

**Biological Studies of Bottlenose dolphins from  
Natal Coastal Waters**

by

Victor Gavin Cockcroft

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Laqhamuka ihlengethwa elwandle,  
Ngegagasi laqonda emhlabathini,  
Ngoba ithwasane beseliqomile,  
Licakile lizophothula,  
Lagijima lesaba malibheke idlozi,  
Licamanga ukuthi ngushaka,  
Abadobi basebelibulala bengaqondile,  
Osochwepheshe basebeqoqa amathambo.

Mzikayasi Mahola, 1989.

## ABSTRACT

The biology of bottlenose dolphins from the east coast of southern Africa is investigated. Births occur predominantly in summer, after a one year gestation period. Calves are born at a length of approximately 103 cm and a mass of nearly 14 kg. Neonates are closely attended by the mother, she determines the calf's respiration rate and behaviour as it swims in a negative pressure vortex high on her flank. The initial weeks are marked by the calf's acquisition of swimming skills and its ability to regulate its own respiration rate. Although the calf takes solid food between six months and one year, suckling may continue for as much as three years. Initial growth is rapid but slows with the approach to puberty.

Females reach sexual maturity at about ten years of age and may undergo a series of rapid ovulations before fertilisation occurs. Subsequently, the mean ovulation rate indicates a three year calving interval. Males show a mass growth spurt at the onset of puberty, between 10 and 12 years, and reach sexual maturity between 12 and 15 years of age. In both sexes, physical maturity and asymptotic size are reached at about 15 years and maximum life-span is in excess of 40 years.

Although a wide variety of fish and cephalopods are taken, the fishes *Pomadasys olivaceum*, *Scomber japonicus*, *Pagellus bellotti*, *Trachurus delagoae*, and the cephalopods *Sepia officinalis* and *Loligo* sp. contribute some 60 % by mass of all prey taken. Different sex and maturity classes of dolphins consume differing sizes and species of prey, implying a partitioning of food resources within the group. Comparisons of stomach volumes with estimates of prey mass and nutritional requirements suggest that calves and lactating females may need to feed more often than other sex and maturity classes.

Examination of shark stomachs indicates that shark predation may be an important component of dolphin natural mortality. Four species of shark, the Zambesi (*Carcharhinus leucas*), the

tiger (*Galeocerdo cuvieri*), the great white (*Carcharodon carcharias*) and the dusky shark (*Carcharhinus obscurus*) are implicated as dolphin predators. Estimates from the number of these four species caught annually and the frequency of occurrence of dolphin flukes and vertebrae in their stomachs suggest that a minimum of 20 bottlenosed dolphins or 2.2 % of the estimated population in southern Natal coastal waters are killed each year by sharks.

Some 32 bottlenose dolphins, about 4 % of the estimated population, are captured in shark nets annually. Calves of two years or less constitute nearly 45 % of the catch, while lactating females make up a further 15 %. An analysis of biological, environmental and physiographic factors associated with each capture, suggest that feeding and probably prey movement and distribution are directly associated with capture.

PCB, t-DDT and dieldrin concentrations in the blubber of male bottlenose dolphins increase with age and reach levels that may impair testosterone production. In females, there is an 80 % decline in residue concentrations after the first or second ovulation. Evidence presented suggests that first born calves receive possibly lethal doses of residues within two months of birth. Residue concentrations in dolphins from different geographical areas varied significantly, implying a degree of isolation of sections of the population.

Investigation of reproductive parameters indicates that mortality of bottlenose dolphins off Natal probably equals or exceeds the replacement rate. The necessity for and requirements of further research on the natural history of bottlenose dolphins off the east coast of southern Africa are summarised.

## PREFACE

The work described in this thesis was undertaken at the Natal Sharks Board and the Port Elizabeth Museum between January 1980 and December 1987 under the supervision of Dr. Graham Ross.

Although a number of individuals have collaborated in aspects of the various chapters, these studies represent the authors own original ideas and work and have not been submitted in any form to another University.



## ACKNOWLEDGEMENTS

By its nature, this work has relied, to a large degree, on a host of individuals who have provided enthusiasm, ideas, discussion, laboratory assistance and many other services. A complete list of your names is not possible here but this in no way lessens my appreciation of your essential contributions.

To my family for accepting my many months away from home. Your constant belief in me and the pride with which you call me husband and father has given me the will to complete this work.

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I thank the Director of the Natal Sharks Board for granting me access to retrieved dolphins and immeasurable logistical support. My particular thanks to the Field Officers of the Natal Sharks Board without whose co-operation and enthusiasm little of the material would have been retrieved. The observations of these officers on the movements and behaviour of dolphins in and around the nets has provided invaluable background understanding to this work.

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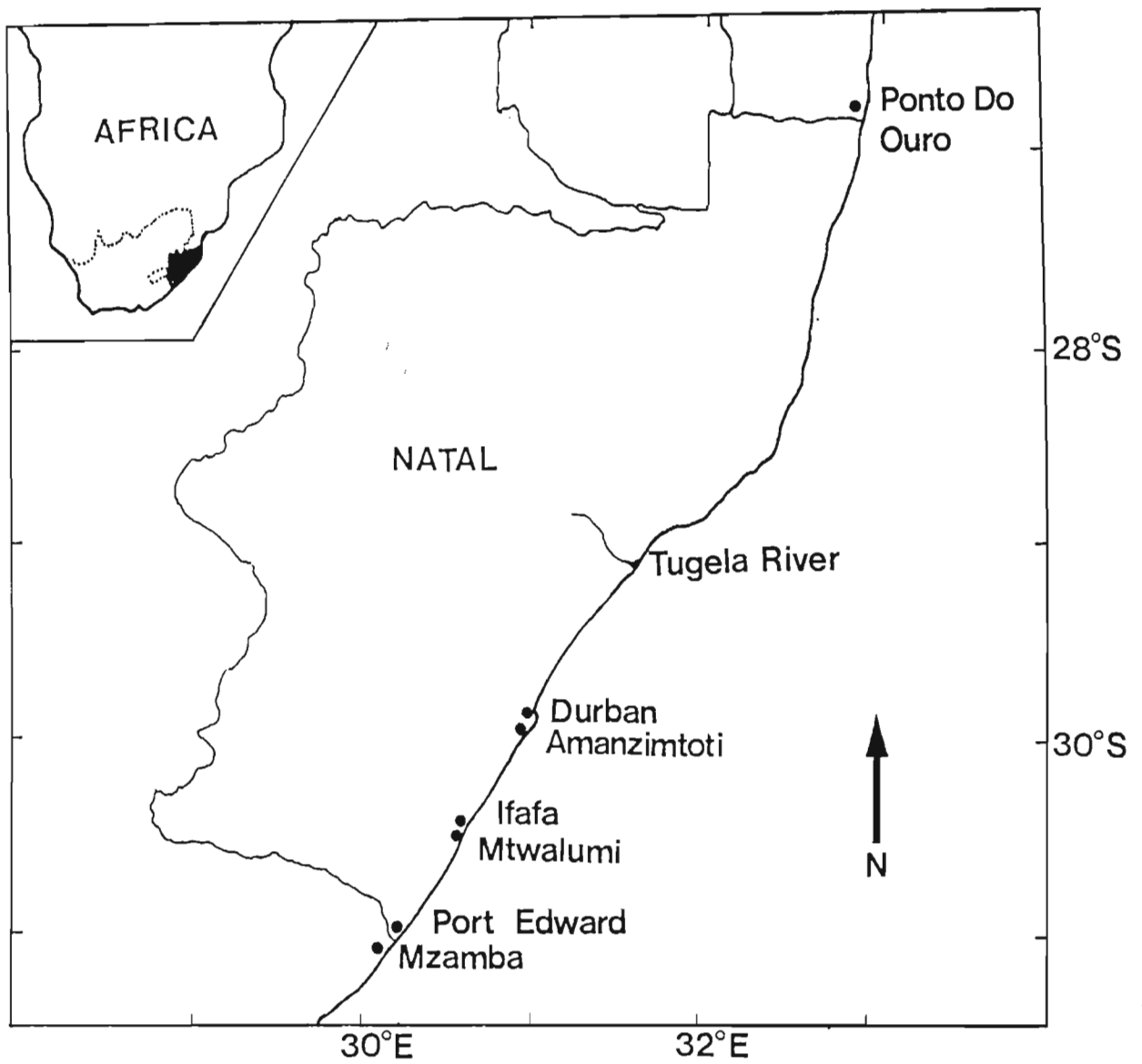
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## INTRODUCTION

The work reported here is part of a wider, ongoing effort to understand the natural history of marine mammals off the coast of southern Africa. More specifically, it is part of an extensive study of the bottlenose dolphin in the nearshore waters of the south east coast of southern Africa, particularly Natal. Bottlenose dolphins inhabiting the near shore region of the east coast of southern Africa are taxonomically similar to a larger form which inhabits offshore waters (Ross & Cockcroft, in press). The distribution of the smaller form of *Tursiops* appears to be governed by water depth, the animals inhabiting the inshore region within the 30 m isobath (Ross *et al.*, 1986). This work is concerned exclusively with the smaller form.

It is not the intention of this introduction to provide a chronological account of the work from which this study originated. Rather, it attempts to provide an appreciation of the progression of ideas which, from the original insights, has lead to this work and subsequently to ongoing research by a number of individuals. Although the majority of ideas and data interpretation are my own, all the work is co-authored, as many individuals contributed ideas and have given unstintingly of their enthusiasm.

Natal lies on the east coast of southern Africa and has approximately 650 km of coastline which extends from about Ponta Do Ouro ( $26^{\circ}50'S$   $32^{\circ}54'E$ ) in the north to Port Edward in the south ( $31^{\circ}03'S$   $30^{\circ}13'E$ ) (Fig. 1). The southern half of this coast, between Zinkwazi Beach in the north ( $29^{\circ}17'S$   $31^{\circ}26'E$ ) and Mzamba (two km south of Port Edward) in the south, is densely populated and is host, most of the year, to hundreds of thousands of tourists who throng to the beaches for their annual holiday. For traditional reasons, this 250 km of holiday coast is divided into three sections, the North Coast, north of Durban, the Upper South Coast, between Durban and Ifafa and the Lower South Coast which extends south of Ifafa to Mzamba.

Durban, as the major tourist centre on the Natal coast, accomidates the vast majority of

tourists and has done so since early this century. Between 1944 and 1952 there was a spate of 21 shark attacks on bathers using the beaches of this coastal city. These attacks had a dramatic and negative affect on the tourist industry and prompted the installation of protective nets in 1952 (Davies, 1964). These nets were apparently successful and few serious attacks have occurred off Durban following their introduction. During the holiday season of 1958 (November 1958 to January 1959) seven shark attacks off resorts on the South Coast lead to a dramatic drop in tourist revenue and prompted some South Coast local authorities to set protective nets to placate the public and maintain the tourist industry (Davies, 1964).

The number of nets and the number of beaches off which they were installed increased rapidly over the next few years, from about 150 nets at 32 beaches in 1968 to the present 416 nets at 45 beaches. Initially, all nets were maintained and serviced by local authorities or by appointed private contractors and few or no records of catches were kept. In 1964 the Natal Anti-Shark Measures Board (later renamed The Natal Sharks Board - NSB) was established, after promulgation of "The Anti-Shark Measures Control Ordinance" (Natal Provincial Ordinance 10). The function of the NSB was to initiate, approve and control measures for safeguarding bathers against shark attacks. From 1966, a liaison officer, appointed to the NSB, monitored some of the catches.

The function of the 416 anti-shark gill nets presently set along the southern half of Natal is to catch and deplete the stocks of large sharks inhabiting or visiting this area in an attempt to reduce the possibility of shark and bather interaction. The number of nets set at each beach depends on its frequency of use by bathers and the number of bathers visiting the area. Each net is 107 m long by 6.1 meters in depth<sup>\*</sup> and is set in water less than 15 m deep, on average some 100 m to 200 m off the surfline and 400 m offshore. Nets have a 25 cm bar so that when set and

\* Triple length nets (304 m in length) are used off Durban.

taut the mesh is diamond shaped with a vertical and horizontal measurement of approximately 35 cm. Nets are visited and maintained daily, weather permitting and excluding weekends, by trained staff of the NSB, who retrieve any dead animals captured in the nets and return them to shore where they are frozen for scientific analysis.

Approximately 17 % of the southern half of the Natal inshore region is covered by gill nets.

That these nets are effective in their purpose is beyond doubt, few, all non-fatal, shark attacks on bathers have occurred in netted areas following the introduction of nets. Some 1400 sharks are captured annually in these nets and there is evidence that the number of sharks captured in the Durban nets has decreased fourfold since 1952 (Cliff *et al.*, 1988).

Regrettably, shark nets are not selective; a number of small sharks and sharks apparently not hazardous to bathers are regularly caught. Even the wisdom of depleting the numbers of large, apparently dangerous, sharks has been questioned because of the possible impact on the Natal inshore environment (van der Elst, 1979). Fisherman have complained that the nets are responsible for a deterioration of fishing off the Natal coast (Mara, 1986). Net non-selectivity also applies to batoids, teleost fish, turtles and marine mammals which are often also captured. The capture of these latter animals, which was for so long ignored, has recently prompted calls for an enquiry into the effect of shark nets on the inshore environment (cf. African Wildlife, vol. 42(3)).

There was little early effort to monitor the capture of dolphins in shark nets, the first known published account being that of Davies (1963) who described two *euprosyne* dolphins, a humpback and bottlenose dolphin. Although it is not stated, the latter two were presumably captured in the Durban nets. In October 1964, 93 common dolphins, one bottlenose and one humpback dolphin were captured in the nets off Durban. A further 10 unidentified dolphins were captured off Umhlanga Rocks during October and November the same year (Anon, 1965). The author of this article notes that "It is an uncommon event for dolphins to be caught in set nets and during the

past six years only one or two young specimens have been found in the nets off Durban". The author further comments that this low capture rate is despite the common sighting of large congregations of dolphins off the beaches of Durban. Unfortunately, few data or material remain from any of these early captures.

The collection of dolphins caught in nets under the control of the NSB was initiated in 1968 by the Port Elizabeth Museum (PEM), to augment a strandings retrieval programme in the Eastern Cape. In 1973 NSB staff were requested to keep records of numbers and species of dolphins seen during operations. Although few dolphins were recovered from the nets, probably because most netting operations were done on contract, it was established that three species, the bottlenose dolphin (*Tursiops truncatus*), the common dolphin (*Delphinus delphis*) and the Indian Ocean humpback dolphin (*Sousa plumbea*), were regularly captured (Best & Ross, 1977). Analyses of the dolphins caught in conjunction with those stranded or captured in the Eastern Cape, lead to work on the taxonomy and biology of the smaller cetaceans of the south east coast of southern Africa, particularly the bottlenose dolphin (Ross, 1977; 1984).

