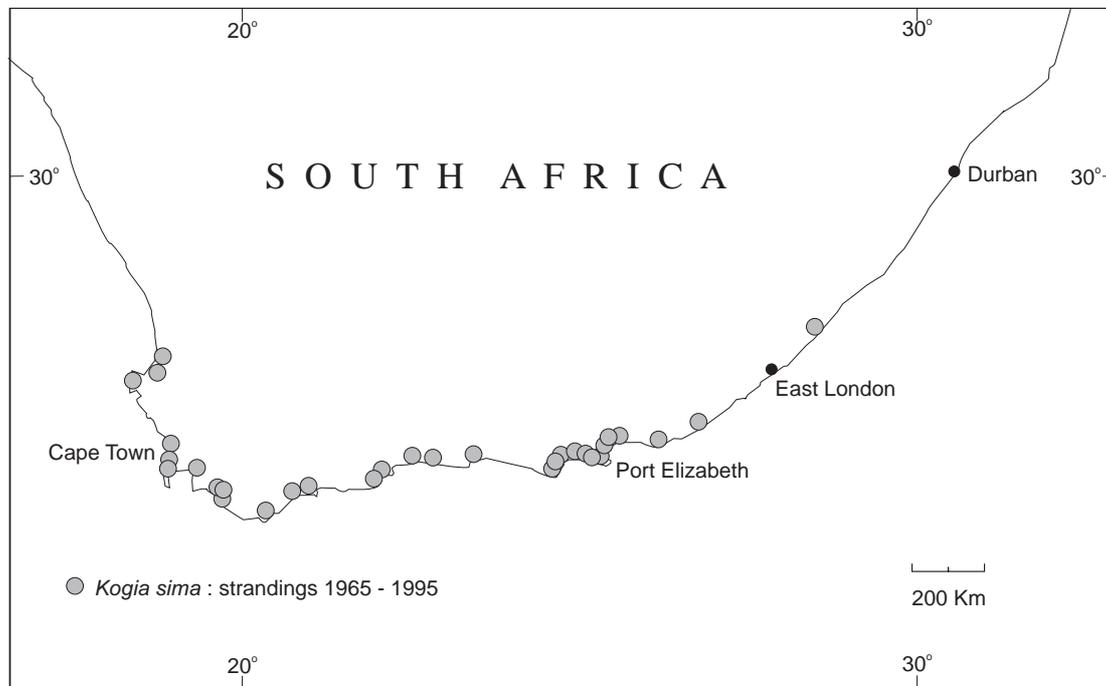
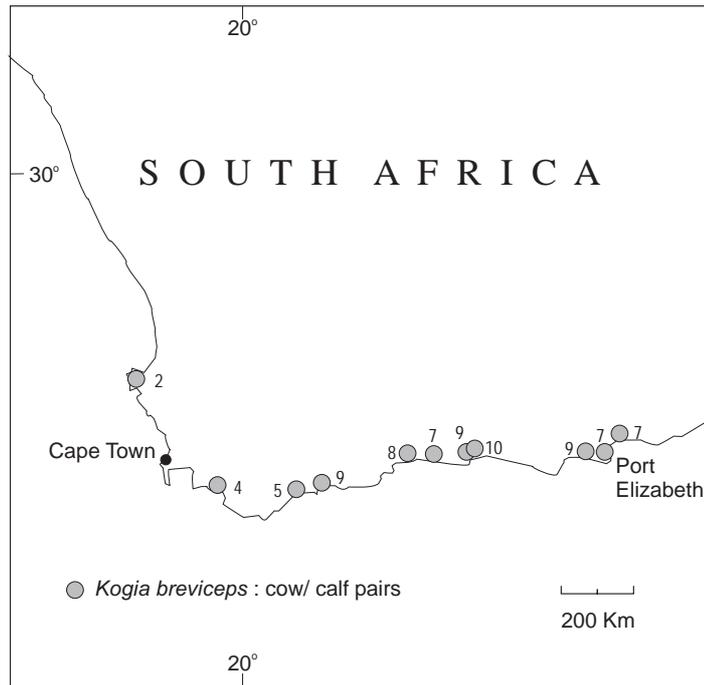


Figure 7.11: Geographical distribution of stranding events of *Kogia breviceps* (a) and *Kogia sima* (b) along the South African coastline from 1965 until 1995.

a)



b)

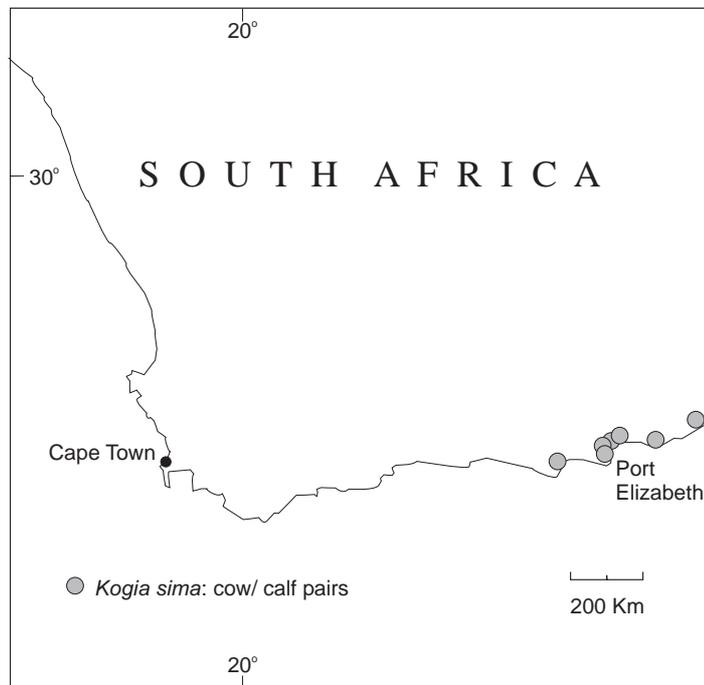
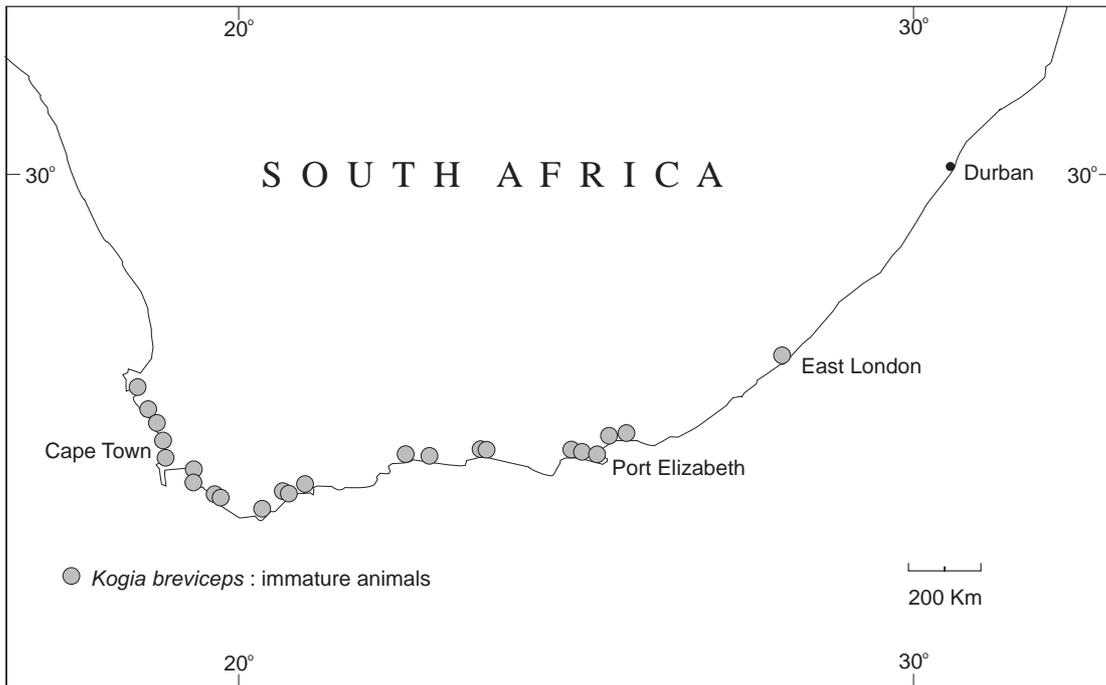


Figure 7.12: Geographical distribution of stranding events of *Kogia breviceps* (a) and *Kogia sima* (b) cow/calf pairs along the South African coastline. The numbers represent the month of the stranding event.

a)



b)

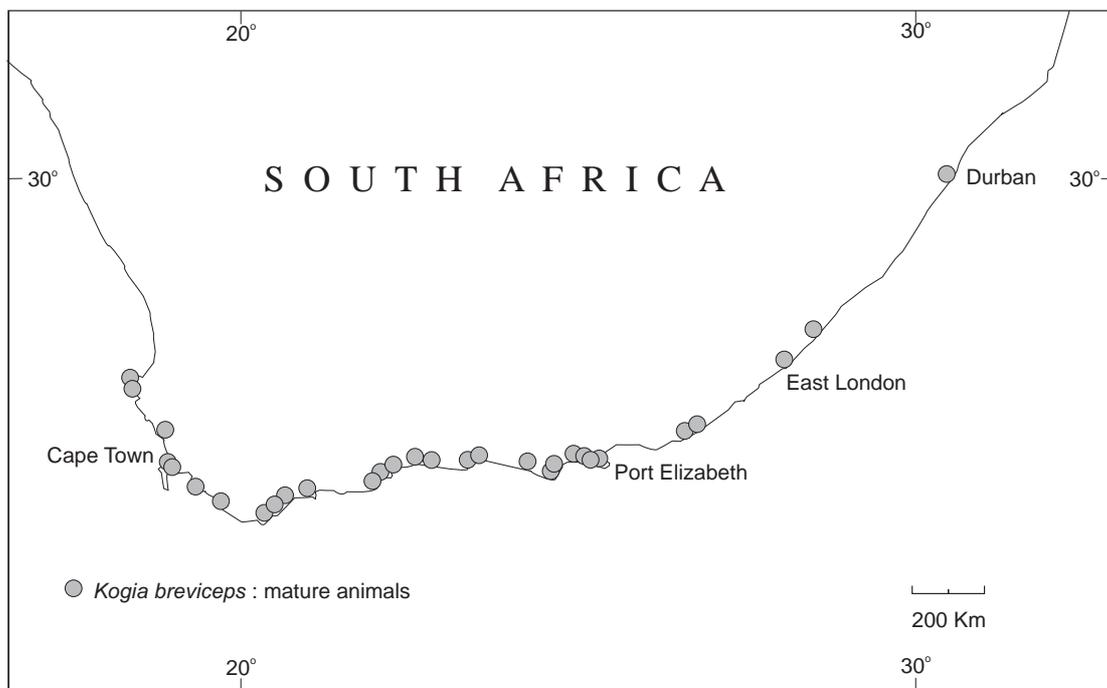
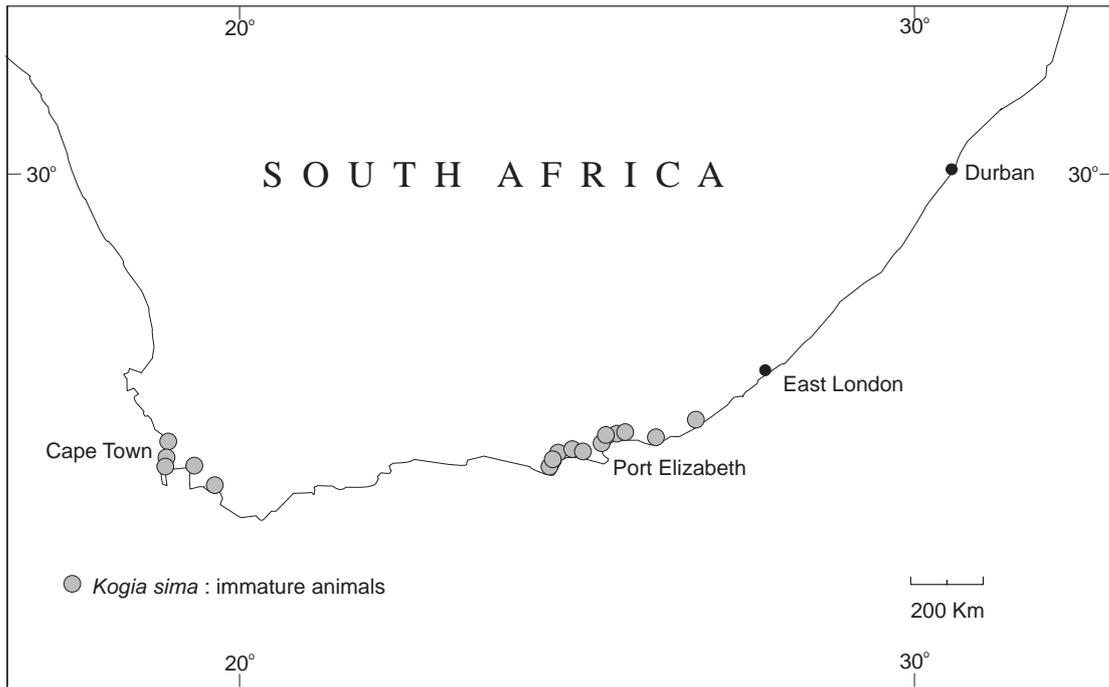


Figure 7.13: Geographical distribution of stranding events of immature (a) and mature (b) *Kogia breviceps* along the South African coastline.

a)



b)

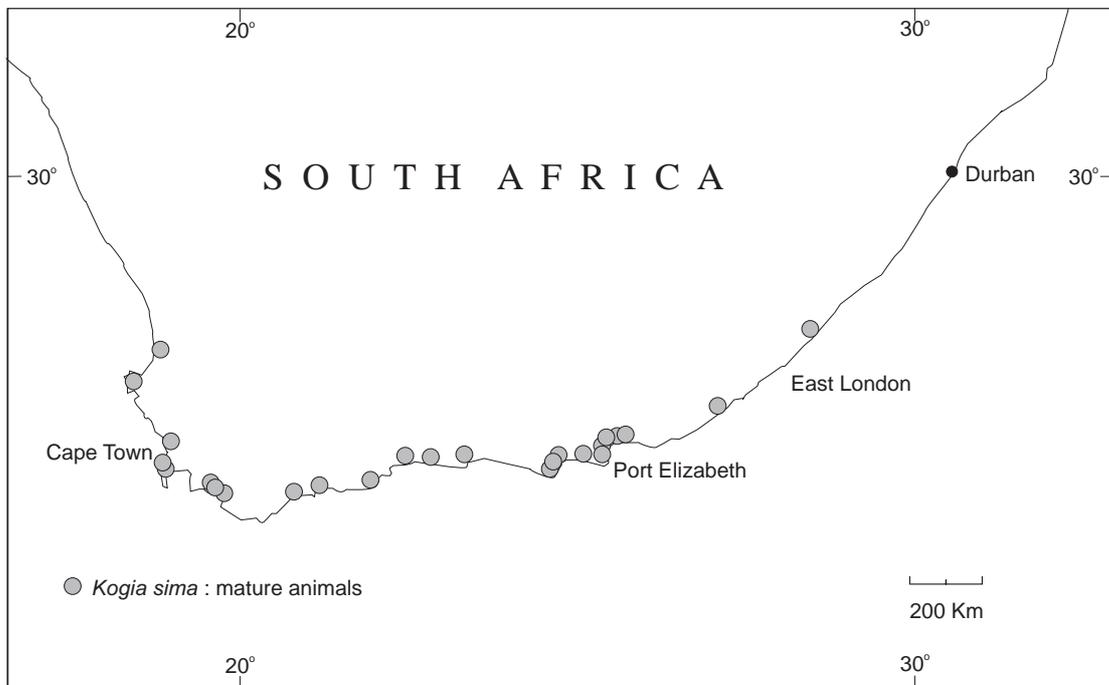


Figure 7.14: Geographical distribution of stranding events of immature (a) and mature (b) *Kogia sima* along the South African coastline.

### 7.3.5 Temperature preferences

In order to elucidate further differences in the stranding patterns of the two species I tested whether there were any significant differences in the sea surface temperatures (SST's) at the time of the stranding. SST's were available from charts issued by the Department of Environment Affairs and held by the J.L.B. Smith Institute of Ichthyology (now SAIAB) in Grahamstown, calculated for decadelts (10-day intervals) for the entire South African coastline. The mean sea surface temperature for strandings of *K. breviceps* was 16.5°C, but 17.9°C for *K. sima*. This difference in temperature was found to be significantly different at the 95% level. Furthermore, live strandings in each species were found to occur at a slightly higher sea surface temperature than dead strandings, but this was not found to be significantly different.

## 7.4 Discussion

### 7.4.1 Composition of stranded animals

The size-frequency of the stranded *K. breviceps* and *K. sima* along the Southern African coastline has already been discussed in Chapter 2 and was found to be biased towards immature males and mature females in *K. breviceps*, while it was normally distributed for *K. sima*.

In a healthy, normal population there are no apparent reasons why either sex should be more prone to strand, and strandings of male and female *K. breviceps* occurred in more or less equal numbers, whereas *K. sima* had a slightly higher rate of female strandings. One possible explanation for this may be that males appear to stay and forage further offshore, while females seem to move closer inshore with their young in order to feed (see Chapter 6). Although a similar trend was seen in *K. breviceps*, this phenomenon was more pronounced in *K. sima*. The more complex inshore environment may be confusing for these animals and cause them to strand.

In addition, a higher rate of stranded females than males may be due to reproductive stress as females of both species may ovulate up to once a year and are often found to be simultaneously lactating and pregnant (see Chapter 5). In particular, monthly peaks in stranding events appear to be related to the calving season (see below).

Furthermore, the majority of the stranded animals were mature and strandings were composed mainly of dead animals rather than live ones. While immature animals

are inexperienced in navigation and as a result more likely to get confused and strand themselves, mature animals may be predominantly sick, old or dead. Adult *Kogia* appear to commonly suffer cardiomyopathy (Bossart *et al.*, 1985) and all adult animals examined by Credle for the south-eastern United States showed this condition, leading her to conclude that it is probably a primary factor responsible for mortality, either at sea or on the beach (Credle, 1988). In addition, *Kogia* seem to suffer heavy parasite loads (see Chapter 1), which may make them more prone to strand. Dead animals are transported by the prevailing currents and eventually may get washed ashore. Of the 94 *K. breviceps* strandings that occurred along the South African coastline before June 1986 Findlay (1989) found the majority (n=47) to be dead strandings, while 21 animals stranded alive. Similarly, out of the 71 *K. sima* strandings the majority of animals stranded dead (n=42), while only 16 animals stranded alive (Findlay, 1989). In contrast, live stranding events far outnumbered strandings of dead animals in Credle's analysis of *Kogia* strandings along the south-eastern United States (Credle, 1988). Most animals were either alive or recently dead (n=270, 80%) (Credle, 1988). Similarly, Brabyn found that the majority of the *K. breviceps* strandings in New Zealand were single, live animals.

The fact that the majority of the strandings for each species were single animals is probably a reflection of the group size of the two species, which appear to be mainly solitary (Carwardine, 1995; Baird *et al.*, 1996; Willis and Baird, 1998) (see Chapter 1). Analysing *Kogia* strandings in the south-eastern U.S. Credle found the majority to be single strandings (n=286, 74%) and concluded that the strandings of single specimens suggest a solitary lifestyle (1988). Observations at sea indicate that *K. breviceps* has a slightly smaller group size of one to six animals (Carwardine, 1995; Baird *et al.*, 1996), while *K. sima* occurs in larger groups of one to seven animals (Wade and Gerrodette, 1993; Davis *et al.*, 1995; Ballance *et al.*, 1996b) (see also Chapter 1). This is reflected in the maximum number of animals that stranded together, which was three for *K. breviceps* and four for *K. sima*. The former group was composed of a pregnant and lactating female accompanied by two smaller, unsexed individuals, while the latter was composed of one immature male and three immature females. Mass strandings in the south-eastern United States, defined as three or more adults stranding together, are rare and make up less than one percent of all events (Credle, 1988). Data from Florida and South Africa suggest that there are different types of groups in both species, namely solitary adult animals of both sexes, cow/calf pairs, and small groups of immature

animals (Ross, 1979a; Leatherwood and Reeves, 1983; Credle, 1988). However, the most common groups, judging from data from stranded animals, seem to be solitary animals or cow/calf pairs (Ross, 1979a; 1984; Credle, 1988).

#### 7.4.2 Stranding trends over time

The temporal analysis of *Kogia* strandings over the years showed more definite peaks for *K. sima* than for *K. breviceps* strandings. This may indicate some correlation with environmental factors influencing inshore/offshore movement of *K. sima*, which does not appear to influence *K. breviceps*. Exactly which factors are responsible for the different stranding patterns between the two species is difficult to discern as there are no data available for a number of environmental parameters (such as primary productivity, prey distribution etc), and it is most likely the interaction of a number of parameters that results in the observed differences. One possibility would be the occurrence of El Niño phenomena, and although there was no direct correlation with El Niño events, which were reported to be strong in 1972/73, 1976/77 and 1982/83, there was an increase in the number of stranded *Kogia* around these time periods. Since El Niño events primarily affect water temperatures, the initial change in an ecosystem would occur at the planktonic level, resulting at a change in fish and squid abundance and distribution some time after that (Kawasaki, 1992). Studies on environmental effects on squid populations are rare, but the literature available indicates that at least some species undertake seasonal migrations in response to fluctuations in food availability, water temperature and spawning (Brodziak and Hendrickson, 1999). Furthermore, the distribution of neritic species appears to be more influenced by environmental factors than that of oceanic species (Brodziak and Hendrickson, 1999). As *Kogia* are close to the top of the food chain there may be a certain lag phase until the effects of El Niño events would become reflected in an increased number of strandings. However, no such studies have been undertaken on cetaceans to date and it is therefore difficult to predict the extent of such a lag phase.

No obvious explanation is available for the general decrease in the number of strandings in the 1990's, although an increase in the squid fishery off the South African coastline may be playing a role in that (see below and Chapter 6).

### 7.4.3 Seasonality of strandings

The analysis of strandings by month indicated that *K. breviceps* stranded more frequently during the austral winter and spring (July to October), while *K. sima* stranded in more or less equal numbers throughout the year, with small peaks in late summer and winter (April and July, respectively). Unfortunately no seasonal analyses of cetacean strandings have been carried out in Southern Africa to date, so that no comparison can be made with the seasonality of strandings of species other than *Kogia*. A previous analysis of *Kogia* strandings from southern Africa did not find any seasonality in the stranding events for either species (Ross, 1984), but Findlay (1989) reports peaks of *K. breviceps* strandings in late winter (July-September), while *K. sima* has a stronger seasonal occurrence of strandings in late summer/ early autumn (February-June) (Findlay, 1989). These data are in agreement with the above findings for *K. breviceps*.

Odell (1985) suggests that a seasonal peak in the stranding events in Florida is linked to the inshore-offshore movement of the Gulf Stream. Individual animals may follow warm water plumes shooting off from the stream and travelling towards the coast. They may get confused in the more complex inshore waters and subsequently strand, as strandings appear to occur more frequently when the Gulf Stream is positioned further offshore. Although the hydrographic structure of the Agulhas Current is very similar to that of other large western boundary currents such as the Gulf Stream (Gründlingh, 1983), no strong seasonal behaviour was found in its flow behaviour (Lutjeharms *et al.*, 1989). However, it may be possible that meanders and plumes shooting off the current and travelling towards the coast are more prevalent at a certain time of year and thus may result in increased strandings. Meanders and eddies have been reported off the south-eastern Cape coast, but not off the east coast of South Africa, where the current flows closely along the continental shelf edge, and plumes of warm Agulhas water were recorded offshore from Port Elizabeth (Lutjeharms *et al.*, 1989).

The most common stranding months for the two *Kogia* species in the south-eastern U.S. were August and September (late summer) when 26% of all whales stranded (Credle, 1988). Overall, over 50% of the strandings occur on the east coast of Florida, while less strandings in the Gulf of Mexico suggest a lower density or a seasonal migration (Credle, 1988). Credle (1988) concludes that an increase in stranding events in one month or at a particular location could be equally attributed to an increased mortality as to actual movement of animals. In this respect an increase in stranding events during

August/ September in the south-eastern U. S. was interpreted as the result of an increase in storms as that is the peak of the hurricane season (Credle, 1988).

A seasonal movement of *Kogia* based on the seasonal occurrence of strandings has also been suggested for Australia and New Zealand (Hale, 1962) and New Caledonia (Sylvestre, 1988). However, such seasonality in stranding events may also be linked to the seasonal inshore/offshore movement of the main prey and/or the animals themselves and this will be discussed in more detail below under section 7. 4.6.

Peaks in the number of live strandings in relation to month appear to be associated with reproductive events such as calving and weaning as they occur just after the end of the calving season. In *K. breviceps* a protracted calving season was found from March to August and lactation appeared to last just under a year (see Chapter 5). Thus the increase in the number of live stranding events in September, just after the end of the calving season, is probably due to of cow/calf pair strandings, resulting from a combination of factors such as difficulties during birth, unsuccessful weaning of the calf, reproductive stress for the cow associated with simultaneous pregnancy and lactation, and, lastly, a slight migration further inshore. An increase in live strandings in *K. sima* was found from March to May, which can also be attributed to an increase in cow/calf strandings. In this species calving occurred from December to March and lactation was estimated to also last about one year (see Chapter 5). Females and immature animals of both species have a different prey preference than males, feeding closer inshore (see Chapter 6). This inshore movement possibly also provides additional shelter, ensures that the cow does not have to dive as deeply in search of prey and thus may not leave her offspring unattended at the surface for long periods. It may, however, also increase the possibility of stranding as the animals find themselves in a more complex environment than the one they are used to.

It is remarkable, however, that no strandings of *K. sima* have been recorded during June over the last 30 years. June is the coldest month in the austral winter and therefore sea surface temperatures (SST's) are the lowest off the Southern African coastline during this month. Further indications about SST preferences will be discussed below. The absence of live stranding events in October for *K. sima* is unclear.

#### **7.4.4 Stranding distribution and habitat preferences**

The analysis of *Kogia* peak stranding locations by longitude indicated that *K.*

*breviceps* stranded in both the Western and Eastern Cape regions, but had a “peak” location at around 20°E in the Western Cape. In contrast, *K. sima* almost exclusively stranded in the Eastern Cape at around 26°E and was only found to strand in the Western Cape during the summer months. This indicates a clear preference of *K. sima* for the Eastern Cape region. As mentioned earlier the shelf regions of the Eastern Cape (i.e. in particularly east of 24°E) are strongly influenced by the warm waters of the Agulhas Current (Boyd *et al.*, 1992). In this respect the above results would indicate that *K. sima* prefers warmer water temperatures, especially as it is only found in the cooler waters of the Western Cape during the summer months, when water temperatures are the highest. In contrast, *K. breviceps* appears to frequent both the Western and Eastern Cape to almost equal amounts, perhaps with a slight preference for the Western Cape.

Such a difference in habitat preference and distribution is further supported by the general stranding distribution of the two species: the shorter strip of coastline along which *K. sima* stranded is still influenced by the warm Agulhas Current, whereas *K. breviceps* had a much broader stranding range, occurring even along the coast of Namibia, which is predominantly influenced by the cold Benguela system. However, those data were not included in the present analysis. The three records of *K. breviceps* from Namibia that Ross presented in 1979 formed a substantial proportion of all the records from this territory, which has over 1000km of uninhabited coastline (Ross, 1979a). In contrast, the Natal coast has a higher human population, but it appears to have a relatively low stranding rate for all species of cetaceans, which may possibly be a result of the narrow continental shelf and the fast, directional flow of the prevailing current parallel to the coastline (Ross, 1979a). As *K. breviceps* appears to be distributed across an entire spectrum of oceanographic conditions (see Chapter 1) it appears unlikely that the distribution of this species could be correlated with a particular water mass (Ross, 1979a).

Historical records of *Kogia* distribution and habitat preferences are difficult to interpret since either only one or up to seven species of *Kogia* were recognized (Yamada, 1954; Handley, 1966; Ross, 1979a; Willis and Baird, 1998). Allen (1941) comments on the record by Hirasaka (1937) from Independencia Bay, Peru, that it was “interesting as occurring in the region of the cool Humboldt Current, though it may, of course, have washed in from a warmer area of the adjacent seas”. Ross (1984) notes that while records for *K. breviceps* extend from Cape Cross in Namibia to the Natal coastline, the majority of strandings occur along the Cape south coast (Ross, 1984). This is in

contrast to his findings for *K. sima*, with most of the strandings (72%) reported from the south-east coast (Ross, 1984). He suggests that the apparent restriction of stranding records to the southern part of the South African coastline may in fact represent the true distribution of *K. sima*, which may be associated with the mixed water region in this area formed by the interaction of the Agulhas with the Benguela Current (Ross, 1979a; 1984). He suggests further that this region over the Agulhas Bank is a possible nursery area for immature *K. sima* (Ross, 1984). In contrast, no clear pattern was found for *K. breviceps*, although strandings of immature animals are also restricted to the southern Cape coast (Ross, 1984). He speculates that mature animals of this species may disperse more widely once they move offshore (Ross, 1984). Findlay's findings support those of Ross' (Findlay, 1989), with *K. breviceps* strandings found along the entire South African coastline from 22°S on the west coast to 29° 50'S on the east coast, while *K. sima* was only reported to strand between Cape Colombine (32°49'S, 17°50'E) and approximately 28°E (just east of Port Elizabeth (see Figure 7.2).

The apparent eastward movement of *K. breviceps* cow/calf pairs may be a result of the eastward migration of the main prey item of the cow/calf pairs and/or may be related to the reported eastward movement of Benguela water at the same time as the strandings occur (see section 7.4.6). Credle (1988) reports a westerly migration for both *Kogia* species towards the Gulf of Mexico, which was reflected in strandings in the Florida Keys in late winter/spring (February to April) and late summer/ autumn (August to October). She suggests that *K. sima* moves into the eastern Gulf in late summer/early fall, followed by a westward movement towards Texas in late fall/early winter, but did not provide any explanation for this phenomenon (Credle, 1988). No data were provided for *K. breviceps*.

In contrast to *K. breviceps* cow/calf strandings those of *K. sima* occurred exclusively in two bays in the Eastern Cape, namely Algoa Bay and Jeffrey's Bay. As mentioned previously this is an area strongly influenced by the Agulhas Current (Goschen and Schumann, 1988). These differences in the stranding distribution of cow/calf pairs between the two species together with the observed differences of the general stranding distribution indicate that the Agulhas Current may in fact play a greater role in the general ecology of *K. sima*, since it is the major oceanographic feature influencing the marine environment off the Eastern Cape coast. It has been suggested before that the seasonal fluctuation of the Gulf Stream off Florida may play a role in stranding events of both *Kogia* species as strandings occur in greater numbers when the

Gulf Stream is further from shore (Odell, pers. com.). In contrast to the Gulf Stream the Agulhas current does not show any seasonal inshore/offshore movement. It is more or less constrained by its path along the continental shelf throughout the year, with plumes of warm water shooting off periodically. These plumes possibly play a role in *K. sima* strandings. The role of nearshore currents in *Kogia* strandings along the Florida coast has been speculated before. However, a correlation between individual warm nearshore currents and individual stranding events is extremely difficult to test due to the small time scales involved (Dan Odell, pers. com.). Credle (1988) reports that the distribution of live strandings is not significantly different from a random distribution based on the analysis of 116 strandings in the south-eastern U.S.. However, data for both live and dead animals combined show a clumped distribution, which may indicate stranding “hot spots” caused by the prevailing currents, occurring in areas where the Gulf Stream runs close to shore (Credle, 1988). In addition, live strandings have a geographically random distribution, but occur in sites with geomagnetic field strengths above average and on magnetically “quiet days compared to passive stranding events (Credle, 1988).

The apparently more “clumped” distribution of strandings of immature *Kogia* along the South African coastline, which was particularly pronounced in *K. sima*, may indicate that mature and immature animals do in fact form different groups.

#### 7.4.5 Temperature preferences

The differences in SST at the stranding location between live *K. breviceps* and *K. sima* further support the above indication that *K. sima* appears to prefer warmer temperatures and probably has a closer association with the Agulhas Current than *K. breviceps*. The maximum temperatures recorded for the Agulhas Current ranged from 26°C in summer to 22-23°C in winter in the surface waters, while the surrounding water masses were on average about 6°C cooler (Goschen and Schumann, 1988). Data reviewed above on the distribution at sea of the two *Kogia* species also suggest that *K. sima* may prefer somewhat warmer waters than *K. breviceps*. Survey data indicate that *K. sima* is found near the coast (Wade and Gerrodette, 1993) and prefers warm, deep waters (Ballance and Pitman, 1998). Both species of *Kogia* are found in higher water temperatures than other cetacean species included in surveys (Davis *et al.*, 1995), but are also found along thermal fronts, which may be related to foraging (Davis *et al.*, 1995; 1998; Griffin, 1999; Baumgartner *et al.*, 2000). Such data in combination with the

stranding data may indicate that both *Kogia* species have an affinity for western boundary currents, which are usually warm currents and provide the necessary oceanographic conditions of thermal fronts that the two species need for foraging (see also sections 7.4.6 and 7.4.7 below).

Cetaceans have a number of physiological and morphological adaptations according to the habitat they live in. Species that have a more offshore habitat, which may require the need to dive longer and perhaps deeper, have greater blood volumes, haemoglobin concentrations, and packed cell volumes, thus facilitating a greater oxygen carrying capacity, than inshore species (Ridgway and Johnston, 1966; Hersh and Duffield, 1990). Total blood-oxygen content estimates are nearly three times higher for offshore species, such as Dall's porpoise *Phocoenoides dalli* than for coastal species like the bottlenose dolphin *T. truncatus* (Ridgway and Johnston, 1966). The discovery of different types of haemoglobin present in the latter aided in the differentiation of two ecotypes (Hersh and Duffield, 1990). Additionally, the two forms also have distinct morphological differences with offshore animals exhibiting a longer body with a shorter snout and smaller flippers (Hersh and Duffield, 1990). The smaller size of coastal animals as well as larger flipper size is probably an adaptation to aid greater manoeuvrability in a more complex inshore environment and a representation of a warm-water habitat (Hersh and Duffield, 1990). In this context, these characteristics are thought to present a warm, shallow-water ecotype (as opposed to a cool, deep-water ecotype) than simply an inshore one (Hersh and Duffield, 1990). Additional differences in skull dimensions may reflect the differing food preferences observed between the two forms and the morphological differences may indicate population differentiation based on resource exploitation (Hersh and Duffield, 1990). In similar situations where morphological characteristics differ a difference in the haematology of these animals is also expected (Hersh and Duffield, 1990).

Sighting data from the short-finned pilot whale *Globicephala macrorhynchus* reveal a thermal segregation between the two forms (or ecotypes) found off Japan (Kasuya *et al.*, 1988). However, additional factors such as bathythermal structure or food availability are also thought to control the distribution of the two forms (Kasuya *et al.*, 1988). Subsequent studies suggest the segregation of a northern and southern form into different sub-species based on differing distribution ranges (Kasuya and Tai, 1993). The northern form, which is also slightly larger, appears to occupy the colder northern part influenced by the cold Oyashio Current, with water temperatures ranging between 12°C

and 24°C. In contrast, the southern form has a smaller body and appears to occupy the warmer southern Kuroshio Current with water temperatures between 20°C and 31°C (Kasuya *et al.*, 1988; Kasuya and Tai, 1993). This seems to result in larger neonates in the northern form than in the southern form (Kasuya and Tai, 1993). In addition, the two forms appear to have different reproductive seasonalities, although they seem to occupy similar niches.

Previous morphological studies on both *Kogia* species indicate that although *K. breviceps* has the bigger body length of the two species, *K. sima* has larger extremities such as flippers, dorsal fin and flukes (Ross, 1979a). Unfortunately the data did not allow a statistical comparison of the size of these structures. The regulation of heat loss from the appendages as a response to exercise, diving activity, or change in water temperature is extremely important in cetaceans (Whittow, 1987; Pabst *et al.*, 1998; Rommel *et al.*, 1998). Thus these data may support the idea that *K. breviceps* has a more temperate, cold-water habitat and therefore smaller extremities in order to conserve body heat, while *K. sima* has a more tropical, warm water habitat, thus no need to conserve as much heat and subsequently has larger extremities. This may be especially important for species, which undertake long and deep dives as is assumed for *Kogia* (see Chapter 6).

Further supporting evidence comes from the description of a counter-current heat exchange system in the dorsal fin of odontocetes, which functions as a cooling system for the intra-abdominal testes (Rommel *et al.*, 1992; 1998; Pabst *et al.*, 1995). It appears that the size of the dorsal fin may be an indication of the size of the testes i.e. the larger the testes the greater is the need for a larger surface area of the dorsal fin to act as an efficient cooling mechanism (Ann Pabst, pers. com.). In the case of *Kogia* the larger dorsal fin of *K. sima* may well reflect the larger testes as established in Chapter 4. However, it may also indicate that the animal lives in a warmer environment, thus needs a larger surface area in order to cool the testes down than an animal that lives in a cooler environment, such as *K. breviceps* with its smaller dorsal fin.