In addition to the estimated 20 to 30 bottlenose dolphins captured annually in the nets, an unknown number on the east coast were thought to be harpooned illegally by fisherman (Best & Ross, 1977). Also, preliminary organochlorine analyses indicated that bottlenose and humpback dolphins in Natal waters carried high organochlorine loads (Ross, 1982). Concern for the effects of captures, illegal killings and habitat degradation on the populations of dolphins, particularly bottlenose dolphins, prompted the first census of dolphins on the south east coast of southern Africa (Ross, 1982). Transect-line density estimates from this preliminary survey suggested that about 3000 bottlenose dolphins inhabited Natal, although the calculations included areas where bottlenose dolphins were known not to occur, which implied that real numbers were probably far lower. Humpback dolphin sighting rates were very low and suggested that these animals were extremely sparse in Natal. Recommendations stemming from this exercise were that a specific survey be undertaken to determine the offshore distribution of bottlenose

dolphins.

Coincident with the first aerial survey, the NSB attained control of the majority of net installations, including the Durban installation of 23 triple length nets. Discussions with net meshing officers at this juncture revealed that many of the captured dolphins were retrieved but were subsequently eaten by staff, the officers being unaware of the need to keep the animals for scientific purposes. Over the following two years, by which time the NSB had attained control of all netting operations, an intensive effort was made by the PEM to have all captured dolphins retrieved and frozen for scientific study. The recording of sightings of dolphin groups, which had lapsed in 1977, was reinstated. Cameras and film were donated by KODAK South Africa and meshing officers were exhorted to obtain photographs of dolphins, particularly humpback and bottlenose dolphins displaying distinguishing marks.

The ideas and directions for the study of bottlenose dolphins, particularly those off Natal, are a result of these beginnings. Knowledge of the natural history of bottlenose dolphins in Natal was needed not only because of their capture in the nets but also because little was known of the dolphin fauna in Natal waters. The capture of dolphins in the shark nets provided a unique sample. Most dolphin studies are based on stranded animals and the information gained, although useful and in many cases the only data available, is tainted by the knowledge that it is from stranded animals. In contrast, incidentally captured free-ranging animals are 'healthy' at their death and can provide unbiased information on the natural history of the animal. Most incidental catches of dolphins occur in commercial fishing gear which is seldom set in the same area and, for numerous reasons, access to dolphin catches is often limited. The Natal shark nets provide an ideal sample of incidentally captured dolphins as nets are always set in the same area, are maintained by trained staff and access to catches is relatively easy. Additionally, the trained staff are able to collect environmental and other pertinent information pertaining to each capture.

Preventing captures became a priority and efforts were begun to test dolphin repellent devices on the nets (Peddemors *et al.*, in press). However, the low capture rate, some 32 bottlenose dolphins per year in any of 416 nets, meant that this type of study was too time consuming in light of the apparent low population number and needed to be conducted in concert with other work.

Population estimates of the bottlenose dolphin in Natal waters were essential. An aerial study on the offshore distribution of bottlenose dolphins off the North Coast of Natal, and a boat study in Algoa Bay, Eastern Cape, showed that in both areas these animals had a preference for shallow water between 15 m and 20 m deep (Ross *et al.*, 1986). The vast majority of the Natal sightings were within 1 km of the shore, making the animals particularly vulnerable to capture in inshore nets. This survey also suggested that future surveys could be flown along the shoreline. A subsequent census of bottlenose dolphin numbers off Natal and Transkei, flying along the shore and 1 km offshore, suggested that there were probably no more than about 900 bottlenose dolphins in Natal inshore waters (Ross *et al.*, in press). This number was far lower than was previously thought following the original 1980 survey. It suggested that net captures, at the rate of some 32 bottlenose dolphins per year, may be depleting the population, particularly if, as the grouping of sighting data seemed to imply, groups of these animals were spatially separated and could be 'home range' bound so that high catches in specific areas, such as Durban, selectively depleted particular groups (Ross *et al.*, 1987).

An early analysis of the catch statistics showed that most captures of bottlenose dolphins occurred at only a few beaches, suggesting a clumped longshore distribution. A study of this distribution, using catch statistics and sighting data collected by NSB staff, indicated that although catch per net was random along the coast, there were six areas where dolphins were sighted more frequently than elsewhere (Ross *et al.*, 1987). These six 'preferred areas' were of similar length, all about 35 km, which suggested that they may be home ranges. Although there was evidence that groups often crossed the boundaries of these 'preferred areas' and that mixing



of groups may thus occur (Richards & Cockcroft, in prep), this confirmed the suspicion that particular groups may be more at risk of capture than others.

These studies underscored the need for extensive research on the natural history of bottlenose dolphins off Natal. This work is a culmination of efforts, begun in 1980, to understand the natural history of Natal's bottlenose dolphins. It attempts, through several published or submitted papers, to provide detailed biological data and information on possible sources of mortality which, in conjunction with the results of other studies, are required for a better understanding of the bottlenose dolphin off the south east coast of southern Africa.

#### Chapter outline:

Chapter Two examines the growth and development, both behavioural and physical, of a captive-born bottlenose dolphin. It provides much of the necessary background knowledge against which the biological data from the net catches were viewed. This chapter has been accepted for publication in a book entitled "The Bottlenose Dolphin" (Edited by S. Leatherwood and R.R. Reeves).

Chapter Three investigates the age, growth and reproductive biology of bottlenose dolphins captured in the shark nets, with additional material from stranded and captive animals in the Eastern Cape. From a management viewpoint this is, in some respects, the most important of the six chapters as it defines preliminary estimates of the reproductive capacity of the Natal population of bottlenose dolphins. This chapter has been submitted for publication to Fishery Bulletin, United States.

Chapter Four is a study of the feeding biology of bottlenose dolphins in Natal, examines the diet and attempts to determine aspects of group social structure from differences in diet. This chapter has been accepted for publication in a book entitled "The Bottlenose Dolphin" (Edited by S. Leatherwood and R.R. Reeves).

Chapter Five outlines the net catch, giving the numbers, sexes and sizes of animals captured between January 1980 and December 1987, and examines its impact on the estimated Natal population. Further, it attempts, through an analysis of the biological, environmental and physiographic data pertaining to each catch, to determine reasons for the capture of bottlenose dolphins in the shark nets and to propose measures which may prevent their capture. This chapter has been accepted for publication in an International Whaling Commission special publication entitled "Cetaceans and Cetacean Research in the Indian Ocean Sanctuary" (Edited by G. Donovan and S. Leatherwood).

Chapter Six investigates the possible minimum mortality of bottlenose dolphins through shark predation. This chapter has been accepted for publication in a forthcoming issue of the South African Journal of Zoology.

Chapter Seven examines the occurrence of agricultural and industrial organochlorines, and their possible affects, in bottlenose dolphins. This chapter has been accepted for publication in a forthcoming issue of the South African Journal of Marine Science.

Chapter Eight presents conclusions drawn from this work and attempts to present guidelines for future research.

## CHAPTER TWO

Observations on the early development of a captive bottlenose dolphin calf.

V.G. Cockcroft and G.J.B. Ross,

Port Elizabeth Museum, P.O. Box 13147, Humewood 6013.

Republic of South Africa.

## ABSTRACT

The physical and behavioral development of a captive born bottlenose dolphin calf was monitored from birth to an age of two years through a series of 12 and 24 h observations. The first three weeks of the calf's life were marked by a number of behavioral and physical changes which began his progressive independence from the mother. The development of axial musculature and some motor control made the calf less dependant on the mother's pressure wave, allowing him to determine his own respiration and suckling frequency. Over the following two years the calf developed physically and acquired the behavioral skills necessary to attain complete independence from the mother. The volume of milk ingested by the calf at each suckle was estimated at 40 ml from the excised mammary gland of an incidentally killed female. Observations showed that the calf's suckling frequency decreased with age suggesting a decreased milk and energy intake with age. From an age of 321 days the calf took solid food but continued suckling. Just prior to weaning the calf's estimated energy intake was only 17 % of that immediately post weaning.

## INTRODUCTION

The relatively easy access to lactating female pinnipeds and their pups has facilitated studies of mother and calf interactions, calf energetics, suckling behavior and early growth (Tedman *et al.*, 1981; Fedak and Anderson, 1982; Lavigne *et al.*, 1982). Bonner (1984) reviewed pinniped lactation strategies. Apart from the constituent analysis of cetacean milk, similar energetic and early developmental studies of cetaceans are almost completely lacking.

This is partly due to the difficulties inherent in observing free ranging cetaceans. In the wild, access to mother and calf pairs is rarely practical and such pairs are often secretive and elusive. Despite these difficulties a few short-term studies of wild births and subsequent behavioral development have been undertaken. For example Norris *et al.* (1977) studied the movements and respiration patterns of gray whale (*Eschrichtius robustus*) mother and calf pairs in Magdalena Bay, Mexico, and Taber and Thomas (1982) observed the first four months of calf development, mother-calf spatial relationships and yearling behavior in southern right whales (*Eubalaena australis*) off Argentina.

Captive births of small cetaceans provide an ideal opportunity for studies of mother and calf interactions and the development of the calf. As a result, many behavioral and developmental studies of captive small cetaceans have been undertaken (McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavalga and Essapian, 1951; Essapian, 1953; Tayler and Saayman, 1972; Saayman and Taylor, 1977; Drinnan and Sadlier, 1982). However, even in captivity there is a natural reluctance to allow investigators physical contact at the risk of imposing additional stress on neonates and their mothers. Consequently, the majority of studies on captive mother and calf pairs have been brief or cursory.

This paper presents the results of a study of the relationships between suckling, respiration, growth and behavioral development of an Indian Ocean bottlenose dolphin (*Tursiops truncatus*)

observed from birth to two years of age.

## MATERIALS AND METHODS

Observations were made in the L-shaped dolphin lake ( $4.72 \times 10^6$  liter, maximum depth 5 m) at the Port Elizabeth Oceanarium. An underwater viewing facility provides a view of over 80% of the pool area.

'Simo' was born at 16h36 on 3 February 1982. His mother, 'Thandi', had been captured 36 days prior, and was still largely untrained. Observations were initiated at 17h15, and maintained until last light at approximately 19h15. The following day observations began at 08h00 and were intermittent throughout the day for a total of about five hours. Subsequently, a 12 h continuous watch was kept once per week and a 24 h watch once per month. This sequence was altered occasionally to allow more or less observation when needed. Over the two years we used three additional observers trained by one or both of us. Night observations were aided by a 1500 W tungsten light which illuminated most of the pool area sufficiently to permit observations to continue. The light illuminated before sunset and extinguished after dawn to prevent any sudden changes in light intensity. A total of 829 h was spent observing Simo from birth to 16 December 1983. Data were recorded in diary fashion, specifying time and the relevant behavior.

Initially, almost any action or behavior by mother or calf was noted. Subsequently, only distinctive features of mother and calf activity were recorded. Of the calf's behaviors these included: All feeding or attempted feeding; the side (left or right) from which he fed; the length of the feed and the calf's pre and post-suckling behavior. Suckling entailed the insertion of the rostral and mandibular tips into either of the mammary slits and the ensuing intake of milk (Tavolga and Essapian, 1951). Suckling time was measured from the moment of contact with the nipple to the moment of release. Other relevant behaviors, not directly

associated with feeding, were also recorded. One of these, termed bumping, consisted of the calf's swimming beneath the mother and bumping her mammary area with the top of his head: it occurred both before and after suckling.

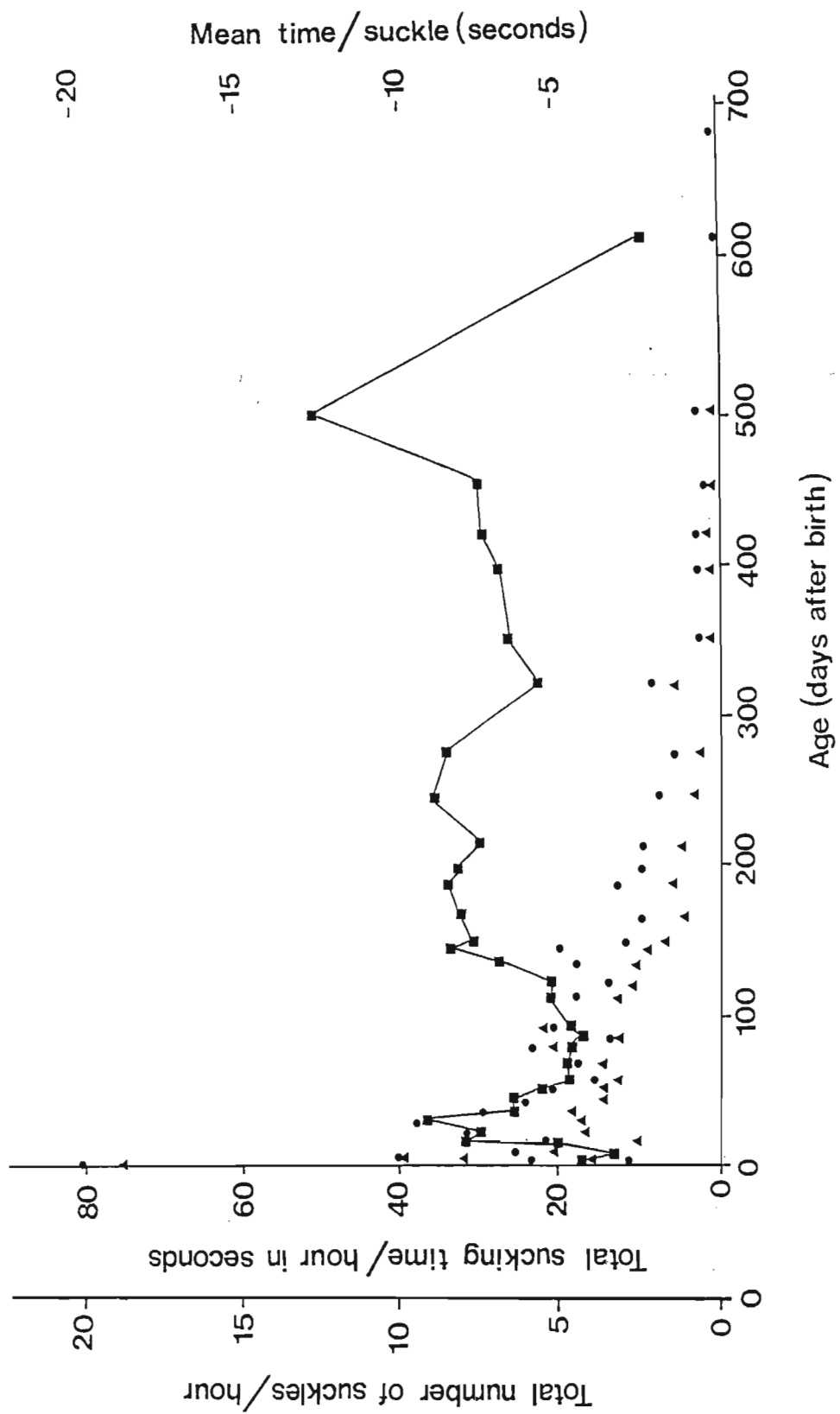
Three types of presentation by the mother during suckling were recognised and recorded. In side presentations Thandi turned to one side, arching her back and presenting the calf with her mammary area. In vertical presentations she arched her back while in the normal swimming position (without turning to either side), the mammary area was thus below her, forcing the calf to feed while on his side. Combined presentations were combinations of these two forms. If no presentation occurred prior to a feed this was also recorded.