The evidence presented above for ecotypes of both *T. truncatus* and *G. macrorhynchus* would indicate that a similar scenario may be true for *Kogia*. Within the ceacea more examples can be found that, among closely related species or two ecotypes of the same species, the forms living in the colder environment show similar life history or morphological traits to each other. Similarly, the forms found in the warmer environment also exhibit similar life history traits and morphologies. Such patterns of differing ecologies between closely related species will be discussed in more detail in

Chapter 9.

Based on an analysis of the stranding data the distributions of the two *Kogia* species off South America were found to extend further south on the east coast of South America than on the west coast, which seems related to the prevalence of the warm Brazilian Current, particularly during the highest flow peak in the austral summer (Muñoz-Hincapié *et al.*, 1998). Similarly, Muñoz-Hincapié *et al.* (1998) suggest that the distribution range of *Kogia* on the west coast is linked to the cool, northward flow of the Perú Current. However, the similarities drawn by Muñoz-Hincapié *et al.* (1998) between the distribution of *Kogia* off South America and the distribution and clear link to the main currents off South Africa does not hold. While there were some clear patterns observed by different researchers off Southern Africa (Ross, 1979a; 1984; Findlay *et al.*, 1992) (present study), the sample size for *Kogia* off South America is not large enough to demonstrate a clear trend in distribution patterns as found for other species (Hussenot *et al.*, 1996; Silva and Sequeira, 2003).

#### 7.4.6 Distribution determined by diet

The distribution of many marine mammal species is to a large extent determined by their prey (Kenney and Winn, 1986; Payne and Heinemann, 1993; Young and Cockcroft, 1994). The Agulhas Bank is a major spawning ground for both pelagic fish and squid (Chapman and Largier, 1989; Augustyn *et al.*, 1992; 1994). Unfortunately, little is known about the biology of most squid species as some may be actively avoiding the catching nets deployed to study them (see Chapter 6). However, some data are available on those species that are commercially exploited (Augustyn *et al.*, 1994; Roberts and Sauer, 1994). Unfortunately, however, these may not be the species that *Kogia* are feeding on. Mother and calf pairs of *K. breviceps* mainly feed on *Sepia* sp. (see Chapter 6) and it is possible that the eastward movement throughout the year reflected in the cow/calf pair strandings may be an indication that the animals follow the migration of their prey. Incidentally, the flow pattern of Benguela surface water is from north to south during the summer months (December to February), inshore along the west coast, while it flows eastwards along the south-west coast in winter (Duncan and Nell, 1969). Thus the prevalent currents during that time period may aid in the migration of cephalopod prey or the whales themselves. Although data on the distribution *Sepia* sp. are rare, information available on other cephalopods indicate that the waters off the

Eastern Cape coast, in particular between Plettenberg Bay and Algoa Bay, may be important habitats for some squid species, which are usually found over the Agulhas Bank, but may migrate further east in order to spawn (Roeleveld *et al.*, 1993; Augustyn *et al.*, 1994). Data for both the cuttlefish *Sepia australis* and the commercially exploited chokka squid indicate that the species use the inshore waters of the Eastern Cape region as spawning grounds (Roeleveld *et al.*, 1993; Augustyn *et al.*, 1994). It has been speculated that topographically induced upwelling areas inshore of large western boundary currents sustain large populations of squid as these provide productive environments with appropriate temperatures for all life stages of the cephalopods (O’Dor, 1992). The Agulhas Current forms the western boundary current of the southern Indian Ocean (Goschen and Schumann, 1988) and swift western boundary currents govern most of the inshore processes along their coastlines (Lutjeharms, 1981). They commonly show upwelling along the inshore front of the current (Schumann and van Heerden, 1988) and such an inshore upwelling cell is found just off Port Elizabeth and thus may further support the fact that *Kogia* cow/calf pairs come closer inshore to feed. In addition, they may also seek a sheltered and protected environment, where females with their calves would not have to dive as deep in search of food and thus would not have to leave their calves unattended at the surface for too long. However, being pelagic animals they may get confused in the more complex inshore environment and subsequently strand themselves.

These circumstances may also play a role in strandings of immature animals, which prey on the same cephalopod species as cow/calf pairs (see Chapter 6). These animals may still be lacking navigational skills since they strand in only a few locations along the coast, which are predominated by onshore currents from the Agulhas Current.

#### **7.4.7 Population sizes and population “hotspots”?**

Credle (1988) concludes that the mere occurrence of strandings of *Kogia* along a coastline indicates that there must be a minimal population present in the area. As no other odontocete exhibits such a high number of stranding events in the area, *Kogia* may be either especially abundant in the region or have extreme mortality (Credle, 1988). Consequently, the high number of strandings of both *Kogia* species along the South African coastline would lead to the conclusion that both *Kogia* are also abundant in this region, but unfortunately, the data available to date do not allow any estimate of

population sizes off the subcontinent.

It is noteworthy that the peak stranding areas for *Kogia* species worldwide such as the south-eastern United States, South Africa, the east coast of the North Island of New Zealand and potentially Japan, are all influenced by western boundary currents. Although the above discussion indicates that the interrelationship between these oceanographic conditions, the biology of the squid, and the distribution of the whales is as yet not fully understood, attempts by Ross (1979a), Odell *et al.* (1985), and in the present study indicate, that these ecosystems appear to be a preferred habitat for *Kogia*, or may in fact represent calving and nursery areas as suggested by some authors (Ross, 1979a,b; Tuohy *et al.*, 2001).

However, it is generally believed that these so-called stranding “hotspots” represent separate populations of *Kogia* due to their shear distance from each other. This assumption is examined in more detail in the following chapter (Chapter 8).

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## *Chapter 8: Population genetics*



## **8.1 Theoretical background**

While the previous chapters concentrated on aspects of the life history and ecology of the two *Kogia* species, the present chapter examines the population genetics of the two species in order to address questions of how distinct the South African populations are from others in the Southern Hemisphere and how much exchange there may be between them.

Since data on the movements of wild animals are currently unavailable for either *Kogia* species, their population structure or the degree of mixing of animals from different regions is unknown. Movements of small odontocetes appear to be restricted in most species (Mate *et al.*, 1995; Pichler *et al.*, 1998; Rosel *et al.*, 1999a, b; Pichler *et al.*, 2001a) and it seems unlikely that cetaceans the size of *Kogia* travel between continents over long oceanic distances. In addition, both in South Africa and New Zealand, females of both species strand frequently with calves. This has led to the suggestion that both areas represent calving grounds (Ross, 1984; Tuohy *et al.*, 2001). Therefore it has commonly been assumed that these stranding “hotspots” represent separate populations that are reproductively isolated to some degree.

Although both *Kogia* species strand in high numbers in certain geographical areas, such as Florida, South Africa and New Zealand (see Chapter 7), surprisingly few tissue samples are available from either species for genetic analysis. The main reason for this may be that the animals often strand in an advanced state of decay, leading researchers to dismiss the prospect of collecting tissue samples. Furthermore, the majority of tissue samples available for *Kogia* have been preserved in formalin and this can create problems during the process of DNA extraction. Museum and other research collections have only in recent years taken to preserving material in ethanol. In contrast, teeth and bones of *Kogia* are routinely accessed to collections. Although traditionally employed in the research of extinct species as well as past populations, ancient DNA research can now aid in studying contemporary populations of cetaceans for which no direct sampling method can be used (Dalebout *et al.*, 1998; Pichler *et al.*, 2001b).

### **8.1.1 The study of “ancient” DNA**

During the last 15 or so years the development of new techniques for the examination of so-called “ancient DNA” has enabled researchers to study past

organisms, including extinct species (Higuchi *et al.*, 1984; Pääbo, 1989; Neimanis *et al.*, 2000), of both plant (Golenberg, 1994) and animal origin (Janczewski *et al.*, 1992; Huynen *et al.*, 2003). “Ancient DNA” (also referred to as aDNA) is defined as being “any bulk or trace of DNA from a dead organism or parts of it” and therefore it is “any DNA that has undergone autolytic or diagenetic processes or any kind of fixation” (Herrmann and Hummel, 1994). This indicates that the source material for aDNA is immense and any preserved organism, parts of it and/or products made from biological material can potentially supply aDNA (Herrmann and Hummel, 1994).

The first successful attempt to amplify DNA from dead animal remains was made from mummified muscle tissue connected to the hide of a quagga (Higuchi *et al.*, 1984) and to date aDNA has been successfully extracted from such diverse sources as bird feathers (Ellegren, 1994), remnants on eggshells (Cooper, 1994), herbarium specimens (Taylor and Swann, 1994), plant seeds (Rollo *et al.*, 1994), mummified skin (Nielsen *et al.*, 1994) as well as bones (Hagelberg, 1994), teeth (Matisoo-Smith *et al.*, 1997; Tebbutt *et al.*, 2000; Pichler *et al.*, 2001b) and hair (Greenwood and Pääbo, 1999).

More studies have successfully amplified ancient mitochondrial DNA than ancient nuclear DNA (Herrmann and Hummel, 1994), which is due to the high copy number of mtDNA per cell and the possibility that organellar DNA is preserved better than nuclear DNA in aDNA samples (Hagelberg, 1994; Nielsen *et al.*, 1994; Rollo *et al.*, 1994; Huynen *et al.*, 2003). In addition, dense tissues such as bone/teeth and seeds appear to preserve DNA better than more porous material as they do not contain water and enzymes and offer mechanical protection (Cooper *et al.*, 1992; Herrmann and Hummel, 1994; Hummel and Herrmann, 1994a; Matisoo-Smith *et al.*, 1997). This is supported by the fact that longer fragments can be amplified from ancient bone than ancient tissue remains (Hagelberg, 1994).

Three types of cells present sources of aDNA in extractions from bones: (i) osteocytes, (ii) osteoblasts, and (iii) osteoclasts (Hummel and Herrmann, 1994b). Further possible sources are blood cells and epithelial cells of the Haversian canals as well as residues of cartilage cells in the better preserved specimens (Hummel and Herrmann, 1994b). Teeth are composed of dentine, enamel and cementum (for more detail see Chapter 3). While the enamel and the dentine do not contain any cells (Klevezal’ and Kleinenberg, 1967; Symons, 1976), the pulp cavity of the tooth holds a number of cells which present sources of aDNA: (i) odontoblasts, which lie on the boundary between the pulp cavity and the dentine and which have long processes that extend almost to the

outer surface of the dentine, (ii) fibroblasts and (iii) defence cells (Symons, 1976). In addition, a number of blood vessels and nerve fibres are present in the pulp tissue (Symons, 1976). While the enamel has very little organic content and the dentine only contains around 18-21% organic material (Symons, 1976; Berkovitz *et al.*, 1978), the cementum has the highest organic content with about 23% (Berkovitz *et al.*, 1978). Three types of cells are sources for aDNA in cementum: (i) fibroblasts, (ii) cementoblasts and (iii) cementocytes (Klevezal' and Kleinenberg, 1967). Therefore tissue remains in the pulp cavity as well as cells contained within the cementum present the best sources for aDNA in teeth. As a result of the low water and lipid content of bones and teeth each osteocyte or cementoblast appears to undergo individual mummification (Hummel and Herrmann, 1994a). This in addition to the fact that they are completely surrounded by protective hard tissue, which aids against physical and biochemical decay by microorganisms, ensures the long term preservation of genetic information in these materials (Hummel and Herrmann, 1994a).

A number of review articles deal with the problems encountered when working with aDNA, including DNA damage, (Pääbo, 1990; Hummel and Herrmann, 1994a; Austin *et al.*, 1997) and discuss the differential preservation of DNA in a number of different tissues and under differing preservation conditions (Lindhal, 1993; Cooper, 1994; Höss *et al.*, 1996). In addition, guidelines for the minimization of contamination have been established (Pääbo, 1990; Cooper, 1994; Austin *et al.*, 1997).

The rapid progress in aDNA studies over the last decade is not least due to the invention of the polymerase chain reaction (PCR), which enables the synthesis of many copies of a small number of intact DNA molecules in the presence of a vast excess of damaged molecules (Thomas *et al.*, 1989; Herrmann and Hummel, 1994; Austin *et al.*, 1997). However, due to the high contamination risk involved in PCR, dramatic results with aDNA should be viewed with skepticism (Lindhal, 1993). The DNA molecule is generally not expected to survive longer than 10 000 to 100 000 years and even if it does survive it will be highly fragmented (Austin *et al.*, 1997). However, the extent of fragmentation of DNA from “ancient” samples does not appear to be related to the age of the sample, but rather the preservation conditions (Hagelberg *et al.*, 1989; Pääbo, 1989; Cooper, 1994; Hagelberg *et al.*, 1994). Therefore many historical specimens of interest are likely to yield only short mitochondrial fragments of DNA (Höss and Pääbo, 1993a; Cooper, 1994). Although a number of studies have claimed to have extracted DNA from plant or animal remains millions of years old, such as insect inclusions in

amber dated from 120-135 million years before present (Poinar *et al.*, 1994), most of the reports on DNA older than 50 000 years have not been authenticated (Austin *et al.*, 1997). The oldest authenticated records of aDNA come from woolly mammoths frozen in permafrost in Siberia and are around 50 000 or more years old (Hagelberg *et al.*, 1994; Höss *et al.*, 1994). Recently, DNA was successfully extracted from a 60 thousand year old human fossil from Australia (Adcock *et al.*, 2001), although this study still remains to be authenticated.

Because aDNA studies allow the investigation of both spatial and temporal genetic changes (Relethford, 2001), a number of studies have concentrated on extinct species in order to determine the phylogenetic affiliation with extant species (Higuchi *et al.*, 1984; Thomas *et al.*, 1989; Janczewski *et al.*, 1992) as well as trace biogeographic relationships (Cooper *et al.*, 1992). However, aDNA studies have also been used to compare past and present populations of organisms and one of the first such study was carried out on the kangaroo rat (*Dipodomys panamintinus*) (Thomas *et al.*, 1990; Villablanca, 1994). Subsequently, population studies utilizing aDNA material have been especially popular in the field of paleoanthropology (Hagelberg *et al.*, 1989; Adcock *et al.*, 2001), either to examine past human populations directly (Hauswirth *et al.*, 1994) or to study non-human markers of human migrations (Matisoo-Smith *et al.*, 1998).

Ancient DNA techniques have also been used to study a number of cetacean species by extracting aDNA from the bones and teeth of odontocetes, such as the Hector's dolphin (Pichler *et al.*, 1998), members of the Ziphiidae family (Dalebout *et al.*, 1998), and the sperm whale *P. macrocephalus* (Tebbutt *et al.*, 2000; Pichler *et al.*, 2001b), as well as from the baleen of mysticetes like the blue whale *Balaenoptera musculus* (Kimura *et al.*, 1997) and northern right whale *Eubalaena glacialis* (Rosenbaum *et al.*, 1997). Since samples from cetaceans are often difficult to obtain due to the elusive nature of some species, the technique of analyzing bones and teeth containing aDNA now enables researchers to access the often extensive collections of cetacean material located in museums, universities and research institutes. In this way studies on little known species for which too few samples are available to use conventional techniques, like for example the Ziphiids, can now be initiated. Similarly, such material can help to elucidate the population structure of past organisms and aid in determining the conservation status of present populations (Pichler *et al.*, 1998). In addition, sampling collection costs will be reduced, retrospective and non-invasive sampling is possible, and sample sizes may be increased (Kimura *et al.*, 1997). In many

cases the technique presents a valuable instrument in studying animals, which are otherwise inaccessible in the wild (Rosenbaum *et al.*, 1997; Pichler *et al.*, 2001b), such as *Kogia*.

### **8.1.2 MtDNA as a molecular marker**

A number of reviews discuss the advantages and disadvantages of using mitochondrial DNA (mtDNA) as a genetic marker (Wilson *et al.*, 1985; Moritz *et al.*, 1987; Harrison, 1989; Avise, 1994; Meyer, 1994; Villablanca, 1994; Wallis, 1999), but the three main advantages of mtDNA, namely i) its haploid, non-recombining nature, ii) its maternal inheritance (Moritz *et al.*, 1987; Harrison, 1989; Villablanca, 1994), and iii) its relatively rapid evolutionary rate (Moritz *et al.*, 1987; Harrison, 1989; Villablanca, 1994), led to its widespread use in population biology studies and phylogenetic analyses (Moritz *et al.*, 1987). As mtDNA is present in a haploid state, its genetic and sequencing analysis is not complicated by the presence of a second allele at any locus (Avise, 1994). Because it does not recombine, the entire circular genome (which is approximately 16 kilobases long in most animals) is inherited intact in a clonal fashion, and thus the molecule's genealogical history can be traced simply (Avise, 1994). The fact that mtDNA is maternally inherited allows conclusions about the maternal phylogenies and maternally mediated gene flow within and among populations (Moritz *et al.*, 1987; Villablanca, 1994). Thus mtDNA markers are expected to show quite different patterns than nuclear markers, especially if the mating or dispersal/philopatry strategy differs between the sexes of a species (Moritz *et al.*, 1987; Villablanca, 1994; Lyrholm *et al.*, 1999). As mtDNA exhibits considerable variation among individuals, both within and between populations, and thus provides enhanced resolving power for the detection of genetic diversity among closely related populations, it has proven to be an effective marker of population structure and patterns of intraspecific geographic variation (Harrison, 1989; Wada *et al.*, 1991). Furthermore, the effective population size of the mitochondrial genome is roughly a quarter that of the nuclear genome, thus leading to a higher rate of local differentiation by random genetic drift (Baker and Palumbi, 1997). This ability to detect local differentiation may be enhanced by the rapid evolutionary rate of mtDNA in relation to nuclear DNA, which has been found to vary among taxa (Moritz *et al.*, 1987; Harrison, 1989; Meyer, 1994; Rand, 1994). It results in high levels of intraspecific variation, thus again aiding in resolution (Schaeff *et al.*, 1991). In

mammalian species, like whales and dolphins, mtDNA studies may be particularly meaningful, because social organization is often female-based and dispersal is sex-biased (Baker and Palumbi, 1997; Dizon *et al.*, 1997a).

#### **8.1.2.1. Cytochrome *b***

Cytochrome *b* is probably one of the best-understood mitochondrial genes with respect to its structure and function (Irwin *et al.*, 1991; Meyer, 1994), and its widespread use as a genetic marker allows for the resulting data to be compared with a larger body of work (Harrison, 1989; Meyer, 1994).

#### **8.1.3 Species identification**

Although described as two distinct species (Handley, 1966; Ross, 1979), the overall similarity in appearance between *Kogia breviceps* and *K. sima* often make identification to species level difficult (Caldwell and Caldwell, 1989) (see Chapter 1). In addition, both species frequently strand in an advanced state of decay, which intensifies the problem of species identification. However, accurate species identification is necessary for obtaining useful information from the stranded animals for ecological, distributional and life history studies.

Other studies on cetaceans have encountered similar problems. Some described beaked whale species are only known from a few specimens, which may not be representative of the respective species (Henshaw *et al.*, 1997), and even studies on well-known cetaceans such as the common dolphin *Delphinus delphis* benefit from the examination of species identity by molecular means (Rosel *et al.*, 1994). Although most species can be identified according to morphological characteristics, some species are difficult to identify in the field and the process often requires detailed examination in a laboratory (Dalebout *et al.*, 1998). In recent years molecular methods have equipped researchers with additional tools of species identification, which allows identification from only small samples of tissue or blood (Cronin *et al.*, 1991; Baker and Palumbi, 1994). More recently, a web-based tool for the identification of whales, dolphins, and porpoises has enabled researchers to identify unknown specimens by aligning their DNA sequences to a validated data set of reference sequences (Ross *et al.*, 2003).

### 8.1.3.1 Species identification in *Kogia*

To date the only genetic confirmation of an identification based on morphological characteristics in a species of *Kogia* was carried out by Hückstädt and Antezana (2001) on a female *K. breviceps* stranded in Chile. However, recent studies using electrospray ionization mass spectrometry (ESIMS) on specimens from the North Atlantic, Gulf of Mexico, the eastern North Pacific and Indian Ocean have verified two definite *Kogia* species (Duffield *et al.*, 2003). As accurate species identification is unavailable for a substantial number of *Kogia* strandings due to either an advanced state of decay, age-size related confusion or inexperienced stranding personnel, any study on *Kogia* should involve a verification of species identification (Duffield *et al.*, 2003).

### 8.1.4 Population genetic studies of cetaceans

As many marine mammals today face the threat of extinction due to habitat destruction, pollution, overexploitation or other human-related causes, the identification of distinct populations of marine mammal species has become increasingly important over the last few decades. Population genetics is the study of determining how genetic principles apply to entire populations (Hartl and Clark, 1989). However, the question of what constitutes a population is not always an easy one. Phylogeography refers to the analysis of natural populations using molecular techniques in order to identify genetic relationships among individuals of known geographic origin (Palumbi *et al.*, 1991; Avise, 1994). Knowledge of patterns of genetic relatedness can then be related to features of the environment in order to determine if a continuously distributed species exhibits genetic heterogeneity across its range or if an ecological discontinuity is matched by a genetic discontinuity (Palumbi *et al.*, 1991). The ability to discern these geographic patterns allows inferences to be made about migration, demographic processes, or historical events in the evolution and persistence of populations or species (Palumbi *et al.*, 1991). Avise *et al.* (1987) review the literature on geographic patterns of population structure.

Molecular methods are an indirect way to estimate levels of gene flow between populations (Slatkin, 1987) and the variety of molecular methods that are available today to analyze gene frequencies in natural populations indicate that species differ greatly in the extent of gene flow they experience (Slatkin, 1985). Reviews of the different

mechanisms of gene flow and their effect on natural populations are given by Slatkin (1985; 1987).

Studies on cetacean populations indicate a similar level of genetic variability as found in other large mammal species (Anonymous, 1991). An overview of population genetic studies as well as other molecular analyses on marine mammals in general is presented by Dizon *et al.* (1997b), and for cetaceans in particular by Hoelzel (1991; 1994). Specific reviews of population genetic analyses are available for only a few marine mammals, namely the walrus *Odobenus rosmarus* (Scribner *et al.*, 1997a), the polar bear *Ursus maritimus* (Scribner *et al.*, 1997b), the sea otter *Enhydra lutris* (Scribner *et al.*, 1997c), and the harbour porpoise *Phocoena phocoena* (Rosel, 1997).

#### **8.1.4.1 Stock boundaries**

Definitions of stock boundaries based on experience drawn from the study of terrestrial mammals have proven to be inadequate for cetaceans as they have evolved a high degree of motility and versatility in the marine environment, and these characteristics are reflected in the genetic structure of cetacean populations (Hoelzel, 1994). In the marine environment the processes affecting genetic differentiation are not nearly as well understood as those in the terrestrial environment. Many cetacean species are capable of migrating great distances and in some cases baleen whale breeding populations mix on feeding grounds, which they visit annually and which can be up to thousands of kilometers away (Hoelzel, 1994; Baker *et al.*, 1998a). In addition, recent studies also suggest some mixing on the breeding grounds (Garrigue *et al.*, 2002). This may allow gene flow to occur over wide distances, thus preventing genetic differentiation of populations, which are separated by thousands of kilometres. But even among species that both breed and forage in the same geographic range, intraspecific differences in the feeding ecology can lead to the genetic differentiation of local populations (Hoelzel and Dover, 1991; Hoelzel, 1994). The unusual dispersion and social behaviour of some cetacean species makes the geographic identification of some genetic stocks difficult and in many cases an insight into the ecological context of the species under examination is central to the interpretation of behaviour and genetic structure (Hoelzel, 1994).

#### 8.1.4.2 Migrations and temporal movements

Migrations and temporal movements are main reasons for patterns of genetic diversity in cetaceans. Although little is known about seasonal movements of odontocetes, it is evident that the seasonal movement of prey, which is more pronounced in temperate and polar regions, largely determines movement patterns of odontocetes (Hoelzel, 1994). For example, significant genetic differentiation was found between geographically distinct summering groups, which are most likely a result of maternal fidelity to summer migration areas in belugas *Delphinapterus leucas* (Brown Gladden *et al.*, 1997; O'Corry-Crowe *et al.*, 1997; 2002). Long annual migrations between feeding and breeding grounds are characteristic for many of the large baleen whales and molecular analyses so far indicate that mixing between reproductive groups of minke whales *Balaenoptera acutorostrata* takes place on the feeding grounds (Hoelzel, 1994). This is in contrast to the main pattern observed for humpback whales where whales from more than one feeding ground mix in one breeding area (Baker *et al.*, 1993), although females show considerable site fidelity to feeding grounds (Clapham and Mayo, 1990). Furthermore, the minimum number of migration events could be calculated from the current geographical distribution of haplotypes (Baker *et al.*, 1993). The most extensive study of genetic variation within and between baleen whale populations was carried out by Wada and Numachi on *Balaenoptera* species (Wada and Numachi, 1991).

For a number of species with a worldwide distribution, like the fin whale *B. physalus* and the sei whale *B. borealis*, there is little genetic differentiation between ocean basins, while for others there is considerable variation between populations in the different ocean basins like in the minke whale *B. acutorostrata* and the humpback whale *Megaptera novaeangliae* (Hoelzel, 1994).

#### 8.1.4.3 Sympatric, genetically different populations

In some species sympatric, genetically different populations co-exist in the same habitat, but show differing patterns in habitat utilization (e.g. mammal versus fish-eating killer whales *Orcinus orca* (Hoelzel and Dover, 1991), inshore versus offshore bottlenose dolphins *Tursiops truncatus* (Curry and Smith, 1997), and common dolphins *D. delphis* (Rosel *et al.*, 1994)). A special situation appears to exist among populations of spinner dolphins *Stenella longirostris* in the eastern tropical Pacific. Although four distinct stocks are recognized for management purposes based on morphology and

geographical distribution, molecular analysis reveals an equally high within-population variation as between-population variation and great genetic interchange for at least two of the stocks (Dizon *et al.*, 1991).

When different populations become geographically isolated it can result in the species becoming variously subdivided. The most extreme form of geographic isolation occurs in species that are endemic to a certain geographical area such as the North Island Hector's dolphin *Cephalorhynchus hectori* (Pichler *et al.*, 1998) or the vaquita *Phocoena sinus* (Rosel and Rojas-Bracho, 1999).

#### **8.1.4.4 Kinship patterns**

Different patterns of kinship are another main reason for differing patterns of genetic diversity in cetaceans. Kinship patterns in cetaceans concur with general mammalian patterns in that a number of species form stable, matrifocal groups in which females are philopatric, while males disperse, which is expressed in greater within pod variation than between pod variation (Hoelzel, 1994). This is particularly the case for social dolphin species such as long-finned pilot whales *Globicephala melas* (Amos *et al.*, 1991) and bottlenose dolphins *T. truncatus* in Sarasota (Duffield and Wells, 2002), although there is some indication of female movement between groups in the latter. In contrast, in mammal eating killer whales *O. orca* the social organization indicates serial polygyny, which could lead to a less structured pattern of genetic variation at the population level (Hoelzel, 1994). The degree of male dispersal varies between species and is most distinct in sperm whales *P. macrocephalus*, where the sexes form separate groups, which only come together for breeding (Hoelzel, 1994; Lyrholm and Gyllensten, 1998; Lyrholm *et al.*, 1999). Four species of baleen whales are known to migrate over long distances to travel between their feeding and breeding grounds, namely the humpback whale *M. novaeangliae*, the gray whale *Eschrichtius robustus*, the northern right whale *E. glacialis* and the southern right whale *E. australis*, while the breeding and feeding ecology of the remaining baleen whale species is poorly understood (Hoelzel, 1994). However, of these four species only the breeding behaviour of the humpback whale has been investigated with molecular techniques (Baker *et al.*, 1993; Hoelzel, 1994). The results indicate at least partial reproductive isolation between feeding grounds and segregation of mtDNA lineages (Baker *et al.*, 1993; 1998a, b). Similarly, significant genetic differentiation was found between two wintering grounds of southern

right whales (Baker *et al.*, 1999). These results contribute to the emerging picture of stock structures within oceanic populations of baleen whales in the absence of obvious geographical barriers (Baker and Palumbi, 1997).

One result of the high degree of sociality found in dolphins could be a low level of genetic variation within local populations as found in killer whales and pilot whales (Amos *et al.*, 1991; Hoelzel and Dover, 1991). Furthermore, a loss of genetic diversity was seen in a number of species which have been subject to overexploitation, either directly through hunting (Malik *et al.*, 2000) or indirectly due to fisheries bycatch (Rosel and Rojas-Bracho, 1999; Pichler and Baker, 2000). Low diversity as a result of founder events has been suggested for the Black Sea harbour porpoise *P. phocoena* (Rosel, 1997) and the Hawaiian population of humpback whales *M. novaeangliae* (Baker *et al.*, 1993).

Although studies involving life history and genetic structure have in the past been conducted separately in cetaceans, in recent years, molecular studies on cetaceans have increasingly incorporated both life history and environmental data (Rosenbaum *et al.*, 2002). A recent study on humpback whales *M. novaeangliae* in the North Atlantic showed how subtle differences in life history traits among individuals, such as differential reproductive success in females, can alter certain aspects of the population genetic variability (Rosenbaum *et al.*, 2002), while studies on bottlenose dolphins *T. truncatus* in the Gulf of Mexico (Duffield and Wells, 2002) and long-finned pilot whales *G. melas* in the North Atlantic (Fullard *et al.*, 2000) were able to relate distributions of genetic lineages with current systems and sea-surface temperatures. The increased use of combining genetic data with information on environmental factors and life history will help elucidate patterns of population structures in different cetacean species in the future.

In most population studies on cetaceans biopsy samples for genetic analysis are obtained from animals that are already known to the researcher from previous photo-identification studies. The genetic analysis of populations is most effective when it is interpreted within a demographic, behavioural, morphological or comparative framework (Baker and Palumbi, 1997). However, when species are intractable to demographic study, as well as highly mobile and relatively inaccessible, as is the case with *Kogia*, genetic studies may be the only way for describing the structure and historic demography of a species (Baker and Palumbi, 1997; Scribner *et al.*, 1997b).

#### 8.1.4.5 Molecular studies on *Kogia*

Previous molecular studies on *Kogia* are limited to the analysis of the karyotype of *K. breviceps* (Arnason and Benirschke, 1973) and a microsatellite analysis of cow/calf pairs (Tuohy *et al.*, 2001). Contrary to other cetacean species, which have 44 chromosomes, the chromosome number for both *K. breviceps* and the sperm *P. macrocephalus* whale were found to be  $2n=42$  (Arnason and Benirschke, 1973). A microsatellite analysis was carried out on seven *K. breviceps* cow/calf pairs stranded in New Zealand in order to determine the relatedness of the animals (Tuohy *et al.*, 2001). Five of these pairs were related, while two were possibly not, although they had stranded together (Tuohy *et al.*, 2001). More recently, a *K. breviceps* sequence from the present study has been used to present the outgroup for a dataset of ziphiid sequences used in the web-based molecular identification tool for cetaceans (Ross *et al.*, 2003). A review of the phylogenetic analysis of cetaceans including *Kogia* has been given in Chapter 1.

Knowledge of the genetic as well as spatial and temporal aspects of intraspecific population structure is the foundation of good and appropriate management of cetacean populations (Dizon *et al.*, 1991). Different populations of the same species have often been called geographic forms, stocks, races etc. (Dizon *et al.*, 1991). In genetic terms, the female component of a population is demographically the most important and this makes the analysis of maternally inherited mtDNA appropriate for decisions about population definition as well as for management plans (Dizon *et al.*, 1997a). Furthermore, assessments of the status of marine mammals require knowledge of the intraspecific population structure of the species concerned and in this context a variety of data, including molecular genetic data, aid in unravelling the complexities of intraspecific structure (Dizon *et al.*, 1997a).

#### 8.1.5 Aim of the present chapter

In this respect the aim of this part of the study was threefold: a) it was necessary to determine whether the two species were genetically distinct and whether previous identification based on morphological characteristics had been correct, b) to determine how many populations of *K. breviceps* as well as *K. sima* are found off South Africa and to examine the genetic variation within these populations, and c) to determine how genetically distinct the South African *Kogia* populations are in relation to other

populations in the Southern Hemisphere. The latter could unfortunately only be addressed in a preliminary manner for *K. sima* due to a limited number of samples from different geographic locations. However, the results of the present analysis will help to establish the conservation status of *Kogia* populations off South Africa, Australia and New Zealand as well as aid in developing management directives for the two species.

## **8.2 Materials and methods**

### **8.2.1 Samples**

The geographical origins of the samples are given in Figure 8.1. Tissue samples, including muscle, skin, liver and heart tissue (see Appendix D), were obtained from four *K. breviceps* and three *K. sima* stranded along the South African coastline, 48 *K. breviceps* stranded along the New Zealand coastline, and seven *K. breviceps* and five *K. sima* (including two cow/calf pairs) stranded along the Australian and Tasmanian coastline (Table 8.1). In addition, there were two samples (one from South Africa, one from Australia), which had only been identified to genus level (Table 8.1). Soft tissue material preserved in ethanol was available for both *Kogia* species from the 1990's onwards. The earliest samples of soft tissue for *K. breviceps* were from 1988 (Australia), 1994 (New Zealand) and 1998 (South Africa). For *K. sima* the first samples of soft tissue preserved in ethanol dated from 1992 (Australia) and 2000 (South Africa). As indicated in Table 8.1 the sample size was increased dramatically for both *Kogia* species with the access of teeth and bone from museum collections for DNA analysis. Teeth and/or bone samples were available from 67 *K. breviceps* and 48 *K. sima* from South Africa and 25 *K. breviceps* and two *K. sima* from Australia (Table 8.1). Three samples from South Africa had been identified only to genus level (Table 8.1). For comparative purposes one tooth each from a *K. breviceps* and a *K. sima* stranded in Peru and one tooth from a *K. sima* from Chile were included in the analysis (Table 8.1). The oldest samples available for *K. breviceps* dated from 1880 and 1899 and originated from South Africa (see Appendix D). The oldest samples for *K. sima* were from 1958 and 1959 (Australia) and 1969 (South Africa) (see Appendix D). However, due to inherent problems with the extraction of DNA from such old samples (Hagelberg, 1994; Hagelberg *et al.*, 1994), the oldest samples yielding DNA dated from 1930, 1957 and 1959 for *K. breviceps* and from 1971 for *K. sima* (see Appendix D). Thus the majority of samples of aDNA date from

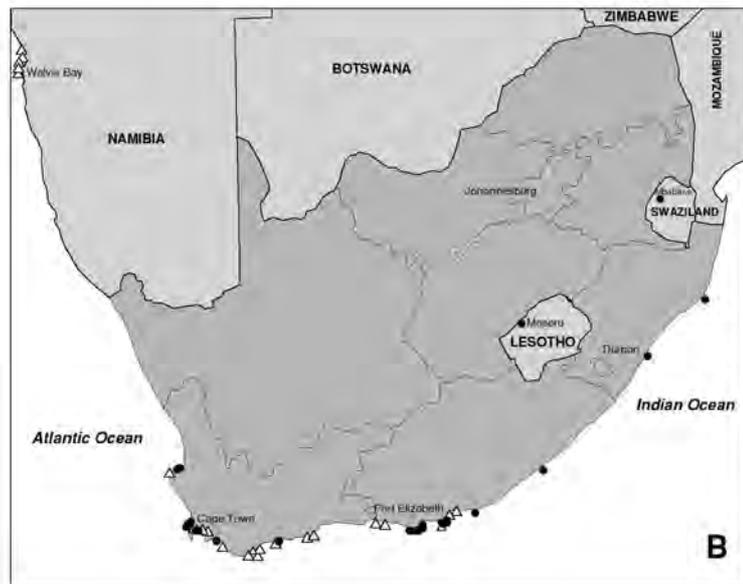
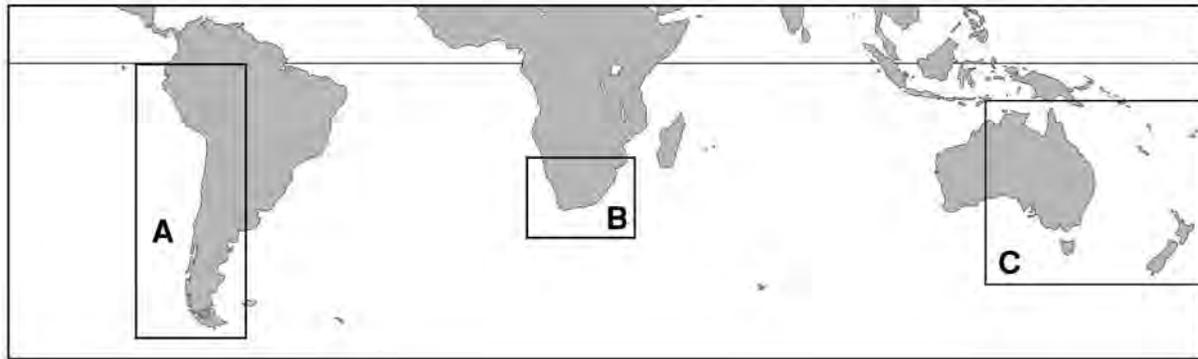


Figure 8.1: Geographical locations of *K. breviceps* (△) and *K. sima* (●) samples from South America (A), South Africa (B), and Australasia (C) used in the genetic analysis.

1970 onwards for both *Kogia* species.

Table 8.1: Sample sizes available for extraction sorted by tissue types for the different geographic locations in the Southern Hemisphere. Data in parentheses indicate specimens that were tentatively only identified as *Kogia* spp. by the collectors.

Collection location	<i>Kogia breviceps</i>			<i>Kogia sima</i>		
	Tissue*	Teeth and bone	Total	Tissue*	Teeth and bone	Total
South Africa	4	67(+1)	72	3(+1)	48(+2)	54
Australia	7	25	32	5(+1)	2	8
New Zealand	48	-	48	-	-	-
New Caledonia	2	-	2	-	-	-
Peru	-	1	1	-	1	1
Chile	-	-	-	-	1	1
<b>Total</b>	61	94	155	10	54	64

\*= Tissue samples include material from skin, muscle, liver and heart. Teeth and bone samples were obtained from museum collections.

## 8.2.2 DNA extractions

### 8.2.2.1 From tissue samples

Genomic DNA was extracted from all tissue samples by standard proteinase K digestion, followed by a phenol-chloroform extraction and ethanol precipitation of the DNA (Sambrook *et al.*, 1989) as modified for small samples by Baker *et al.* (1994). Precipitated DNA pellets were washed in 70% ethanol, dried, resuspended in TE buffer (10mM Tris-HCl, pH 7.6, 1mM EDTA, pH 8.0) and stored at -20° C (Baker *et al.*, 1994).

### 8.2.2.2 From bones and teeth (“ancient material”)

All reagents for the DNA extraction from the “ancient” material were purchased exclusively for this project and kept separate from reagents used for genetic work on other marine mammals. The reagents were prepared in laboratories which do not handle any animal DNA, and the extraction procedure itself was conducted in a designated “ancient” DNA room, equipped with a laminar flow cabinet, in which no work on modern cetaceans or other animals had been carried out. In addition, the preparation for the PCR was conducted in the designated “ancient” DNA room. Working surfaces were

washed with sodium hypochlorite (10%) and ethanol (70%) and all equipment was sterilized by bleaching and autoclaving. Teeth were cleaned with sterile, fine grained sandpaper and ethanol (100%) to remove all traces of foreign DNA and stored in the freezer at -80°C for at least 12 hours, if possible longer, in order to make them brittle. Especially designed tooth crushing sets consisting of a stainless steel tray, well and bolt were used for crushing whole teeth by placing the well on the tray, inserting a tooth into the well and placing the bolt on top. Teeth were crushed by means of a hammer until a fine powder was obtained, which was then transferred into sterile, labelled 2ml Eppendorf tubes. These were stored in the freezer at -80°C until further use. The crushing sets were washed in sodium hypochlorite (10%), followed by a wash of hydrochloric acid (0.1%) and autoclaved prior to every use and each set of crushers was used for one tooth specimen only. In addition, working surfaces were cleaned between the processing of individual teeth using 10% sodium hypochlorite and 70% ethanol and all disposable equipment was replaced. The DNA was extracted using the silica-based method designed for “ancient” DNA samples (Höss and Pääbo, 1993b) as modified by Matisoo-Smith *et al.* (1997).

### 8.2.3 Amplification and sequencing

Nested fragments of the cytochrome *b* region of the mtDNA ranging from 300-430 base-pairs (bp) in length were amplified for either species from both modern and “ancient” tissue extractions using PCR. In addition, an approximately 550bp section of the control region of the mtDNA was amplified for a subset of *K. breviceps* (mainly from New Zealand) and *K. sima* specimens (all from South Africa) for comparative purposes. The PCR reactions followed standard protocols (Palumbi, 1996).

For modern tissue samples the oligonucleotide primers *tgludg* (5'-TGA CTT GAA RAA CCA YCG TTG-3') and *cyb2* (5'-CCC TCA GAA TGA TAT TTG TCC TCA-3') (Palumbi, 1996) were used to amplify the larger cytochrome *b* fragment. For the majority of samples from aDNA this fragment was not amplified successfully as expected from extractions from such material (Höss *et al.*, 1996). Instead, these specimens are represented by a smaller fragment nested inside the larger one, which was amplified using the primers *cyb1* (5'-CCA TCC AAC ATC TCA GCA TGA TGA AAA-3') (Palumbi, 1996) and *cyb2*. For amplification of the control region fragment the

primers M13Dlp1.5 (5'-TGT AAA ACG ACG GCC AGT TCA CCC AAA GCT GRA RTT CTA-3') and Dlp5 (5'-CCA TCG WGA TGT CTT ATT TAA GRG GAA-3') or Dlp8G (5'-GGA GTA CTA TGT CCT GAA CA-3') were used (Baker *et al.*, 1993). For both loci, fragments were sequenced in both directions in some cases to confirm variable nucleotide positions.

All amplifications used the same conditions: 1X Perkin Elmer PCR Buffer II, 2.5mM MgCl<sub>2</sub>, 0.4μM each primer, 0.25mM dNTP and one unit of AmpliTaq. For museum specimens 0.5mg/mL bovine serum albumin (BSA) was added to help overcome the effects of inhibiting substances that often accumulate in such material (Pääbo, 1990). Amplifications were initiated by a 3-minute, 94°C denaturation step, followed by 35 cycles of 92°C (40 seconds), 54°C (40 seconds) and 74°C (40 seconds). Amplified DNA was run on standard agarose gels, visualized under UV light after ethidium bromide staining, and were compared to a 123bp ladder to confirm successful amplification.

Prior to sequencing the PCR products were purified using *Concert*<sup>TM</sup> Rapid Gel Extraction Systems (Life Technologies) or *QiaQuick*<sup>TM</sup> PCR product purification kits (Qiagen). Cycle sequencing reactions used ABI Big Dye reagents, and sequencing products were analysed using an ABI 377 automated sequencer.

#### 8.2.4 Sequence analysis

Sequences were examined and aligned using the program *Sequencher*<sup>TM</sup> (Gene Codes Corporation) including confirmation of polymorphic sites. Sequences obtained from aDNA material were authenticated by alignment with those from the tissue material (Thomas *et al.*, 1990). Unique haplotypes were determined using MacClade (Maddison and Maddison, 1992). Phylogenetic reconstruction was carried out using the maximum-parsimony algorithm in PAUP\* (Swafford, 2000). For the analysis of population structure the program Arlequin Vs. 2.000 (Schneider *et al.*, 2000) was used.

Some samples were assumed to originate from cow/calf pairs based on the fact that the animal stranded together. MtDNA sequences from these pairs were compared and examined in order to determine whether they were identical as expected for cow/calf pairs. If this was the case, only one sequence was used to represent the pair for the population analysis.

Published cytochrome *b* and control region sequences for *Kogia* and the sperm

whale *P. macrocephalus* from Genbank were included in the phylogenetic analysis. These were as follows: cytochrome *b*- AF304073 (Cassens *et al.*, 2000) for the sperm whale, U72040 (from California) (Milinkovitch *et al.*, 1996), X92542 (Arnason and Gullberg, 1996) (from South Carolina), and U13134 (Milinkovitch *et al.*, 1994) (from the Western North Atlantic) for *K. breviceps*, and AF304072 (Milinkovitch *et al.*, 1994) and AF334482 (Hamilton *et al.*, 2001) for *K. sima*; control region- M93154 (Dillon and Wright, 1993) for the sperm whale and X72201 (Arnason *et al.*, 1993) for *K. breviceps*; no published sequences were available for *K. sima*.

### 8.2.5 Assignment to species level

Five samples (four from South Africa, one from Australia) were obtained from animals that had been identified only to genus level. As the two *Kogia* species are so similar in appearance and thus easily misidentified (especially if the animals are in an advanced state of decay as is often the case with stranded individuals of both species), a number of researchers have now taken to only identify the two species only to genus level. Therefore the sequences obtained from the samples were later aligned to sequences from specimens with known and reliable species identification and assigned to either *K. breviceps* or *K. sima* accordingly.

### 8.2.6 Analysis of population structure

For the phylogenetic analysis a maximum-parsimony tree was constructed for both the cytochrome *b* and the control region with the sperm whale *P. macrocephalus* as an outgroup (Figures 8.3 and 8.5).

For the phylogeographic analysis only the cytochrome *b* sequences were used and the samples from the different locations were grouped into sub-populations (Table 8.4) in order to prevent the loss of any fine scale phylogeographic patterns in the data. For South Africa the sub-populations were Namibia, as defined by its political boundaries, as well as the West Coast and East Coast. As animal distributions do not adhere to political borders, geographical boundaries rather than political ones were applied in some cases in order to divide subpopulations. Thus Cape Agulhas was used as the border between Western and Eastern South Africa rather than the political border, since it is the point where the cold Benguela current from the West Coast meets the

warm Agulhas current from the East Coast. For Australia the sub-populations were considered to be East Coast and South Coast and for New Zealand West Coast and East Coast. Sample sizes for other geographical regions like South America and New Caledonia were very small and therefore were excluded from this statistical analysis.

$\Phi_{ST}$  statistics were calculated for *K. breviceps* in order to examine intra-population structure and for this purpose the sub-populations were pooled together by region (Table 8.5).

### **8.2.7 Sex determination**

For samples from animals without prior determination of gender based on anatomical examination or necropsy (21 of the *K. breviceps* samples from New Zealand as well as one *K. sima* from Australia) sex determination was carried out following the methods of Gilson *et al.* (1998).

## **8.3 Results**

### **8.3.1 Success of aDNA extractions**

Out of a total of 148 aDNA samples, cytochrome *b* sequences were successfully obtained for 69 specimens, which corresponds to 46.62%. Split up into species, out of 94 *K. breviceps* aDNA samples sequences were obtained for 43 specimens (45.7%) and out of 54 *K. sima* aDNA samples sequences were obtained for 26 specimens (48.15%). The number and geographic origin of the samples that yielded sequences for analysis is listed in Table 8.2.

Table 8.2: Sample sizes from successful extractions sorted by tissue types for the different geographic locations in the Southern Hemisphere.

Collection location	<i>Kogia breviceps</i>				<i>Kogia sima</i>			
	Tissue*	Teeth and bone	Total	Sex (M/F/unknown)	Tissue*	Teeth and bone	Total	Sex (M/F/unknown)
South Africa	3	26	29	12/ 11/ 6	1	24	25	6/ 13/ 5
Australia	6	16	22	11/ 11/ 0	2	1	3	1/ 2/ 0
New Zealand	42	-	42	21/ 19/ 2	-	-	-	-
New Caledonia	2	-	2	1/ 1/ 0	-	-	-	-
Peru	-	1	1	0/ 0/ 1	-	-	-	-
Chile	-	-	-	-	-	1	1	0/ 1/ 0
<b>Total</b>	53	43	96	45/ 42/ 9	3	26	29	7/ 16/ 5

\*= Tissue samples include material from skin, muscle, liver and heart. Teeth and bone samples were obtained from museum collections. M= male; F= female; unknown= unknown sex.

### 8.3.2 Analysis of cytochrome *b* sequences

Fragments of the cytochrome *b* region of the mtDNA ranging from 300-430 base-pairs (bp) in length were successfully amplified using PCR for 96 *K. breviceps* specimens and 29 *K. sima* specimens. A 279bp consensus region was examined for both species.

In *K. breviceps*, 27 polymorphic sites were observed and 26 unique haplotypes were identified from the 96 individuals examined. All the polymorphic sites were transition substitutions, 15 of which were purines and 12 were pyrimidines. Eight of the substitutions occurred in first codon position, one in the second position and 18 in the third position. Eight amino acids were polymorphic.

In *K. sima* 12 polymorphic sites were found in the 279bp consensus region, which related to 12 unique haplotypes among the 29 individuals examined. All the polymorphic sites were transition substitutions, five of which were purine and seven were pyrimidine transitions, with three of the substitutions occurring in the first codon position, two in the second position and seven in the third position. Three amino acids were found to be polymorphic.

The results indicate that *K. breviceps* and *K. sima* fall into two clearly separate clades, with a high bootstrap support of 100 (Figure 8.2). In fact, only one specimen originally identified as a *K. breviceps* fell into the *K. sima* clade. In contrast to the strong division on the species level, there was no characteristic phylogeographic structure

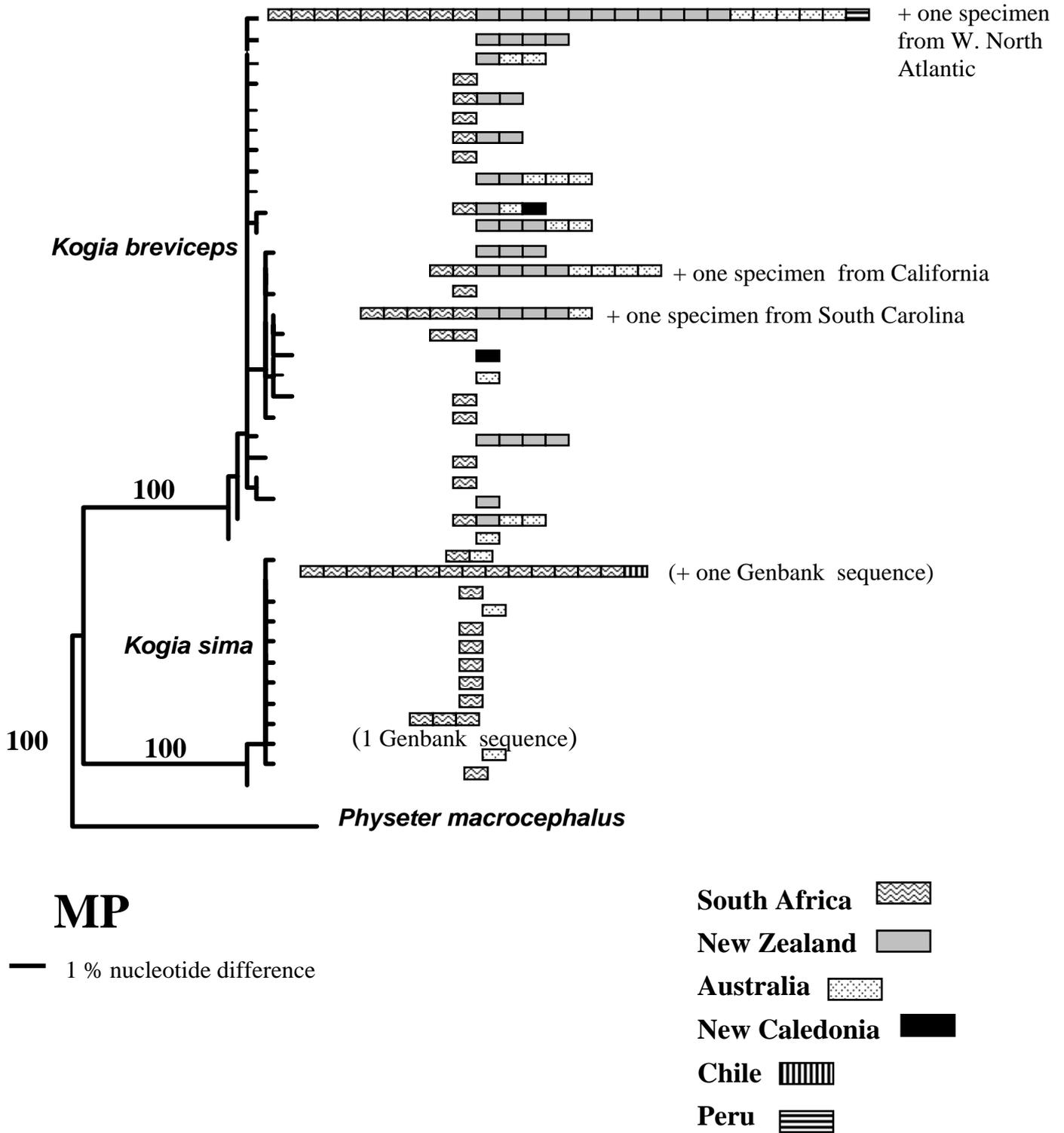


Figure 8.2: Phylogenetic tree of unique *Kogia* cytochrome *b* sequences constructed using the maximum-parsimony algorithm with *Physeter macrocephalus* as an outgroup. Each box represents an individual with that particular haplotype, and indicates the sampling location it originated from. Bootstrap values (based on 100 iterations) greater than 50% are also indicated.

within the two species.

The most common haplotype for *K. breviceps* (h1) included 26 individuals (nine from South Africa, 11 from New Zealand, five from Australia as well as the individual from Peru) and accounted for 27.08% of all the individuals sequenced. Thirteen haplotypes (i.e. half of all the haplotypes for *K. breviceps*) were represented by only one individual.

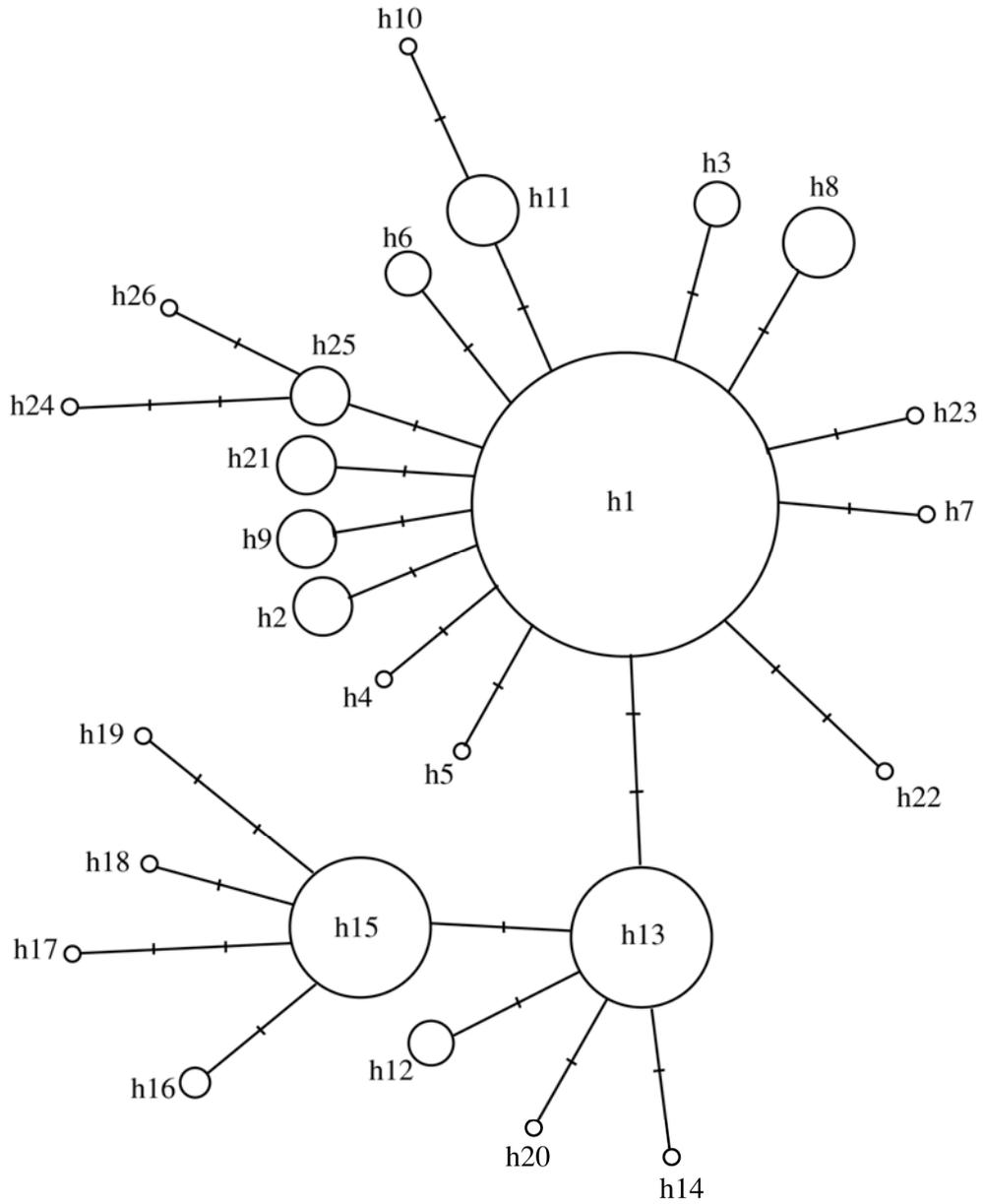
Interestingly, one of the specimens from New Caledonia grouped with individuals from these three major sampling locations, while the other represented a unique haplotype. The sequences obtained from Genbank for *K. breviceps*, which all originated from the Northern Hemisphere, surprisingly grouped with rather common haplotypes found in the Southern Hemisphere sample.

Unfortunately, the majority of samples for *K. sima* originated from South Africa, so that not much can be said about the population structure of this species in the Southern Hemisphere. However, it was interesting to see that the sample from Chile (i.e. the eastern Pacific Ocean) shared a haplotype with specimens from South Africa. In fact this was the most common haplotype (h2) and made up 51.72% of the individuals sequenced. Another haplotype (h1) was shared by an individual from South Africa and one of the animals from Australia (from Hobart, Tasmania). Nine haplotypes (i.e. three quarters of all haplotypes identified) were represented by only one individual. Unfortunately the geographical origin of the Genbank sequences included in the phylogenetic reconstruction for *K. sima* could not be determined.

Minimum-spanning-networks for both the *K. breviceps* and *K. sima* cytochrome *b* sequences were calculated by Arlequin and are shown in Figures 8.3 and 8.4, respectively. The network for *K. breviceps* showed three major clusters (centered on h1, h13 and h15), from which rarer haplotypes radiated out. In contrast, the network for *K. sima* was more star-shaped, showing only one, dominating haplotype (h2), from which all others, represented by fewer individuals, radiated out.

### 8.3.2 Analysis of control region sequences

For the analysis of the control region, sequences of 505bp were examined for 41 *K. breviceps* and three *K. sima*. 29 unique haplotypes were identified for *K. breviceps* (nucleotide diversity ( $\pi$ ): 2.07+/-1.1; haplotype diversity (*h*): 0.9810+/-0.0108) and three for *K. sima* ( $\pi$ : 1.0; *h*: 1.0). As the majority of the *K. breviceps* samples originated from



— 1

Figure 8.3: Minimum spanning network for cytochrome *b* haplotypes of *Kogia breviceps*. The numbers inside the circles indicate haplotype code numbers. The size of the circles is approximately proportional to the number of individuals per haplotype. Cross-bars indicate base substitutions.

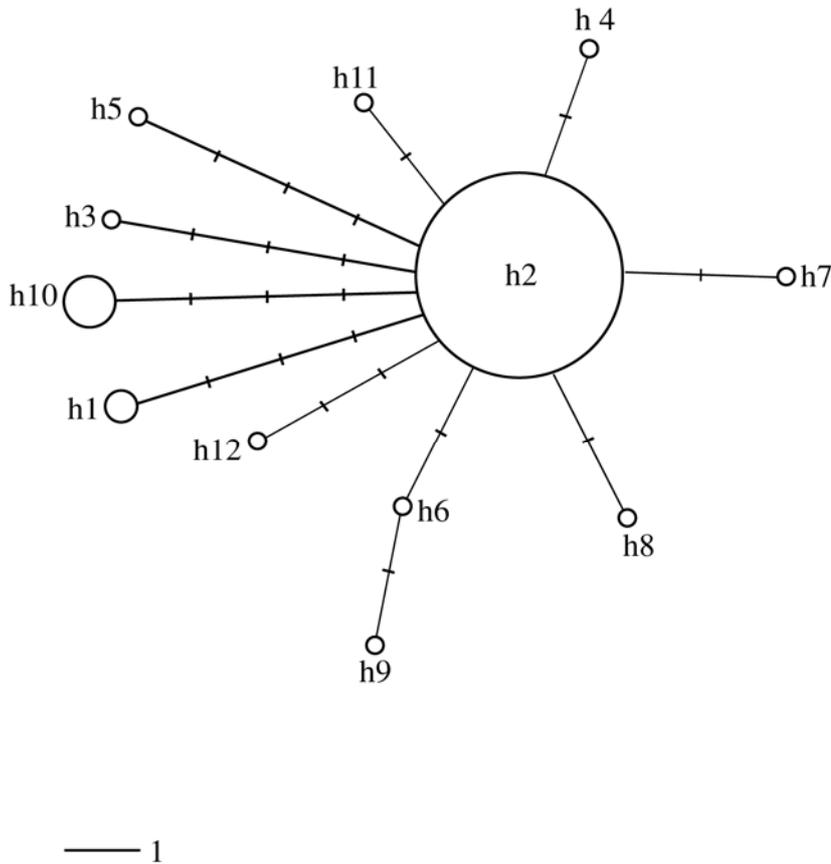


Figure 8.4: Minimum-spanning network for cytochrome *b* haplotypes of *Kogia sima*. The numbers inside the circles indicate haplotype code numbers. The size of the circles is approximately proportional to the number of individuals per haplotype. Cross-bars indicate base substitutions.

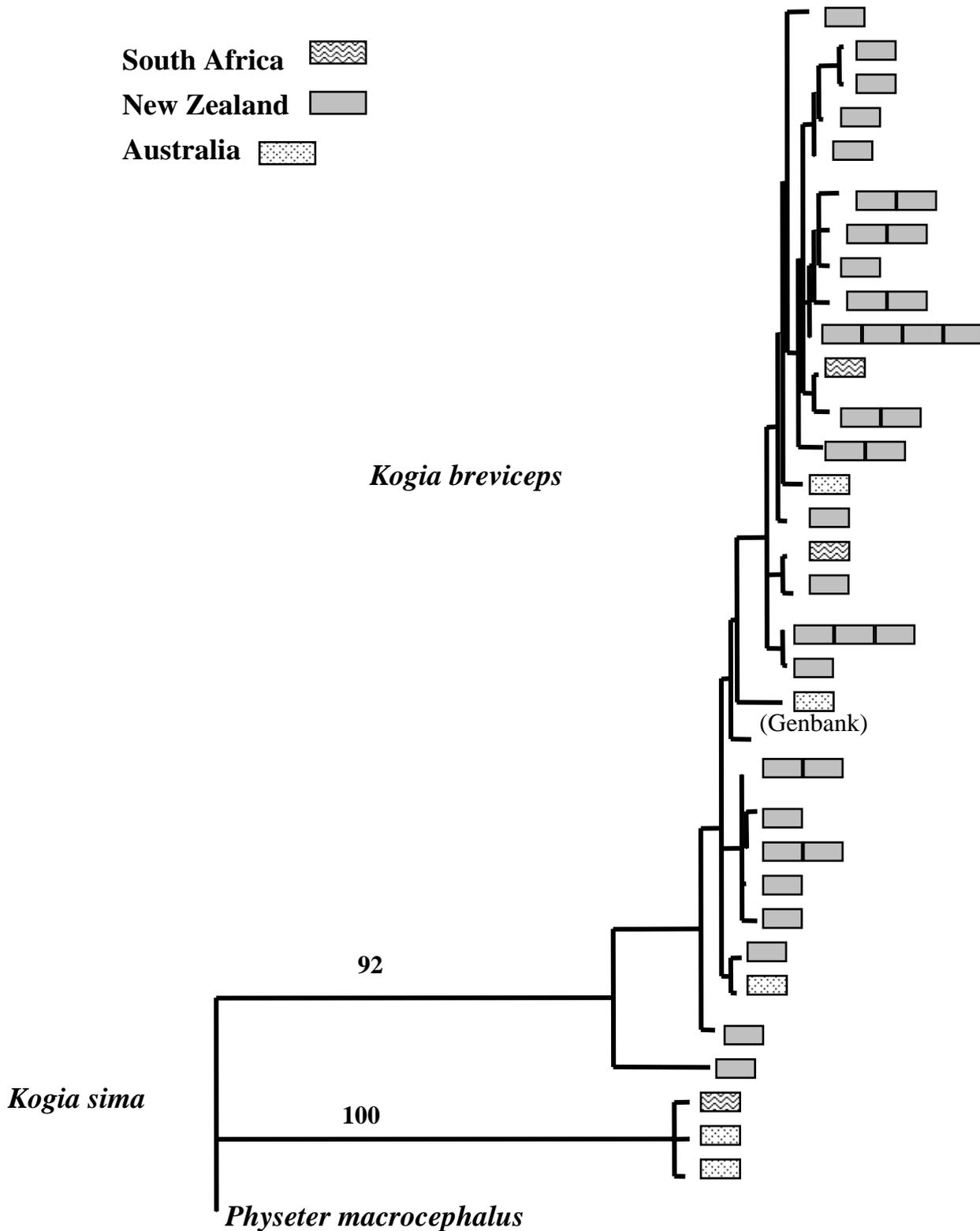
New Zealand only little can be said about the phylogeographic structure (Figure 8.5). It is interesting to note, however, that individuals from South Africa and Australia included in this analysis are nested among the New Zealand samples.

### 8.3.3 Comparison of cytochrome *b* and control region

For 39 *K. breviceps* sequences were available for both the control region and cytochrome *b*. The comparison of the analyses for the two loci for the same specimens showed that the 419bp consensus region for the control region had 37 variable sites and identified 27 unique haplotypes, while the 279bp consensus region of the cytochrome *b* gene showed 12 variable sites and identified 13 unique haplotypes. Overall a similar grouping of sequences into haplotypes was found for both loci, although the control region analysis subdivided individuals into more haplotypes. In one case the control region analysis grouped different haplotypes from the cytochrome *b* analysis into one.

### 8.3.4 Comparison with other cetaceans

The overall nucleotide diversity in % for both samples of *K. breviceps* and *K. sima* are shown in Table 8.3. The nucleotide diversity for the whole *K. breviceps* sample is  $0.82 \pm 0.5$  and thus more than twice that of *K. sima* ( $0.40 \pm 0.3$ ). For the control region, overall nucleotide diversity for the subset of *K. breviceps* samples is relatively high ( $2.07 \pm 0.011$ ) compared to other odontocetes (Table 8.3). This is almost as high as that of the humpback whale *M. novaeangliae*, which had a nucleotide diversity of 2.18 calculated for all three major ocean basins combined (Baker and Medrano-González, 2002) (Table 8.3). In contrast, the nucleotide diversity for the closest relative of the Kogiidae, the sperm whale *P. macrocephalus*, was found to be extremely low and only 16 control region haplotypes have been identified for this species worldwide (Lyrholm and Gyllensten, 1998) (Table 8.3). Although this is a similarly low nucleotide diversity to that calculated here for *K. sima* from cytochrome *b*, it has to be kept in mind that the *K. sima* data were calculated primarily from animals from South Africa, while the data for the sperm whale are based on samples from all three major ocean basins. In contrast, the data for the control region of *K. sima* were 2.5 times higher than that of the sperm whale, although based only on three samples.



**MP** — 5 changes

Figure 8.5: Phylogenetic tree of unique *Kogia* control region sequences constructed using the maximum-parsimony algorithm with *Physeter macrocephalus* as an outgroup. Each box represents an individual with that particular haplotype, and indicates the sampling location it originated from. Bootstrap values (based on 100 iterations) greater than 50% are also indicated.

Table 8.3: Nucleotide diversities ( $\pi$ ) in % for cytochrome *b* and control region loci in a number of cetacean populations.

Species	Locus examined	
	cytochrome <i>b</i>	control region
<i>Kogia breviceps</i> Pygmy sperm whale (S. Hemisphere) (present study)	0.82+/- 0.5	2.07+/- 1.1
<i>Kogia sima</i> Dwarf sperm whale (S. Hemisphere) (present study)	0.40+/- 0.3	1.0*
<i>Physeter macrocephalus</i> Sperm whale (world-wide) (Lyrholm and Gyllensten, 1998)	-	0.39 +/- 0.03
<i>Phocoena phocoena</i> Harbour porpoise (Northwest Atlantic) (Rosel <i>et al.</i> , 1999b)	-	0.99+/-0.569
<i>Phocoena phocoena</i> Harbour porpoise (Northeast Atlantic) (Rosel <i>et al.</i> , 1999b)	-	0.47+/-0.311
<i>Phocoena phocoena</i> Harbour porpoise (western N. Atlantic) (Rosel <i>et al.</i> , 1999a)	-	0.99-1.26
<i>Phocoenoides dalli</i> <i>Dall's porpoise</i> (Bering Sea + western N. Pacific) (McMillan and Bermingham, 1996)	-	0.45-0.64
<i>Phocoenoides dalli</i> <i>Dalls porpoise</i> (Sea of Japan and N. Pacific) (Hayano <i>et al.</i> , 2003)	-	1.06
<i>Cephalorhynchus hectori</i> Hector's dolphin (North Island, New Zealand) (Pichler and Baker, 2000)	-	0.0044
<i>Cephalorhynchus hectori</i> Hector's dolphin (East Coast South Island, New Zealand) (Pichler and Baker, 2000)	-	0.0030
<i>Delphinus delphis</i> Common dolphin-short- beaked form (California) (Rosel <i>et al.</i> , 1994)	-	1.61
<i>Delphinus delphis</i> Common dolphin-long- beaked form (California) (Rosel <i>et al.</i> , 1994)	-	1.17
<i>Lagenorhynchus obscurus</i> Dusky dolphin (New Zealand) (Harlin <i>et al.</i> , 2003)	-	2.2+/-1.1
<i>Monodon monoceros</i> Narwhal (North-west Atlantic) (Palsbøll <i>et al.</i> , 1997)	-	0.17
<i>Delphinapterus leucas</i> Beluga whale (Alaska + Canada) (Brown Gladden <i>et al.</i> , 1997)	-	1.0+/-0.6
<i>Delphinapterus leucas</i> Beluga whale (Alaska + Canada) (O'Corry-Crowe <i>et al.</i> , 1997)	-	0.51
<i>Orcinus orca</i> Killer whale Eastern N. Pacific (Hoelzel <i>et al.</i> , 1998)	-	0.54
<i>Hyperoodon ampullatus</i> Northern bottlenose whale (western N. Atlantic) (Dalebout, 2002)	-	0.15

<i>Megaptera novaeangliae</i> Humpback whale (world-wide) (Baker and Medrano-González, 2002)	-	2.18
<i>Eubalaena australis</i> Southern right whale (S. Hemisphere) (Rosenbaum <i>et al.</i> , 2000)	-	2.68+/-1.40
<i>Eubalaena glacialis</i> Northern right whale (N. Atlantic) (Malik <i>et al.</i> , 2000)	-	0.6
<i>Eubalaena australis</i> Southern right whale (Southern Ocean) (Patenaude, 2002)	-	2.68

\*= Preliminary estimate from only three *K. sima* from South Africa and Australia.

### 8.3.5 Phylogeographic analysis of cytochrome *b* sequences

#### *K. breviceps*

The examination of the population structure of *K. breviceps* showed both a high nucleotide and haplotype diversity within the sub-populations, with little difference between locations (Table 8.4). The lowest nucleotide and haplotype diversities were observed for the Eastern Cape region of South Africa ( $\pi$ : 0.61±0.4;  $h$ : 0.85±0.077) and for the South coast of Australia ( $\pi$ : 0.74±0.5;  $h$ : 0.88±0.058) (Table 8.4).

Table 8.4: Intra- population diversity of *Kogia breviceps* sub-populations in the Southern Hemisphere. Data in parentheses present the numbers of samples per sub-population.

Geographical area	Nucleotide diversity ( $\pi$ in %)	Haplotype diversity ( $h$ )
<b>Namibia (5)</b>	1.02+/-0.8	1.0+/-0.127
<b>West coast South Africa (8)</b>	1.01+/-0.7	0.96+/-0.077
<b>East coast South Africa (16)</b>	0.61+/-0.4	0.85+/-0.077
<b>East coast Australia (8)</b>	0.78+/-0.6	0.93+/-0.084
<b>South coast Australia (14)</b>	0.74+/-0.5	0.88+/-0.058
<b>West coast New Zealand (8)</b>	0.92+/-0.6	0.93+/-0.929
<b>East coast New Zealand (26)</b>	0.84+/-0.5	0.93+/-0.027

In order to examine whether significant genetic differences exist between individuals of *K. breviceps* from the three major regions (i.e. South Africa, Australia and New Zealand), the sub-populations were pooled accordingly and an Analysis of Molecular Variance (AMOVA) was performed. The resulting  $\Phi_{ST}$ 's indicate the difference between two populations: a  $\Phi_{ST}$ -value of 1 indicates that two populations are completely different from each other, with no overlap, while 0 indicates that the two

populations are the same, with no differences between them. In this respect the results indicate that the difference between animals from Australia and New Zealand is virtually zero i.e. the two populations being very similar (Table 8.5). Although there was some genetic differentiation between the populations from South Africa and Australia, this was not significant. The only significant difference was observed between South Africa and New Zealand (0.0423, which was significant at the 0.05 level) (Table 8.5). However, this  $\Phi_{ST}$ -value is still quite small, indicating only little genetic differentiation between these geographical regions. The overall  $F_{ST}$ -value value from the AMOVA was 0.02499; it was not significant at the 0.05 level ( $p=0.078$ ).