Calf respiration frequency was recorded for a maximum of 15 min in each hour of observation. Respiration was considered to have occurred if Simo broke the surface. The time of each respiration was recorded as was the identity of any associated adult. Only if a minimum of five consecutive breaths with any one partner were recorded were these included in calculations. This excluded very short periods of partner association which were not representative of longer term patterns. The general activity of the calf, resting or active, was also noted. If an activity precluded the monitoring of respiration, recording was terminated and only resumed when respirations could again be adequately monitored.

Handling of Simo was prohibited during his first year and estimates of his body length were made from a series of photographs of him with his mother. To avoid errors of parallax, these were usually taken when he was directly below the mother. Thandi measured 241 cm in length at capture and 242 cm 19 months later. Photographs were taken frequently, at irregular intervals, for the first nine months and less often thereafter. On a few occasions after the first year it was possible to estimate Simo's length from the number of floor tiles between the tip of his rostrum and fluke notch. As the tiles were square and of known dimensions, length could be estimated, a suitable account being taken of inter-tile spacing. The first direct measurement of Simo was



Figure 1: Simo's total number of suckling bouts per hour (triangles), his total suckling time (seconds) spent suckling per hour (dots) and the mean time of each suckle (squares) plotted against his age (days after birth).



made 14 months after birth.

Simo's mass at age was estimated from 74 shark net caught bottlenose dolphin calves less than 210 cm in length. To estimate mammary gland volume, a mammary gland was excised from PEM N1182, a heavily lactating female caught in the shark nets. The gland, measuring 360 mm x 100 mm x 38 mm, was washed, filled with X-ray opaque fluid and X-rayed. Subsequently, a resin cast was made by filling with slow acting resin (7 days to mature). Her uterus was slightly distended and a large corpus was evident in her right ovary. Unfortunately, no information is available for her calf.

## RESULTS

### Suckling and Feeding:

Eighty four (5.2 %) of 1622 recorded suckling bouts were either untimed or uncertain and have been excluded from these results. There was no significant difference in Simo's use of left and right mammary glands ( $P < 0.01$ , Student's t-test - 829 left and 793 right, mean suckling time on both sides = 4.7 s) and therefore, no distinction has been made between suckling from the left or right.

No diurnal trends were evident in Simo's mean hourly suckling times during the first 16 weeks, suggesting no regular peak suckling time and no daily suckling pattern (Spearman's Rank Order Correlation Coefficient, all p values  $< 0.25$ ). Suckling almost always took place while mother and calf circuited the deepest part of the pool, directly in front of the viewing window. Circuiting was characterized by a repetitious circling of the same route and a slow, regular breathing pattern.

Simo's hourly suckling frequency and total number of suckles per hour decreased with age, particularly over the first four months (Fig. 1). Conversely, the mean suckling time per feed

Figure 2: Simo's mean daily weight of ingested food after his first solid food intake at day 321  
<sup>triangles</sup>  
(squares). The food intake as a percentage of body weight is also shown ((open circles)  
calculated from estimated body weights; (closed circles) calculated from actual weights).

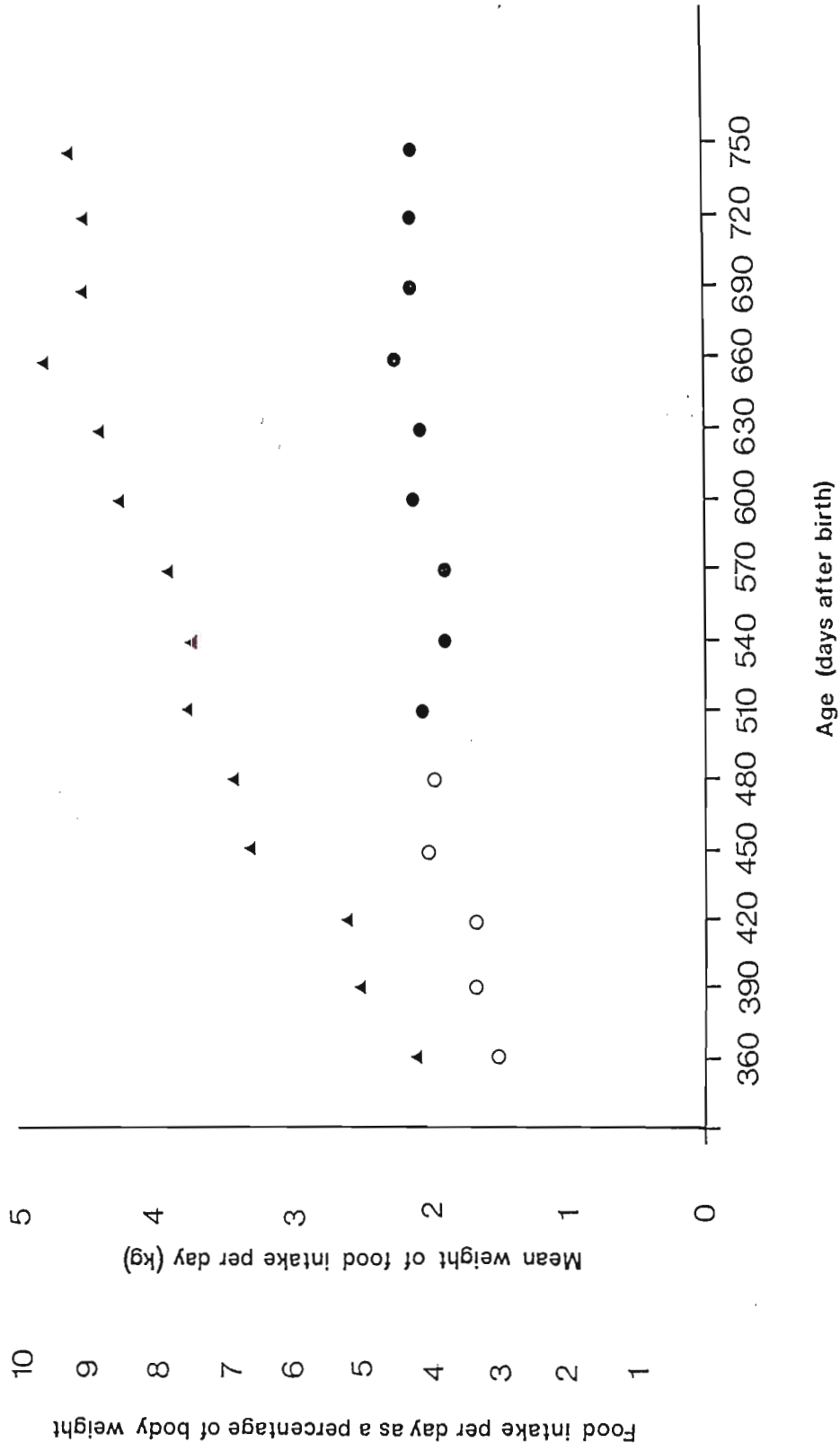


Figure 3: The influence of age on the percentage of Simo's suckles preceded by his bumping his mothers mammary area.

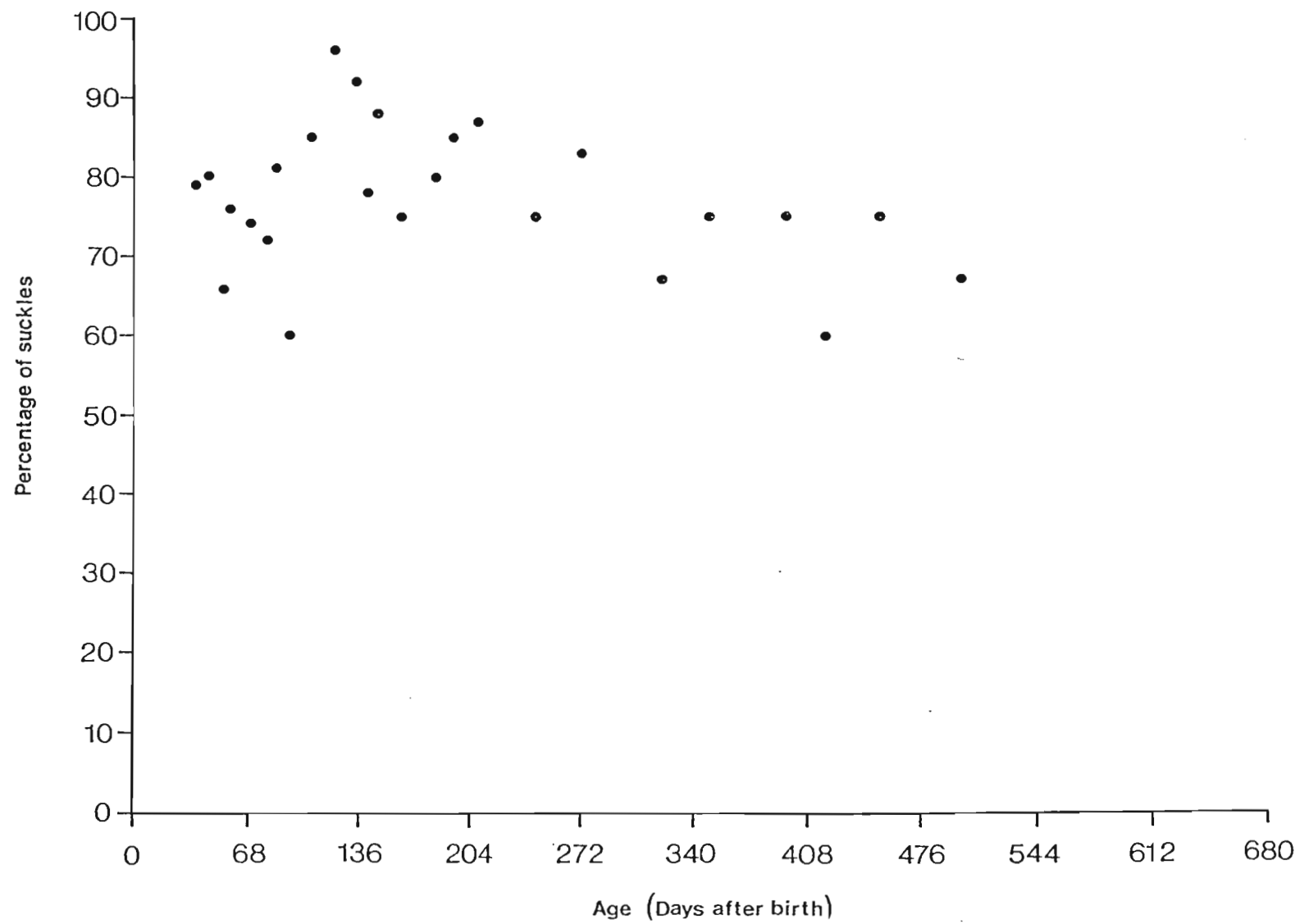


Figure 4: The change with age in the percentage of Simo's suckles preceded by Thandi presenting sideways (A), vertically (B) and a combination of the two (C).