Table 8.5: Inter-population structure of *Kogia breviceps* populations in the Southern Hemisphere as indicated by pair-wise  $\Phi_{ST}$  statistics. Data in parentheses indicate the number of samples analyzed per population. Data above the diagonal are the levels of probability for the exact tests of population differentiation.

Geographical area	South Africa	Australia	New Zealand
South Africa (29)	-	0.1313	0.11420
Australia (22)	0.0293	-	0.29060
New Zealand (42)	0.0423*	-0.0036	-

\*= significant at the 0.05 level.

In summary, for *K. breviceps* high genetic diversity was observed within the sub-populations, but little genetic structure was found between the major regions (Table 8.4 and Table 8.5). Only little genetic differentiation was found between the populations that are the furthest apart, South Africa and New Zealand, and this was the only significant difference observed (Table 8.5). No significant genetic differentiation was found between the populations off New Zealand and Australia or Australia and South Africa. As such the null hypothesis that these animals form part of the same population could not be rejected.

### *K. sima*

For *K. sima* both nucleotide and haplotype diversities varied greatly between the different geographical regions analysed (Table 8.6). The results indicated a relatively high genetic diversity within the sub-populations, although it is unclear to what extent these results are influenced by differences in sample size (Table 8.6). It is interesting to

note that both the nucleotide and haplotype diversity are substantially lower in the Eastern Cape ( $\pi$ :  $0.24 \pm 0.2$ ;  $h$ :  $0.57 \pm 0.127$ ) than in the Western Cape region of South Africa ( $\pi$ :  $0.65 \pm 0.5$ ;  $h$ :  $0.89 \pm 0.111$ ). However, Nei's Student t-test for testing differences between diversities showed that both the nucleotide and the haplotype diversities between the Eastern and Western Cape were not significant at the 0.05 level ( $t=0.76$  and  $1.89$ , respectively) (Nei, 1987). On the other hand, analyses indicated significant genetic differentiation between the Eastern and Western Cape of South Africa ( $\Phi_{ST}=0.077 \pm 0.018$ ,  $p < 0.05$ ). However, a Nei's Student T-test for testing differences between diversities showed, that both the nucleotide and the haplotype diversities between the Eastern and Western Cape were not significant at the 0.05 level ( $p=0.76$  and  $1.89$ , respectively) (Nei, 1987). The overall nucleotide diversity was lower in *K. sima* than *K. breviceps*, but again this was not significantly different at the 0.05% level ( $p=0.72$ ) (Nei, 1987).

Table 8.6: Intra-population diversity of *Kogia sima* sub-populations in the Southern Hemisphere. Data in parentheses present the numbers of samples per sub-population.

Geographical area	Nucleotide diversity ( $\pi$ in %)	Haplotype diversity ( $h$ )
West coast South Africa (8)	0.65+/-0.5	0.89+/-0.111
East coast South Africa (17)	0.24+/-0.2	0.57+/-0.127
Australia (3)	0.72+/-0.7	1.0+/-0.272

## **8.4 Discussion**

### **8.4.1 Species identification**

The clear separation of *K. breviceps* and *K. sima* into two clades with a bootstrap support of 100 not only indicates that there are two clearly distinct *Kogia* species, but also that the morphological characteristics used for species identification are reliable and provide a good guideline for researchers dealing with stranded animals. Only one sample (SA PEM N1869, originally identified as a *K. breviceps*) out of the 214 samples identified to species level based on morphological characteristics was misidentified. It was subsequently placed with the other *K. sima* samples. Considering the overlap in some morphological characters between the two species as well as the overall similarity this result is encouraging for researchers dealing with stranded and/or dead animals on

the beach as it supports the identification criteria currently used.

#### 8.4.2 Success of aDNA extractions

In the present sample 46.62% of the extractions from “ancient” material resulted in clean sequences, which could be used for analysis of population structure in *Kogia*, with little difference between the two species. Data on the success of this technique are scarce, but a number of factors like contamination with human material, leaching of DNA from bones and teeth due to inadequate preparation or storage of the material, and poor preservation of DNA in bones and teeth could all add to a potential failure in extracting DNA successfully from this material. In view of the scarcity of tissue material from the two *Kogia* species the present result from the aDNA extractions is encouraging and once again indicates that “ancient” material presents a good source of material for the molecular analysis of cetaceans.

#### 8.4.3 Phylogeographic structure of *K. breviceps* in the Southern Hemisphere

The distribution of mtDNA variation in *K. breviceps* from different geographical locations in the Southern Hemisphere suggests a very close evolutionary relationship among these populations. The presence of haplotypes common to all subpopulations examined are an indication of ancestral mtDNA lineages that remain widespread following the divergence of populations (Brown Gladden *et al.*, 1997). According to Avise *et al.*'s categorisation of possible phylogeographic patterns theoretically observable in natural populations, the pattern shown here for *K. breviceps* would fall into Category IV- phylogenetic continuity, with a lack of spatial separation (1987). This transcribes into a number of closely related mtDNA haplotypes found within the species, each being geographically widespread (Avise *et al.*, 1987). Such a pattern would arise due to extensive and historically recent gene flow in the absence of zoogeographic barriers (Avise *et al.*, 1987). In addition, it would require a life history strategy, which is conducive to dispersal (Avise *et al.*, 1987). Although less common among cetaceans, this pattern has also been described for many marine fish species, birds and to a lesser extent, humans (Avise *et al.*, 1986; 1987; Graves, 1998). In the marine environment a number of species have great dispersal abilities and there are often no obvious barriers to gene

flow (Graves, 1998). In this context, cosmopolitan marine fishes with continuous distributions exhibited far less genetic structuring than species with discontinuous distributions (Graves, 1998).

A lack of significant phylogeographic structure and the high number of haplotypes found may indicate a substantial gene flow among populations, which would be facilitated by the movement of individuals among populations, thus inhibiting genetic differentiation of local populations (Palumbi *et al.*, 1991; Avise, 1994). In this respect genetic data only present an average view of the recent genetic structure of a population and not a snap-shot of the current ecological reality (Palumbi *et al.*, 1991; Avise, 1994). Over the short-term there appears to be some restriction to movement between the South African and New Zealand populations as indicated by significant  $\Phi_{ST}$  values. This suggests that the South African population is somewhat isolated from others in the Southern Hemisphere.

Cetaceans have evolved a high degree of motility and versatility in the marine environment, and these characteristics are reflected in the genetic structure of cetacean populations (Hoelzel, 1994). Social cohesion can affect genetic differentiation through its effect on the range of dispersal and by the tendency for kin to associate in groups (Hoelzel, 1994). *K. breviceps* are known to be solitary or occur in rather small groups (Ross, 1979; 1984; Baird *et al.*, 1996; see also Chapter 1). Such a social structure would facilitate a high genetic diversity within species, but low phylogeographic diversity, if animals travel independently and over wide ranges and do not have designated breeding grounds.

There were no indications in the results that there was any greater phylogeographic structure in females than in males for *K. breviceps*. If *K. breviceps* exhibited a common mammalian pattern of male dispersal and female philopatry, one would expect to see a high level of genetic structure in the maternally inherited mtDNA. However, the results presented here appear to indicate that female *K. breviceps* have a relatively high degree of dispersal. Unfortunately, mtDNA data reflect only the history and movement of females (Hoelzel, 1994) and in this context it would be interesting to examine some nuclear markers in order to elucidate male dispersal patterns of *K. breviceps*.

As seasonal changes in prey distributions are more pronounced in temperate and polar regions it would affect the seasonal movement of odontocetes inhabiting those regions (Hoelzel, 1994). Unfortunately, little is known about migration patterns of

cephalopods (the primary food source of *Kogia*) off the South African coastline (see Chapter 6). There seems to be some indication that the chokka squid (*Loligo vulgaris*) has an eastward migration off the South African coast as the year progresses (Augustyn *et al.*, 1994), but this species only contributes little to the diet of *K. breviceps* (see Chapter 6). However, the stranding data of cow/calf pairs suggest that there may be a slight seasonal eastward movement along the coast as the year progresses (see Chapter 7), which may be related to the movement of some of their prey species. In general, *K. breviceps* has a very generalist diet (see Chapter 6), which suggests that the species is not bound to a particular prey item, which may facilitate extensive movements reflected by the phylogeographic pattern shown by the mtDNA data. The above results indicate what a central role the ecological context and the knowledge of life history parameters play in interpreting the genetic structure of a species (Hoelzel, 1994).

However, a lack of phylogeographic structure as determined by mtDNA analysis may also indicate a lack of sufficient resolution by the genetic marker used. Not all markers are equally informative, because the level of detectable polymorphisms varies greatly between them (Palumbi *et al.*, 1991; Scribner *et al.*, 1997b). Furthermore, it may reflect the inability of mtDNA analysis to detect genetic differentiation that occurs over relatively short time scales e.g. less than about 50 000 years (Palumbi *et al.*, 1991). The relatively high evolutionary rate of animal mtDNA facilitates rapid development of genetic differentiation among populations, but this rate is slow in comparison with ecological and demographic processes. Thus a failure to detect genetic differences among populations does not prove that there is currently ecological or demographic exchange among them (Palumbi *et al.*, 1991).

Furthermore, the reliance on a single locus may diminish the power to detect significant spatial structure in the *Kogia* populations. This is due to the fact that genetic drift in populations results in random changes in gene frequencies and these changes will occur with differing frequencies at different loci (Baker and Palumbi, 1997). Therefore an investigation of spatial or temporal genetic structure should ideally consider a number of different loci and the resulting patterns (Baker and Palumbi, 1997). The concordance or contrasts of these patterns across several loci provides the best insight into the historical processes of the species considered (Baker and Palumbi, 1997).

#### 8.4.4 Phylogeographic structure of *K. sima* in the Southern Hemisphere

In contrast to *K. breviceps*, the data on the phylogeographic structure of *K. sima* are somewhat restrictive as the majority of the samples originate from South Africa. Nevertheless, both nucleotide and haplotype diversities were markedly lower than in *K. breviceps* and more similar to those for other small cetacean populations such as the harbour porpoise *P. phocoena* (Rosel *et al.*, 1999a), Dall's porpoise *P. dalli* (Hayano *et al.*, 2003), and common dolphin *D. delphis* (Rosel *et al.*, 1994). The minimum-spanning network also indicated a central haplotype from which all the other haplotypes radiated out, suggesting a recent founder effect. In this respect it is interesting to note that the animal from Chile was included in the most common haplotype from South Africa, as well as the grouping of an Australian and South African animal in a common haplotype. This indicates that there is some gene flow between these populations. However, additional samples of *K. sima* from other populations need to be included in the analysis in order to determine the degree of isolation between them.

The above differences in population structure between *K. breviceps* and *K. sima* may suggest a difference in population size between the two species. Unfortunately there are no population estimates available for either *K. breviceps* or *K. sima*. However, judging from stranding data *K. breviceps* appears to have a bigger distribution and higher stranding rates than *K. sima* (see Chapter 7), which appears to support the notion that *K. breviceps* has a bigger population size. This is consistent with the higher mtDNA diversity within *K. breviceps*.

These data do once again support the fact that although both species of *Kogia* are very similar in many aspects of their external appearance and general biology, there are some pronounced genetic differences between the two.

#### 8.4.5 Dispersal

Although there is not necessarily a simple relationship between dispersal and genetic structure of metapopulations (Lidicker and Patten, 1987), the results of the genetic analysis presented here seem to indicate a relatively wide dispersal of *K. breviceps* in the southern Hemisphere. The detailed pattern of dispersal is of critical importance to nearly all aspects of a species' ecology and behaviour, from the dynamics of its population to the nature of social interactions (Horn, 1983). There are a number of

reasons why animals move, including seasonal migrations related to changing environmental conditions, foraging, predator avoidance and to find mates (Pyke, 1983). The data on *Kogia* life histories are as yet not sufficient to make definite conclusions as to why *K. breviceps* would disperse so widely in the southern Hemisphere. In evolutionary terms, the species appears to have been even crossing the equator at some stage as suggested by the fact that animals in both hemispheres share common haplotypes. Furthermore, too little data are available on the potential impact of predators (such as sharks) as well as on the dynamics of prey (i.e. cephalopod) distribution and biology.

#### **8.4.5.1 Possible factors influencing dispersal in *K. breviceps***

##### 8.4.5.1.1 Nutritional requirements

However, there are three different possible explanations for the wide dispersal of *K. breviceps*. One possibility is that the energetic requirements that facilitate annual reproduction in female *K. breviceps* may be so high that reproductively active females disperse in search of sufficient and high quality food. To date nothing is known about *Kogia* home range sizes. Among adult female vertebrates the primary determinant of home range size is access to food and thus the animals' metabolic requirements as well as food quality and food quantity should be the main determinants of home range size (Greenwood and Swingland, 1983; Mace *et al.*, 1983). Thus the closest relationship between home range size and energetic need should be found in females (Mace *et al.*, 1983). There are no aseasonal habitats in any environment and certain periods of year are relatively worse than others either due to climatic changes or fluctuations in population density (Sinclair, 1983). Thus the food availability prior to birth is a very strong selection for the female to place itself in an environment where there is a super-abundant food supply prior to breeding (Sinclair, 1983). In addition, there is some evidence that suggests that metabolic requirements may vary between the sexes in some species (e. g. *K. breviceps* females and calves feed on different prey than adult males and non-reproductive females –see Chapter 6) and home range sizes can also vary with age and seasonality (Mace *et al.*, 1983).

8.4.5.1.2 Prey abundance

Another possible explanation for the wide dispersal of *K. breviceps* is that the abundance of squid (the main food source) may be cyclic, causing the majority of the animals to migrate in search of food at times when food availability is low. One of the main reasons why animals move is to find food and the distribution of animals in space is intimately linked with the distribution and nature of the food supply (Greenwood and Swingland, 1983; Mace *et al.*, 1983). If resources are distributed patchily an animal will have to forage over a much wider area, thus have a larger home range than an animal which feeds on a more evenly and densely distributed food source (Mace *et al.*, 1983). In addition, dispersal is most favourable when the pattern of environmental fluctuations varies from place to place- in such cases there will often be other places where conditions are better (Stenseth, 1983). The relative merit of dispersal is higher when resources change cyclically rather than randomly over time e.g. cyclic food production would result in large litter size, high juvenile survival and low adult survival (Stenseth, 1983), which is a pattern observed in *K. breviceps* (see Chapters 3 and 4). Movement may be the necessary consequence of the exploitation of a temporary habitat (Rogers, 1983). Habitat thus is the driving force for movement and migrants are therefore refugees from deteriorating conditions as the habitat they live in becomes increasingly crowded (Rogers, 1983)- the apparent “hot spots” found in *Kogia* distribution may be an indicator of that. Migrants that are able to feed during migration will have increased survival without reducing productivity i.e. reproduction (Rogers, 1983). If migrants are escaping from deteriorating local conditions (e.g. due to lack of food or predation), it is possible that, even allowing for migration losses, their average survival exceeds that of resident animals (Rogers, 1983).

Most mammals need to find areas where resources are abundant for long enough to allow successful reproduction (Sinclair, 1983). Resource superabundances that last for shorter periods of time cannot be used by these species and thus there should be selection for individuals that can reduce the period of breeding residency or young dependence in environments which are changing rapidly (Sinclair, 1983). Such environments are usually unpredictable in both timing and location of high resource areas and thus selection would favour those that adopted a nomadic existence, moving in unpredictable ways rather than following a prescribed regular migration (Sinclair, 1983). However, there are some examples, like the wildebeest populations in the Tanzanian Serengeti,

where only a proportion of the population migrates, the rest being resident, suggesting these animals are adopting a mixed evolutionary stable strategy (Sinclair, 1983). In general, one should expect a proportion of the population to become resident whenever year-round conditions allow it. The size of the resident and migrant portions of this mixed strategy would depend on the relative abundances of resources available to them (Sinclair, 1983). Just to what extent this may be the case for either *Kogia* species remains to be speculated and more studies exploring the abundance of prey (i.e. cephalopods) as well as predator/prey interactions need to be carried out to elucidate this issue. In addition, studies on wild *Kogia* would help clarify whether animals are resident year-round, or have a migratory phase during part of the year (and if so, whether all animals migrate or just a proportion of the population).

#### 8.4.5.1.3 Predation

Finally, predator/prey interactions between potential predators such as sharks and *Kogia* may be cyclic, causing movement of *Kogia* to other localities. Locally unstable predator-prey interactions may be regionally stabilized by the patchiness and contiguous distribution of prey, and by aggregations of predators at sites of high prey density (Horn, 1983). Drawing predators (such as sharks) to areas of prey abundance allows them to feed efficiently and to preserve their abundance, while it draws predators away from precariously small prey populations and thus provides a refuge in which prey at low density can escape predation (Horn, 1983). The prey (in this instance *Kogia* species) may disperse to homogenize their populations, decreasing regional stability and possibly lowering diversity or the prey may disperse to colonize areas recently denuded and vacated by predators, promoting regional stability and heterogeneity (Horn, 1983). The dispersal of predators can either homogenize their populations and cause regional instabilities or allow predators to converge on areas of high prey abundance and stabilize regional interactions between predator and prey (Horn, 1983). The differences in effect of dispersal are not due to different levels of dispersal, but rather to the pattern of dispersive responses of the prey and predator to their own and each others' local abundances (Horn, 1983). Frequent, copious dispersal is usually associated with species formerly described as r-selected, which are subject to extreme fluctuations in numbers, with high mortality, but also high rates of population growth through fecundity, early breeding, rapid development, and small body size (Horn, 1983). These characteristics

have emerged to be true for the life history strategies of both *Kogia* species (see Chapter 9).

If an animal is at risk from predators when feeding in certain areas of its territory, a resulting change in foraging behaviour to minimize that risk may alter its territorial requirements i.e. one might expect the pattern of foraging and dispersion of individuals to be substantially altered by a high predation risk (Greenwood and Swingland, 1983). Food and predators are the two main factors influencing the diurnal migration of sockeye salmon *Oncorhynchus nerka* (Greenwood and Swingland, 1983). During the day the animals stay at depth, because low light levels protect them from predation at dusk they rise to the surface to feed (Greenwood and Swingland, 1983). A similar combination of finding large food supplies (for reproduction) and avoiding predators is also found in some ungulate species. Large predators like lion and hyena are much more sedentary in comparison to the ungulates they feed on (Sinclair, 1983). Thus the migratory strategy of wildebeest in the Serengeti, which has one of the most extensive migrations among the African ungulates, allows them to escape their predators in addition to finding a sufficient food supply (Sinclair, 1983). Unfortunately, we have no data on which shark species prey on *Kogia* and to what extent, and thus have no idea how large these potential predators' territories are. However, recent genetic studies on the great white shark *Carcharodon carcharias* indicate that dispersal of individuals is more extensive than has been indicated by tagging studies (Pardini *et al.*, 2001). Great white sharks are thought to inhabit primarily inshore continental shelf waters as well as do extensive oceanic travel and were found to have a preference for depths between 0-5 metres and 300-500 metres, spending 90% of the day at these depths and little time at intermediate depths (Boustany *et al.*, 2002). Furthermore, they were found to be able to tolerate a broad temperature range from 4.8°C to 26°C (Boustany *et al.*, 2002). Both the depth and temperature range coincide with the feeding depth and habitat of *K. breviceps* (see Chapters 6 and 7) and would thus make it a prime prey target species for great whites. Predation on *Kogia* by great white sharks has been reported (Long, 1991; Heithaus, 2001), but direct observations remain scarce.

As seen above the factors leading to a high dispersal rate are intricately interwoven and it is therefore difficult to establish any form of causality. On the one hand, the dispersal of the main food source of *K. breviceps*, namely squid, may have caused the high dispersal rate, which was followed by an increase in predation risk from

sharks, resulting in high adult mortality and thus high reproductive rates. On the other hand high predation pressure may have resulted in wide dispersal as well as an opportunistic feeding behaviour and a high reproductive rate. This is perhaps a more likely scenario as the combined characteristics of predator avoidance by “inking”, predator mimicry by exhibiting “false-gill” markings, a generalist diet and a fast life history strategy all suggest that predator avoidance is a primary selective force in this species.

#### 8.4.5.1.4 Additional factors

Other factors such as mating systems and habitat availability may also influence dispersal patterns in *Kogia*. Mating systems of animals are inextricably linked to their spatial and group dynamics and thus to their population structure. As such, the extent to which animals move from area to area or group to group will have profound consequences for a species’ social organisation (Greenwood, 1983). Thus it is argued that patterns of dispersal are linked to the type of mating system and that differences between mating systems have important implications for the population and social structure of a species (Greenwood, 1983). In this respect the proposed roving-male mating system for the two *Kogia* species (see Chapter 4) would facilitate dispersal of males in search of receptive females. As females also appear to be solitary and not form social groups as seen in other cetacean species with a roving-male strategy, such as the sperm whale *P. macrocephalus* (Connor *et al.*, 2000), dispersal of females may be equally as high.

Furthermore, the movement behaviour of individuals can be determined by the range of habitats available. A species can occupy a variety of environments either because the species has a number of divergent individuals, each a habitat specialist, or because individuals are habitat generalists (Swingland, 1983). If different sections of the population or species are each adapted to their specialized habitat, then polymorphism will result in populations or species with broad habitat use (Swingland, 1983). This niche-variation hypothesis states that species with broader ecological niches should be more variable than those with narrow niches because of the action of disruptive selection. Some researchers believe that environments with high temporal heterogeneity will select for individuals with broad ecological niches and that populations of such individuals might be more likely to show intraspecific differences in movement. This

may be applicable to *K. breviceps* since they have a relatively broad ecological niche in a temporally unstable environment (see Chapter 6). In addition it was shown that certain parts of the population like reproductively active females and immature animals feed on different prey than reproductively inactive females and mature males (see Chapter 6). The corollary is that species in temporally homogenous environments should not show dichotomy in movement patterns because they will have narrower niches, as is suggested for *K. sima* (see Chapter 6) (Swingland, 1983). However, too little is known about *Kogia* movements, in particular the differences in movement patterns between the two species, to speculate too widely to what extent the different mating systems and habitats influence dispersal patterns.

#### 8.4.6 Comparison with other cetaceans

As already outlined in Chapters 3 to 5 the life history strategies of *Kogia* and the harbour porpoise *P. phocoena* are very similar (see Chapter 9). However, the above data indicate that, possibly contrary to expectations, the population genetic structures are very different. Nucleotide diversities of harbour porpoises are higher than that of humpback whales *M. novaeangliae* when averaged over all three ocean basins (Rosel *et al.*, 1995) (Table 8.3). But while at least *K. breviceps* has a wide distribution with interbreeding populations in the Southern Hemisphere, the harbour porpoise shows distinct population structuring throughout its range (Rosel *et al.*, 1995; 1999a, b; Tolley *et al.*, 1999). Thus differences between the two *Kogia* species, in particular *K. breviceps*, and the harbour porpoise, leading to a difference in the phylogeographic patterns, may be due to other parts of their ecology. Rosel *et al.* (1995) suggest that the restricted distribution of the harbour porpoise to coastal waters would have led to the higher degree of reproductive isolation between populations compared to other cosmopolitan species like the humpback whale.

Investigating the diversity of the mitochondrial control region in sperm whales, *P. macrocephalus*, Lyrholm *et al.* (1996) report an unusually low level of intraspecific mtDNA diversity compared to that of other mammals. Both the nucleotide diversity and the haplotype diversity are considerably lower than that of other mammals (see Table 8.3). To date only 16 haplotypes have been described worldwide for the species (Lyrholm and Gyllensten, 1998), which is in stark contrast to the results presented here for the closest relatives of the sperm whale. However, subsequent studies indicate that

significant differences between ocean basins in the maternally inherited mtDNA, while little or no differentiation exists between ocean basins in the biparentally inherited nuclear DNA, indicating a sex-biased dispersal pattern in the species (Lyrholm *et al.*, 1999). A similarly low nucleotide diversity was found in African savannah elephants *Loxodonta africana*, which show a similar social structure with roving males and matrilineal groups like the sperm whale (Weilgart *et al.*, 1996; Nyakaana and Arctander, 1999). In this respect, the lack of social cohesion in *Kogia* would also present one of the main differences between the sperm whale, *P. macrocephalus*, which travels in stable social groups (Hoelzel, 1994; Lyrholm *et al.*, 1999), and *K. breviceps*, and may to a large extent account for the differences seen in the phylogeographic patterns of the two species. Additional contributing factors would be the differences in reproductive rates as well as the lack of matrilines in *K. breviceps*. These findings do not only show that even closely related sister taxa like *Physeter* and *Kogia* can have quite different patterns in genetic variability, but also suggest that, in addition to a possible dispersal by male *Kogia* (see Chapter 4), female *K. breviceps* may disperse widely as well. As described in Chapter 4 both the testis size and the group size suggest a roving male mating strategy for both *K. breviceps* and *K. sima*, similar to that seen in bottlenose dolphins *T. truncatus* or even the sperm whale. The above results for the maternally inherited mtDNA suggest that *Kogia* females disperse widely in the Southern Hemisphere, and perhaps even across the equator. This is an unusual pattern for female mammals (Greenwood, 1983), and in this context it would be interesting to investigate the nuclear DNA of *Kogia* further in order to shed more light on the male dispersal pattern.

Cetacean species, which have a similar offshore habitat to *Kogia* and disperse widely in the Southern Hemisphere would be expected to show similarly high levels of genetic diversity. Contrary to that, studies of beaked whales in the Southern Hemisphere showed surprisingly low levels of nucleotide diversity compared to other wide-ranging cetaceans and terrestrial mammals (Dalebout, 2002). Nucleotide diversity in most wide ranging cetacean species is generally over 1%, even if only regional populations are considered (Rosel *et al.*, 1994; 1999a, b; Hayano *et al.*, 2003). However, a survey of the phylogeographic patterns of the Ziphiidae in the Southern Hemisphere indicated that only Cuvier's beaked whale *Ziphius cavirostris* and the southern bottlenose whale *Hyperoodon planifrons* had nucleotide diversities over 1% ( $\pi$ : 1.18%±0.68% and 3.73%±2.16%, respectively) (Dalebout, 2002). Similarly low levels of genetic diversity

have been attributed to either low abundance or declining population size (Rosel *et al.*, 1995; O’Corry-Crowe *et al.*, 1997), or to a matrifocal social structure as was found in sperm whales (Lyrholm and Gyllensten, 1998; Whitehead, 1998), killer whales *O. orca* (Hoelzel *et al.*, 1998) and narwhals *Monodon monoceros* (Palsbøll *et al.*, 1997). In this respect the results indicate once again that even species that appear superficially similar in their life histories and distributions may have vast differences in population structure.

#### **8.4.7 Recommendations for conservation and management strategies**

Although the genetic structure of a population may often be considered of secondary importance in deciding management strategies, such an analysis can be extremely useful in the preceding decision of identifying populations that are highly independent demographically (Lande, 1991). The above data do indicate that the *Kogia* populations off South Africa are somewhat reproductively isolated from other populations in the Southern Hemisphere. The absence of any detectable genetic differences between a number of populations such as the New Zealand and Australian populations does not necessarily imply that the interchange of individuals between them is so large that the populations could be treated as a single unit for management purposes (Anonymous, 1991). Although these data are reassuring in a time when numerous populations of large and small mammals are under threat from human related causes world-wide, the fact remains that certain locations in the Southern Hemisphere present “hot-spots” for *Kogia*. In the absence of any data from live, wild animals these “hot-spots” are currently indicated by high stranding rates of both live and dead animals, including a high occurrence of cow/calf pairs. Both South Africa and New Zealand represent such “hot-spots” and may present possible breeding grounds for either *Kogia* species (Ross, 1979; 1984; Tuohy *et al.*, 2001). In this context, the continued health of these *Kogia* populations should be monitored closely and the populations should be treated conservatively as separate stocks in the case of any signs of threats (Dizon *et al.*, 1992).

In the absence of detectable genetic differentiation it is also necessary to consider possible morphological, behavioural, geographical and demographic differences (Anonymous, 1991). As these data are widely lacking for most populations of the two *Kogia* species and only basic data are available for the two *Kogia* populations off South Africa, it is at this stage not possible to nominate the populations analysed here as

panmictic super-populations (Dizon *et al.*, 1997a). It is still unknown whether there are differences in life history or morphology between the so-called “hot spots”. Until more data can be gathered to answer these questions unequivocally the continued survival of these “hot spot” populations of these two rare species should be ensured through further research and protection.

#### 8.4.8 Further research

There are two possible reasons for the lack of significant population structure in *K. breviceps* as determined by the mtDNA analysis: a) substantial gene flow may be present among populations or b) there is a lack of sufficient resolution to detect slight genetic differentiation.

Although the analysis of maternally inherited mtDNA is appropriate for determining the population substructure as it represents the female component of a species, the recommendations of the IWC workshop on the genetic ecology of cetaceans clearly states that “a failure to detect genetic differentiation should not be a reason for pooling two putative populations into a single management unit” (Dizon *et al.*, 1997a). A thorough investigation of population structure should involve both nuclear and mtDNA markers (Lande, 1991; Dizon *et al.*, 1997a).

Because mtDNA is maternally inherited, differences in dispersal between males and females can lead to differences in patterns of population differentiation for biparentally versus maternally inherited genes (Palumbi *et al.*, 1991). As the present study only examined maternally inherited mtDNA, examination of nuclear markers may present a very different picture and provide additional information about dispersal patterns of *Kogia* males. Unfortunately the extraction of nuclear DNA from ancient material is still problematic, but a concerted effort could be made to obtain tissue material from contemporary strandings of *Kogia*, which would facilitate the analysis of nuclear DNA in the two species.

In addition, the sample size available from South America was very small. Although it is possible to detect fixed genetic differences between populations with sample sizes of about 20 animals per population, it is recommended to use larger samples than that (between 20 and 50 animals from each population), which should originate from throughout the geographic range, as cetacean populations are often structured into groups of closely related animals (Anonymous, 1991). In this respect, the

addition of further samples, in particular from South America, would elucidate the population structure in the Southern Hemisphere further. Finally, a comparison with populations from the Northern Hemisphere would prove interesting as the current data indicate extensive movement not just throughout the Southern Hemisphere, but possible also across the equator. Genetic exchange across the equator has to date not been shown for any cetacean population and in this respect an examination of this phenomenon would further elucidate the unusual life history strategies employed by the two *Kogia* species.

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## *Chapter 9: General Discussion and Conclusions*

*“The only true voyage of discovery is not to go to new places, but to have other eyes”*

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*Marcel Proust*



## **9.1 Summary of the results from the present study**

### **9.1.1 Sample**

The size-frequency analysis for *Kogia breviceps* showed that the sample was biased towards immature males and mature females, while the sample for *K. sima* was normally distributed.

### **9.1.2 Age and growth**

Teeth from 80 *K. breviceps* and 45 *K. sima* from South African animals were used in the age determination. In addition, age estimates were also available for 27 *K. breviceps* and one *K. sima* from Australia. A good correlation between cemental and dentinal age estimates was found for both species, although cemental readings may not be as reliable in *K. sima* as they are for *K. breviceps*. The clearer GLGs in *K. breviceps* with less accessory layers may reflect the differences in distribution patterns between the two *Kogia* species, with *K. breviceps* inhabiting cooler waters than *K. sima*. Age estimates from Ross' 1979 study and from the present study were not significantly different. No seasonal pattern in dentinal deposition was found for either species of *Kogia*. The pulp cavity started to become occluded as early as 288cm body length and 14 years in *K. breviceps*, while it started to close at 196cm body length and 11 years in *K. sima*. The von Bertalanffy growth equation gave the best fit for the data based on the smallest residual sums of squares values in both *K. breviceps* and *K. sima*. Length at birth for *K. breviceps* was about 120cm and the weight around 53kg, while it was about 103cm and 14kg for *K. sima*. These data indicated that *K. breviceps* neonates were born at 40.5% of mean adult asymptotic length (296cm), whereas it was 40.2% in *K. sima* (mean adult asymptotic length: 256.5cm). The results for the foetal growth rate in cm/day during the linear part of the growth curve using Kasuya's (1977) formula indicated that growth was slightly faster in *K. breviceps* (0.34cm/day) than *K. sima* (0.31cm/day). The asymptotic length for *K. breviceps* females was calculated as 306.04cm by the growth model and for males as 286.08cm. Both sexes reached physical maturity at about the same age of 15 years. The longest female *K. breviceps* in the sample measured 327.6cm and the longest male 330.5cm. The oldest female *K. breviceps* in the sample was estimated to be 22.4 years old. The oldest *K. breviceps* male from South Africa was estimated to be 13.33 years old and the oldest Australian male

was 16 years old. This indicated a life expectancy between 16 and 23 years in *K. breviceps*. The heaviest female weighed 480kg and the heaviest male weighed 374.03kg. The asymptotic length calculated by the growth model was 249.14cm in *K. sima* females, while the males reached physical maturity at a slightly larger body size of 263.75cm. This corresponds to 13 and 16 years of age for females and males, respectively. The longest animal in the sample was a 274.3cm long female and for male *K. sima* the longest animal measured 260.4cm. The oldest female was 21.5 years and the oldest male was estimated to be 17 years old. These data indicated a life expectancy of 17-22 years in *K. sima*. The heaviest female in the sample weighed 264kg, and the heaviest male weighed 303kg. In *K. breviceps* age at ASM and age at physical maturity was the same for both sexes. In contrast, length at both sexual and physical maturity was shorter in males than in females. Thus these results would indicate that females are larger in body size than males in *K. breviceps*. A different pattern could be seen in *K. sima*, where females were both older and longer at ASM, but males “overtook” them and were older and longer at physical maturity. *K. breviceps* females had a smaller growth rate constant ( $k$ ) than *K. sima*, which is in agreement with the general trend that smaller species have higher growth rates than larger ones. The data for males did not support this trend. Growth constants for both male *K. breviceps* and female *K. sima* were remarkably higher than for other odontocetes of similar size. Appendages such as pectoral fins, dorsal fin, and flukes were larger in *K. sima* than *K. breviceps*.

### 9.1.3 Male reproduction

Reproductive organs from 19 *K. breviceps* and 19 *K. sima* males were examined to determine the reproductive status of the individual animals. The histology of the testes of immature males, animals in early spermatogenesis, and animals in late spermatogenesis was described and histological and morphological parameters for the individual stages of sexual maturity were given. In male *K. breviceps* ASM occurred between 2.5 and 5 years, 241-242cm and 210.0- 233.6kg, while it occurred between 2.55 and three years of age in male *K. sima*, a body length of 197cm and body weights between 111.8kg-124.0kg. The maximum combined testis weight made up 1.04% of the total body weight in *K. breviceps* and 2.00% in *K. sima*. Based on data on testes size, sexual size dimorphism, signs of intraspecific fighting, and group size a polygynous mating system with a roving male strategy was proposed for both species. A detailed

examination of seasonality of spermatogenesis was not possible due to the small sample size, but the year-round presence of *K. sima* males in late spermatogenesis suggested an absence of seasonal testicular activity in this species. Examination of sperm morphology indicated that the spermatozoa of *K. breviceps* and *K. sima* were similar in shape and size, with *K. breviceps* having a more rounded sperm head, while it was more bullet-shaped in *K. sima*. In both species the surface area of the sperm head was the same and the midpiece was short and comprised of spherical mitochondria arranged in rows and columns. Both species had five to six rows of spherical mitochondria, with five mitochondria per row, resulting in 25 to 30 mitochondria. While the mean total length of the sperm was larger in *K. breviceps*, the mean length of the head of the spermatozoon was slightly but significantly larger in *K. sima*.