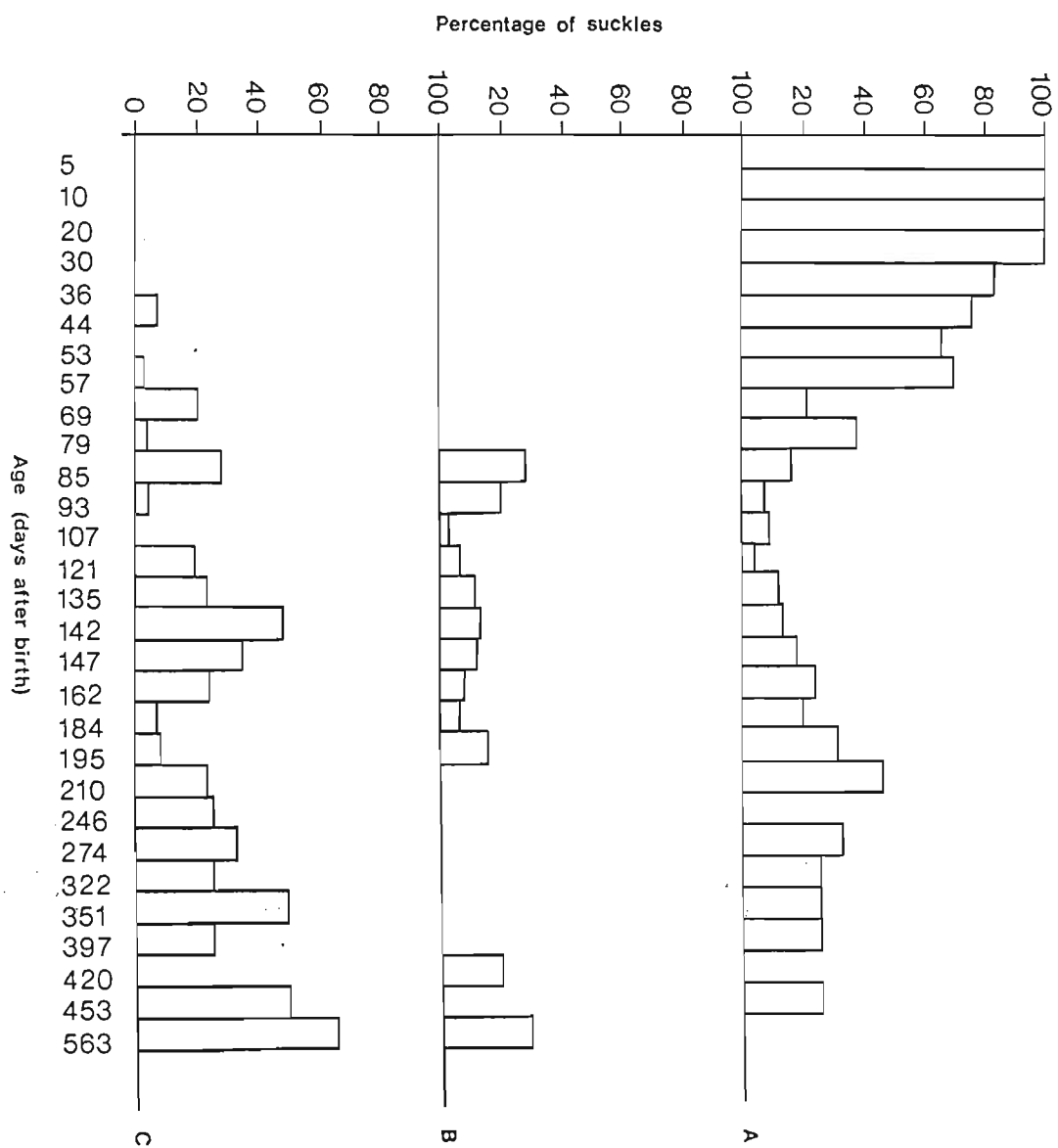
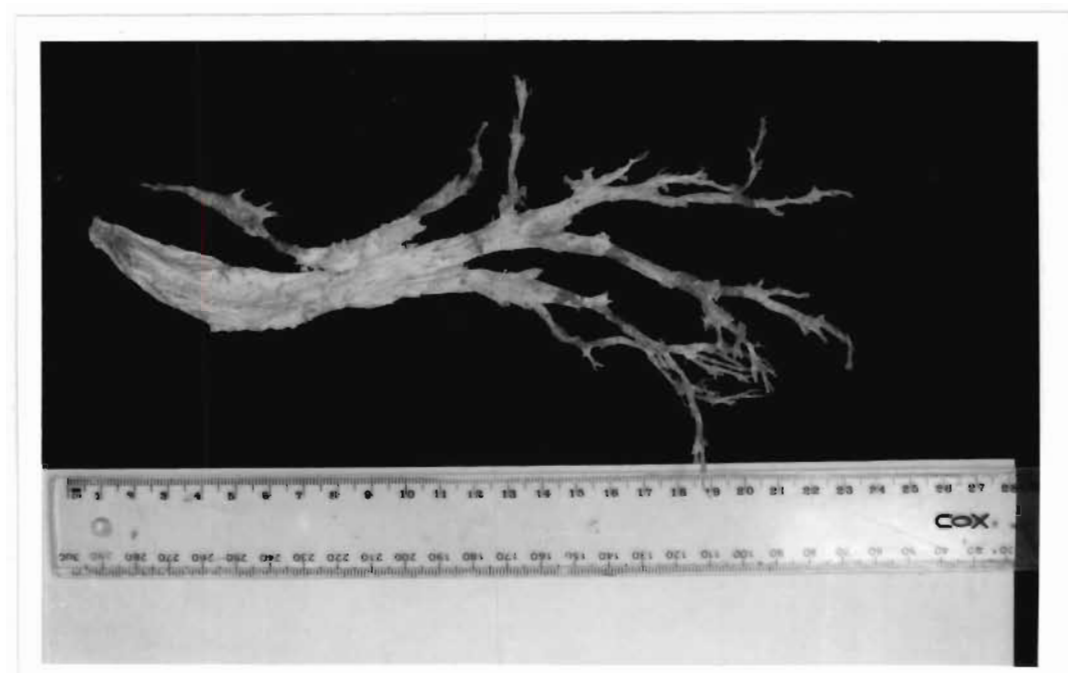
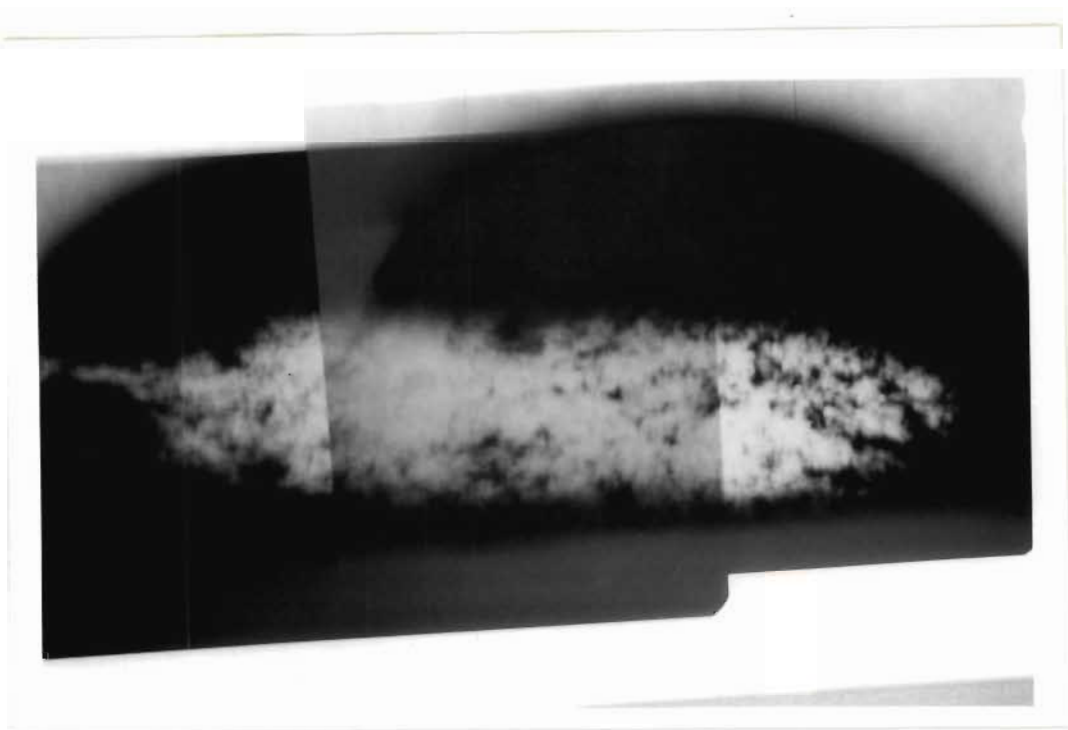


Plate 1: X-ray (Mammograph) of the mammary gland of a lactating *T. truncatus* (PEM N1182).

Plate 2: Resin cast of the mammary gland in Plate 1. The main ducts and mammary cistern are shown.



was highly variable but increased with age, reached a plateau between 5 and 16 months and then decreased rapidly (Fig. 1). The date of Simo's last suckle is unknown. During the last observation, on day 710, he suckled once within the 24 h period.

Simo's first known solid food intake was on day 321 (600 g of maasbanker -*Trachurus trachurus*). Regular solid food intake did not begin until day 331. Simo's mean daily fish intake increased with his mass, although the mass of this food as a percentage of his body mass remained fairly stable at around 4 % throughout (Fig. 2).

Less than 1 % of suckles were followed, within 3 min, by bumping. The percentage of suckles preceded by bumping (within 3 min prior to suckling) ranged between 58 % and 96 % throughout, except during initial observations when bumping was not specifically recorded. Bumping frequency outside these times remained constant with age but its proportion to the total number of bumps increased as suckling and presuckling bumping frequency decreased (Fig. 3).

All Simo's suckles over the first four weeks were associated with side presentations by the mother (Fig. 4). At about six weeks Thandi began combining side presentations with vertical presentations. Subsequently, the frequency of side presentations decreased, while that of vertical and combined presentations showed high variability and no obvious pattern (Fig. 4). By one year only half of all suckles were accompanied by some change in the mother's posture.

The mammograph of PEM N1182 and a resin cast of the mammary gland are shown in plates 1 and 2 respectively. 140 ml of X-ray opaque fluid were used to fill the mammary gland for X-ray and 147 ml of resin were used in the drip to make the cast. The similarity of these two figures suggests that they are reasonable estimates of the total volume of this gland. The volume of the cistern and major ducts only was estimated from the resin cast, by displacement, at 40 ml.

Figure 5: The change with age in the proportional amount of time that Simo respired alone (A) and with his mother (B).

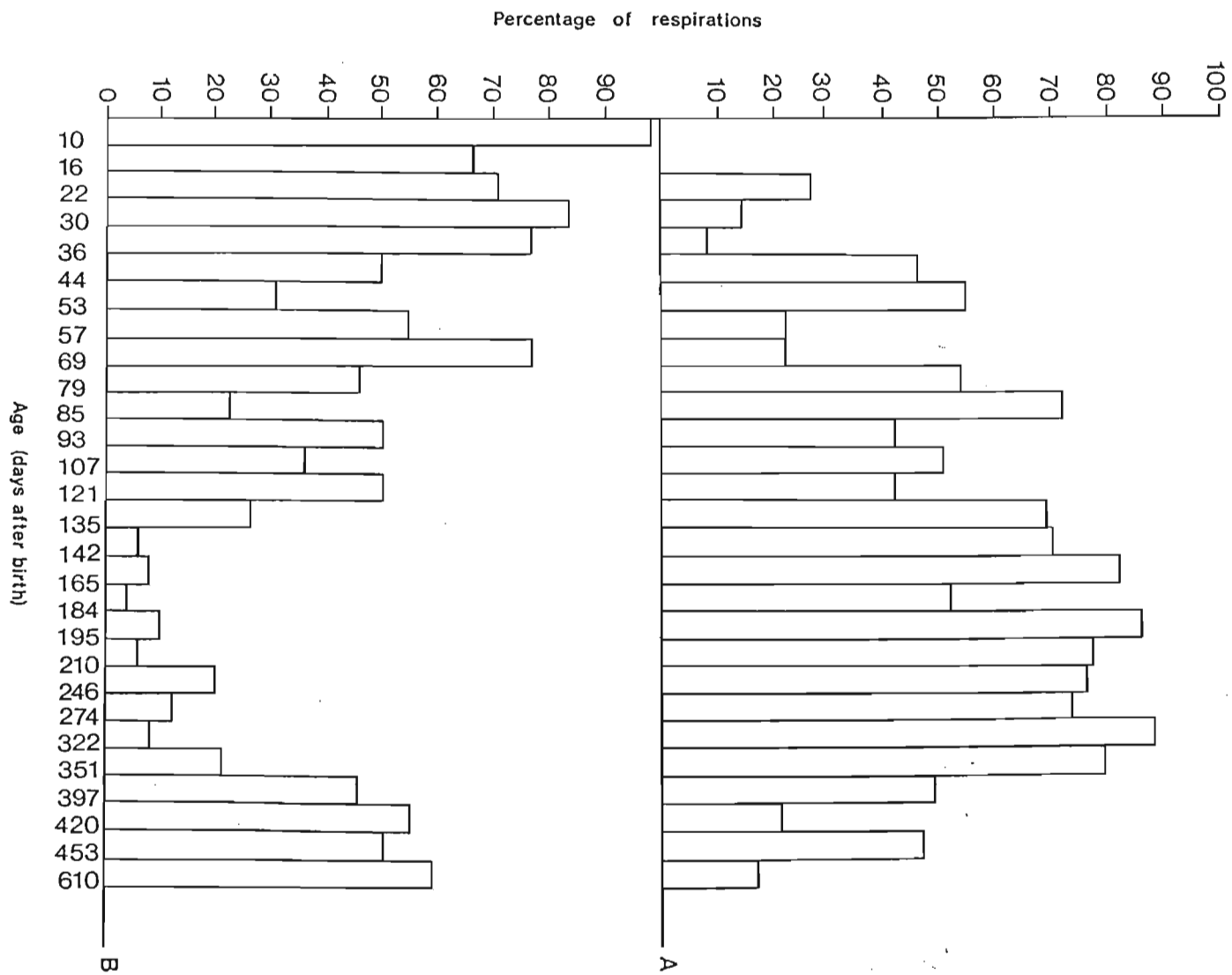


Figure 6: The influence of age on Simo's mean time between respiration's while swimming alone (A) and with his mother (B).







Figure 7: Simo's growth from birth to two years. The mean of photographic length estimates showing ranges where more than one estimate was made (closed circles); length estimates based on tile counts (triangles) and direct length measurements (open circles). Simo's calculated weight increase over this period (broken line) is also shown.

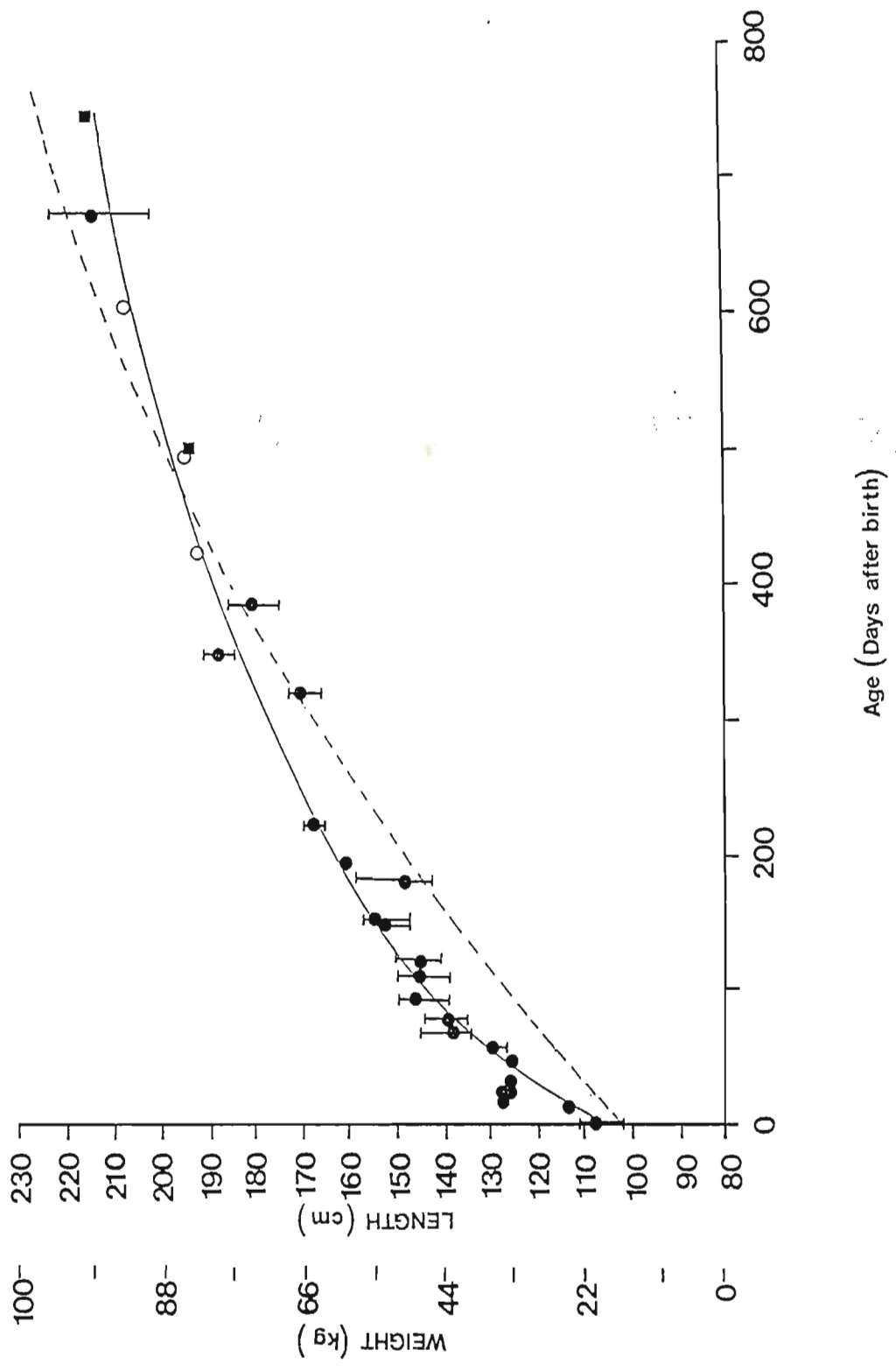
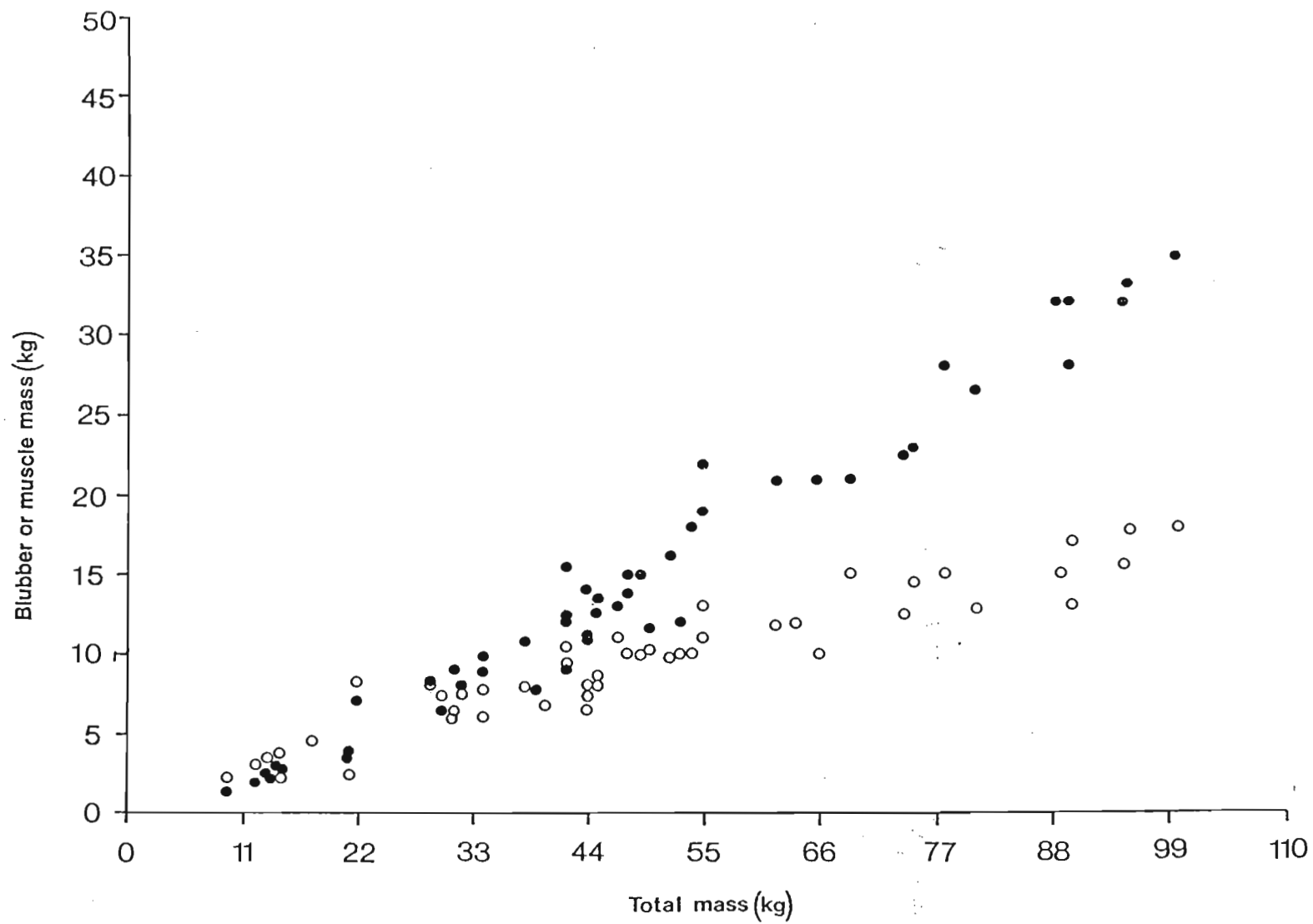


Figure 8: A plot of muscle mass (closed circles) and blubber mass (open circles) against total mass for *Tursiops truncatus* under 2.1 m total length.



### Growth and Development:

Simo's growth pattern over the two years was based on 61 length estimates from photographs and other measurements and his estimated body mass at age was based on the length/mass relationship of 71 calves caught in shark nets (Cockcroft, unpublished data) (Fig. 7). Simo's estimated length at birth was 108 cm to 111 cm; the best photographic estimate was 109 cm.

At birth the proportion of blubber to total mass is greater than that of muscle (Fig 8). This trend is reversed at a mass of approximately 22 kg or an age of between four and five weeks. Simo displayed this phenomenon quite graphically. At birth he was noticeably thin, with lean flanks and a large head in relation to his body. This leanness appeared to be primarily due to underdevelopment of the epiaxial musculature. Only after day 30 did he fill out and develop the sleek proportions of the adults.

At birth Simo's dorsal surface was darkly pigmented and the ventral 'anchor' mark, anterior to the flipper insertions, was very evident. Most of this had changed by day 10 and given way to the typical grey cape pattern (Ross, 1984). The umbilical wound had healed by day 22 and was reduced to a small scar by day 44. By day 22 the rostral whiskers had also disappeared and the foetal creases were apparent only as lightly pigmented lines but were still visible, under certain light conditions, up to day 62. The first maxillary teeth had erupted by day 91 and most teeth were visible in both jaws by day 163. Associated with the acquisition of teeth Simo began mouthing the other dolphins in the pool. Fresh rake marks were often evident on the other animals, particularly on their flippers and dorsal caudal areas. Simo was first heard whistling on day 2, but sonar clicks were not heard until day 42. Directly after birth Simo swam high up on his mother's flank, within a few centimeters of her, maintaining this position most of the day by infrequent fluke strokes. Whenever Thandi accelerated as in times of fright or emergency Simo moved along next to her. At such times she appeared to adjust her course to maintain the calf's proximity. Simo's relative passivity in this position was often shown when the females in the pool competed for him. Any female was able to take him from another, by swimming past very

closely at speed.

The spatial relationship of the mother and calf changed with time. By day 9 Simo's positioning was no longer as close to the mother's flank as previously. He still used irregular fluke beats to maintain this position but began to swim underneath his mother, between her pectoral fins, and sometimes rose alone to breathe. By day 16 he was further removed from the mother and breathed alone more often. Subsequent to day 22 he swam approximately 70 cm to 100 cm from the mother's flank and constantly moved his flukes much as the other animals did. By day 36 swam beneath Thandi as much as at her side, appearing to maintain contact beneath her with his dorsal fin. Only some 50% of his time was, however, spent swimming with his mother during circuits of the deepest part of the pool. Circuiting occurred irregularly, lasting from a few minutes to half an hour. Simo swam beneath his mother increasingly and by three months very little swimming was done at her side. Subsequent to day 79 Simo only swam at his mother's side when alarmed or frightened, at which time Thandi would accelerate and swim away rapidly with him at her flank. This behavior continued until Simo was well over a year old. Between about three months and fifteen months Simo progressively spent more of his time independently of his mother (Fig. 5). When together he swam beside her increasingly as the other animals did. By two years he swam beneath Thandi only when distressed or when bumping and suckling during short periods of slow circuiting.

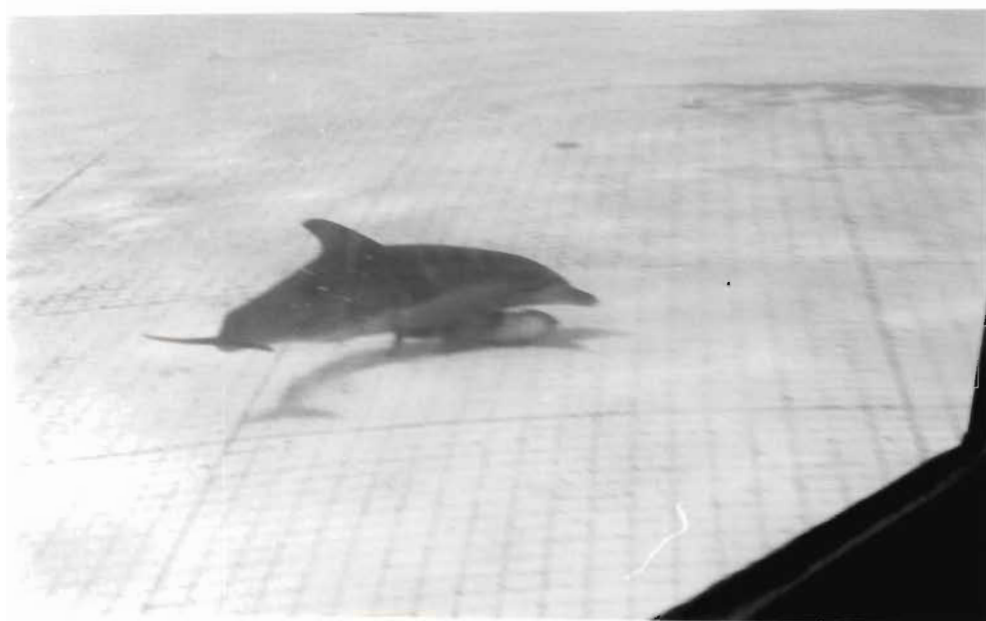
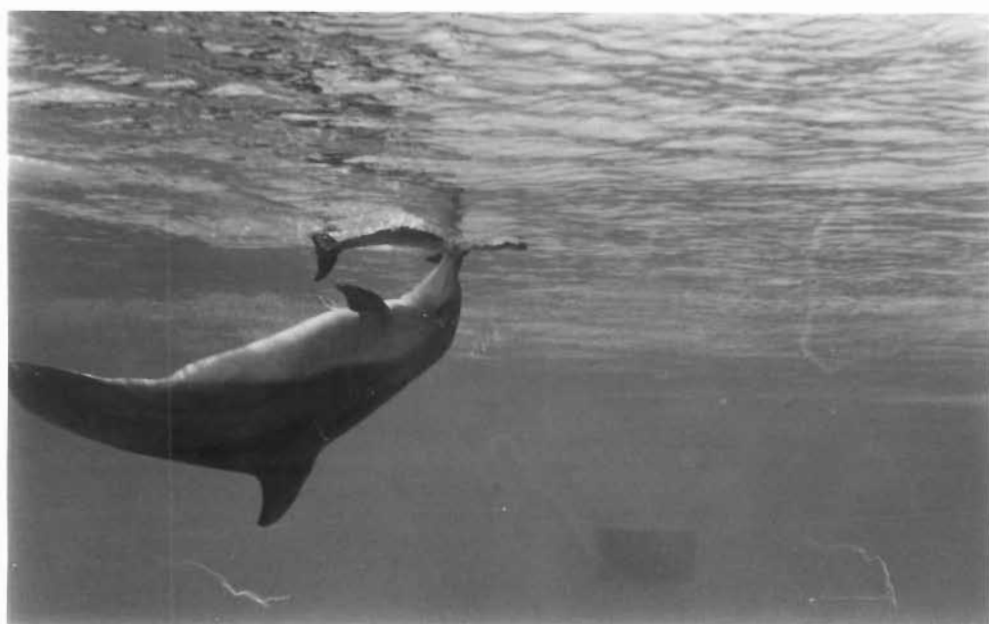
Simo's development of swimming control was also progressive and linked to his physical development. At birth he was unable to maintain an even keel and was constantly required to make minor adjustments. He was positively buoyant and tended to drift upwards and was unable to neutralise his buoyancy, by releasing air, until six months of age. This is consistent with the proportionally high blubber mass of early neonates (Fig. 8).

On a number of occasions Thandi exhibited maternal care behaviors when Simo wandered from her side. On a number of occasions between days 2 and 23 Thandi pushed Simo above the surface (Plate

Plate 3: The female *T. truncatus* chastising her calf by lifting him clear of the surface.

Plate 4: The female *T. truncatus* chastising her calf by rolling on him and forcing him to remain on the floor of the pool.





3) and held him on the pool bottom (Plate 4). On other occasions Thandi whistled and Simo immediately returned to her. These whistles were not recorded and no audible distinction was possible between these and other whistles made by the mother.

## DISCUSSION

The behavioral and physical development of the young dolphin is marked by a progressive independence from the mother through physiological development and the acquisition of behavioral skills. This is especially marked in the first four weeks after birth, when a series of rapid physical and behavioral developments take place. Tavalga and Essapian (1957) described how young calves become more independent of their mothers at about two weeks (see also Tavalga, 1966; Gurevich 1977). Taber and Thomas (1982) outlined a similar process in right whale calves of one to three months old.

The newborn calf appears unable to swim efficiently, probably because it lacks both the muscular development and motor co-ordination. Its high proportional blubber mass acts as an insulator and probably increases its buoyancy, making submergence difficult. Under these circumstances the neonate's ability to maintain a position at the mother's side is of prime importance (Essapian, 1953).

The positioning of newborn dolphin calves, high on and probably touching the mother's flank, has been noted by a number of authors (McBride and Hebb, 1948; McBride and Kritzler, 1951; Tavalga and Essapian, 1957; Prescott, 1977; Dudock van Heel, 1977 ; Herman and Tavalga, 1980; Norris and Dohl, 1980). In this position newborn dolphins are probably riding in the pressure wave caused by the mother's body (Norris and Prescott, 1961) thus conserving energy (Prescott, 1977). Though Norris and Dohl (1980) claimed that calves lack movement in this position, Simo actively maintained his station by infrequent fluke strokes.