#### 9.1.4 Female reproduction

Reproductive organs from 25 female *K. breviceps* and 26 female *K. sima* from South Africa were examined to determine the reproductive status of the individual animals. The morphological characteristics and colour of the ovaries in both species of *Kogia* were in agreement with previous reports. Ovulations occurred equally in both ovaries in *K. breviceps*. The onset of sexual maturity in female *K. breviceps* was estimated to be at about 262cm and around five years and the weight at the onset of sexual maturity was between 272.2kg and 301kg. The ovulation rate of 0.9 per year for *K. breviceps* indicated that, on average, ovulations occurred about every 13.3 months. The gestation length calculated based on a neonate length of 120cm was 353.3 days or 11.8 months, while the monthly occurrence of foetuses and juveniles suggested a gestation period of approximately 11 months. There was a reproductive season with conceptions occurring from April to September and births possibly occurring from March to August in *K. breviceps*. Weaning may start after a year of lactation, but lactation may continue for two years. The foetal sex ratio in *K. breviceps* was biased towards males and this trend was even stronger in the juvenile sex ratio. In *K. sima* the left ovary was significantly more active than the right one. The onset of sexual maturity for *K. sima* females occurred at about 215cm and around five GLGs and between 155.6kg and 169kg. *K. sima* females had an ovulation rate of 0.7 per year, which means that ovulations occurred about every 17.1 months (or roughly one and a half years). Using Kasuya's (1977) formula the estimated gestation length, based on a neonate length

of 103cm, was 333.3 days or 11.1 months, while the monthly occurrence of foetuses and neonates suggested a gestation length of 12 months. For *K. sima* both conceptions and births occurred between December and March. Lactation may last at least one year, but weaning can start as early as six months. 11.5% of mature female *K. sima* that stranded along the Southern African coast were found to be simultaneously lactating and pregnant. These data indicated that *K. sima* may also show annual reproduction, if the conditions are right, although that may be facultative and some animals may only reproduce every two years. The reproductive strategy determined for both *Kogia* species indicated that lactation lasts about one year in both species, but may extend to two years. A relatively high percentage of females was simultaneously lactating and pregnant in both species, but the accumulation rate of corpora indicated that although *K. breviceps* may have an annual reproduction, at least some *K. sima* females may only reproduce every two years. Both species exhibited seasonal reproduction, but while *K. breviceps* appeared to have a protracted mating and calving season of six months, *K. sima* exhibits a shorter mating and calving season over the period of four months with births occurring during the warmest part of the year. The mating and calving seasons overlapped slightly between the two *Kogia* species off South Africa. Post-partum ovulation was suggested for both species.

### **9.1.5 Diet**

Stomach contents of 42 *K. breviceps* (21 females, 20 males and one animal of unknown sex) and 33 *K. sima* (20 females and 13 males) stranded along the South African coastline were examined. The diet of *K. breviceps* comprised 50 different cephalopod species from 22 families and 17 other prey species including fish (12 species), crustaceans (five species), and colonial salps (one species). In contrast, *K. sima* fed on a smaller range of prey species made up of 32 cephalopod species from 17 families and six others (three fish and three crustacean species).

The results of the dietary analysis indicated that both *Kogia* species, which are sympatric off the coast of Southern Africa, shared the same ecological niche in terms of prey species. Statistical analyses using both the Simpson and Shannon-Weaver diversity indices showed that the diets of *K. breviceps* and *K. sima* were significantly different in terms of diversity of prey species ( $p < 0.0005$  and  $p < 0.0001$ , respectively). In addition, the diet of the two *Kogia* species was also significantly different in terms of species richness

( $p < 0.0001$ ). However, the niche overlap index of 0.86 (where 1.0 indicates complete overlap and 0.0 indicates none) indicated that the diet and therefore the foraging areas of the two species overlapped to a great extent. While both *Kogia* species fed on the same main prey items (*Histioteuthis* sp. and *Lycoteuthis diadema*), each whale species fed on a suite of prey species which differed between the two whale species. An examination of prey size indicated that little difference existed between the sizes of prey consumed by *K. breviceps* and *K. sima*. However, the data indicated some separation of the niche in the form of trophic segregation, spatial segregation, and temporal segregation. *K. breviceps* was more of a generalist feeder than *K. sima*, which could be considered a specialist feeder, and the data on prey size indicated that *K. sima* fed on slightly larger prey than *K. breviceps*, although the latter fed on a larger range of prey sizes. No clear preference for either ammoniacal or muscular squid could be observed in either whale species. The diet of both *Kogia* species included benthic prey, indicating that they could dive to the bottom at least in coastal waters up to 200m in depth. Furthermore, they also fed over the continental shelf and over the slope. The presence of some deep-water species in the diet of *K. breviceps* indicated that this species also foraged over the lower slope and slope edge, while *K. sima* foraged at lesser depths. This segregation of the niche along the spatial dimension does not only concentrate on depth, but also resulted in an inshore/offshore segregation. Deep-diving species are able to exploit more offshore areas and gain access to prey that is unavailable to the shallower diving species and are thus often found over deep ocean areas, while the shallower foraging/diving species, in this case *K. sima*, is restricted to the shallower inshore waters. These results also have implications for the distribution ranges of the two *Kogia* species. The ultimate controlling factor for the distribution of cetaceans is food and offshore species of cetaceans feed on a higher variety of prey, allowing them to be distributed over a wide range. Equally, a large range results in the animal encountering more types of prey and thus in having a larger niche breadth, thus the causality in this case is unclear. In this respect the generalist diet of *K. breviceps* allows it to have a larger distribution than *K. sima* and travel more widely. In terms of temporal segregation the feeding strategy (being either generalist or specialist) can have an effect on the pattern of reproduction. *K. breviceps*, being the generalist feeder, had a longer mating and calving period extending over a period of six months, while *K. sima*, which was more of a specialist feeder, had a shorter mating and calving period of four months. The observed differences in reproductive seasonality in the two *Kogia* species off South Africa may have been

selected for in order to prevent utilisation of the same resource at a time when energetic demands are the highest.

In addition, the diets of males and females, immature and mature animals, and animals belonging to group 1 (sexually mature males and sexually mature females neither lactating, pregnant or accompanied by a calf) and group 2 (immature animals of both sexes and females that were lactating and/or pregnant and/or accompanied by a calf) within each species were also overlapping to great extent as indicated by niche overlap indices. It is thought that the partitioning into subgroups and the use of different foraging ranges, different prey sizes, and different prey species aids in resource partitioning and thus segregation of the niche. In both *Kogia* species females fed to a larger extent on *Histioteuthis* sp. than males, which had a more diverse diet. In *K. breviceps* males fed to a larger extent on fish than females, which in turn showed a preference for crustaceans. The sexual dimorphism found in *K. breviceps* was also reflected in the prey size preferences in *K. breviceps*, with females taking same-sized as well as slightly larger prey than males. In both species of *Kogia* mature animals consumed more fish than immature animals. In addition, in *K. breviceps* mature animals foraged predominantly on a different species of fish (*Phosichthys argenteus*) to immature animals (*Merluccius capensis*). In *K. sima* there was also some difference in the type of cephalopod consumed: while mature animals consumed mainly *Loligo vulgaris*, immature animals fed predominantly on *Sepia papillata*. While in both species mature animals fed mainly on larger prey than immature animals (80-100mm), immature *K. sima* foraged predominantly on much smaller prey (0-20mm) than immature *K. breviceps* (60-80mm). This may present further subtle differences in niche segregation between the two *Kogia* species. In *K. breviceps* animals belonging to group 1 showed a clear preference for *Loligo vulgaris reynaudii* and for fish. Animals of both *Kogia* species from group 2 foraged predominantly on *Sepia* sp. and *Sepia papillata*. It is interesting to note that group 1 in *K. sima* fed almost twice as much on *Lycoteuthis diadema* than group 2, while animals from group 2 in *K. breviceps* consumed more *Lycoteuthis diadema* than those from group 1. This seems to present a further overlap between the two *Kogia* species with *K. breviceps* from group 2 and *K. sima* from group 1 feeding to large extents on *Lycoteuthis diadema*, and may indicate some spatial overlap in foraging area between the two groups of the two *Kogia* species. Interestingly, the size-frequency analysis of the prey indicated that in both species animals belonging to group 1 fed predominantly on prey that was 80 to 100mm in size, while animals from group 2

fed on prey 60-80 mm in size. In addition, *K. sima* from group 2 also fed on smaller prey 0-20mm in size. In both *Kogia* species females accompanied by calves and immature young fed on smaller prey and closer inshore than mature males and non-reproducing mature females. This inshore movement may be due to the fact that the cow would not have to dive as deep in search of prey as she would over the edge of the continental shelf. Thus she would not have to leave her calf unattended on the surface for too long or reduce her own foraging success, because the calf would not be able to dive for as long or as deep. The preferred prey of animals belonging to group 1 (*Sepia* sp.) inhabits shallower waters and contains more calcium than other cephalopods and may thus be important in the diet of lactating females and growing immature animals.

### **9.1.6 Stranding patterns**

In order to determine stranding patterns of the two *Kogia* species along the South African coastline 106 strandings of *K. breviceps* and 85 strandings of *K. sima* between 1880 and 1995 were analysed. Strandings of male and female *K. breviceps* occurred in more or less equal numbers, whereas *K. sima* had a slightly higher rate of female strandings. This may be due to the fact that females seem to move closer inshore with their young in order to feed or due to reproductive stress as females of both species may ovulate up to once a year and are often found to be simultaneously lactating and pregnant. The majority of the stranded animals were mature and strandings comprised mainly dead animals. The fact that the majority of the strandings for each species were single animals is probably a reflection of the group size of the two species, which appear to be mainly solitary. The maximum number of animals that stranded together was three for *K. breviceps* (composed of a pregnant and lactating female accompanied by two smaller, unsexed individuals) and four for *K. sima* (composed of one immature male and three immature females). The temporal analysis of *Kogia* strandings over the years showed clearer peaks for *K. sima* than for *K. breviceps* strandings. This may indicate some correlation with environmental factors influencing inshore/offshore movement of *K. sima*, which does not influence *K. breviceps*. A general decrease in the number of strandings of both species was observed in the 1990's. *K. breviceps* stranded more frequently during the austral winter and spring (July to October), while *K. sima* stranded in more or less equal numbers throughout the year, with small peaks in late summer and winter (April and July, respectively). Although no strong seasonal changes were found in

the flow of the Agulhas Current off the South African coastline, it may be possible that meanders and plumes shooting off the current and travelling towards the coast are more prevalent at a certain time of year, resulting in an increased number of strandings. Peaks in the number of live strandings in relation to month in both *Kogia* species appeared to be associated with reproductive events such as calving and weaning as they occurred just after the end of the calving season, probably resulting from a combination of factors such as difficulties during birth, unsuccessful weaning of the calf, reproductive stress for the cow associated with simultaneous pregnancy and lactation, and, lastly, a slight migration further inshore. In addition, the inshore movement in relation to feeding observed in cow/calf pairs and immature animals may also increase the possibility of stranding as the animals find themselves in a more complex environment than the one they are used to. No strandings of *K. sima* were recorded during June over the last 30 years. June is the coldest month in the austral winter and therefore sea surface temperatures (SST's) are the lowest off the Southern African coastline during this month. The analysis of *Kogia* peak stranding locations by longitude indicated that *K. breviceps* stranded in both the Western and Eastern Cape regions, but had a "peak" location at around 20°E in the Western Cape. In contrast, *K. sima* almost exclusively stranded in the Eastern Cape at around 26°E and was only found to strand in the Western Cape during the summer months. This indicated a clear preference of *K. sima* for the Eastern Cape region and shows that the species preferred warmer water temperatures, especially as it was only found in the cooler waters of the Western Cape during the summer months, when water temperatures were the highest. In contrast, *K. breviceps* appeared to frequent both the Western and Eastern Cape almost equally, perhaps with a slight preference for the Western Cape. This difference in habitat preference and distribution was further supported by the general stranding distribution of the two species: the shorter strip of coastline along which *K. sima* stranded was still influenced by the warm Agulhas Current, whereas *K. breviceps* had a much broader stranding range, occurring even along the coast of Namibia, which is predominantly influenced by the cold Benguela system. An eastward movement of strandings of *K. breviceps* cow/calf pairs throughout the year may have been a result of the eastward migration of the main prey item of the cow/calf pairs and/or may have been related to the reported eastward movement of Benguela water at the same time as the strandings occurred. In contrast cow/calf strandings of *K. sima* occurred exclusively in two bays in the Eastern Cape, namely Algoa Bay and Jeffrey's Bay, which are strongly influenced by the Agulhas Current. These differences

in the stranding distribution of cow/calf pairs between the two species together with the observed differences of the general stranding distribution indicated that the Agulhas Current may in fact play a greater role in the general ecology of *K. sima*, since it is the major oceanographic feature influencing the marine environment off the Eastern Cape coast. The more “clumped” distribution of strandings of immature *Kogia* along the South African coastline, which was particularly pronounced in *K. sima*, indicated that mature and immature animals form different groups. Differences in sea-surface temperatures at the stranding location of live *K. breviceps* and *K. sima* further supported the above indication that *K. sima* appears to prefer warmer temperatures and probably has a closer association with the Agulhas Current than *K. breviceps*. Survey data in combination with the stranding data indicated that both *Kogia* species had an affinity for western boundary currents, which are usually warm currents and provide the necessary oceanographic conditions of thermal fronts that the two species need for foraging. Previous morphological studies on both *Kogia* species indicated that although *K. breviceps* had the bigger body length of the two species, *K. sima* had larger extremities such as flippers, dorsal fin, and flukes. These data supported the idea that *K. breviceps* has a more temperate, cold-water habitat and therefore smaller extremities in order to conserve body heat, while *K. sima* has a more tropical, warm water habitat, thus no need to conserve as much heat and subsequently has larger extremities. Conservation of body heat may be especially important for species, which undertake long and deep dives as is indicated by the diet data for *K. breviceps*. In contrast *K. sima* forages in shallower waters, which probably results in shorter dive times and a lesser need to conserve body heat. This in turn may lead to larger appendages. Strandings of both species of *Kogia* may also be related to the migration of their main prey, but too little is known about the biology and distribution of most cephalopod species off Southern Africa to draw any conclusions.

### 9.1.7 Population structure

In order to analyse the population structure of both *Kogia* species in the Southern Hemisphere cytochrome *b* sequences were available for 96 *K. breviceps* and 29 *K. sima*. For comparative purposes sequences of the control region were available for 41 *K. breviceps* and three *K. sima*. 46.62% of the extractions from “ancient” material resulted in clean sequences, which could be used for analysis of population structure in *Kogia*. A clear separation of *K. breviceps* and *K. sima* into two clades with a bootstrap support of

100 indicated that there were two clearly distinct *Kogia* species and that the morphological characteristics used for species identification were reliable and provided a good guideline for researchers dealing with stranded animals. The distribution of mtDNA variation in *K. breviceps* from different geographical locations in the Southern Hemisphere suggested a very close evolutionary relationship among these populations and the presence of haplotypes common to all subpopulations examined were an indication of ancestral mtDNA lineages that remain widespread following the divergence of populations. Such a pattern would arise due to extensive and historically recent gene flow in the absence of zoogeographic barriers and would require a life history strategy, which is conducive to dispersal. A lack of significant phylogeographic structure in *K. breviceps* and the high number of haplotypes found indicated substantial gene flow among populations, which would be facilitated by the movement of individuals among populations, thus inhibiting genetic differentiation of local populations. Over the short-term there appeared to be some restriction to movement between the South African and New Zealand populations, which suggested that the South African population is somewhat isolated from others in the Southern Hemisphere. *K. breviceps* are known to be solitary or occur in rather small groups and such a social structure would facilitate a high genetic diversity within species. However, it would also result in a low phylogeographic diversity, if animals travel independently and over wide ranges and do not have designated breeding grounds. There were no indications in the results that there was any greater phylogeographic structure in females than in males for *K. breviceps*. In contrast to *K. breviceps*, the data on the phylogeographic structure of *K. sima* were somewhat restrictive as the majority of the samples originated from South Africa. Nevertheless, both nucleotide and haplotype diversities were markedly lower than in *K. breviceps* and more similar to those for other small cetacean populations. The grouping of samples from Chile and Australia with common haplotypes from South Africa indicated that there is some gene flow between these populations. Additional samples of *K. sima* from other populations need to be included in the analysis in order to determine the degree of isolation between them. The higher mtDNA diversity within *K. breviceps* than within *K. sima* suggested a bigger population size for the former. The results of the genetic analysis indicated a relatively wide dispersal of *K. breviceps* in the southern Hemisphere. In evolutionary terms, the species appeared to have even crossed the equator at some stage as suggested by the fact that animals in both hemispheres shared common haplotypes. The following three different possible explanations for the

wide dispersal of *K. breviceps* were explored: the energetic requirements that facilitate annual reproduction in female *K. breviceps* may be so high that reproductively active females disperse in search of sufficient and high quality food, the abundance of squid (the main food source) may be cyclic, causing the majority of the animals to migrate in search of food at times when food availability is low, or predator/prey interactions between potential predators such as sharks and *Kogia* may be cyclic, causing movement of *Kogia* to other localities. In comparison with other cetaceans, such as the sperm whale *Physeter macrocephalus*, which shows very low levels of nucleotide diversity in the mitochondrial control region, *K. breviceps* had levels comparable to those exhibited by the humpback whale *M. novaeangliae*, which has the highest nucleotide diversity observed in a cetacean. The lack of social cohesion in *K. breviceps* compared to the sperm whale, *P. macrocephalus*, which travels in stable social groups, may to a large extent account for the differences seen in the phylogeographic patterns of the two species. Additional contributing factors would be the differences in reproductive rates as well as the lack of matriline in *K. breviceps*. The data resulting from the genetic analysis indicated that the *Kogia* populations off South Africa are somewhat reproductively isolated from other populations in the Southern Hemisphere. The absence of any detectable genetic differences between a number of populations such as the New Zealand and Australian populations does not necessarily imply that the interchange of individuals between them is so large that the populations could be treated as a single unit for management purposes. As data on the morphological, behavioural, geographical and demographic differences between different *Kogia* populations are widely lacking and only basic data are available for the two *Kogia* populations off South Africa, it is at this stage not possible to nominate the populations analysed here as panmictic super-populations.

While chapters 3 to 5 give indications of the life history strategies of the two *Kogia* species, chapters 6 to 8 present information on the general ecology. However, both the life history strategies and ecologies of *K. breviceps* and *K. sima* are intimately linked as is discussed in detail in the following sections.

## **9.2 Life history theory**

Determining the status and natural history of a species is important in order to

acquire a basic understanding about its biology as well as to determine its conservation status and ensure its continued survival. On a broader scale natural history data gain importance when viewed in terms of general mammalian or evolutionary biology.

### **9.2.1 The slow-fast continuum**

In recent years the theory of the evolution of life histories and in particular about its determining factors has changed dramatically (Charnov, 1991; Stearns, 1992; Kozlowski and Weiner, 1997). Previously body size, as well as brain size (Sacher and Staffeldt, 1974; Sacher, 1980), and metabolic rate (McNab, 1980) were believed to be key determinants of life history variation. In particular, body size appeared to be a strong determining factor and these thoughts led to the concept of the “slow-fast continuum” of life histories in mammals (Stearns, 1992) (Figure 9.1). In general larger bodied mammal species live slower lives, have lower mass-specific metabolic rates, longer gestation lengths, wean later, reach sexual maturity at a higher age, produce a lower number of young less frequently, and have longer maximum recorded lifespans, while smaller species are shorter lived, attain sexual maturity at an earlier age and shorter body length, have larger litter sizes and reproduce more frequently and have lower maximum lifespans (Read and Harvey, 1989; Promislow and Harvey, 1990; Purvis and Harvey, 1995) (Figure 9.1). This slow-fast continuum, driven by body size, seemed to explain the great variation in life history strategies observed throughout the mammalian orders, and this allometric relationship can also be seen within the Cetacea. Small odontocetes like the porpoises and small dolphins of the Genus *Cephalorhynchus* are located closer to the fast end of the slow-fast continuum as they reach sexual maturity relatively early and have a life expectancy of around 20 years (Gaskin *et al.*, 1984; Sooton, 1991; Read and Hohn, 1995; Hohn *et al.*, 1996) (see Appendix F). At the slow end of the continuum are the large mysticetes, like the bowhead whale *Balaena mysticetus*, that reach sexual maturity as late as 15 years of age and live up to a hundred years or longer as recent studies have shown (George *et al.*, 1997) (see Appendix F). The most diverse cetacean group with respect to body size and longevity are the Delphinidae, with ages at attainment of sexual maturity ranging from five years in female Commerson’s dolphins

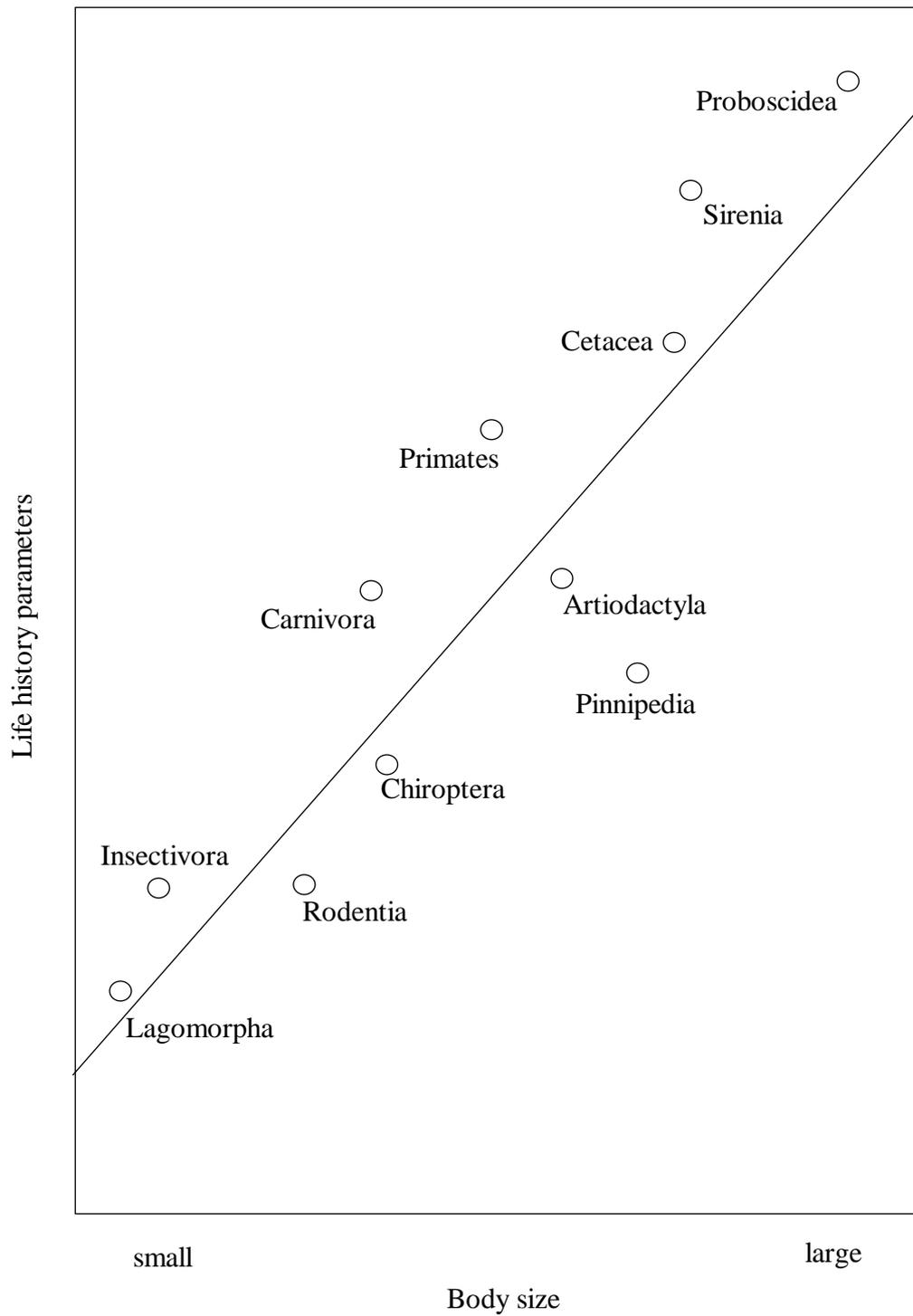


Figure 9.1: Slow-fast continuum of life histories for mammals.  
After Harvey and Purvis, 1999.

*Cephalorhynchus commersonii*, six years in common dolphins *Delphinus delphis*, and seven years in Hector's dolphins *Cephalorhynchus hectori*, to 16 years in killer whales *Orcinus orca* (Appendix F). However, most medium-sized delphinids attain sexual maturity between eight and 12 years of age (Perrin and Reilly, 1984). In this context it has been argued that porpoises, in particular the harbour porpoise *Phocoena phocoena*, represent one extreme of life history strategies among cetaceans in that they have an extremely short life span (maximum recorded age is 24 years) (Hohn and Brownell, 1990; Lockyer, 1995), early maturity (between three and four years of age) (Read, 1990a; Sørensen and Kinze, 1994; Read and Hohn, 1995), and very high reproductive rates (annual reproduction) (Sørensen and Kinze, 1994; Read and Hohn, 1995) compared to other cetaceans like the larger odontocetes or mysticetes (Read and Hohn, 1995). Similar results have also been presented for the Dall's porpoise *Phocoenoides dalli* (Ferrero and Walker, 1999). Furthermore, it was suggested that this trend represents part of the general allometric pattern observed in mammals as outlined above (Western, 1979; Read and Hohn, 1995).

### **9.2.2 The new model**

However, during the last decade the general thinking about mammalian life history strategies and in particular the factors influencing them has changed dramatically (Harvey and Purvis, 1999) and recent research indicates that in fact the ecology of a species plays a more prominent role in shaping its life history strategy than was previously assumed (Austad and Fischer, 1991; Charnov, 1991; Austad and Fischer, 1992; Kozłowski and Weiner, 1997). Although the general perception that body size is an indicator of life history strategy holds true, the slow-fast continuum remains even when the effects of body size are removed (Read and Harvey, 1989). Thus body size alone is not a reliable indicator for life history strategies. It rather appears that species with a high mortality rate (either extrinsic or intrinsic) mature early (Charnov, 1990; Promislow and Harvey, 1991) and that size at sexual maturity is determined by growth rates, which in turn are set by assimilation and respiration rates (Charnov, 1991; Purvis and Harvey, 1995; Kozłowski and Weiner, 1997) (Figure 9.2). Age at maturity, adult and juvenile mortality rates, and annual fecundity were all shown to be linked in mammalian life history strategies, even when body size was held constant (Harvey and Zammuto, 1985; Read and Harvey, 1989; Promislow and Harvey, 1990; Charnov, 1991)

(Figure 9.2). Higher adult mortality rates result in a lower age at maturity (Charnov, 1990) and in fact mortality rates may represent the primary link between ecology and life history evolution (Promislow and Harvey, 1991) (Figure 9.2). High rates of both extrinsic and

intrinsic mortality were found to be correlated not only with low age at sexual maturation, but also with other life history traits such as large litters and short gestation lengths and short inter-birth intervals (Promislow and Harvey, 1991). Factors affecting the extrinsic mortality rate include predators and parasites, whereas intrinsic mortality can be understood as resulting from choices of resource allocation for reproduction and a high reproductive turnout may increase the intrinsic mortality rate (Promislow and Harvey, 1990; 1991).

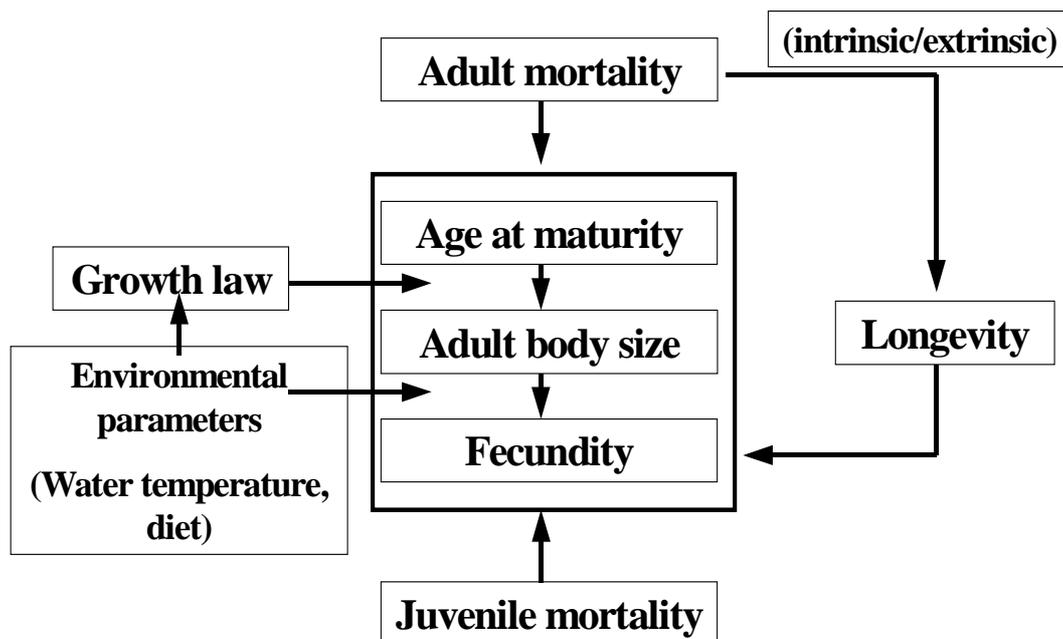


Figure 9.2: Model for mammalian life history strategies, after Charnov (1991) and Harvey and Purvis (1999).

The importance of knowledge of animal life histories for the development of conservation strategies has become ever more evident in recent years. Relating life history variation to environmental predictability and population processes may provide insights into species specific conservation as species with “slow” life histories (with characteristically late onset of maturity, slow growth, and low reproductive rates) require

larger areas and live at lower densities in more unpredictable environments (Ferguson and Larivière, 2002). As a result such species are more susceptible to the exploitation of adults in comparison to related species with “faster” life histories (Ferguson and Larivière, 2002).

### **9.3 Life history strategy of *Kogia***

Little comparative work has been done on the life history strategies of cetaceans (Kasuya, 1995) and previously, little information was available on the natural history of the genus *Kogia*. However, the data from the present study allow first conclusions to be drawn about the life history strategies of both *Kogia* species. Both species of *Kogia* are regarded as belonging to the medium to larger sized odontocetes and are located close to the similar sized dephinids on the slow-fast continuum (Figure 9.3a). The maximum recorded lengths for animals from Southern Africa show that *K. sima* has similar body lengths to the bottlenose dolphin *Tursiops truncatus* off South Africa (Cockcroft and Ross, 1990), while *K. breviceps* is somewhat larger (Table 9.1). Thus when age parameters are considered (like age at sexual maturity versus maximum age, Figure 9.3b) one would expect the age at sexual maturity and the lifespan of *Kogia* to be similar to that of a similar-sized odontocete, like the bottlenose dolphin *T. truncatus*. However, both *Kogia* species exhibit surprisingly fast life histories, with low ages at sexual maturity (between three and five years), relatively short lifespans (around 22 years), and high reproductive rates (annual reproduction) (Table 9.1). Thus they group closer with the smaller odontocetes like the porpoises and the Hector’s dolphin *C. hectori* when age parameters are considered (Figure 9.3b). In contrast, most medium-sized odontocetes, like the bottlenose dolphin, reach sexual maturity between eight and 12 years of age and dolphins of similar size reach maximum ages of between 40 and 60 years (Perrin and Reilly, 1984) (see Appendix F). A female *K. breviceps* stranded in Florida exhibited a total of 29 corpora in her ovaries (Jenness and Odell, 1978). Unfortunately no age estimate was available for this female, but if we assume attainment of sexual maturity around five years and annual ovulation as found in the present study, this female would have been around 34 years old. So, although *Kogia* elsewhere may well reach higher maximum ages overall they do not live as long as one would expect of an animal their size and similar life histories are usually only found in much smaller odontocetes, for example in some porpoises. Therefore the allometric explanation of the slow-fast

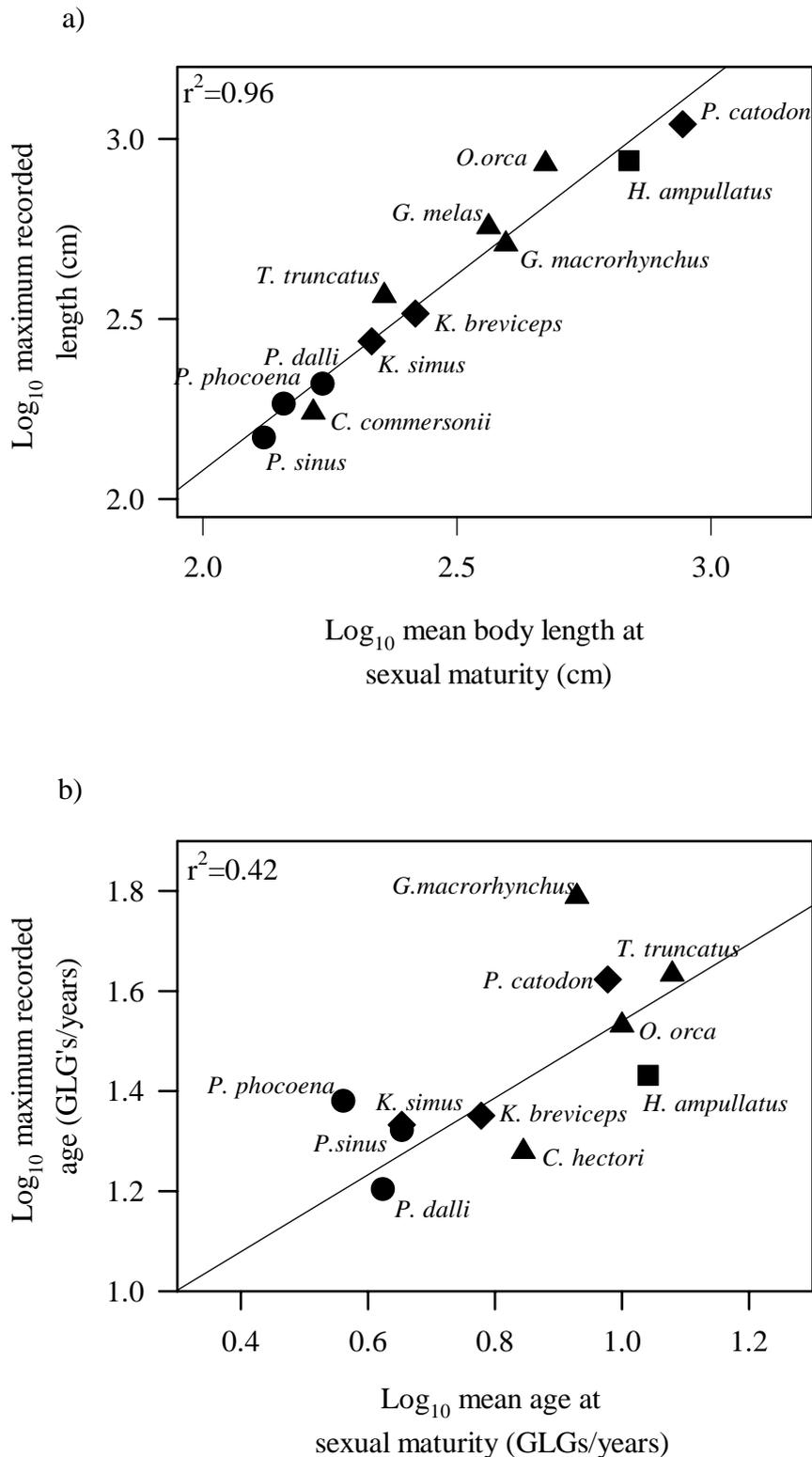


Figure 9.3: Slow-fast continuum for female odontocetes as indicated by length at sexual maturity versus maximum body length (a) and age at sexual maturity versus maximum age (b). The data are based on mean values calculated from publications listed in Appendix F. If a range was provided the median of that range was used.

continuum does not satisfactorily explain the life history strategies of *Kogia*.

Table 9.1: Summary of life history parameters of *Kogia* from South Africa from the present study.

Life history parameter		<i>K. breviceps</i>	<i>K. sima</i>
Length at birth (cm)	♂/♀	120	103
Age at sexual maturity (GLGs)	♀	~5	~5
	♂	2.5-5	2.55-3
Length at sexual maturity (cm)	♀	262	215
	♂	241-242	197
Maximum age (GLGs)	♀	22.4	21.5
	♂	13 (16*)	17
Maximum body length (cm)	♀	327.6	274.3
	♂	330.5	260.4
Gestation length (months)		11-12	11-12
Ovulation rate/ year		0.9 (1 every 13.3 mths)	0.7 (1 every 17.1 mths)
Lactating and pregnant females (%)		24.1	11.5

According to the new model for life history evolution, however, the life history parameters of low ages at sexual maturity, short lifespans, and high reproductive rates observed in the two *Kogia* are indicative of high mortality rates (Figure 9.4). These could be a result of high intrinsic mortality, due to the demands and resource allocation necessary for annual reproduction, or they could be ascribed to high extrinsic mortality such as predation pressure or parasitism. These scenarios are described in detail below (see section 9.3.2). And although mortality is not the single driving force in the evolution of life histories it does serve as an important link between various demographic and ecological factors. Body size is largely determined by environmental variables such as water temperature and prey quantity and quality, which in turn affect the so-called growth law or growth rate (Figure 9.4). Although the two *Kogia* species follow the general trend seen in mammals, with smaller species (*K. sima*) having higher growth rate constants than larger ones (*K. breviceps*), the growth rate constants for male *K. breviceps* and female *K. sima* were remarkably higher compared to those of other similar-sized odontocetes (see Chapter 3). In considering the role that ecological factors play in shaping mammalian life histories the new model (Figure 9.2) based on Charnov's (1991) and Harvey and Purvis' (1999) ideas now explains the previously little understood

observation how different sized species may exhibit rather similar life history strategies.