Plate 5: The successive frames of a calf 'riding' at his mothers flank, showing the matching colouration. Note the effect of the light in the bottom frame. The tips of the calf's dorsal fin and flippers are barely visible.



The first few weeks are also a learning period for the calf during which the mother constantly monitors its position, behavior and safety (Tavolga and Essapian, 1957; Tavolga, 1966; Taber and Thomas, 1982) and punishes its misbehavior (Tavolga, 1966; Tayler and Saayman, 1972). Simo spent his early days apparently resting and sleeping as Tavolga and Essapian (1957) observed for other neonates. Right whale calves spend the majority of their first month in close proximity to and almost in continuous contact with the mother (Taber and Thomas, 1982). It is during this early, close association with its mother that a calf learns how to recognize her and find the nipples (Herman and Tavolga, 1980). Only after learning this essential behavior can the young dolphin acquire a measure of independence.

At about three weeks Simo began to gain independence from Thandi and the assistance of her pressure wave. This coincided with the development of axial musculature and a reduction in proportional blubber mass, increasing his ability to swim alone and reducing his reliance on the mother's pressure wave. The loss of rostral vibrissae at this time is also of interest, for the calf may be aware of the mother's pressure wave through its sensory rostral pits (Ling, 1974). The sensitivity of these pits may be enhanced by vibrissae, allowing a better perception of the pressure wave during the critical first weeks of life. McBride and Kritzer (1951) also record the loss of vibrissae in bottlenose dolphin calves of approximately one month. Herman and Tavolga (1980), however, note that in *Tursiops* and *Stenella* sp. the vibrissae may remain until the end of nursing.

The color patterns of mother and calf may be important for the protection of the dependent calf. During early infancy the calf is positioned in the mother's pressure wave for most of the time and is protected by its ability to remain in this wave and be accelerated away from danger. The blending of the calf's dark dorsal cape with that of the mother and a similar blending of their lighter flank areas may provide additional calf protection (Plate 5). When the calf begins to swim beneath the mother it is no longer in the safety of the pressure wave but is still very dependent upon her. In this position the calf is beneath the posterior, ventrally sweeping,

Plate 6: The calf swimming below his mother in typical fashion. The close match in the pigmentation of the mother and calf provides disruptive colouration.



flank pattern of the mother such that his flank color and light ventral area appear as extensions of hers (plate 6). This has the effect of making the pair appear as one large animal, particularly at low light intensities such as would be found in the natural environment. It is important that, in later life, Simo returned immediately to this position whenever alarmed.

Simo's respiration frequency decreased with age, as did that of the calves observed by McBride and Kritzer (1951) and Gurevich (1977). When with Thandi, Simo's behavior was characterized by rhythmic breathing (resting), and it is probable that his respiration frequency was determined by her. For some three weeks after birth, when he was dependent upon her, Simo's respiration frequency more or less matched his mother's. For the next four weeks his dependence declined and his respiration frequency increased markedly (Fig. 6). In the subsequent three weeks Simo's respiration frequency declined gradually, though the reasons for this are unclear. Perhaps the calf's rate is determined by the mother when he is completely dependent upon her. However, as the calf's swimming proficiency increases and his dependency decreases he begins determining his own respiration rate.

Gurevich (1977) found that the respiration rate of a young bottlenose dolphin varied depending on time of day and activity. During his first year Simo displayed no time preference for rest or play and no diurnal pattern was observed in his respiration rate, the rate varying considerably depending on activity. Thereafter, his daylight activities were similar to those of the other adults. At night, however, Simo's activity pattern remained similar to his daylight activity. The other adults appeared to rest, with a reduced respiration, in the early hours of the morning either lying on the pool floor or hanging upside down, rostrum on the floor, for about 3.5 min.

As all feeds in the first four weeks of Simo's life were preceded by side presentations it suggests that this particular posture has significance to the neonate. Side presentations



probably make suckling easier for the calf when its respiratory and swimming efficiency are low. It is feasible that in early infancy the calf is stimulated to suckle by the mother's presentation, the mother initiating suckling in response to pressure in her mammary glands. The change in the mother's presentation posture coincided with an increase in the number of suckling bouts being preceded by bumping.

Although bumping was not specifically recognized and monitored for the first four weeks, its high frequency of occurrence, once identified, suggests it was probably not present early in the calf's life. It is significant that once identified and monitored the high proportion of feeds preceded by bumping remained fairly constant (Fig. 3). This suggests some relationship between bumping and suckling. It is possible that bumping marks the onset of the calf's initiation of suckling bouts, indicating to the mother the calf's need to feed and allowing the mother time to ready herself and present. It is also possible that bumping may provide the calf with information on the relative fullness of the mammary gland.

On a number of occasions just prior to suckling, it was obvious that Thandi's mammary glands were full. When she twisted or turned, milk was expelled. This is common in lactating delphinids (Tavolga and Essapian, 1957; Arvy, 1974; Drinnan and Sadlier, 1981) and it seems probable, therefore, that the milk reservoir is normally full prior to suckling, despite the calf's relatively high suckling frequency. Bumping may hasten or stimulate the 'let down' of milk from the alveoli into an empty gland allowing the calf to maintain its high suckling frequency. Ely and Petersori (1941; In Folley, J.S. 1952) postulated that 'let down' is normally governed by circulating adrenalin and oxytocin released when the enervated teat is tactually stimulated. This reflex is conditionable, apparently, and bumping may be the operant stimulus.

Bumping behavior appears either not to have occurred in other mother-calf pairs observed or was not noticed. Gurevich (1977) noted that a bottlenose dolphin calf initiated nursing by nudging

its mother in the mammary region. This nudging behavior was observed in practically all of Simo's sucklings, but is distinct from bumping.

Drinnan and Sadlier (1981) showed that, during the first month after its birth, a beluga (*Delphinapterus leucas*) calf displayed no circadian suckling pattern. Simo's suckling behavior similarly showed no diurnal pattern. His first day was characterised by a high number of suckles (19/h). The reasons for this are uncertain but may include the mother's inability to provide milk at this time and the calf's inexperience, both of which could contribute to unsuccessful suckles. Over the following weeks Simo's suckling frequency, although highly variable, was similar to that observed for a bottlenose dolphin calf of the same age (Gurevich, 1977). The latter calf nursed four times per hour; the duration of each feed lasting 7 -10 s. Simo's nursings, at this age, ranged between 3 s and 9 s, with a mean of 5.6 s (Fig. 1). Gurevich (1977) noted a decrease in the suckling time per hour and an increase in the number of bouts per hour at three months. At six months the calf increased the time of each suckling bout while the number of suckles per hour decreased. He attributed these variations to changes in the mothers posture during bouts (Gurevich, 1977). Simo showed none of these variations as Thandi's presentation posture changed. His suckling rate and the duration of each event decreased steadily. Similar reductions in nursing frequency have been observed for bottlenose dolphins (McBride and Kritzler, 1951) and for belugas (Drinnan and Sadlier, 1981). This apparent decrease in milk, and perhaps energy, consumption during the course of suckling, is interesting.

There are two methods of estimating the amount of milk and energy Simo consumed. The amount and energy value of milk consumed can be estimated from the volume of the mammary gland. The amount of energy consumed can also be estimated from the difference in Thandi's food consumption during and subsequent to pregnancy and lactation.

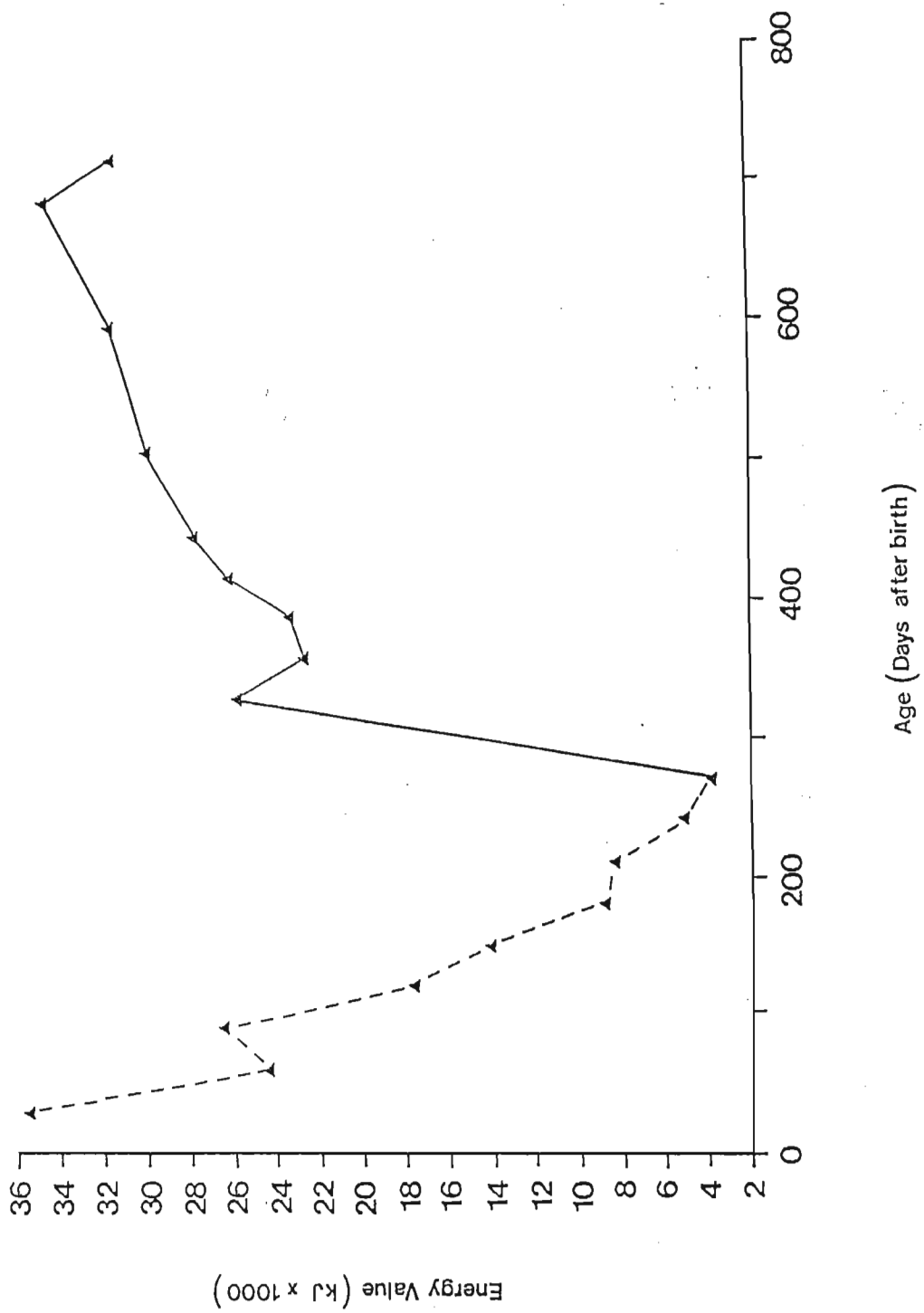
The mammary gland volume of the heavily lactating female was estimated at approximately 145 ml.

Given an hourly suckling frequency of 4.5 (less than six weeks old) and presuming the entire mammary is emptied, Simo's daily milk intake would amount to 15.7 l. However, the mammary alveoli (Plate 1) are minute and their flow resistance is probably too great for the milk to be available to the calf during the brief suckling period. It is more probable that only the cistern and larger ducts of the mammary gland are emptied. The volume of the ducts and cistern were estimated at 40 ml (Plate 2). On this basis Simo's daily intake would be approximately 4.3 l, based on a suckling frequency of 4.5/h.

Information on the fat, lactose and protein composition of bottlenose dolphin milk is scanty and reported values vary considerably. Eichelberger *et al.* (1940, in Arvy, 1974) reported a range of values for fat, lactose and protein, with means of 14.1 %, 0.6 % and 10.4 %, respectively. Ackman *et al.* (1971) found a fat content of 19 % in the milk. It seems likely that Thandi's milk was of similar composition to those above. If the fat, protein and lactose proportions of her milk are assumed to be 14.5%, 10% and 1%, respectively, the estimated energy value of the milk would be approximately 827 kJ/100 g of milk and Simo's daily intake would be approximately 35600 kJ. (Energy conversions of fat, protein and lactose were calculated using the figures of Brody, 1945, in Crisp, 1971).

Thandi's mean food intake during lactation averaged 13.5 kg of fish per day (6.5 kg *Sardinops ocellatus*, 4.5 kg *Merluccius capensis* and 2.5 kg *Scomber japonicus*) but dropped to 8.5 kg per day (4.5 kg *M. capensis* and 4 kg *S. ocellatus*) three years after Simo's birth. Thandi's mean mass during this period was 163 kg. During the stress of lactation she required 8.3 % of her body mass in food per day compared to the 5.2 % subsequent to the birth and lactation. The additional energy required for lactation was contained in 5 kg of fish per day. The energy value of this fish was estimated at about 37000 kJ from energy values for food species (Ross and Cockcroft, 1989). The estimated daily milk energy consumed by Simo represents 96 % of the additional food energy ingested by Thandi. The close agreement of these derived figures and consideration of Thandi's assimilation efficiency suggests that great energetic demands are

Figure 9: Estimated energy content of Simo's daily food intake, milk only (broken line), fish plus milk (solid line).



placed on the mother during lactation. Unless she has sufficient fat reserves to last the almost five months of high suckling frequency she must be capable of either reducing her energy requirements or increasing her food consumption. In a captive situation both these alternatives may be possible. However, the ability of free-ranging lactating females to conserve energy is unknown. The existence of nursery groups within free-ranging schools may facilitate energy reduction and the ability of lactating females to obtain additional food as discussed by Cockcroft and Ross (1989).

The pattern of Simo's estimated daily energy intake, from birth, shows an apparent gradual decrease in the energy consumed until weaning (Fig. 9), which is clearly related to the decreased suckling rate observed in this and other studies (see above). Immediately solids were consumed energy intake increased dramatically. Thereafter it remained approximately constant and at about the same level as initial milk energy consumption. It is improbable that the calf's energy requirements decrease prior to weaning. Energy requirements to overcome thermoregulatory stress may decrease with growth, but more energy is required for growth and activity. It is unlikely that milk production or milk energy value increases during lactation. Arvy (1974) suggested that milk production at the beginning of lactation is probably greater than at the end. Further, although nutritional changes in milk during lactation are well known (Arvy, 1974; Oftedal, 1984), this has not been recorded in cetaceans.