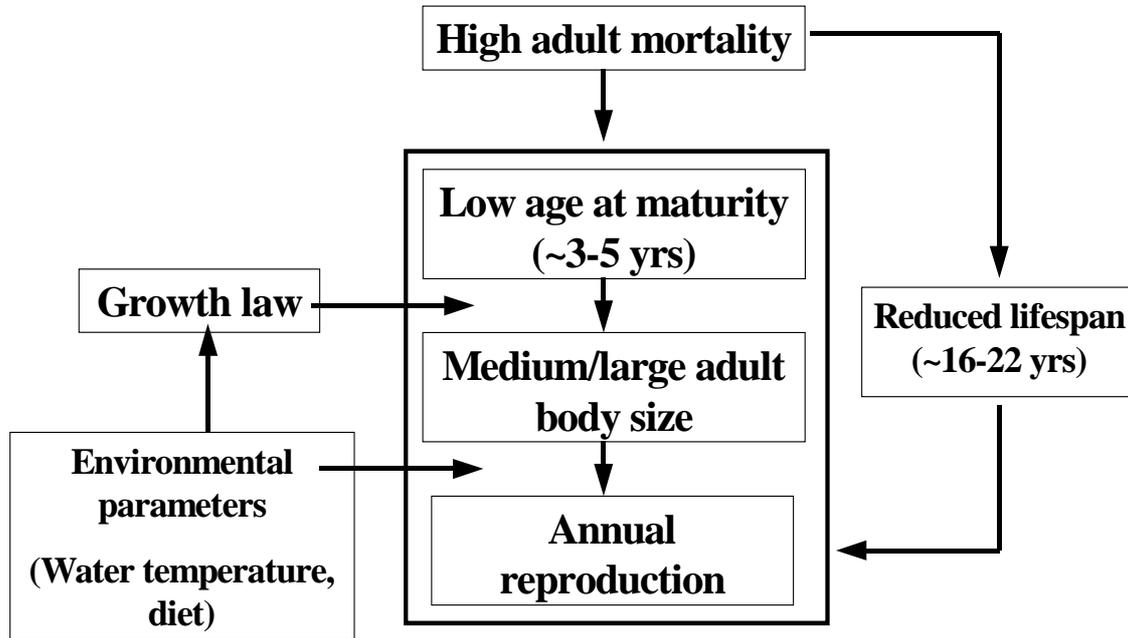


Figure 9.4: Life history strategy for *Kogia*.

### 9.3.1 Annually reproducing cetaceans

And in fact the range in body size observed in cetacean species that commonly exhibit annual reproduction is rather impressive. Those species range from the smallest odontocetes, like the Dall's porpoise *P. dalli* and harbour porpoise *P. phocoena*, over *Kogia*, which are large to medium sized odontocetes as already established, to the larger baleen whales like the minke whale *Balaenoptera acutorostrata* and the humpback whale *Megaptera novaeangliae* (Table 9.2). All have relatively low ages at sexual maturity as well as short lifespans. And it is also remarkable that those species that do not have a strictly annual reproduction, like *K. sima* and the humpback whale, also show longer gestation periods than those species with a strictly annual reproduction (Table 9.2). Estimates for mortality rates in cetaceans are difficult to obtain for obvious reasons and we know little about the mortality rates of these species, but considering the similarities between the other life history parameters one would expect them to be similarly high. Additionally, the demands of resource allocation to maintain annual reproductive rates in these species would also lead to increased intrinsic mortality rates.

One species listed here that does not exhibit annual reproduction is the blue whale, which is the largest mammal on earth. Unfortunately, no data are available on its longevity, but the low age at sexual maturity of five years is remarkable (Table 9.2). This wide range of body sizes found in cetaceans that live the fast life reflects how each species optimal body size depends upon its combination of ecological parameters.

Table 9.2: Comparison of cetacean species that commonly exhibit pregnancies in successive years.

Species	Gestation (months)	Lactation (months)	Annual reproduction?	Age at sexual maturity (yrs)	Lifespan (yrs)	Mortality rates
Dall's porpoise <i>Phocoenoides dallii</i> <sup>1</sup>	10-11	-	yes	4-5	15/22	?
Harbour porpoise <i>Phocoena phocoena</i> <sup>2</sup>	10.5	9	yes	3-4	24	?
Dwarf sperm whale <i>K. sima</i> <sup>3</sup>	12	6-12	yes (facultative)	3-4	21.5	?
Pygmy sperm whale <i>K. breviceps</i> <sup>4</sup>	11	~12	yes	5	22.4	?
Minke whale <i>Balaenoptera acutorostrata</i> <sup>5</sup>	10	3-6	Yes	6-7	50	?
Humpback whale <i>Megaptera novaeangliae</i> <sup>6</sup>	10-12	10-12	sometimes	5-7	48	?
Blue whale <i>Balaenoptera musculus</i> <sup>7</sup>	11	7	No	5	-	?

<sup>1</sup>: Newby, 1982 in: Ferrero and Walker, 1999; Ferrero and Walker, 1999; <sup>2</sup>: Gaskin *et al.*, 1984; Hohn and Brownell, 1990; Read, 1990a,b; Sørensen and Kinze, 1994;

Lockyer, 1995; Read and Hohn, 1995; <sup>3</sup>: present study; <sup>4</sup>: present study;

<sup>5</sup>: Williamson, 1975; Masaki, 1979; Best, 1982; <sup>6</sup>: Chittleborough, 1965; Clapham and Mayo, 1990; Clapham, 1992; <sup>7</sup>: Lockyer, 1984; Evans, 1987.

It is interesting to note that most species listed in Table 9.2 in which the females are commonly observed to reproduce in successive years and consequently possibly have high mortality rates (namely the harbour porpoise *P. phocoena* (Read, 1990b), Dall's porpoise *P. dalli* (Ferrero and Walker, 1999), the humpback whale *M. novaeangliae* (Clapham and Mayo, 1990; Straley *et al.*, 1994; Clapham, 1996) and *K. breviceps*) also

show reversed sexual size dimorphism (Ohsumi, 1966; Gaskin *et al.*, 1984; Kasuya, 1995; Clapham, 1996). Reversed sexual size dimorphism would be in agreement with the proposed life history strategy for *Kogia*. It has been suggested that mortality may influence the evolution of sexual size dimorphism, because if sexual dimorphism is costly to achieve in males due to delays in growth to maturity, and if, in addition, these costs must be offset by increased fecundity, species with high mortality rates may not be able to afford sexual dimorphism (Promislow and Harvey, 1991). In these cases males with low probabilities of survival cannot afford to delay growth because they run the chance of dying before beginning to reproduce (Promislow and Harvey, 1991). As other traits in the life history of *Kogia* indicate that both species may suffer high mortality rates, the little sexual size dimorphism or even possible lack thereof (i.e. both sexes being of equal size) may be explained by the idea that the resources are rather allocated to reaching sexual maturity early and beginning to reproduce than in reaching a larger body size. Ralls (1976), reviewing mammalian species in which females are larger than males, concluded that this phenomenon can be explained by the fact that larger females are better mothers. In this context the argument that the body condition of females determines the length of the reproductive cycle holds true as well. Since reversed sexual dimorphism may appear counter intuitive in a species where males fight over access to females, as in the humpback whale *M. novaeangliae* (Clapham, 1996) suggests that the relative size of the two sexes may be the result of two very different selective forces as the energetic constraints of lactation may to a greater degree favour larger size in females than does competitive ability in males.

Further similarities observed in those cetacean species that frequently exhibit annual ovulation are a relatively short gestation and lactation period and a low age at ASM. Kasuya (1995), listing similarities between the life history strategies of mysticetes and phocoenids, remarks on the short parental investment in both groups, which may also be true for *Kogia* as data from the present study indicate. He furthermore suggests that the maximum reproductive output of over 20 calves found in mysticetes may have evolved to compensate for the high juvenile mortality resulting from short parental investment. Indeed it has been suggested that species with a low probability of adult survival should be selected to produce large numbers of offspring and invest small amounts in any one offspring (Promislow and Harvey, 1991). Thus the same species will raise offspring from conception to independence as quickly as possible and consequently have small offspring with relatively short gestation and lactation lengths (Promislow and

Harvey, 1991). In porpoises the short calving interval suggests a high lifetime production (Kasuya, 1995). Although the low age of sexual maturity at three to four years and a maximum longevity of up to 24 years (Gaskin *et al.*, 1984; Hohn and Brownell, 1990; Sørensen and Kinze, 1994; Lockyer, 1995) suggests that the harbour porpoise *P. phocoena* may have up to 20 offspring per lifetime it was suggested that only a few offspring are produced per lifetime (Gaskin *et al.*, 1984; Read, 1990a). Due to the annual ovulation rate and facultative annual ovulation rate found in *K. breviceps* and *K. sima*, respectively, one can expect a high number of offspring per lifetime for the two *Kogia* species. However, the success rate of pregnancies and calf and juvenile mortality rates are unknown for the two *Kogia* species and it may well be that only a few offspring produced per lifetime survive to adulthood and reproduce. Another similarity found between mysticetes and porpoises was that apart from the mother-calf bond no other stable or long lasting social associations are reported for the two groups (Kasuya, 1995). Both stranding data and observations in the wild as well as the genetic data indicate that this is also the case in *Kogia*.

Although the proposed high mortality rate of *Kogia* may explain the low age at sexual maturity and low life expectancy it does not explain the differences in female reproductive strategy observed between the two species. When phylogenetically related species have similar physiologies and live in similar environments slight differences among the species may be due to an accumulation of small differences in morphology, physiology, ecology or behaviour (Harvey and Purvis, 1999). One possible explanation may be that the two species are threatened to differing degrees by predation due to their different group sizes. *K. breviceps* are solitary animals and may therefore be more prone to predation than *K. sima*, which occur in small groups. Previous studies on variation of predation pressure with varying group size in antelope would support this argument (Jarman, 1974). An additional explanation may be that a combination of ecological factors such as prey density and quality as well as temperature regimes have an influence on the reproductive strategy employed in cetaceans.

In conclusion the new model for life history evolution based on the ideas of Charnov (1991) and Harvey and Purvis (1999) explains how species with different body sizes may have similar life history strategies and reproductive strategies. It also shows how similar-sized species, like for example the bottlenose dolphin *T. truncatus* and *K. sima*, can exhibit very different strategies. The model indicates that body size is an adaptation to the life history of a species rather than a determinant and that ecological

processes play more important roles in the evolution of mammalian life histories than allometric constraints. In this respect the comparison of life history strategies in cetaceans may present an underlying model for testing the effects of different environments on the shaping of their life histories.

### **9.3.2 Extrinsic mortality rates in *Kogia* –predation and parasitism**

A lowered age at sexual maturity resulting from high mortality rates as a result of exploitation has been reported for populations of spotted striped dolphins (Perrin *et al.*, 1976; Kasuya, 1985) and exploited species often compensate by producing more offspring (Kasuya, 1985; Myrick *et al.*, 1986; Chivers and Myrick, 1993). However, conflicting reactions to exploitation have been reported in cetacean reproductive parameters and not all parameters behaved as expected with change in population density (Perrin and Henderson, 1984; Perrin and Reilly, 1984; Barlow, 1985; Chivers and Myrick, 1993). Furthermore there is no unequivocal evidence whether a species life history represents a strategy that has evolved over time or is a reaction to overexploitation (Kasuya, 1995). However, there is no evidence that either *Kogia* species has been subjected to excessive exploitation, but both exploitation as well as predation pressure result in higher mortality rates, thus putting the same pressure on the population (Kasuya, 1985).

#### **9.3.2.1 Predation**

One rather fascinating aspect of the biology of *Kogia* that is quoted frequently is the fact that both species appear to squirt ink in a similar way as do squid and other cephalopods (Baird *et al.*, 1996; Willis and Baird, 1998). This behaviour has previously been described as a “startle response” (Yamada, 1954; Scott and Gordaro, 1987; Caldwell and Caldwell, 1989; Baird *et al.*, 1996; Willis and Baird, 1998) and may represent a predator escape mechanism, similar to that found in cephalopods. A comparable mechanism in terrestrial mammals is found in the skunk, but such behaviour has to date not been reported for any other cetacean and it seems possible that the inking behaviour of *Kogia* has evolved as a camouflage mechanism to avoid predation by sharks or killer whales. In addition, the false gill marking characteristic for *Kogia* as well as the underslung jaw may represent a form of mimicry and consequently stranded

*Kogia* have often been mistaken for sharks by laymen (Baird *et al.*, 1996; Willis and Baird, 1998; Graham Ross, pers. com.). Credle (1988) noted that the resemblance to sharks may result in incorrect information concerning a stranding to be passed on to local authorities. Although predator mimicry is often observed in terrestrial invertebrates, for example in a number of moths, to date there is no report on a mammal exhibiting this phenomenon. Shark attacks on *Kogia* have been reported before for *K. breviceps* (Long, 1991), and in the present study two *K. breviceps* (one live animal, one dead animal) and two *K. sima* (one live animal, one dead animal) were reported to have stranded with signs of shark bites. Although these observations suggest that both *Kogia* species may be preyed upon by sharks even prior to death, the suggestion that extensive predation pressure has led to a fast life history strategy in *Kogia* remains a hypothesis that will be hard to test.

However, there are a number of factors in addition to the signs of predator avoidance and mimicry that may suggest that predation pressure plays an important role in the shaping of the life histories of the two *Kogia* species.

Predation risk is a major factor influencing group composition, size, and habitat use and it furthermore has been suggested as the selective pressure leading to the evolution of sociality in odontocetes (Heithaus, 2001). However, due to the logistic difficulties involved the interactions between predators and marine mammal prey have been little studied. A number of natural predators have been identified to prey on marine mammals. These include the killer whale *O. orca*, false killer whale *Pseudorca crassidens*, pygmy killer whale *Feresa attenuata*, polar bear *Ursus maritimus* and a variety of sharks (Heithaus, 2001). Examining the predator-prey interactions between sharks and odontocetes, Heithaus (2001) found evidence that the great white shark *Carcharodon carcharius*, tiger shark *Galeocerdo cuvier*, dusky shark *Carcharhinus obscurus*, bull shark *Carcharhinus leucas*, oceanic whitetip shark *Carcharhinus longimanus* and shortfin mako *Isurus oxyrinchus* all can be considered predators of marine mammals. In addition, the sixgill shark *Hexanchus griseus* and sevengill shark *Notorhynchus cepedianus* may be considered as predators (Heithaus, 2001). Although only the great white shark has been found to prey on *Kogia*, in particular the sixgill shark may be a potential predator as it is a large deepwater species, which is the dominant predator along the outer continental shelf and upper slope (Heithaus, 2001) and thus has a similar habitat to *Kogia*. However, recent genetic studies on the great white shark indicate that dispersal of individuals is more extensive than has been indicated by

tagging studies (Pardini *et al.*, 2001). In addition, recent data indicate that great white sharks inhabit primarily inshore continental shelf waters as well as undertake extensive oceanic travel and have a preference for depths between 0-5 metres and 300-500 metres, spending 90% of the day at these depths and little time at intermediate depths (Boustany *et al.*, 2002). Furthermore, they are able to tolerate a broad temperature range from 4.8°C to 26°C (Boustany *et al.*, 2002). Both the depth and temperature range coincide with the feeding depth and habitat of *K. breviceps* (see Chapters 6 and 7) and would thus make it a prime prey target species for great whites. However, the extent of predation by sharks on odontocetes remains difficult to quantify. As Heithaus points out, the lack of scars in an odontocete population does not necessarily indicate a low predation rate, because smaller individuals or species will be taken more often and thus scarred less frequently than large ones (2001). In South Africa marine mammals were found to be the most important prey of large juvenile white sharks between 1983 and 1988, with dolphins making up the majority of the marine mammal prey (Cliff *et al.*, 1989).

Group formation is one way animals can reduce predation risk, but groups may also form for other reasons entirely, such as food finding and reproduction (Krebs and Davies, 1981). Another way to reduce predation risk is to avoid encounters with predators and therefore many species select habitats where predation risk is relatively low (Heithaus, 2001). However, predation risk is not purely determined by the number of predators in a given location, the ability of predators and prey to detect each other and the probability of capture after detection play important roles as well (Heithaus, 2001). One possibility in the pelagic environment is for predation risk to be vertically stratified, due to changes in light level and the vertical stratification of shark species (Heithaus, 2001). Upper water layers would be frequented by oceanic whitetip and mako sharks and occasionally tiger, dusky and white sharks, while deep-diving cetaceans would face large deep water sharks such as sleeper and sixgill sharks (Heithaus, 2001).

Thus if predation pressure is a real factor in the shaping of life histories of the two *Kogia* species it remains unclear why they do not form groups as a preventative mechanism to predation. However, the mechanisms of predator avoidance and mimicry described above should prove efficient against predators like sharks in a pelagic environment. While inking would help at the surface where light levels are high, resulting in a visual camouflage mechanism, it would also aid at depth if it paralyzes the olfactory sense of predator, as suggested for squid ink and, similarly, for skunk secretions. The latter would be particularly effective for predators like sharks which rely

more on olfactory than visual cues to locate their prey. In addition, shark-like appearance would give them a shark-like resemblance at low light levels.

It is interesting to note that harbour porpoises *P. phocoena*, which show a similar life history strategy to *Kogia*, are also frequently preyed upon by sharks (Arnold, 1972) and that the effects of shark predation were largely ignored in assessing the status of harbour porpoises in the north-western Atlantic (Brodie, 1995). In this respect the postpartum oestrus described for harbour porpoises (Read, 1990b), which was also considered to be possible in *Kogia*, would indicate that calving and subsequent mating takes place over a very brief time period compared to other cetaceans, which in turn may also present an adaptation to high predation pressure in *Kogia*. In addition, Rutberg (1987) speculated that a highly synchronized calving season may represent an adaptation to avoid predation on the young. A study on 27 lizard species showed that species that use flight to escape predators and actively hunt for their prey have a smaller clutch mass for a given body weight than species that use crypsis and obtain their food more passively (Vitt and Congdon, 1978). This indicates that reproductive effort may have co-evolved with predator escape and foraging strategies and therefore ecologically analogous species (i.e. species with similar adult mortalities, environmental conditions, and resource abundance and quality) should exhibit similar reproductive efforts (Vitt and Congdon, 1978).

### **9.3.2.2 Parasitism**

Another factor that may result in increased extrinsic mortality in *Kogia* is parasitism as many of the animals in the present study as well as those documented in the literature appeared very heavily parasitised. However, no quantitative studies have been carried out on the parasite load of *Kogia* to date and therefore this point also remains unsupported.

One question that remains unanswered in this evaluation of life history strategies in cetaceans in general and *Kogia* in particular is why *Kogia* should be more vulnerable to predation than other cetaceans? If it is assumed that predators were the main cause of high mortality rates in the other cetacean species, which share similar life history traits to *Kogia*, what evolutionary pressure lead to *Kogia* developing mimicry and camouflage or escape mechanisms while the other species did not develop similar mechanisms? Only

further research into the elements that shape life history variation in cetaceans will lead to satisfactory clarification of this issue. Mortality is not the single driving force in the evolution of life histories, but it does serve as an important link between the various demographic and ecological factors and as such may provide further insight in the future as will additional data on the relative importance of intrinsic versus extrinsic sources of mortality in natural populations (Promislow and Harvey, 1991).

#### **9.4 Ecology of *Kogia***

As already established according to the new model on the evolution of life histories phylogenetically closely related species with similar physiologies inhabiting similar environments may express slight differences in life history strategies as a result of the accumulation of small differences in morphology, physiology, ecology or behaviour. However, few cetacean studies have compared life history strategies between two species of the same genus (Perrin *et al.*, 1976; 1977; Kasuya *et al.*, 1988; Slooten, 1991; Hohn *et al.*, 1996) or different populations of the same species (Kasuya and Tai, 1993; Read and Hohn, 1995). Ecological parameters like distribution range, water temperature and food availability are intimately linked and a synthesis of the few data available from the literature reveals an interesting trend in the variation of life history parameters between closely related odontocetes (Table 9.3). The vaquita *P. sinus*, which is slightly smaller than the closely related harbour porpoise *P. phocoena*, inhabits waters with a higher mean temperature, has a smaller distribution range and exhibits a two year reproductive cycle (Hohn *et al.*, 1996). In contrast, the harbour porpoise inhabits cooler waters, has a larger distribution range, and exhibits annual reproduction (Read and Hohn, 1995). Similarly the data for the smaller *Kogia* species, *K. sima*, indicate that it prefers warmer waters and has a more limited distribution than *K. breviceps*, which is found in cooler waters. Accordingly, the larger species exhibits an annual ovulation rate, while the smaller one appears to have facultative annual ovulation. There are further similarities between the harbour porpoise and the vaquita and *K. breviceps* and *K. sima*. Both porpoise species have a strongly seasonal reproductive cycle (Read and Hohn, 1995; Hohn *et al.*, 1996) as do *K. breviceps* and *K. sima*. The seasonal pattern in the vaquita, which inhabits warmer waters, is shifted two to three months earlier than in the harbour porpoise (Hohn *et al.*, 1996) and a similar trend was also seen in *K. sima*. Additional data on the two forms of short-finned pilot whales *Globicephala*

*macrorhynchus* off Japan support the trend that in pairs of closely related species of the same genus or two populations of the same species the larger species or form appears to inhabit cooler waters, shows a shorter reproductive cycle, and has a higher percentage of simultaneously lactating and pregnant females in the population (Table 9.3).

Table 9.3: Comparison of some life history and environmental parameters of closely related odontocetes. The larger species of a genus is always listed first.

Species	Total length (cm)	Preferred temperature/distribution range	Morphology	Reproductive parameters
<b>Harbour porpoise</b> <i>Phocoena phocoena</i> <sup>1</sup> (w. North Atlantic)	160-184	<20°C, larger range	larger total length	1yr reproductive cycle
<b>Vaquita</b> <i>Phocoena sinus</i> <sup>2</sup> (Gulf of California)	140.6♀ 134.9♂	>20°C, restricted range	smaller total length	2yr reproductive cycle
<b>Pygmy sperm whale</b> <i>K. breviceps</i> <sup>3,4</sup> (South Africa)	327.6♀ 330.5♂	colder waters, larger range	larger total length, but smaller flippers and dorsal fin	1yr reproductive cycle
<b>Dwarf sperm whale</b> <i>K. sima</i> <sup>3,4</sup> (South Africa)	274.3♀ 260.4♂	warmer waters, smaller range	smaller total length, but larger flippers and dorsal fin	1yr (2yr) reproductive cycle
<b>Short-finned pilot whale Northern form</b> <sup>5,6</sup> (Japan)	395♀ 560♂	colder waters <24°C summer 8-21°C winter, larger range	larger total length	length @ ASM:3.9-4m; mean calving interval: 5.1-7.1yrs; % females simultaneously pregn. + lact.: 9.6%; ann. pregn. rate: 14-20%
<b>Short-finned pilot whale Southern form</b> <sup>5</sup> (Japan)	316♀ 422♂	warmer waters >24°C summer >20°C winter, smaller range	smaller total length	length @ ASM:3.16cm; mean calving interval: 7.78yrs; females simultaneously pregn. + lact.: n=3; ann. pregn. rate: 12.8%

<sup>1</sup>= Read and Hohn, 1995; <sup>2</sup>= Hohn *et al.*, 1996; <sup>3</sup>= present study; <sup>4</sup>= Ross, 1979; <sup>5</sup>= Kasuya and Tai, 1993; <sup>6</sup>= Kasuya and Marsh, 1984.

It may be possible to explain the differences in body size in terms of the thermoregulatory requirements in relation to surface area to volume ratios. A larger distribution range indicates that a larger area can be utilized in search of food and thus body condition may overall be better in these animals. Larger bodies can store more fat reserves, which would in turn mean a better physiological condition for the maintenance of pregnancies in successive years (Ralls, 1976; Wiley and Clapham, 1993). The majority of the world's oceans have very low temperature regimes and in the marine environment colder waters are more nutrient rich than warmer waters (Mann and Lazier, 1991). Thus the data presented in Table 9.3 would indicate that the species inhabiting colder waters have access to more food for two reasons: colder waters are richer in biomass and the animals may have access to a larger area for foraging. This may also explain the larger body size for animals in cooler waters as the thermoregulatory requirements can more easily be met with a smaller surface-area to volume ratio. Harvey and Zammuto (1985) suggested that larger animals can defend themselves better against predators and survive longer without food and that higher nutrition levels can result in early maturation and decreased lifespan within and among mammal species. Three allometric components reflect a species' ecology, namely mortality rate, assimilation rate and respiration rate (Harvey and Purvis, 1999). Growth rates (or assimilation rates) are governed by the resources available as well as other environmental conditions and thus one can surmise that the resources and ecology determine the growth rate and thus the size at sexual maturity, as well as the body condition and reproductive rate. The annual reproduction observed in some cetaceans is a result of a combination of environmental factors, like resource availability and/or quality, which in turn affects body condition, as well as juvenile and adult mortality rates since higher prey availability would result in higher assimilation and respiration rates. Higher food availability for the harbour porpoise *P. phocoena* population in the western North Atlantic was suggested to be the reason for annual reproduction as opposed to a two year reproductive cycle for the population found off California (Hohn and Brownell, 1990; Read and Hohn, 1995). Similarly the principal factor determining the length of the calving interval in humpback whales *M. novaeangliae*, which frequently show reproduction in successive breeding seasons (Clapham and Mayo, 1990; Straley *et al.*, 1994), was suggested to be food

availability (Clapham, 1996).

As adult mortality rates influence the age at ASM as well as the lifespan of a species it can be assumed, looking at the data in Table 9.3, that species with similar age at ASM and similar lifespans, like for example *K. breviceps* and *P. phocoena* experience similar adult mortality rates. This does, however, not imply that species which are similar in that respect have to exhibit similar body size. It is rather the case that growth (assimilation) and metabolic rate (respiration) are determined, in part, by the environment and therefore different availability, utilization as well as quality of resources lead to different body sizes. Furthermore the characteristics of the habitat itself, as discussed above in relation to water temperature, almost certainly play a role as well. A review of existing life history models shows that differences in trophic conditions and mortality are the main sources of inter- and intraspecific variation in body size (Kozłowski, 1992). Production rate and mortality always act together in determining age and size at maturity (Kozłowski, 1992). This explains why, after the effects of body size are removed, a positive interspecific relationship exists between the age at maturity and adult lifespan (Kozłowski, 1992).

Different reproductive strategies can be exhibited by species that have otherwise similar life history traits. This can be observed when comparing the life histories of the harbour porpoise *P. phocoena* and the vaquita *P. sinus*, which show different life history strategies, but are similar in most other respects. The main reason for these differences can be put down to energetic constraints. It is costly to reproduce annually and therefore such a strategy will only evolve and be maintained in an environment that holds sufficient high quality resources. This scenario is supported by data from two different harbour porpoise populations off California and in the western North Atlantic which show similar ages at sexual maturity (around four years), but exhibit a two year and an annual reproductive cycle, respectively (Hohn and Brownell, 1990; Read and Hohn, 1995). The reason for this difference was thought to be the higher prey abundance in the western North Atlantic (Read and Hohn, 1995). Therefore the list of cetacean species presented here which have some similar life history traits, but differ in others (like body size and reproductive rates) may present an underlying model for testing the effects of different environments on the shaping of life history strategies in cetaceans in the future as new results on that subject become available.

In summary the life history strategy of *K. sima* may represent an intermediate strategy between that of harbour porpoises and *K. breviceps* on the one hand and most

delphinids on the other hand. Factors that may have lead to a longer calving interval in *K. sima* than in *K. breviceps* include a larger group size, presumably resulting in a somewhat reduced predation pressure and a smaller habitat due to preferred higher water temperatures (see Chapter 7), which may result in lower food availability. Further differences between the two species may be a slightly different male mating strategy as indicated by the somewhat larger relative testis weight in *K. sima* (see Chapter 4). The opportunistic mating system proposed for both *Kogia* species supports the opportunistic lifestyle observed for both species. Although both species appear to share the same ecological niche as indicated by the stomach content analysis (see Chapter 6) different peaks in the seasonality of reproduction may have evolved to avoid direct competition for the same resources at a time when energetic demands are the highest (see Chapter 5 and 6).

As the above data indicate, although life histories are often regarded as strategies employed by animals, they may well have arisen as an effect of environmental conditions and demographic constraints (Sutherland *et al.*, 1986; Purvis and Harvey, 1997). A more detailed understanding of cetacean as well as mammalian life history evolution will emerge as more information on the combined roles of the environment and demography as well as behaviour, genetics and physiology becomes available. However, it is still unknown in which way the environment affects mortality rates and influences life history strategies, both directly and indirectly (Promislow and Harvey, 1991). Environmental factors are not easily quantified and there are likely to be many environmental factors that influence each other in complex ways and affect life history traits (Promislow and Harvey, 1991).

### **9.5 Additional factors influencing life history strategies**

The social system of a species can modify life histories in terrestrial mammals (for example the hunting dog with a colonial social structure has unusually large litters) and new social systems are found in cetaceans that do not appear to have an equivalent in terrestrial mammals (Marsh and Kasuya, 1986; Kasuya, 1995; Kasuya *et al.*, 1997). Therefore it would not be surprising to find modified life history strategies in cetaceans. In fact, recent evidence for the life history of Baird's beaked whale suggests that members of the Ziphiidae may exhibit very different strategies to other cetaceans

(Kasuya *et al.*, 1997). Furthermore, the aquatic environment may present different evolutionary constraints on species than the terrestrial environment.

## **9.6 Conclusions**

Although *Kogia* would be placed near the slow end of the fast-slow continuum when all mammals are considered they can be placed nearer the fast end of life history strategies of Cetacea. However, a fast life history does by no means ensure a healthy population. The harbour porpoise *P. phocoena* populations in the North Sea and western North Atlantic, which exhibit a very similar life history strategy to *Kogia*, are currently under threat due to extensive bycatch in fishing gear. Although there are very few reports of *Kogia* getting entrapped in fishing gear, both species are known to swallow plastic bags, which they probably mistake for squid. As these present major obstructions in the digestive tract the animals almost invariably starve to death. However, the threat posed to *Kogia* populations from these sources of pollution has to be monitored more closely in the future before a definite assessment of its impact can be made. In the meantime the data presented here, in particular the relatively high reproductive rates should not be seen as an insurance for the continued survival of the *Kogia* populations off southern Africa, but rather be interpreted as a starting point for more research efforts into the biology of these two little understood species.

The above data for cetaceans support Charnov's (1991) and Harvey and Purvis' (1999) model of life history strategies in mammals as they show that mortality rates and ecological parameters like water temperature and, possibly related to that, food availability determine not just body size, but also other related parameters like age at ASM and reproductive rates. Although the slow-fast continuum still holds among cetaceans, it is intriguing to note that there appears to be a pattern between closely related species of the same genus or two populations or ecotypes of the same species. Additionally, the evidence presented for *Kogia* in the present study reflects the possibility of closely related species inhabiting a similar environment (and thus being subject to similar environmental constraints), but showing slightly differing life history strategies, which would further support Charnov's (1991) and Harvey and Purvis' (1999) model. Ultimately the data from the present study support the idea that optimal body size varies among species due to ecological differences, because it corresponds to a particular growth rate, age at maturity, adult and juvenile mortality, and other related parameters

(Purvis and Harvey, 1997). Therefore each species' optimum size depends upon its combination of ecological parameters. The reason why it has proved so hard to correlate life history differences with ecology is that related species with differing ecologies are expected to be of different sizes and life history variation correlated with size differences is commonly factored out in comparative studies (Purvis and Harvey, 1997).

Although the present study may have resulted in more additional questions being asked about the general biology of *Kogia* than were answered, it presents a first insight into the biology of these two lesser known cetacean species and it is hoped that the resulting questions will inspire and initiate further research on these truly fascinating whales.

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# *Appendices*



## APPENDIX A

### Stranding records of pygmy sperm whales *Kogia breviceps* along the South African coastline in reverse chronological order.

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length</u> (cm)	<u>Lat</u> (S)	<u>Long</u> (E)	<u>Locality</u>	<u>Event</u> <u>Condition</u>
N2758	19/10/99	M	231	34° 03'	23° 03'	Knysna	single, live, unsuccessfully refloated
N2757	12/10/98	M	246	34° 00'	25° 53'	Blue Horizon Bay	single, live, unsuccessfully refloated, died in rehabilitation
N2754	02/09/98	M	183	33° 42'	26° 41'	Kenton-on-Sea	single, live, unsuccessfully refloated
N2641	20/08/97	F	242	33° 58'	22° 34'	Wilderness	single, live
96/17	20/05/96	F	184	34° 30'	20° 29'	3km E of Klipkoppie, De Hoop Nature Reserve	cow/calf? fresh
96/16	19/05/96	Fp	281.5	34° 30'	20° 29'	3km E of Klipkoppie, De Hoop Nature Reserve	cow/calf? decomposing
95/13	18/10/95	M	268	34° 31'	20° 28'	Klipkoppie, De Hoop Nature Reserve	single, decomposing
94/09	25/06/94	Flp	263	34° 24'	20° 50'	Breede River Mouth	double?, fresh
-	29/06/94	-	180	34° 24'	20° 50'	Breede River Mouth	double? (cow/calf?), refloated
N2115	18/10/93	M	275	34° 14'	21° 56'	6km W of Danabaai, Mossel Bay	single, decomposed
N1888	18/10/93	F	324	33° 43'	26° 30'	10km E of Alexandria State Forest Station	single, decomposed
93/16	01/09/93	M	195	34° 48'	20° 03'	Struisbaai	single, live
93/14	06/07/93	M	180.5	34° 25'	20° 24'	De Hoop Nature Reserve	single, decomposing
92/14	16/09/92	Flp	300	34° 24'	20° 50'	Breede River Mouth	triple, live
N1863	05/09/91	Mc	213	34° 00'	23° 27'	Keurboomsstrand, Plettenberg Bay	cow/calf?, live
N1862	02/09/91	F	320	34° 00'	23° 27'	Keurboomsstrand, Plettenberg Bay	cow/calf?
91/26	08/06/91	F	285	34° 20'	21° 54'	East bank of Gouritz River Mouth	single, live
N1831	26/01/91	F	221	33° 59'	23° 34'	Natures' Valley	single, live
N1707	23/07/90	Fp	286	34° 08'	22° 10'	Batnon, between Lusbaai and Boggansbaai	single
N1377	19/05/87	M	229	28° 24'	32° 22'	3km N of St. Lucia, Natal	single

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length</u> (cm)	<u>Lat</u> (S)	<u>Long</u> (E)	<u>Locality</u>	<u>Event</u> <u>Condition</u>
87/10	?05/03/87	M?	ca320	34° 31'	20° 28'	Klipkoppie, De Hoop Nature Reserve	single, decomposing
87/06	03/03/87	M	232.7	34° 08'	22° 10'	Bokkumsbaai, Mossel Bay	single, live
86/22	25/05/86	M	218	33° 25'	18° 18'	15km S of Ysterfontein	single, live
86/17	09/04/86	F	321	34° 31'	20° 28'	Klipkoppie, De Hoop Nature Reserve	single, freshish
N1174	12/07/85	F	290	34° 05'	22° 58'	Buffels Bay, Knysna	double?
N1079	12/09/84	Mc	194	33° 59'	25° 18'	Beach View	cow/calf
N1078	12/09/84	Fpl	262	33° 59'	25° 18'	Beach View	cow/calf
84/26	04/09/84	F	238	22° 57'	14° 30'	Walvis Bay, Namibia	single, freshish
84/24	10/08/84	F	301	34° 21'	19° 02'	Kleinmond	single, decomposing
N1011	08/12/83	M	301	34° 02'	25° 45'	Cape Recife	single, decomposed
N989	26/09/83	M	-	34° 01'	25° 22'	Seaview, PE	-
83/33	23/09/83	F	256.5	34° 25'	19° 14'	Hermanus	single, fresh
83/27	11/06/83	M	147+	34° 23'	18° 52'	Holbaai, False Bay	single
83/26	03/06/83	-	300	34° 07'	22° 07'	Hartenboos River Mouth, Mossel Bay	single, fresh
83/21	06/05/83	Mc	191	34° 24'	20° 50'	Breede River Mouth	cow/calf, fresh
83/20	06/05/83	Flp	301	34° 24'	20° 50'	Breede River Mouth	cow/calf, fresh
82/21	26/09/82	M	215+	34° 24'	20° 50'	Breede River Mouth	cow/calf?, live
82/20	26/09/82	F	299	34° 24'	20° 50'	Breede River Mouth	cow/calf?
82/27	31/08/82	Fp	300	22° 40'	14° 34'	Swakopmund, Namibia	single, live
N854	23/07/82	Mc	202	34° 04'	22° 56'	1.5km W of Goukamma River Mouth	cow/calf, fresh
N853	23/07/82	Fl	297	34° 04'	22° 56'	1.5km W of Goukamma River Mouth	cow/calf, fresh
82/04	06/02/82	Flp	288	32° 52'	17° 52'	Noordwesbaai, N of Saldanha Bay	double(cow/calf?) live
81/22	31/12/81	F	301	34° 06'	18° 29'	Sunrise Beach, Muizenberg	single, live
N771	29/08/81	F	216	34° 00'	24° 56'	Kabeljous River Mouth	single, live
80/26	?29/10/80	F	ca255	34° 29'	19° 22'	De Plaat, Walker Bay	single
N16	08/02/80	-	-	33° 43'	25° 51'	Sundays River Mouth	skull on beach
79/18	?06/08/79	?	246.4	22° 50'	14° 34'	20km N of Walvis Bay, Namibia	single, decomposing

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length</u> (cm)	<u>Lat</u> (S)	<u>Long</u> (E)	<u>Locality</u>	<u>Event</u> <u>Condition</u>
80/03	01/08/79	?	339	21° 15'	13° 14'	Dunrissa Bay, Namibia	single, freshish
N408	18/07/79	F	276	34° 02'	25° 34'	1.2km E of Skoenmakerskop	single
N378	23/09/78	-	-	34° 11'	24° 33'	Gibson Bay, 10km W of Oyster Bay	- *
N377	23/09/78	M	270	34° 08'	24° 27'	Huisklip, Tsitsikamma River Mouth	single, decomposed
78/26	01/09/78	M	229	33° 06'	18° 02'	Langebaan	single, decomposing
78/25	ca27/8/78	Fp	-	22° 51'	14° 34'	18km N of Walvis Bay, Namibia	single
N368	25/07/78	F	247	33° 43'	25° 57'	7.9km E of Sundays River Mouth	single, decomposing
78/20	07/07/78	F	ca295	34E39'	19E29'	Pearly Beach, near Gaansbaai	single, fresh
78/19	12/06/78	Fl	292.5	34° 07'	18° 28'	Muizenberg, False Bay	single, live
78/13	22/03/78	M	242	34° 06'	18° 29'	Sunrise Beach, Muizenberg, False Bay	single, live
N342	11/02/78	M	276	34° 03'	24° 55'	Jeffrey's Bay	single, live
76/24	?30/11/76	M	186	33° 40'	18° 24'	7.6km N of Melkbosstrand	single, decomposing
N284	03/10/76	F	304	34° 13'	24° 50'	Cape St. Francis, between E St. Francis and Lighthouse	single, live
76/19	16/09/76	M	179	34° 10'	18° 52'	Gordons Bay, False Bay	single, live
N278	21/08/76	Fc	204	33° 58'	22° 34'	Wilderness	cow/calf
N277	21/08/76	Flp	266	34° 00'	22° 34'	Wilderness	cow/calf
76/17	30/07/76	M	167	34° 11'	18° 26'	Simons Town Naval Dockyard	single, live
76/04	late02/76	F?	306	34° 35'	20° 22'	16km E of Arniston	single, decomposing
75/12	15/12/75	M	310	33° 43'	18° 26'	Melkbosstrand	single, fresh
75/07	07/10/75	M	241	22° 57'	14° 30'	Walvis Bay, Namibia	single, live
N225	25/12/74	M	234	33° 59'	25° 39'	King's Beach, PE	single, live
74/08	10/08/74	F	ca236	34° 29'	19° 22'	De Plaat, Walker Bay	single, decomposing
N179	18/07/72	M	197	34° 01'	25° 31'	Skoenmakerskop, in Reserve nearer to Sardinia Bay than	cow/calf?
N178	18/07/72	Fp	309.5	34° 01'	25° 31'	Skoenmakerskop Skoenmakerskop, in Reserve nearer to Sardinia Bay than Skoenmakerskop	cow/calf?