Simo's estimated mean daily mass gain between day 100 and day 150 was 240 g. The daily mass gain of blubber and muscle as a proportion of this increase can be estimated as 49.2 g of muscle and 53.8 g of blubber (Fig. 8). The energy value of this mass of muscle and blubber is 310 kJ and 2127 kJ, respectively (Lockyer, 1978). At this age (day 100 - 150) it appeared that the calf's energy intake was equal to or less than needed to maintain this level of growth (Fig 9). One logical interpretation of these phenomena is that weaning is a response to the increase in energy requirement which the calf is unable to fulfill through nursing. This interpretation is supported by the increased growth which occurred concurrent with the commencement of solid food

intake (Fig. 7).

Although Simo continued suckling past his first year, and probably beyond the second, it appears that he received a progressively decreasing energetic contribution from his mother's milk. However physically independent the calf may be, it is not yet fully grown or behaviorally independent. Suckling probably remains important in mother and calf interactions subsequent to the calf's intake of solid food. During its second year the calf continues acquiring the necessary behavioral, respiratory and feeding skills for complete independence. Complete independence may not occur until a number of years later. Progressive independence may be reflected in free-ranging bottlenose dolphin schools by the presence within them of subgroups of larger calves (Leatherwood, 1977). These subgroups may themselves be important in the continuing learning process.

All reported values for bottlenose dolphin milk fat are markedly less than values reported for other delphinids. Milk fat values for *Stenella attenuata*, *S. longirostris*, *S. coeruleoalba* and *Delphinus delphis* were all greater than 29% (Pilson and Waller, 1970; Kawai and Fukushima, 1980; Ross, 1984). It is impossible to evaluate why these differences between dolphin groups occur without additional information on growth, metabolic and suckling rates. However, if suckling frequency of calves of other species is similar to Simo's, it suggests that females of these species would be subject to enormous stress during lactation. This may lead to earlier weaning and a reduction in the period of mother and calf interaction, apparently so important in the calf's development. It is possibly a reflection of the smaller school size and inshore habitat of some bottlenose dolphins which may require greater maternal care and a longer learning period for the young to attain total independence. These factors are as yet unexplored in the literature, but suggest that delphinid species may have evolved diverse strategies for the development and care of their young.

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## CHAPTER THREE

Age, growth and reproduction in bottlenose dolphins from the east coast of southern Africa.

V.G. Cockcroft and G.J.B. Ross

Port Elizabeth Museum, P.O. Box 13147, Humewood. 6013. Republic of South Africa.

## ABSTRACT

Age and reproductive parameters were determined for 174 bottlenose dolphins captured in shark nets off Natal, on the south east coast of southern Africa. Calibration of dentinal and cemental GLG readings using a known age, captive born dolphin indicated that dentinal and cemental GLGs are deposited annually, at least up to an age of six years. Female growth in length and mass and male growth in length is best described by Von Bertalanffy growth curves. Male growth in mass is characterised by a growth spurt at puberty. Most growth occurs during the suckling years. Both males and females reach physical maturity and their asymptotic size, 243 cm, 176 kg and 238 cm, 160 kg, respectively, between 12 and 15 years. Males and females have similar life expectancies and may reach a maximum age of about 43 GLGs (years). Females attain sexual maturity between 9 and 11 years of age, two or three years earlier than males. Mating and birth are seasonally diffuse, although there is a peak of births in summer. The calf is born at a mean length and mass of 103 cm and 13.8 kg, respectively, after a gestation period of about one year. Lactation lasts approximately two years, although there is evidence of an extended mother and calf association of up to three years. Post pubertal female ovulation rate is 0.32/year and the estimated calving rate is approximately three years. There is no evidence that females become reproductively senescent with increasing age. Estimates of population replacement suggest that man induced mortality may equal or exceed the replacement rate.



## INTRODUCTION

Many populations of small inshore delphinids are exploited either directly or indirectly (Mitchell, 1975; Beddington, Beverton & Lavigne, 1985; Northridge & Pilleri, 1986) and their continued survival depends on adequate management based on knowledge of their life history. In this context knowledge of the reproductive parameters of a species is important in formulating management and conservation proposals. In particular the reproductive biology of females is crucial to an understanding of the likelihood of a species's survival.

An estimated 900 bottlenose dolphins inhabit Natal, along a stretch of some 400 km of coastal waters, on the south east of southern Africa (Ross *et al.*, in press). Between January 1980 and December 1987 a minimum of 212 of these animals were captured in non commercial inshore nets set to catch and deplete the numbers of large sharks off bathing beaches (Cockcroft & Ross, in press). The annual catch of dolphins varies between 2 % and 4.5 % of the estimated population and is of concern in the continued survival of these animals off Natal (Ross *et al.*, in press; Cockcroft & Ross, in press).

Feeding studies on the bottlenose dolphins off Natal have shown that groups are segregated by sex and size. Lactating females and their calves frequent and feed in the near shore zone, adolescents feed slightly further offshore while resting females and adult males feed further offshore (Cockcroft & Ross, 1989a). Consequently, the catch of these animals in the shark nets is biased, with calves less than two years old and lactating females constituting almost 60 % of the total (Cockcroft & Ross, in press). Other age and sex classes, particularly pregnant females and adolescents, are, therefore, probably under-represented.

This study was undertaken to establish the reproductive potential of bottlenose dolphin off Natal, as part of a more extensive investigation of the natural history of these animals and

severity of the threat to the population through capture in shark nets. Where appropriate, recognition is given to the effects of biases in sex and size composition, noted above, which reduce the accuracy of deductions made from catch data (Perrin & Reilly, 1984).

## MATERIALS AND METHODS

Routine necropsies were performed on all bottlenose dolphins retrieved from the Natal shark nets. A large number of biological and morphological parameters, including sex, total length and mass were recorded for each animal, based on the recommendations of Norris (1961) and Mitchell (1975). Collected organs were stored in 10 % formalin for varying periods and then transferred to 50 % ethyl alcohol.

Testes were excised, weighed after removal of the epididymis and the three dimensions (length, maximum height and width) measured. The epididymis was visually checked for the presence of sperm and scored as present or not. Testes from young animals (combined testis mass less than approximately 100 g) were preserved whole, while only a section removed from the bigger testis of older males was kept. Standard histological slides, approximately 5  $\mu$ m thick and stained with haematoxylin and eosin, were prepared from whole testes or from three locations (outer, middle and inner) of sections of large testes. From each slide the diameter of a minimum of 10 circular tubules was measured at a magnification of 125 using an ocular reticule. Testis development stage was also estimated using the criteria of Mitchell & Kozicki (1984).

Lactating females and calves caught together were considered mother and calf pairs. Both left and right ovaries were routinely collected and preserved from all females. These were sectioned serially at about 1 mm intervals and the number and dimensions of corpora albicantia in each recorded. The length and mass of any foetus present in the uterus was recorded before preservation. Mammary glands were assessed for the presence of milk. For most lactating females the width, length and depth of one mammary gland was measured.

The state of physical maturity of animals was assessed from the degree of fusion of the epiphyses to the centra of mid thoracic vertebrae (immature = unfused, maturing = fusing, mature = fused). The brain mass of neonates and calves was measured directly while that of adults was estimated from the braincase volume. Braincase volume was estimated by filling the skull with coarse dry sand, after first sealing all apertures with adhesive tape. The volume of sand was then measured in a measuring cylinder and the volume assumed to represent the brain mass.

Age was determined from the number of growth layer groups (GLGs; sensu Perrin & Myrick, 1980) counted in the dentine and cement of longitudinal thin sections of teeth. The largest mandibular or maxillary teeth were used. Numerous methods of obtaining thin sections were employed. These included hand grinding on 1200 grade Carborundum paper or between glass sheets using 'jewelers rouge' or obtaining thin (about 20  $\mu\text{m}$ ) ground sections using a geological Carborundum wheel. However, the best results were achieved with a purpose-built, slow speed saw and diamond lapidary blade that cut thin (120  $\mu\text{m}$ ) sections. These were etched in 5 % formic acid for 5 minutes, washed in running water for 1 hour and dried and mounted on perspex slides using cyanoacrylate glue. Sections were then viewed, at 8 x magnification, through a binocular microscope using both transmitted polarised light and reflected light on the pencil-rubbed etched surface of the tooth.

Dentinal GLGs in all teeth were counted three times by each of two independent observers. Additionally, one observer (VGC) made a minimum of three cemental GLG counts in all teeth where the pulp was occluded but only in a selection of teeth in which the pulp was not occluded. Initially, age estimated from dentinal and cemental GLG counts was assessed separately. The mean of any three GLG counts (dentinal or cemental) that were within 15 % of one another was accepted as the age of the animal. However, in teeth where counts varied by more than 15 %, further counts were done until any three were within 15 % of one another. Finally, for teeth where the pulp cavity was open, the mean of a combination of GLG counts in both cement and dentine was

Plate 1: A thin etched section of a tooth from 'Dolfie', a captive born bottlenose dolphin. The neonatal line (N) and the end of each of six growth layer groups are marked.

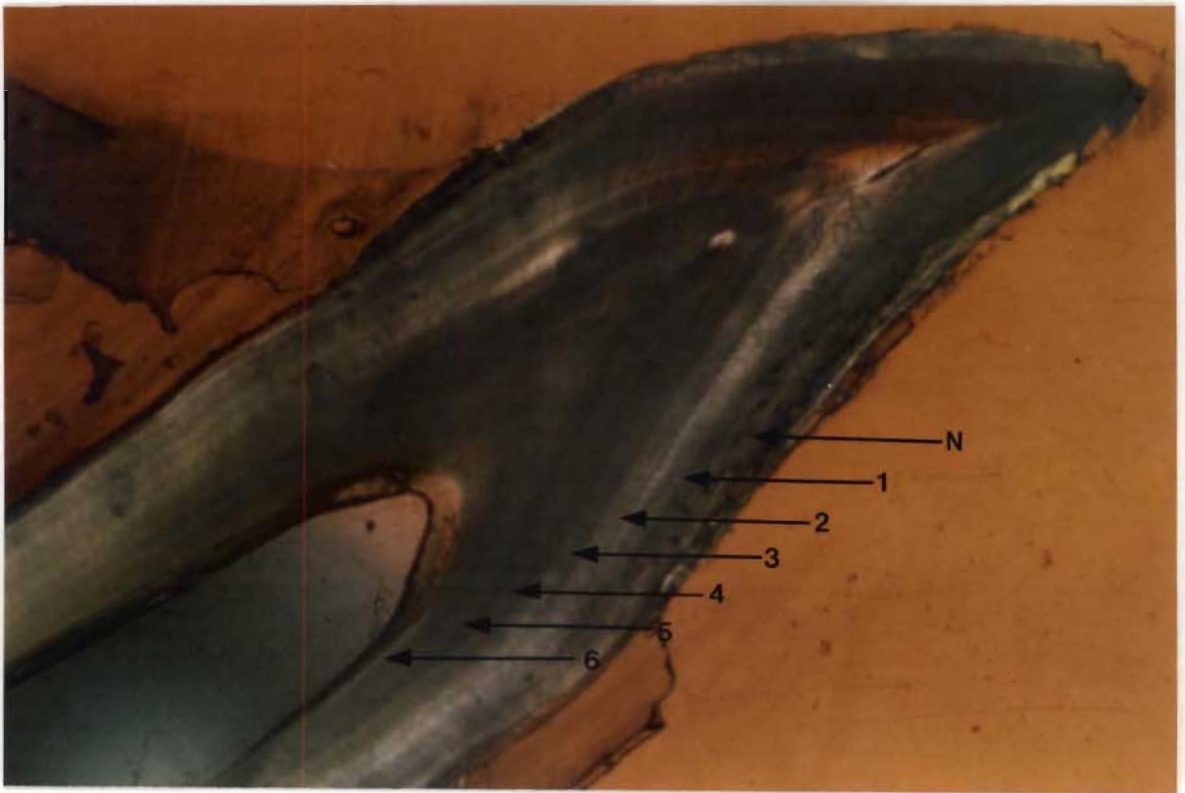
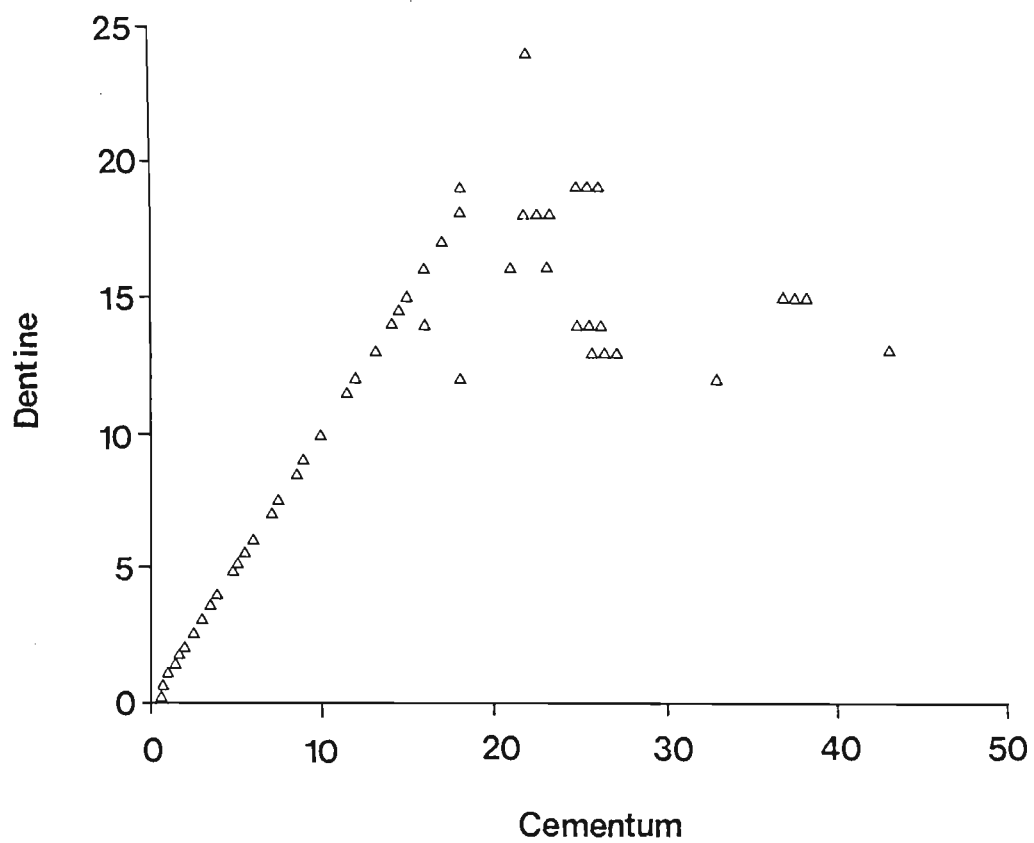
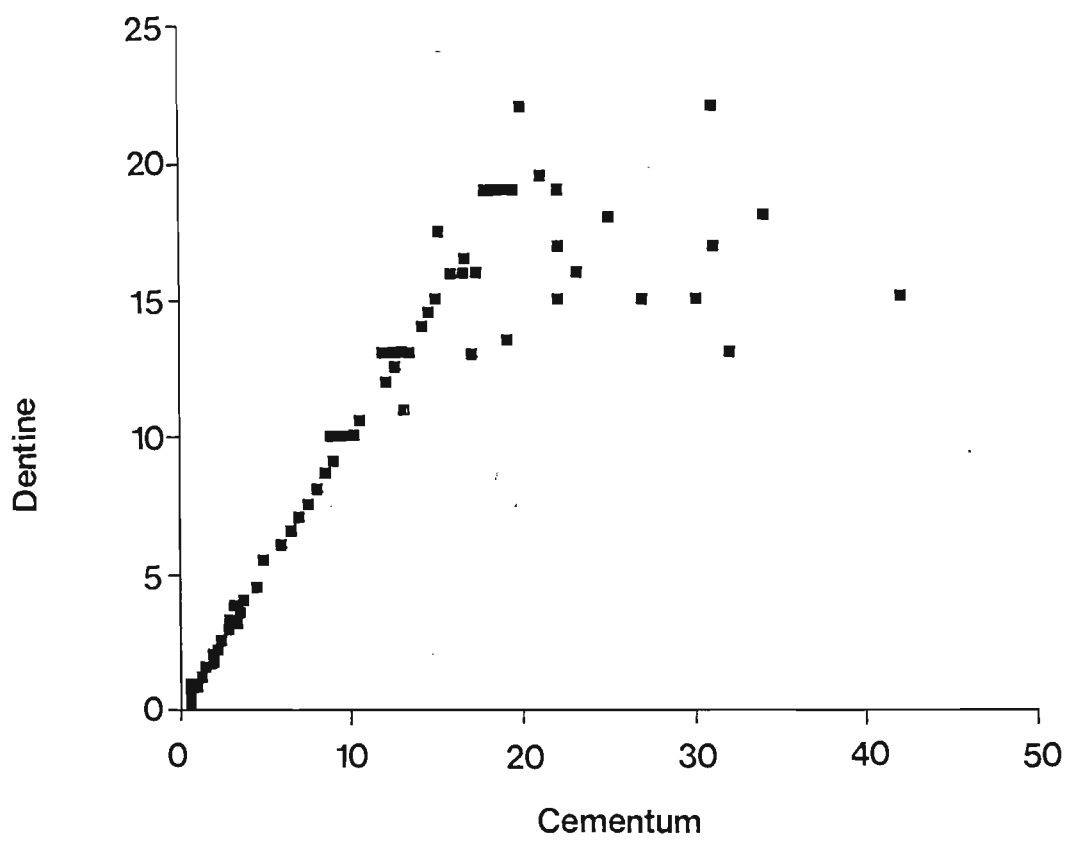