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length (cm)</u>	<u>Lat (S)</u>	<u>Long (E)</u>	<u>Locality</u>	<u>Event Condition</u>
N177	11/07/72	M	202	33° 48'	25° 42'	Salnova, Coega River Mouth	cow/calf?
N176	11/07/72	Fp	305.5	33° 48'	25° 42'	Salnova, Coega River Mouth	cow/calf?
N172	02/04/72	F?	327.6	33° 42'	26° 40'	640m W of Bushmans River Mouth	single, decomposed
N152	18/07/71	F	289.6	34° 02'	25° 33'	Skoenmakerskop, PE	single
N138	14/03/71	Fp	305	33° 59'	25° 18'	457m from Maitlands River Mouth	single, decomposed
-	Jan/Feb 1971	-	ca305	21° 47'	14° 01'	7km S of Cape Cross, Namibia	- *
N132	21/11/70	M	325	33° 58'	25° 14'	Van Stadens River Mouth	single, decomposed
N110	29/08/70	M	196.6	34° 02'	25° 33'	Skoenmakerskop, PE	single
72/14	end07/beg 08 1970	-	275	34° 29'	20° 31'	Koppie Alleen, De Hoop Nature Reserve	double, fresh
-	end07/beg 08 1970	-		34° 29'	20° 31'	Koppie Alleen, De Hoop Nature Reserve	double, fresh
N85	06/12/69	-	305	33° 59'	25° 18'	Beach View, PE	single, decomposed
N82	07/11/69	F	188	33° 23'	27° 19'	Bira River Mouth, near East London	(single?)-live
69/15	06/11/69	M	304.8	34° 42'	20° 15'	3.22km W of Arniston	single, decomposing
N68	Jan 1969	-	-	33° 46'	26° 20'	Woody Cape, Algoa Bay	skull only *
37126	1969	-	-	21° 45'	13° 57'	Cape Cross, Namibia	partial skeleton *
68/13	30/04/68	M	194.31	34° 29'	19° 22'	De Plaat, Walker Bay	double(cow/calf?), live
1513/87	22/07/67	M	293.5	33° 50'	25° 40'	St. Georges Strand, PE	-
N42	08/03/67	M	270	33° 58'	23° 34'	Natures' Valley	-
66/08	03/12/66	M	266.7	34° 02'	18° 21'	Hout Bay	single, live
-	Oct 1966	-	ca366	26° 38'	15° 10'	Lüderitz, Namibia	- *
-	Sep1966	-	-			Natal North Coast	-cow/ calf *
N41	?/10/65	Fpl	269.5	33° 58'	23° 34'	Natures' Valley	cow/calf?
N40	?/10/65	-c	211	33° 58'	23° 34'	Natures' Valley	cow/calf?
-	14/04/65	F	ca305	34° 17'	21° 55'	Vleesbaai, Mossel Bay	- *
-	10/06/64	M	330.5	33° 23'	27° 19'	Bira River Mouth, near East London	- *
N425	24/01/64	F	-	33° 02'	27° 55'	East London	- *
N27	20/11/63	M	297	33° 51'	25° 38'	Amsterdamhoek, PE	single, live *
-	11/04/62	-	ca270	33° 58'	22° 34'	Wilderness	- *

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length</u> (cm)	<u>Lat</u> (S)	<u>Long</u> (E)	<u>Locality</u>	<u>Event</u> <u>Condition</u>
N424 ELM 674	Aug/Sep 1960	M	ca275	32° 59'	27° 57'	Nahoon Beach, East London	- *
ELM 616a	31/05/58	F	-	32° 27'	28E39'	Mazeppa Bay, Transkei	- *
-	24/10/56	-	ca305	29° 56'	31° 01'	Brighton Beach, Durban	- *
282	01/1955	-	-	34° 03'	23° 22'	Plettenberg Bay	- *
-	1951/52	Fp	ca305	34° 03'	23° 22'	Plettenberg Bay	- *
-	ca1940	-	-	33° 58'	22° 34'	Wilderness	- *
17690	02/08/33	-	-	33° 53'	18° 27'	Table Bay	-double, sighting? *
34018	15/12/30	-	-	33° 52'	18° 27'	Milnerton Beach, Cape Town	- *
3912	1899	-	-	34° 02'	23° 02'	Knysna	- *
3911	1896	F	175.5	33° 55'	18° 24'	Green Point, Table Bay	- *
35074	1880	-	-	34° 05'	22° 58'	Buffels Bay, Knysna	- *

\*: taken from Ross (1979). F: female; M: male; p: pregnant; l: lactating; c: calf

Remarks:

-94/09 was possibly associated with a 1.8m individual, which stranded live 4 days later ca 600m east of it. It may have been its calf.

-92/14 stranded live with at least two other, smaller individuals, one of which may have been its calf. The two other individuals got refloated.

-N1174 stranded apparently with a calf.

-82/04 stranded live with a smaller, ca. 1.5m individual, which may have been its calf.

-N408 was possibly pregnant and foetus was removed.

-N278 had eight plastic bags and one paper bag in the stomach on autopsy.

-N82 had three pieces of string and two plastic bags in its stomach on autopsy.

**Stranding records of dwarf sperm whales *Kogia sima* along the South African coastline in chronological order.**

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length</u> (cm)	<u>Lat</u> (S)	<u>Long</u> (E)	<u>Locality</u>	<u>Event</u> <u>Condition</u>
N2774	11/04/99	-c	160	34° 08'	22° 10'	Bokkumsbaai, Mossel Bay	cow/calf
N2773	11/04/99	F	286	34° 08'	22° 10'	Bokkumsbaai, Mossel Bay	cow/calf
N2772	21/04/99	M	262			Hartenbos	single, live
N2760	09/02/99	M	220	34° 03'	24° 55'	Jeffrey's Bay	single
N2755	30/07/98	F	165	34° 01'	25° 23'	Kini Bay	single
-	29/02/96	M	198	29° 50'	31° 02'	Central Beaches, Durban	single, live
N2243	04/08/94	M	197	33° 59'	25° 18'	500m E of Maitland Caravan Park	single
N2041	17/05/93	M	202.5	29° 51'	31° 02'	Snake Park Durban, Natal	single
N1869	04/10/91	-	215	33° 09'	27° 41'	(North Beach) Kidd's Beach, East London	single

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length (cm)</u>	<u>Lat (S)</u>	<u>Long (E)</u>	<u>Locality</u>	<u>Event Condition</u>
90/41	?07/12/90	-	ca400?	32° 47'	18° 10'	Velddrif, St. Helena Bay	single, decomposing
90/34	16/10/90	M	238	32° 36'	18° 18'	Rocher Pan, N of Dwarskersbos	single
N1564	05/01/89	M	230	33° 59'	25° 41'	Flat Rocks Road House	single, live
88/20	?14/07/88	F	231	34° 36'	19° 24'	Uilkraalmond, near Franskraal, Gansbaai	single, fresh
88/02	27/01/88	Fp	225.5	34° 23'	20° 51'	Eastern Side of Breede River Mouth	single, live, refloated unsuccessfully
N1322	01/12/86	Fp	236	33° 58'	25° 39'	King's Beach, PE	single
86/34	?14/09/86	-	244.4	34° 48'	20° 03'	Struisbaai	single, decomposing
N1248	02/11/85	M	196	33° 59'	24° 59'	5km E of Kabeljous River Mouth	single, v. fresh
85/02	08/03/85	F	251	34° 31'	20° 28'	Klipkoppie, De Hoop Nature Reserve	single, decomposing
N1132	17/01/85	F	-	34° 02'	25° 45'	0.5-1km N of Cape Recife	double, propeller wound?
N1131	17/01/85	M	228	34° 02'	25° 45'	0.5-1km N of Cape Recife	double
84/36	26/11/84	M	178	34° 07'	18° 28'	Muizenberg, False Bay	double
84/35	26/11/84	M	230	34° 07'	18° 28'	Muizenberg, False Bay	double
84/21	16/07/84	M	211	34° 13'	21° 58'	Between Mossel Bay and Vlees Baai	single, fresh
N1082	-	-	-			11km S of Sodwana Bay, Natal	no record
N884	29/10/82	F	234	33° 58'	25° 02'	8km E of Kabeljous River Mouth	single decomposing
N837	05/05/82	M	220	34° 00'	23° 27'	Keurboomsstrand	single, live
N832	08/04/82	Fl	232	33° 58'	22° 34'	Wilderness	double, calf? refloated
N830	27/03/82	Fc	103	33° 48'	25° 42'	Salnova Pipeline, Coega River Mouth	cow/calf live, refloated unsuccessfully
N829	30/03/82	Fl	238	33° 48'	25° 42'	Salnova Pipeline, Coega River Mouth	cow/calf, live
N687	25/04/81	M	216	34° 05'	22° 58'	Buffels Bay	single, live
N682	27/03/81	F	265	33° 44'	25° 50'	3km W of Sundays River Mouth	single
81/03	24/03/81	Fp	215	34° 02'	18° 21'	Hout Bay, Cape Peninsula	single, live
N679	03/03/81	Mc	103.5	33° 58'	25° 02'	8km E of Kabeljous River Mouth, near Gamtoos River Mouth	cow/calf
N678	03/03/81	Fl	241	33° 58'	25° 02'	8km E of Kabeljous River Mouth, near Gamtoos River Mouth	cow/calf
80/10	19/05/80	M	204.5	34° 29'	19° 22'	De Plaat, Walker Bay	single, live
N384	12/01/79	F	181	34° 00'	24° 57'	2km E of Kabeljous River Mouth	single
N372	27/08/78	M	256	34° 03'	24° 55'	Jeffrey's Bay	single

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length (cm)</u>	<u>Lat (S)</u>	<u>Long (E)</u>	<u>Locality</u>	<u>Event Condition</u>
78/17	20/04/78	F	255	34° 30'	20° 28'	7.3km E of Skipskop, Arniston	single, decomposing
N338	22/11/77	M	171	33° 59'	25° 18'	Maitlands River Mouth	single, live
N323	05/09/77	F	216	34° 00'	24° 57'	2km E of Kabeljous River Mouth	single decomposed
N317	01/08/77	Fl	220	33° 34'	26° 58'	Port Alfred, between Riet Point and Rufanes River	cow/calf, prev. night, very thin
N318	30/07/77	Fc	147	33° 34'	26° 58'	Port Alfred, between Riet Point and Rufanes River	cow/calf
N440	21/12/76	Fp	250	33° 01'	27° 54'	Orient Beach, East London	single, live
76/18	09/08/76	F	209	34° 07'	18° 50'	The Strand, False Bay	single, live
76/14	08/04/76	M	225	34° 25'	19° 17'	Grotto Beach, Hermanus	single, fresh
76/09	03/04/76	M	190.5	34° 06'	18° 22'	Noordhoek, Cape Peninsula	single, fresh
76/03	29/02/76	Fl	264	34° 29'	19° 22'	De Plaat, Walker Bay	single, freshish
76/02	?15/02/76	F	255	34° 08'	18° 19'	Kommetjie, Cape Peninsula	single, decomposing
N244	17/09/75	Fc	161	33° 43'	25° 51'	Sundays River Mouth	cow/calf, live
N243	17/09/75	Fp	224	33° 43'	25° 51'	Sundays River Mouth	cow/calf
75/06	12/07/75	F	222	34° 07'	18° 26'	Clovelly, False Bay	single, prob. died at sea
N239	10/07/75	M	201	34° 10'	24° 50'	Sea Vista Beach, Cape St. Francis	quadruple, fresh
N238	10/07/75	F	209	34° 10'	24° 50'	Sea Vista Beach, Cape St Francis	quadruple, fresh
N237	10/07/75	F	206	34° 10'	24° 50'	Sea Vista Beach, Cape St. Francis	quadruple, live
N236	10/07/75	F	189	34° 10'	24° 50'	Sea Vista Beach, Cape St. Francis	quadruple, fresh
N228	09/02/75	M	181	33° 58'	25° 14'	0.5km W of Van Stadens River Mouth	single, decomposing
N227	Feb 1975	-	-	33° 58'	25° 10'	Between Van Stadens River Mouth and Gamtoos River Mouth	bleached skull
N224	19/08/74	M	252	33° 56'	25° 36'	North End Beach, PE	single, fresh
N207	26/02/74	F	189	33° 58'	25° 39'	King's Beach, PE	single, fresh, live?
N205	05/02/74	F	215	33° 56'	25° 36'	North End Beach, PE	single
72/16	31/12/72	M	ca245	33° 03'	17° 58'	Blouwaterbaai, Saldanha Bay	double, ?
72/15	31/12/72	F	264	33° 03'	17° 58'	Blouwaterbaai, Saldanha Bay	double, live
36729	SAM got it in Aug '72	-	-	34° 07'	18° 28'	Muizenberg, False Bay	- *
N185	23/08/72	Fp	240	33° 43'	25° 57'	8.05km E of Sundays River Mouth	double cow/calf? decomposing

<u>No.</u>	<u>Date</u>	<u>Sex</u>	<u>Length (cm)</u>	<u>Lat (S)</u>	<u>Long (E)</u>	<u>Locality</u>	<u>Event Condition</u>
N185a	23/08/72	-c	ca130	33° 43'	25° 57'	8.05km E of Sundays River Mouth	double cow/calf? decomposing
72/09	13/05/72	-	-	33° 54'	18° 27'	Between Woodstock and Milnerton, Table Bay	single, decomposed
N154	04/09/71	F	274.3	33° 58'	25° 18'	Between Beachview and Maitlands Beach	single decomposed
-	18/07/71	-	-	34° 08'	18° 26'	Fish Hoek, False Bay	- *
N149	April'71	-	-	34° 11'	22° 08'	Mossel Bay	decomposed *
N148	02/05/71	M	238.8	34° 01'	25° 22'	Seaview, P.E.	single
N146	14/04/71	Fc	152.4	33° 51'	25° 38'	Amsterdamhoek, P.E.	cow/calf, live
N145	14/04/71	Fpl	235	33° 51'	25° 38'	Amsterdamhoek, P.E.	cow/calf, live
N140	24/03/71	Fc	135.9	33° 46'	26° 27'	1.61km W of Cape Padrone	cow/calf, live
N139	24/03/71	Fpl	ca244	33° 46'	26° 27'	1.61km W of Cape Padrone	cow/calf, decomposed
N104	10/05/70	Mc	152.4	33° 44'	24E49'	9.65km E. of Hougham Park, P.E.	decomposed cow/calf
N103	10/05/70	Fl	230.5	33° 44'	24° 49'	9.65km E. of Hougham Park, PE	decomposed cow/calf
N102	28/04/70	Mc	151.9	33° 49'	25° 39'	St. Georges Strand, PE	decomposed cow/calf
N101	28/04/70	Fpl	231.2	33° 49'	25° 39'	St. Georges Strand, PE	cow/calf
70/04	01/02/70	M	197.5	33° 55'	18° 28'	Woodstock Beach, Table Bay	single, live
N88	01/01/70	M	254	34° 04'	24° 55'	3.22km W. of Jeffrey's Bay	single
69/17	30/11/69	M	177.8	34° 08'	18° 26'	Fish Hoek, False Bay	single, live
N77	20/10/69	M	260.4	34° 05'	24° 55'	Seeköe River Mouth	single, fresh
68/10	02/12/68	M	215.3	33° 48'	18° 27'	Bloubergstrand, Table Bay	single, decomposing
63/01	20/05/63	M	247	33° 03'	18° 02'	Leentjies Klip Beach, Saldanha Bay	single
-	1962?	-	-	33° 48'	18° 27'	Bloubergstrand, Table Bay	-
N43	April'62	-	241	33° 40'	26° 02'	Springmount, Algoa Bay	- *
-	16/07/60	M	ca244	33° 01'	27° 55'	Eastern Beach, East London	- *
N423	12/01/55	-	-	33° 06'	27° 48'	Kaiser's Beach, East London	- *
-	1954	M	252	34° 05'	22° 58'	Buffels Bay, Knysna	- *
-	-	M	185	-	-	-	-

\*: taken from Ross (1979). F: female; M: male; p: pregnant; l: lactating; c: calf

#### Remarks:

- N1322 stranded with a large shark bite.
- N1132 stranded with an adult male (N1131).
- N832 stranded with a calf, which was successfully refloated.
- N244 had a shark bite.
- 72/16 was reported fighting with 72/15 prior to stranding.
- N139 possibly had a shark bite.

## APPENDIX B

Specimens and associated samples available for the present study.

### *Kogia breviceps*

#### Port Elizabeth Museum (PEM).

No.	Sex	Date of stranding	Total length (cm)	Body weight (kg)	Teeth	Gonads	Stomach contents
N2641	F	20/08/97	242	-	-	-	√
N1888	F	18/10/93	324	-	√	-	-
N1862	F	02/09/91	320	480	-	-	√
N1831	F	26/01/91	221	-	√	-	-
N1707	Fp	23/07/90	286	372	√	-	√
N1174	F	12/07/85	290	-	√	-	-
N1078	Fpl	12/09/84	262	-	√	√	√K
N853	Fl	23/07/82	297	-	-	√	√K
N771	F	29/08/81	216	-	√	√	√K
N408	F	18/07/79	276	-	√	-	√K
N368	F	25/07/78	247	-	√	-	√K
N284	F	03/10/76	304	-	√	-	-R
N278	Fc	21/08/76	204	130	-	*	√R
N277	Fpl	21/08/76	266	301	√	√	√R
N178	Fp	18/07/72	309.5	-	√	√	-R
N176	Fp	11/07/72	305.5	-	√	√	-R
N172	-	02/04/72	327.6	-	√	-	-R
N152	F	18/07/71	289.6	-	*√	√	-R
N138	Fp	14/03/71	305	-	√	2	-R
N82	F	07/11/69	188	83.5	-	√	-
N41	Fpl	?/10/65	269.5	-	-	-	-
N2757**	M	12/10/98	246	220	1	1	1
N2754**	M	02/09/98	183	77	1	1	1
N2115	M	18/10/93	275	-	-	-	√
N1863	Mc	05/09/91	213	168	√	√	√
N1377	M	19/05/87	229	210	√	√	√K
N1079	Mc	12/09/84	194	122	√	√	√K
N1011	M	08/12/83	301	-	-	-	√K

N989	M	26/09/83	-	-	√	-	√K
N854	Mc	23/07/82	202	123	√	√	√K
N377	M	23/09/78	270	-	√	-	√K
N342	M	11/02/78	276	374.03	√	√	√K
N225	M	25/12/74	234	-	√	√	-R
N179	M	18/07/72	197	-	*	-	-R
N177	M	11/07/72	202	-	√	√	-R
N132	M	21/11/70	325	-	*	-	-
N110	M	29/08/70	196.6	145.2	-	-	-
1513/87	M	22/07/67	293.5	-	-	-	-
N42	M	08/03/67	270	-	√	-	-
N424	M	30/08/60	275	-	√	-	-
N85	-	06/09/83	305	-	-	-	-
N40	-c	?/10/65	211	-	*	-	-

F= female; M= male; l= lactating; p= pregnant; c= calf

\*\*= animal stranded at the time of write-up and was therefore not included in the analysis.

However, length and weight data were included in the growth analysis (Chapter 3).

<sup>1</sup>= stranded at the time of write-up, samples not yet available for analysis.

<sup>2</sup>= incomplete i.e. only one ovary/testis available.

\*= original tissue not available, results taken from Ross 1979, 1984.

√K= original stomach contents not available, but raw data were available from Klages *et al.*, 1989.

√R= original stomach contents not available, but raw data were available from Ross, 1979.

-R= original stomach contents not available, results taken from Ross, 1979.

-= no data.

#### Foetuses from the Port Elizabeth Museum (PEM).

No. of mother	Sex	Date	Length (cm)	Weight (g)
N1707	M?	23/07/90	27.5	288.6
N1078	M	14/09/84	48	2950
N277	-	21/08/76	31	-
N178	M	18/07/72	17.9	160.8
N176	M	11/07/72	45.8	-
N138	M	14/03/71	113.5	2300*
N41	F	?/10/65	19.5	-

**South African Museum (SAM).**

<b>No.</b>	<b>Sex</b>	<b>Date of stranding</b>	<b>Total length (cm)</b>	<b>Body weight (kg)</b>	<b>Teeth</b>	<b>Gonads</b>	<b>Stomach contents</b>
96/17	F	20/05/96	184	-	√	√	-
96/16	Fp	19/05/96	281.5	-	√	√	-
94/09	Flp	25/06/94	263	-	√	√	-
92/14	Flp	16/09/92	300	394.1	√	√	-
91/26	F	08/06/91	285	-	√	-	-
86/17	F	09/04/86	321	480	√	√	√S
84/26	F	04/09/84	238	est159	√	√	√S
84/24	F	10/08/84	301	-	√	√	√S
83/33	F	23/09/83	256.5	272.2	√	√	√S
83/20	Flp	06/05/83	301	-	√	√	√S
82/27	Fp	31/08/82	300	-	√	-	√S
82/20	F	26/09/82	299	328	-	√	√S
82/04	Flp	06/02/82	288	343.6+	√	√	-
81/22	F	31/12/81	301	425	√	√	√S
80/26	F	?29/10/80	ca255	-	√	-	-
78/25	Fp	ca27/8/78	-	-	√	√	-
78/20	F	07/07/78	ca295	-	√	-	√S
78/19	Fl	12/06/78	292.5	445.5	-	√	√S
74/08	F	10/08/74	ca236	-	√	<sup>2</sup>	-R
95/13	M	18/10/95	268	-	√	-	-
93/16	M	01/09/93	195	123.1	√	√	-
93/14	M	?06/07/93	180.5	-	√	-	-
87/06	M	03/03/87	232.7	182	√	√	√S
86/22	M	25/05/86	218	185.9	√	√	√S
83/27	M	11/06/83	147+	69	√	√	√S
83/21	Mc	06/05/83	191	127	√	√	√S
82/21	M	26/09/82	215+	160.8+	√	√	√S
78/26	M	01/09/78	229	182.8	-	√	√S
78/13	M	22/03/78	242	233.6	-	√	√S
76/24	M	?30/11/76	186	-	√	-	-
76/19	M	16/09/76	179	72.6	√	√	√S
76/17	M	30/07/76	167	85.3	√	√	√S

No.	Sex	Date of stranding	Total length (cm)	Body weight (kg)	Teeth	Gonads	Stomach contents
75/12	M	15/12/75	310	-	-	-	√S
75/07	M	07/10/75	241	197.4	√	√	√S
69/15	M	?06/11/69	304.8	-	√	-	-R
68/13	M	30/04/68	194.31	-	√	-	-
66/08	M	03/12/66	266.7	-	√	√	-R
87/10	M?	?05/03/87	ca320	-	√	-	-
83/26	-	03/06/83	300	-	√	-	-
80/03	-	01/08/79	339	-	√	-	-
79/18	-	?06/08/79	246.4	-	√	-	-
76/04	F?	late02/76	306	-	√	-	√S

F= female; M= male; p= pregnant; l= lactating; c= calf

<sup>2</sup>= incomplete material i.e. only one ovary/testis available.

√S= original stomach contents not available, but raw data were available from Sekiguchi *et al.*, 1992.

-R= original stomach contents not available, results taken from Ross, 1979.

-= no data.

#### Foetuses from the South African Museum (SAM).

No. of mother	Sex	Date	Length (cm)	Weight (g)
96/16	M	19/05/96	23	265.9
94/09	M	25/06/94	28.6	-
92/14	F	16/09/92	38	-
83/20	F	06/05/83	21	-
82/04	F	06/02/82	49	-
78/25	F	ca27/08/78	27	-

#### *Kogia sima*

##### Port Elizabeth Museum (PEM).

No.	Sex	Date of stranding	Total length (cm)	Body weight (kg)	Teeth	Gonads	Stomach contents
N2755**	F	30/07/98	165	75			
N1322	Fp	01/12/86	236	169	√	√	√K
N1132	F	17/01/85	-	38.7	-	-	-
N884	F	29/10/82	234	-	√	-	√K

No.	Sex	Date of stranding	Total length (cm)	Body weight (kg)	Teeth	Gonads	Stomach contents
N832	Fl	08/04/82	232	178	-	√	√K
N830	Fc	27/03/82	103	31.5	√	-	empty
N829	Fl	30/03/82	238	175	-	√	√K
N682	F	27/03/81	265	-	-	√	√K
N678	Fl	03/03/81	241	183.3	-	√	√K
N440	Fp	21/12/76	250	-	√	*	-
N384	F	12/01/79	181	-	-	-	√K
N323	F	05/09/77	216	-	-	-	√R
N318	Fc	30/07/77	147	62.5	-	√	√R
N317	Fl	01/08/77	220	-	√	√	√R
N244	Fc	17/09/75	161	59.42	√	√	√R
N243	Fp	17/09/75	224	-	√	√	√R
N238	F	10/07/75	209	142.4	-	√	√R
N237	F	10/07/75	206	155.6	√	√	√R
N236	F	10/07/75	189	112.9	√	√	√R
N207	F	26/02/74	189	129.3	-	√	√R
N205	F	05/02/74	215	-	√	√	-
N185	Fp	23/08/72	240	-	-	-	-
N185a	-c	23/08/72	ca.130	-	-	-	-
N154	F	04/09/71	274.3	-	-	-	-
N146	Fc	14/04/71	152.4	61.7	√	√	√R
N145	Fpl	14/04/71	235	208.7	-	√	√R
N140	Fc	24/03/71	135.9	47.2	√	-	-
N139	Fpl	24/03/71	ca.244	-	√	-	-
N103	Fl	10/05/70	230.5	-	-	-	-
N101	Fpl	28/04/70	231.2	-	-	√	√R
N2760**	M	09/02/99	220	-	1	1	1
-	M	29/02/96	198	106	-	-	-
N2243	M	04/08/94	197	124	-	√	-
N2041	M	17/05/93	202.5	128	√	-	-
N1564	M	05/01/89	230	240	√	-	-
N1248	M	02/11/85	196	-	√	√	√K
N1131	M	17/01/85	228	202.5	√	√	√K
N837	M	05/05/82	220	-	√	-	√K
N687	M	25/04/81	216	186	-	√	√K

N679	Mc	03/03/81	103.5	14.5	-	-	empty
N372	M	27/08/78	256	303	√	√	√K
N338	M	22/11/77	171	98.5	-	√	√R
N239	M	10/07/75	201	135.9	√	√	√R
N228	M	09/02/75	181	-	√	-	√R
N224	M	19/08/74	252	-	√	√	√R
N148	M	02/05/71	238.76	-	√	√	√R
N104	Mc	10/05/70	152.4	-	-	-	-
N102	Mc	28/04/70	151.9	-	-	-	-
N88	M	01/01/70	254	-	√	-	-
N77	M	20/10/69	260.4	272.2	√	-	-
-	M	-	185	111.8	√	√	√
N1869	-	04/10/91	215	-	√	-	-
N1082	-	-	-	-	√	-	-

F= female; M= male; p= pregnant; l= lactating

\*\*= animal stranded at the time of write-up and was therefore not included in the analysis.

However, the length and weight data were included in the growth analysis (Chapter 3).

\*=original tissue not available, results taken from Ross (1979, 1984).

√K= original stomach contents not available, but raw data were available from Klages *et al.*, 1989.

√R= original stomach contents not available, but raw data were available from Ross 1979.

<sup>1</sup>= stranded at time of write-up, samples not yet available for analysis.

-= no data.

#### Foetuses from the Port Elizabeth Museum (PEM).

No. of mother	Sex	Date	Length (cm)	Weight (g)
N101	-	28/04/70	-	-
N139	-	27/03/71	-	-
N145	F	14/04/71	7.2	6.4
N243	F	18/09/75	32.5	-
N440	M	21/12/76	108	1297.5
N185	-	23/08/72	20-25	-
N1322	M?	01/12/86	9.1	29

**South African Museum (SAM).**

No.	Sex	Date of stranding	Total length (cm)	Body weight (kg)	Teeth	Gonads	Stomach Contents
88/20	F	?14/07/88	231	173.4	√	√	√S
88/02	Fp	27/01/88	225.5	177.7	√	√	√S
85/02	F	08/03/85	251	-	√	-	√S
81/03	Fp	24/03/81	215	176.9	√	√	√S
78/17	F	20/04/78	255	-	√	√	-
76/18	F	09/08/76	209	142.9	√	√	√S
76/03	Fl	29/02/76	264	264	√	√	√S
76/02	F	?15/02/76	255	-	√	<sup>2</sup>	√S
75/06	F	12/07/75	222	135.2	√	√	√S
72/15	F	31/12/72	264	-	√	-	-R
90/34	M	16/10/90	238	190.5	-	√	-
84/36	M	26/11/84	178	109.5	√	√	√S
84/35	M	26/11/84	230	199.6	√	√	√S
84/21	M	16/07/84	211	114.5+	√	√	√S
80/10	M	19/05/80	204.5	151	√	√	√S
76/14	M	08/04/76	225	176.9	√	√	√S
76/09	M	03/04/76	190.5	-	√	√	√S
70/04	M	01/02/70	197.5	-	-	√	-R
69/17	M	30/11/69	177.8	104.3	-	√	-R
68/10	M	02/12/68	215.3	-	√	-	-R
63/01	M	20/05/63	247	-	√	-	-R
90/41	-	?07/12/90	ca400?	-	√	-	-
86/34	-	?14/09/86	244.4	-	√	-	-

F= female; M= male; p= pregnant; l= lactating

<sup>2</sup>= incomplete i.e. only one ovary/testis available.

√S= original stomach contents not available, but raw data were available from Sekiguchi *et al.*, 1992.

-R= original stomach contents not available, results taken from Ross, 1979.

= no data.

**Foetuses from the South African Museum (SAM).**

No. of mother	Sex	Date	Length (cm)	Weight (g)
88/02	M	27/01/88	57.5	-
81/03	M	24/03/81	11.1	-



## **APPENDIX C**

### **Australian specimens of *Kogia breviceps* and *Kogia sima***

Museum of Victoria: provided by Lina Frigo

#### ***Kogia breviceps***

No.	Sex	Length	Date	Lat.(S)	Long.(E)	Locality	Sample
C23489	M	323	09/07/79	39°02'	146°20'	Mouth of Tidal River, Norman Bay, Victoria	teeth
C23565	M	161	04/05/93?	38°49'	146°07'	Sandy Point, Victoria	teeth
C24972	M	-	22/06/75	37°49'	148°44'	Cape Conran	tooth
C24975	M	-	19/08/75	37°49'	148°36'	Nr Point Ricardo	teeth
C24976	M	330	21/01/80	37°52'	148°04'	Shelly Beach	teeth
C29469	F	210	18/08/90	38°20'	142°01'	Lake Yambuk	teeth

CSIRO Australia, Division of Wildlife & Ecology: provided by Richard Schodde and John Wombey

#### ***Kogia breviceps***

No.	Sex	Length	Date	Lat/Long	Locality	Sample
ANWC M16210	F	-	11/03/79	34°25'S/150°52'E	North Beach, Wollongong	tooth

South Australian Museum: provided by Catherine Kemper

#### ***Kogia breviceps***

No.	Sex	Length (cm)	Date	Lat.(S)	Long.(E)	Locality	Sample
M05010 <sup>1,2</sup>	F(c?)	171	25/04/37	34°30'	137°29'	Port Victoria	tooth
M05009 <sup>1,2</sup>	Fpl	290	25/04/37	34°30'	137°29'	Port Victoria	-
M05011 <sup>1,2</sup>	M	19.3	25/04/37	34°30'	137°29'	Port Victoria	-
M05197	-	213-244	Aug. '44	34°54'	135°47'	Sleaford Bay, nr Port Lincoln	tooth
M06156	Mc	172	07/08/57	34°54'	135°47'	Sleaford Bay	tooth
M14157	F	293	07/08/57	34°54'	135°47'	Sleaford Bay	tooth
M06256 <sup>3</sup>	F	-	28/06/59	35°33'	138°37'	Victor Harbour, nr Franklin Parade	tooth
M06257	M	-	28/06/59	35°33'	138°37'	Victor Harbour, nr Franklin Parade	tooth
M06266 <sup>3</sup>	M	273	29/09/59	34°58'	138°32'	Glenelg	tooth

No.	Sex	Length (cm)	Date	Lat.(S)	Long.(E)	Locality	Sample
M06310 <sup>4</sup>	F	192	12/09/61	34°50'	138°29'	2 miles N of Grange	tooth
M10095	-	284.48	15/05/74?	33°00'	138°30'	Stony Point, 0,5 km N of Point Lowly	tooth
M10097/001	Fp	278	20/07/73	36°05'	139°33'	opp. Policemans' Point, on Ocean side of peninsula	tooth
M10097/002	M	30	20/07/73	36°05'	139°33'	opp. Policemans' Point, on Ocean side of peninsula	-
M12915	-	300	July '80	32°43'	134°05'	Cape Bauer	tooth
M15814	M	242	28/10/89	33°18'	137°50'	5km SSW of Port Davis	tooth, testis, stomach contents
M16393	F	210	15/08/88	38°20'	142°02'	Yambuk, W of outlet to sea	stomach contents
M16471	M	289	13/02/91	35°13'	138°28'	2km NNE of Gull Rock	tooth, testis, stomach contents
M16967	M	267	10/11/91	32°13'	133°08'	Point Bell	tooth
s0082	Fp	214	16/11/92	43°28'	147°13'	Cloudy Bay, Tasmania	-

<sup>1</sup>: published in Hale (1939).

<sup>2</sup>: published in Hale (1947).

<sup>3</sup>: published in Hale (1962).

<sup>4</sup>: published in Hale (1963).

Australian Museum: provided by Sandy Ingleby

### *Kogia breviceps*

No.	Sex	Length	Date	Lat.(S)	Long.(E)	Locality	Sample
M19687	M	289.5	7/05/88	33°13'	151°38'	Nth Birdie Beach, 6km N of Budgewoi	teeth
M23800	-	-	Feb 1982	29°49'	153°17'	5 mls N Wooli, SE of Grafton	dentaries
M23823	F	152	26/03/88	30°13'	153°09'	Moonee Beach, 10km N of Coffs Harbour	dentaries
M25479	F	-	02/12/91	29°29'	153°22'	Angourie Back Beach	dentaries
M25869	F	160	20/08/91	30°09'	153°12'	Sandys' Beach, 20km N of Coffs Harbour	dentaries, teeth

Queensland Museum: provided by Steve van Dyk

*Kogia breviceps*

No.	Sex	Length (cm)	Date	Lat.(S)	Long.(E)	Locality	Sample
JM5698	F	477	15/01/87	24°43'	152°17'	Bundaberg, Moore Park Township, 2km N	teeth, uterus
JM10000	Fp	279	08/09/93	26°37'	153°06'	Mudjimba Beach	teeth
JM11586	F	340	30/04/97	24°20'	152°17'	Moore Park, Bundaberg	teeth
JM11587	Fc	157	30/04/97	24°20'	152°17'	Moore Park, Bundaberg	teeth

Western Australian Museum: provided by John Bannister

*Kogia sima*

No.	Sex	Length (cm)	Date	Lat.(S)	Long.(E)	Locality	Sample
M4519	F	216	19/09/59	36°01'	115°44'	Freemantle (Leighton Beach)	teeth



## APPENDIX D

### Genetic samples of *Kogia breviceps* and *Kogia sima*

#### *Kogia breviceps*

Specimen number	Sex	Country of origin	Date of stranding	Lat./Long.	Sample used	Sequenced successfully
N2758	M	SA (PEM)	19/10/99	34°03'S/ 23°03'E	muscle	Y
N2757	M	SA (PEM)	12/10/98	34°00'S/ 25°53'E	muscle	Y
N2754	M	SA (PEM)	02/09/98	33°42'S/ 26°41'E	muscle	Y
N2641	F	SA (PEM)	20/08/97	33°58'S/ 22°34'E	tooth	Y
N1888	F	SA (PEM)	18/10/93	33°43'S/ 26°30'E	tooth	N
N1863	M	SA (PEM)	05/09/91	34°00'S/ 23°27'E	tooth	N
N1862	F	SA (PEM)	02/09/91	34°00'S/ 23°27'E	mammary tissue	N
N1831	F	SA (PEM)	26/01/91	33°59'S/ 23°34'E	tooth	N
N1707	F	SA (PEM)	23/07/90	34°08'S/ 22°10'E	tooth	Y
N1377	M	SA (PEM)	19/05/87	28°24'S/ 32°22'E	tooth	N
N1174	F	SA (PEM)	12/07/85	34°05'S/ 22°58'E	tooth	N
N1079	M	SA (PEM)	12/09/84	33°59'S/ 25°18'E	tooth	N
N1078	F	SA (PEM)	12/09/84	33°59'S/ 25°18'E	tooth	N
N989	M	SA (PEM)	26/09/83	34°01'S/ 25°22'E	tooth	Y
N854	M	SA (PEM)	23/07/82	34°04'S/ 22°56'E	tooth	N
N771	F	SA (PEM)	29/08/81	34°00'S/ 24°56'E	tooth	N
N424	M	SA (PEM)	Aug/Sep1 960	32°59'S/ 27°57'E	tooth, bone	N
N408	F	SA (PEM)	18/07/79	34°02'S/ 25°34'E	tooth	N
N377	M	SA (PEM)	23/09/78	34°08'S/ 24°27'E	tooth	N
N368	F	SA (PEM)	25/07/78	33°43'S/ 25°57'E	tooth	N
N342	M	SA (PEM)	11/02/78	34°03'S/ 24°55'E	tooth	N
N284	F	SA (PEM)	03/10/76	34°13'S/ 24°50'E	tooth	Y
N225	M	SA (PEM)	25/12/74	33°59'S/ 25°39'E	tooth	N
N179	M	SA (PEM)	18/07/72	34°01'S/ 25°31'E	tooth	Y
N178	F	SA (PEM)	18/07/72	34°01'S/ 25°31'E	tooth	N
N177	M	SA (PEM)	11/07/72	33°48'S/ 25°42'E	tooth	Y
N176	F	SA (PEM)	11/07/72	33°48'S/ 25°42'E	tooth	N
N172	F	SA (PEM)	02/04/72	33°42'S/ 26°40'E	tooth	N
N138	F	SA (PEM)	14/03/71	33°59'S/ 25°18'E	tooth	N
N42	M	SA (PEM)	08/03/67	33°58'S/ 23°34'E	tooth	N

N40	-c	SA (PEM)	?/10/65	33°58'S/ 23°34'E	bone	N
96/24	F	SA (SAM)	13/09/96	32°18'S/ 18°21'E	tooth	Y
94/09	F	SA (SAM)	25/06/94	34°24'S/ 20°50'E	tooth	N
93/16	M	SA (SAM)	01/09/93	34°48'S/ 20°03'E	tooth	N
93/14	M	SA (SAM)	06/07/93?	34°25'S/ 20°24'E	tooth	Y
92/14	F	SA (SAM)	16/09/92	34°24'S/ 20°50'E	tooth	N
91/26	F	SA (SAM)	08/06/91	34°20'S/ 21°54'E	tooth	N
88/05	M	SA (SAM)	16/02/88	34°31'S/ 20°28'E	tooth	N
87/26	-	SA (SAM)	?/1986	32°36'S/ 18°17'E	tooth	N
87/12	-	SA (SAM)	09/05//87	34°07' S/ 22°07' E	tooth	N
87/10	M?	SA (SAM)	05/03/87	34°31'S/ 20°28'E	tooth	Y
87/06	M	SA (SAM)	03/03/87	34°08'S/ 22°10'E	tooth	Y
86/22	M	SA (SAM)	25/05/86	33°25'S/ 18°18'E	tooth	N
86/17	F	SA (SAM)	09/04/86	34°31'S/ 20°28'E	tooth	N
84/26	F	SA (SAM)	04/09/84	22°57'S/ 14°30'E	tooth	Y
84/24	F	SA (SAM)	10/08/84	34°21'S/ 19°02'E	tooth	N
83/33	F	SA (SAM)	23/09/83	34°25'S/ 19°14'E	tooth	Y
83/27	M	SA (SAM)	11/06/83	34°23'S/ 18°52'E	tooth	Y
83/26	-	SA (SAM)	03/06/83	34°07'S/ 22°07'E	tooth	Y
83/21	M	SA (SAM)	06/05/83	34°24'S/ 20°50'E	tooth	N
83/20	F	SA (SAM)	06/05/83	34°24'S/ 20°50'E	tooth	Y
82/27	F	SA (SAM)	31/08/82	22°40'S/ 14°34'E	tooth	Y
82/21	M	SA (SAM)	26/09/82	34°24'S/ 20°50'E	tooth	Y
82/04	F	SA (SAM)	06/02/82	32°52'S/ 17°52'E	tooth	Y
81/22	F	SA (SAM)	31/12/81	34°06'S/ 18°29'E	tooth	Y
80/26	F	SA (SAM)	29/10/80?	34°29'S/ 19°22'E	tooth	Y
80/03	-	SA (SAM)	01/08/79	21°15'S/ 13°14'E	tooth	N
79/18	-	SA (SAM)	06/08/79?	22°50'S/ 14°34'E	tooth	Y
78/25	F	SA (SAM)	ca27/8/78	22°51'S/ 14°34'E	tooth	Y
78/20	F	SA (SAM)	07/07/78	34°39'S/ 19°29'E	tooth	N
76/24	M	SA (SAM)	30/11/76?	33°40'S/ 18°24'E	tooth	Y
76/19	M	SA (SAM)	16/09/76	34°10'S/ 18°52'E	tooth	N
76/04	F?	SA (SAM)	late02/76	34°35'S/ 20°22'E	tooth	N
72/14	-	SA (SAM)	end07/ beg08 1970	34°28'S/ 20°30'E	tooth	Y
75/07	M	SA (SAM)	07/10/75	22°57'S/ 14°30'E	tooth	Y
69/15	M	SA (SAM)	?06/11/69	34°42'S/ 20°15'E	tooth	N

68/13	M	SA (SAM)	30/04/68	34°29'S/ 19°22'E	tooth	N
66/08	M	SA (SAM)	03/12/66	34°02'S/ 18°21'E	tooth	N
#34018	-	SA (SAM)	15/12/30	33°52'S/ 18°29'E	tooth	Y
#33577	-	SA (SAM)	-	34°05'S/ 23°36'E	tooth	N
#3912	-	SA (SAM)	1899	34°03'S/ 23°03'E	tooth	N
#35074	-	SA (SAM)	1880	34°05'S/ 23°36'E	tooth	N
C30959	M	AUS (MOV)	26/09/97	37°59'S/ 147°43'E	tooth	Y
C-	F	AUS (MOV)	August '99	38°17'S/ 144°30'E	liver	Y
C29469	F	AUS (MOV)	18/08/90	38°20'S/ 142°01'E	tooth	N
C24976	M	AUS (MOV)	21/01/80	37°52'S/ 148°04'E	tooth	Y
C24975	M	AUS (MOV)	19/08/75	37°49'S/ 148°36'E	tooth	N
C24972	M	AUS (MOV)	22/06/75	37°49'S/ 148°44'E	tooth	N
C23489	M	AUS (MOV)	09/07/79	39°02'S/ 146°20'E	tooth	Y
C23565	M	AUS (MOV)	04/05/93?	38°S49'/ 146°07'E	tooth	Y
M16967	M	AUS (SAUSM)	15/08/88	32°13'S/ 133°08'E	muscle	Y
M16471	M	AUS (SAUSM)	13/02/91	35°13'S/ 138°28'E	muscle	Y
M15814	M	AUS (SAUSM)	30/10/89	33°18'S/ 137°50'E	liver	Y
M14157	F	AUS (SAUSM)	07/08/57	34°54'S/ 135°47'E	tooth	N
M12915	-	AUS (SAUSM)	July '80	32°43'S/ 134°05'E	tooth	N
M10097/001	F	AUS (SAUSM)	20/07/73	36°05'S/ 139°33'E	tooth	Y
M10095	-	AUS (SAUSM)	15/05/74?	33°00'S/ 138°30'E	tooth	N
M06310	F	AUS (SAUSM)	12/09/61	34°50'S/ 138°29'E	tooth	N
M06266	M	AUS (SAUSM)	29/09/59	34°58'S/ 138°32'E	tooth	N
M06257	M	AUS (SAUSM)	28/06/59	35°33'S/ 138°37'E	tooth	N
M06256	F	AUS (SAUSM)	28/06/59	35°33'S/ 138°37'E	tooth	Y
M06156	M	AUS (SAUSM)	07/08/57	34°54'S/ 135°47'E	tooth	Y
M05197	-	AUS (SAUSM)	August '44	34°54'S/ 135°47'E	tooth	N
M05010	F	AUS (SAUSM)	25/04/37	34°30'S/ 137°29'E	tooth	N
M19963	F	AUS (SAUSM)	27/12/96	31°45'S/ 131°49'	skin	Y
M16393	F	AUS (SAUSM)	15/08/88	38°20'S/142°02'E	muscle	Y

Bol592	F	AUS (SAUSM)	18/11/88	30°13'S/153°09'E	liver	Y
ANWC M16210	F	AUS (CSIRO)	11/03/79	34°25'S/150°52'E	tooth	N
JM11587	F	AUS (QM)	30/04/97	24°43'S/ 152°17'E	tooth	N
JM11586	F	AUS (QM)	30/04/97	24°43'S/ 152°17'E	tooth	Y
JM10000	F	AUS (QM)	08/09/93	26°37'S/ 153°06'E	tooth	Y
JM5698	F	AUS (QM)	15/01/87	24°43'S/ 152°17'E	tooth	Y
M25869	F	AUS (AM)	November '91	30°09'S/ 153°12'E	muscle	Y
M25479	F	AUS (AM)	02/12/91	29°29'S/ 153°22'E	tooth	Y
M23823	F	AUS (AM)	26/03/88	30°13'S/ 153°09'E	tooth	Y
M23800	-	AUS (AM)	February '82	29°49'S/ 153°17'E	tooth	N
M19687	M	AUS (AM)	07/05/88	33°13'S/ 151°38'E	tooth	Y
M9722	F	AUS (AM)	02/08/75	35°05'S/ 138°30'E	cartilage	Y
Kbr01	M	NZ	24/03/94	39°09'S/ 177°54'E	skin	Y
Kbr 02	M	NZ	29/03/94	-	skin	Y
Kbr 03	M	NZ	16/12/94	38°20'S/ 175°10'E	skin	Y
Kbr 04	F	NZ	25/02/95	41°13'S/ 174°53'E	skin	Y
Kbr 05	Fc	NZ	16/05/95	-	skin	N
Kbr 06	F	NZ	16/05/95	-	skin	Y
Kbr 08	M	NZ	12/04/95	39°02'S/ 177°35'E	skin	Y
Kbr 09	M	NZ	18/02/94	39°20'S/ 177°20'E	skin	Y
Kbr 10	F	NZ	March '94	38°40'S/ 178°01'E	skin	N
Kbr 11	M	NZ	08/01/97	39°04'S/ 177°52'E	skin	Y
Kbr 12	F	NZ	20/08/97	34°53'S/ 173°04'E	skin	Y
Kbr 13	F	NZ	May '97	34°53'S/ 173°04'E	skin	Y
Kbr 14	F	NZ	21/04/97	39°20'S/ 177°20'E	skin	Y
Kbr 15	M	NZ	05/05/97	-	skin	Y
Kbr 16	M	NZ	-	-	skin	Y
Kbr 17	M	NZ	07/04/98	-	skin	Y
Kbr 18	F	NZ	05/01/98	-	skin	Y
Kbr 19	F	NZ	05/01/98	-	skin	Y
Kbr 20	F	NZ	28/03/98	39°04'S/ 177°25'E	skin	Y
Kbr 21	M	NZ	28/03/98	39°04'S/ 177°25'E	skin	N
Kbr 22	M	NZ	18/02/99	36°22'S/ 174°12'E	skin	Y
Kbr 23	-	NZ	22/03/99	40°50'S/ 175°57'E	skin	Y

Kbr 24	Fl	NZ	02/05/99	39°29'S/ 176°53'E	skin	Y
Kbr 25	Fc	NZ	02/05/99	39°29'S/ 176°53'E	skin	N
Kbr 27	M	NZ	-	-	skin	Y
Kbr 28	M	NZ	29/04/98	39°05'S/ 177°52'E	skin	Y
Kbr 29	Mc	NZ	30/04/98	39°05'S/ 177°52'E	skin	N
Kbr 30	M	NZ	14/05/98	39°04'S/ 177°50'E	skin	Y
Kbr 31	M	NZ	02/06/99?	39°09'S/ 177°54'E	skin	Y
Kbr 32	F	NZ	02/06/99	39°05'S/ 177°52'E	skin	Y
Kbr 33	F	NZ	09/06/99?	39°09'S/ 177°54'E	skin	Y
Kbr 34	F	NZ	09/06/99?	39°09'S/ 177°54'E	skin	Y
Kbr 35	M	NZ	-	39°09'S/ 177°54'E	skin	Y
Kbr 36	M	NZ	12/06/99	39°04'S/ 177°25'E	skin	Y
Kbr 37	M	NZ	-	-	skin	Y
Kbr 38	F	NZ	-	39°05'S/ 177°52'E	skin	Y
Kbr 39	Mc	NZ	09/03/00	39°09'S/ 177°54'E	skin	N
Kbr 40	F	NZ	09/03/00	39°09'S/ 177°54'E	skin	Y
Kbr 41	M	NZ	18/03/00	39°29'S/ 176°55'E	skin	Y
Kbr 42	F	NZ	22/02/00	39°04'S/ 177°52'E	skin	Y
Kbr 43	Fc	NZ	14/05/00	39°09'S/ 177°54'E	skin	N
Kbr 44	F	NZ	14/05/00	39°09'S/ 177°54'E	skin	Y
Kbr 45	F	NZ	16/11/99	38°20'S/ 178°20'E	skin	Y
Kbr 46	F	NZ	20/02/00	39°05'S/ 177°52'E	skin	Y
Kbr 47	M	NZ	19/02/99	39°04'S/ 177°52'E	skin	Y
Kbr 48	M	NZ	27/05/00	39°04'S/ 177°52'E	skin	Y
Kbr 49	M	NZ	11/06/00	39°04'S/ 177°52'E	skin	Y
Kbr 50	F	NZ	30/04/98	39°04'S/ 177°52'E	skin	Y
97-41	F	NC	27/09/97	20°45'S/165°08'E	skin	Y
97-42	M	NC	02/10/97	Magenta, Noumea	skin	Y
KVW1500	-	PE	06/02/87	13°52'S/76°17'W	tooth	Y

***Kogia sima***

<b>Specimen number</b>	<b>Sex</b>	<b>Country of origin</b>	<b>Date of stranding</b>	<b>Lat./Long.</b>	<b>Sample used</b>	<b>Sequenced successfully</b>
N2774	-	SA (PEM)	11/04/99	34°08'S/ 22°10'E	-	N
N2773	F	SA (PEM)	11/04/99	34°08'S/ 22°10'E	tooth	Y
N2772	M	SA (PEM)	21/04/99	-	tooth	N
N2760	M	SA (PEM)	09/02/99	34°03'S/ 24°55'E	tooth	Y

N2755	F	SA (PEM)	30/07/98	34°01'S/ 25°23'E	muscle	N
N2041	M	SA (PEM)	17/05/93	29°51'S/ 31°02'E	tooth	Y
N1869	-	SA (PEM)	04/10/91	33°09'S/ 27°41'E	tooth	Y
N1564	M	SA (PEM)	05/01/89	33°59'S/ 25°41'E	tooth	Y
N1322	F	SA (PEM)	01/12/86	33°58'S/ 25°39'E	tooth	Y
N1248	M	SA (PEM)	02/11/85	33°59'S/ 24°59'E	tooth	Y
N1131	M	SA (PEM)	17/01/85	34°02'S/ 25°45'E	tooth	N
N1082	-	SA (PEM)	-	-	tooth	Y
N884	F	SA (PEM)	29/10/82	33°58'S/ 25°02'E	tooth	Y
N837	M	SA (PEM)	05/05/82	34°00'S/ 23°27'E	tooth	N
N830	F	SA (PEM)	27/03/82	33°48'S/ 25°42'E	tooth, bone	N
N678	F	SA (PEM)	03/03/81	33°58'S/ 25°02'E	mammary tissue	N
N440	F	SA (PEM)	21/12/76	33°01'S/ 27°54'E	tooth	N
N372	M	SA (PEM)	27/08/78	34°03'S/ 24°55'E	tooth	Y
N317	F	SA (PEM)	01/08/77	33°34'S/ 26°58'E	tooth, bone	N
N244	F	SA (PEM)	17/09/75	33°43'S/ 25°51'E	tooth	Y
N243	F	SA (PEM)	17/09/75	33°43'S/ 25°51'E	tooth	N
N239	M	SA (PEM)	10/07/75	34°10'S/ 24°50'E	tooth	N
N237	F	SA (PEM)	10/07/75	34°10'S/ 24°50'E	tooth	Y
N236	F	SA (PEM)	10/07/75	34°10'S/ 24°50'E	tooth	N
N228	M	SA (PEM)	09/02/75	33°58'S/ 25°14'E	tooth	Y
N224	M	SA (PEM)	19/08/74	33°56'S/ 25°36'E	tooth	N
N205	F	SA (PEM)	05/02/74	33°56'S/ 25°36'E	tooth	Y
N148	M	SA (PEM)	02/05/71	34°01'S/ 25°22'E	tooth	N
N146	F	SA (PEM)	14/04/71	33°51'S/ 25°38'E	tooth	Y
N140	F	SA (PEM)	24/03/71	33°46'S/ 26°27'E	tooth	Y
N139	F	SA (PEM)	24/03/71	33°46'S/ 26°27'E	tooth	N
N101	F	SA (PEM)	28/04/70	33°49'S/ 25°39'E	mammary tissue	N
N77	M	SA (PEM)	20/10/69	34°05'S/ 24°55'E	tooth	N
No no.	M	SA (PEM)	-	-	tooth	N
90/41	-	SA (SAM)	~07/12/90	32°47'S/ 18°10'E	tooth	Y
88/20	F	SA (SAM)	14/07/88	34°36'S/ 19°24'E	tooth	Y
88/02	F	SA (SAM)	27/01/88	34°23'S/ 20°51'E	tooth	N
86/34	-	SA (SAM)	14/09/86	34°48'S/ 20°03'E	tooth	N
85/02	F	SA (SAM)	08/03/85	34°31'S/ 20°28'E	tooth	N
84/36	M	SA (SAM)	26/11/84	34°07'S/ 18°28'E	tooth	Y

84/35	M	SA (SAM)	26/11/84	34°07'S/ 18°28'E	tooth	Y
84/21	M	SA (SAM)	16/07/84	34°13'S/ 21°58'E	tooth	N
81/03	F	SA (SAM)	24/03/81	34°02'S/ 18°21'E	tooth	Y
80/10	M	SA (SAM)	19/05/80	34°29'S/ 19°22'E	tooth	N
78/17	F	SA (SAM)	20/04/78	34°30'S/ 20°28'E	tooth	Y
76/18	F	SA (SAM)	09/08/76	34°07'S/ 18°50'E	tooth	N
76/17	M	SA (SAM)	30/07/76	34°11'S/ 18°26'E	tooth	N
76/14	M	SA (SAM)	08/04/76	34°25'S/ 19°17'E	tooth	N
76/09	M	SA (SAM)	03/04/76	34°06'S/ 18°22'E	tooth	N
76/03	F	SA (SAM)	29/02/76	34°29'S/ 19°22'E	tooth	N
76/02	F	SA (SAM)	15/02/76	34°08'S/ 18°19'E	tooth	Y
75/06	F	SA (SAM)	12/07/75	34°07'S/ 18°26'E	tooth	N
72/15	F	SA (SAM)	31/12/72	33°03'S/ 17°58'E	tooth	N
72/09	-	SA (SAM)	13/05/72	33°52'S/ 18°29'E	tooth	Y
68/10	M	SA (SAM)	02/12/68	33°48'S/ 18°27'E	tooth	N
SFRI2000/4	F	SA (SFRI)	05/05/00	32°47'S/ 18°10'E	skin	Y
M4519	F	AUS (WAM)	19/09/59	36°01'S/ 115°44'E	tooth	N
99.260	F	AUS (SAUSM)	27/11/99	-	liver	Y
NT0126	M	AUS	21/08/95	-	skin	Y
PWW2	Ff	TAS (UTAS)	16/11/92	-	skin	Y
Ce004	F	CH	02/02/96	33°50 'S/71°51'W	tooth	Y

F= Female; M= Male; f=foetus

SA= South Africa

NZ= New Zealand

AUS= Australia

TAS= Tasmania

CH= Chile

PE= Peru

NC= New Caledonia

PEM= Port Elizabeth Museum (now Bayworld), Port Elizabeth, South Africa

SAM= South African Museum, Cape Town, South Africa

SFRI= Sea Fisheries Research Institute (now Marine and Coastal Management), Cape Town, South Africa

UA= University of Auckland, Auckland, New Zealand

MNZ= Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand

MOV= Museum of Victoria, Abbotsford, Australia

SAUSM= South Australian Museum, Adelaide, Australia

CSIRO=Commonwealth Scientific and Industrial Research Organisation, Canberra, Australia

QM= Queensland Museum, Brisbane, Australia

AM= Australian Museum, Sydney, Australia

WAM= Western Australian Museum, Perth, Australia

UTAS= University of Tasmania, Hobart







## **APPENDIX F**

Length and age at attainment of sexual maturity of different families of cetacea.

<b>Common Name</b>	<b>Species Name</b>	<b>Male length at ASM (cm)</b>	<b>Female length at ASM (cm)</b>	<b>Male age at ASM</b>	<b>Female age at ASM</b>	<b>Source</b>
<b><u>Phocoenids</u></b>						
Vaquita	<i>Phocoena sinus</i>	127*	131.9*	4.5y	4.5y	Hohn <i>et al.</i> , 1996
Harbour porpoise	<i>Phocoena phocoena</i>	130.8	144.2	2.93y	3.64y	Sørensen and Kinze, 1994
Dall's porpoise	<i>Phocoenoides dalli</i>	179.7	172	5y	4.2y	Ferrero and Walker, 1999
<b><u>Pontoporiidae</u></b>						
Franciscana	<i>Pontoporia blainvillei</i>	131	140	2.5y	2.7y	Brownell, 1984
<b><u>Platanistidae</u></b>						
Susu	<i>Platanista</i>	170*	200*	10y	10y	Brownell, 1984
<b><u>Delphinidae</u></b>						
Hector's dolphin	<i>Cephalorhynchus hectori</i>	140*	125*	7.5y	7y	Slooten, 1991
Commerson's dolphin	<i>Cephalorhynchus commersoni</i>	165	165	8y	5y	Collet and Robineau, 1988
Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>	249	218	9y	8y	Rogan <i>et al.</i> , 1997
Common dolphin	<i>Delphinus delphis</i>	175 200	160 190	3y 6G	4y 6.5G	Perrin and Reilly, 1984
Spinner dolphin	<i>Stenella longirostris</i>	165	164	7.5y	4.5y	Perrin and Reilly, 1984
Spotted dolphin	<i>Stenella attenuata</i>	194 195	182 181	12y 11G	9y 8G	Perrin and Reilly, 1984
Striped dolphin	<i>Stenella coeruleoalba</i>	219 -	216 -	9y 8.9y	9y 8.8y	Perrin and Reilly, 1984; Miyazaki, 1984
Bottlenose dolphin	<i>Tursiops truncatus</i>	238* 252.5	225* 227.5	14.5y 11y	10.3y 12y	Cockcroft and Ross, 1990; Perrin and Reilly, 1984
Melon-headed whale	<i>Peponocephala electra</i>	-	-	3G	4G	Perrin and Reilly, 1984
False killer whale	<i>Pseudorca crassidens</i>	426.5	396.5	12y	12y	Perrin and Reilly, 1984
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	422 560	316 395	17y 17y	9y 8.5y	Kasuya and Marsh, 1984; Kasuya and Tai, 1993

Common Name	Species Name	Male length at ASM (cm)	Female length at ASM (cm)	Male age at ASM	Female age at ASM	Source
Long-finned pilot whale	<i>Globicephala melas</i>	490	365	12y	6.5y	Perrin and Reilly, 1984
Killer whale	<i>Orcinus orca</i>	579	472.5	16y	10y	Perrin and Reilly, 1984
<b><u>Monodontidae</u></b>						
Beluga	<i>Delphinapterus leucas</i>	-	-	8.5y	5.5y	Braham, 1984
Narwhal	<i>Monodon monoceros</i>	390	340	12y	6.5y	Braham, 1984
<b><u>Ziphiidae</u></b>						
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>	750	690	9G	11G	Mead, 1984
Baird's beaked whale	<i>Berardius bairdii</i>	945	1025	8.5y	10.25y	Kasuya <i>et al.</i> , 1997 Best, 1968, 1969, 1970; Best <i>et al.</i> , 1984; Evans, 1987
<b><u>Physeteridae</u></b>						
Sperm whale	<i>Physeter catodon</i>	1190	880	18.5y	9.5y	Best, 1968, 1969, 1970; Best <i>et al.</i> , 1984; Evans, 1987
Pygmy sperm whale	<i>Kogia breviceps</i>	242	262	5G	6G	Present study
Dwarf sperm whale	<i>Kogia sima</i>	197.25	215	4.5G	2.925G	Present study
<b><u>Eschrichtiidae</u></b>						
Gray whale	<i>Eschrichtius robustus</i>	1110	1170	-	-	Lockyer, 1984
<b><u>Balaenidae</u></b>						
Southern right whale	<i>Eubalaena australis</i>	1450	1450	-	-	Lockyer, 1984
Bowhead whale	<i>Balaena mysticetus</i>	1160	1310	15y	15y	Lockyer, 1984; George <i>et al.</i> , 1997; 1999
<b><u>Balaenopteridae</u></b>						
Minke whale	<i>Balaenoptera acuturostrata</i>	720	800	6y	6y	Lockyer, 1984; Williamson, 1975
Bryde's whale	<i>Balaenoptera edeni</i>	1200	1250	-	-	Lockyer, 1984
Humpback whale	<i>Megaptera novaeangliae</i>	1160	1200	6.5y	5y	Lockyer, 1984; Clapham, 1992
Sei whale	<i>Balaenoptera borealis</i>	1360	1400	-	-	Lockyer, 1984
Fin whale	<i>Balaenoptera physalus</i>	1900	2000	-	-	Lockyer, 1984

Common Name	Species Name	Male length at ASM (cm)	Female length at ASM (cm)	Male age at ASM	Female age at ASM	Source
Pygmy blue whale	<i>Balaenoptera musculus brevicauda</i>	1890	1920	-	-	Lockyer, 1984
Blue whale	<i>Balaenoptera musculus</i>	2260	2400	-	-	Lockyer, 1984

LSM= mean length at attainment of sexual maturity; ASM= mean age at attainment of sexual maturity; G= GLG's; y= years.

\* = data were not supplied by the author(s), but estimated (i.e. read off curves and tables) from the paper.

If no mean length/age at sexual maturity was supplied in the literature, data for the shortest/youngest mature animal were used. For females the age at first ovulation, not first calf, was used. If the age at first conception was supplied, the gestation time (roughly 12 months) was subtracted. If a range was supplied the median value was used.

Only complete data sets were used. When complete data sets for different populations were available, only the largest data set was used.

Life expectancy data (i.e. maximum ages) of different families of cetaceans. Note that the data presented are maximum age estimates.

Common Name	Species Name	Males	Females	Males (cm)	Females (cm)	Source
<b><u>Phocoenidae</u></b>						
Vaquita	<i>Phocoena sinus</i>	16y	21y	144	148.2	Hohn <i>et al.</i> , 1996
Harbour porpoise	<i>Phocoena phocoena</i>	24y	24y	160	184	Gaskin <i>et al.</i> , 1984; Hohn and Brownell, 1990; Read and Gaskin, 1990; Read and Hohn, 1995; Sørensen and Kinze, 1994; Lockyer, 1995
Finless porpoise	<i>Neophocaena phocaenoides</i>	23y*	-	192	175	Gaskin <i>et al.</i> , 1984
Dall's porpoise	<i>Phocoenoides dalli</i>	18y	16y	219	209	Gaskin <i>et al.</i> , 1984
<b><u>Pontoporiidae</u></b>						
Franciscana	<i>Pontoporia blainvillei</i>	16y	13y	158	174	Brownell, 1984
<b><u>Iniidae</u></b>						
Boto	<i>Inia geoffrensis</i>	18+y	28y	255	228	Brownell, 1984
<b><u>Platanistidae</u></b>						
Susu	<i>Platanista</i>	28y	-	211	252	Brownell, 1984
<b><u>Delphinidae</u></b>						
Hector's dolphin	<i>Cephalorhynchus hectori</i>	20y	19y	-	-	Slooten, 1991

Common Name	Species Name	Males	Females	Males (cm)	Females (cm)	Source
Commerson's dolphin	<i>Cephalorhynchus commersoni</i>	15G 9y	11G 10y	166.5	174	Perrin and Reilly, 1984; Collet and Robineau, 1988
Dusky dolphin	<i>Lagenorhynchus obscurus</i>	7y	21y	211	193	Perrin and Reilly, 1984
Atlantic white-sided dolphins	<i>Lagenorhynchus acutus</i>	22G 17y	27G 15y	275	243	Perrin and Reilly, 1984; Rogan <i>et al.</i> , 1997
Common dolphin	<i>Delphinus delphis</i>	22y	20y	260	230	Perrin and Reilly, 1984
Spinner dolphin	<i>Stenella longirostris</i>	12-19y	15-23y	235	204	Perrin and Reilly, 1984
Spotted dolphin	<i>Stenella attenuata</i>	40y	46y	257	242	Perrin and Reilly, 1984
Striped dolphin	<i>Stenella coeruleoalba</i>	45.5y 32y	37.5y 28y	256	245	Miyazaki, 1984; Calzada <i>et al.</i> , 1994
Rough-toothed dolphins	<i>Steno bredanensis</i>	32y	30y	265	255	Perrin and Reilly, 1984
Bottlenose dolphin	<i>Tursiops truncatus</i>	42y	43y	381	367	Perrin and Reilly, 1984; Cockcroft and Ross, 1990
Risso's dolphin	<i>Grampus griseus</i>	>13G	>17G	383	366	Perrin and Reilly, 1984
Pygmy killer whale	<i>Feresa attenuata</i>	14G	-	264	243	Perrin and Reilly, 1984
Melon-headed whale	<i>Peponocephala electra</i>	47G	12G	273	257	Perrin and Reilly, 1984
False killer whale	<i>Pseudorca crassidens</i>	20y	22y	596	506	Perrin and Reilly, 1984
Short-finned pilot whales	<i>Globicephala macrorhynchus</i>	44.5y 45.5y	61.5y 62.5y	720 525	510 405	Kasuya and Marsh, 1984; Kasuya and Tai, 1993
Long-finned pilot whales	<i>Globicephala melas</i>	46y	59y	762	570	Perrin and Reilly, 1984; Bloch <i>et al.</i> , 1993
Killer whale	<i>Orcinus orca</i>	35G	34G	975	853	Perrin and Reilly, 1984

Common Name	Species Name	Males	Females	Males (cm)	Females (cm)	Source
<b><u>Monodontidae</u></b>						
Beluga	<i>Delphinapterus leucas</i>	25-30y*	-	-	-	Braham, 1984
Narwhal	<i>Monodon monoceros</i>	50y*	-	470	400	Braham, 1984
<b><u>Ziphiidae</u></b>						
Gervais' beaked whale	<i>Mesoplodon europaeus</i>	-	27G	456	520	Mead, 1984
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	36G	30G	700	754	Mead, 1984
Northern bottlenose whale	<i>Hyperoodon ampullatus</i>	37G	27G	980	870	Mead, 1984
Baird's beaked whale	<i>Berardius bairdii</i>	84y	54y	1010	1045	Kasuya <i>et al.</i> , 1997
<b><u>Physeteridae</u></b>						
Sperm whale	<i>Physeter catodon</i>	42y	42y	1580	1100	Best, 1970; Evans, 1987
Pygmy sperm whale	<i>Kogia breviceps</i>	13.33G (16G)	22.43G	330.5	327.6 (340)	Present study (Australian data)
Dwarf sperm whale	<i>Kogia sima</i>	17G	21.5G	260.4	274.3	Present study
<b><u>Neobalaenidae</u></b>						
Pygmy right whale	<i>Caperea marginata</i>	-	-	-	640	Lockyer, 1984
<b><u>Eschrichtiidae</u></b>						
Gray whale	<i>Eschrichtius robustus</i>	-	-	-	1500	Lockyer, 1984
<b><u>Balaenidae</u></b>						
Southern right whale	<i>Eubalaena australis</i>	-	-	-	1830	Lockyer, 1984
Bowhead whale	<i>Balaena mysticetus</i>	>100y (211y)	-	-	2000	Lockyer, 1984; George <i>et al.</i> , 1997; 1999
<b><u>Balaenopteridae</u></b>						
Minke whale	<i>Balaenoptera acutorostrata</i>	ca50	ca50	980	1070	Lockyer, 1984; Williamson, 1975
Bryde's whale	<i>Balaenoptera edeni</i>	-	-	-	1560	Lockyer, 1984
Humpback whale	<i>Megaptera novaeangliae</i>	-	-	-	1520	Lockyer, 1984
Sei whale	<i>Balaenoptera borealis</i>	-	-	-	1830	Lockyer, 1984
Fin whale	<i>Balaenoptera physalus</i>	114y*	-	-	2600	Lockyer, 1984; Ohsumi, 1979 in: George <i>et al.</i> , 1997
Pygmy blue whale	<i>Balaenoptera musculus brevicauda</i>	-	-	-	2410	Lockyer, 1984

Common Name	Species Name	Males	Females	Males (cm)	Females (cm)	Source
Blue whale	<i>Balaenoptera musculus</i>	110y*	-	-	3100	Lockyer, 1984; Ohsumi, 1979 in: George <i>et al.</i> , 1997

G=GLG's; y=years.

When y and G were available only y were presented here. \* =no indication of sex was provided for these data.

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