Figure 1: Relationship between growth layer group (GLG) counts in the dentine and cement of male (squares) and female (triangles) bottlenose dolphins.



accepted as an estimate of age. Where occlusion of the pulp had occurred, only accepted mean cemental counts were used as an estimate of age.

The number of dentinal and cemental GLGs in the teeth of one known age animal, "Dolfie" (PEM N6) born on 30 December 1972 and died on 9 August 1979, were also counted following the above pattern. In addition, because of the importance of the age estimate of this animal, a third observer (GJBR) counted GLGs in the dentine.

## RESULTS

### Age and Growth:

More than six and a half but less than seven dentinal GLGs were counted in teeth of the known age animal 'Dolfie' (plate 1). This corresponded well with 'Dolfie's' actual age of six years and eight months and indicated an annual deposition of GLGs in the dentine. However, only six GLGs were counted in the cement of this animal indicating that cemental GLGs probably reflect whole years only and may underestimate age by one year. Despite this, cemental and dentinal GLG counts were taken to represent age in years.

Age estimates from dentinal and cemental GLG counts from the teeth of 174 male and female *Tursiops* were well correlated ( $r=0.95$  and  $r=0.96$ , respectively) up to approximately 12 GLGs but, thereafter, counts diverged with increasing age due to the closure of the pulp (Fig. 1). The smallest individual from the nets was 29 kg and 125 cm and had about 15 % of the first GLG formed (approximately two months old). The variation in the length and mass of larger animals meant that the longest was not necessarily the heaviest or oldest. The heaviest male was 204 kg, the longest was 257 cm and the oldest 42 years (GLGs). The corresponding parameters for females were 182 kg, 249 cm and 43 years (GLGs), respectively.



Figure 2: The increase in length with age (growth) of male (closed squares) and female (open squares) bottlenose dolphins. A four stage Von Bertalanffy growth curve is fitted to these data. Mean length for various age classes of males (open circles) and females (closed circles) is also shown.

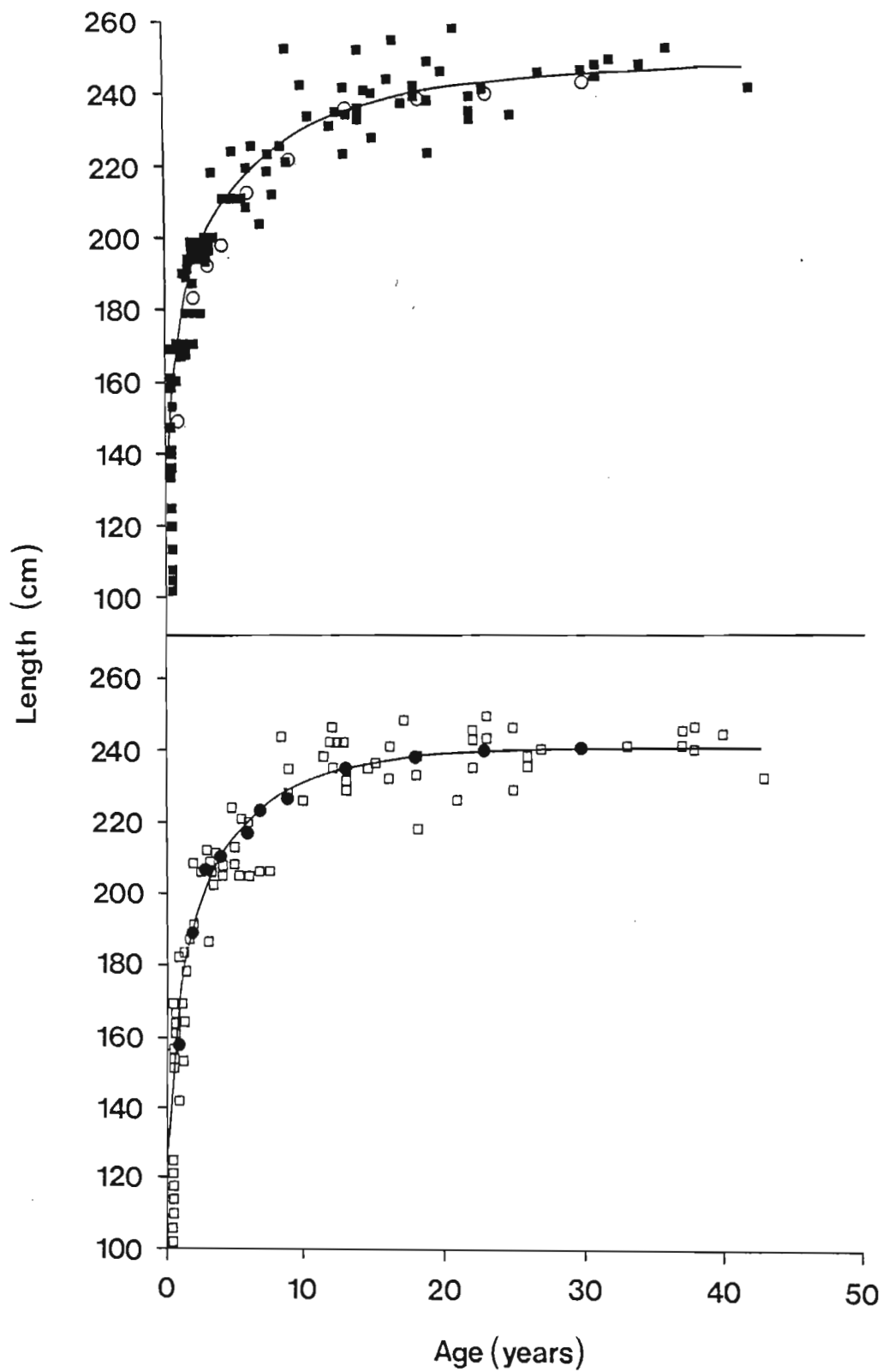


Figure 3: The increase in mass with age of male (closed squares) and female (open squares) bottlenose dolphins. A four stage Von Bertalanffy growth curve is fitted to these data. Mean mass for various age classes of males (open circles) and females (closed circles) is also shown.

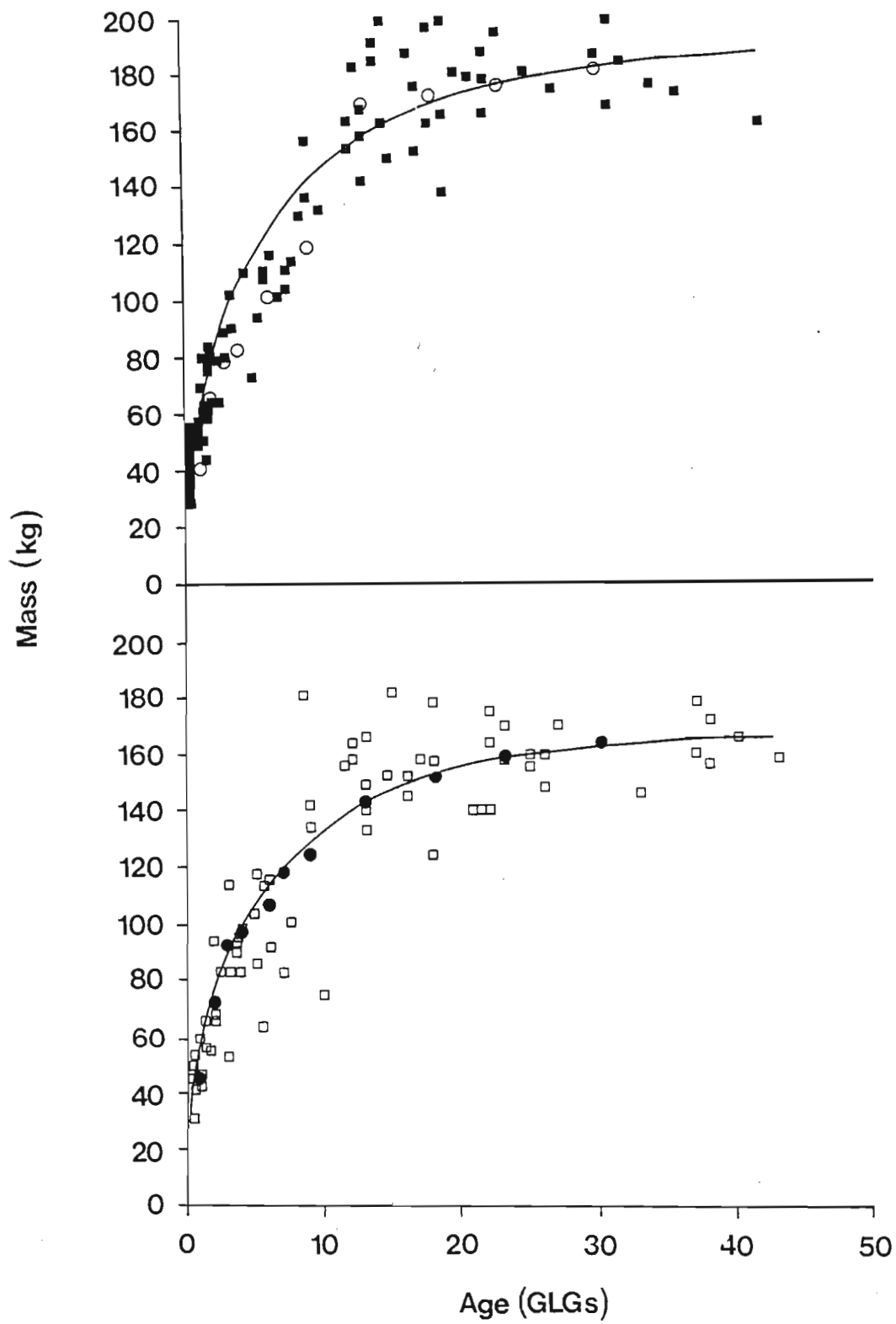


Table 1: Parameters derived from a four stage Von Bertalanfy growth curve ( $l(t) = \text{linf}(1 - e^{-k(t-t_0)})^p$ ) fitted to age-length and age-mass data for male and female bottlenose dolphins.

Parameter	Males		Females	
	Length	Mass	Length	Mass
a	0.09712	0.09105	0.167249	0.099103
b	7.02751	2.00633	5.448886	2.126851
L1	102.775	14.7865	102.0206	14.64186
L2	245.016	185.217	239.9296	165.7209
t0	-0.02261	-0.0676	-0.056844	-0.05725
Linf	245.611	187.254	239.9625	166.8249
k	0.09712	0.09105	0.167249	0.099103
p	0.14229	0.49842	0.183524	0.470179
Lt0	103.4	14.9	102.31	4.8
n	100	88	88	84

Lt0 = Estimated length or mass at birth

The relationship of both body length and mass to age, for captured *Tursiops* and stranded or captive born neonates, were fitted to a number of growth curves, including those of Gompertz, Richards, Putter and Schnute. However, growth with age, for both males and females, was best defined by derived Von Bertalanffy growth curves (Figs. 2 & 3) of the form:

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

Asymptotic length and mass, calculated from the mean length and mass of physically mature males (243 cm and 176 kg) and females (238 cm and 160 kg), were slightly overestimated by the derived curve (Table 1) but both show that the asymptotic length and mass of males is greater than that of females. There was no significant difference between the mean mass of lactating and non-lactating mature females ( $t=0.236$ ,  $P<0.01$ ) which could have contributed to this sexual dimorphism.

Length and mass at birth predicted by the Von Bertalanffy growth curves (Table 1) were almost identical to length and mass at birth (103 cm, range 86 -115 cm, s.d. = 7.6 n = 26 and 13.8 kg, range 9.1 - 21 kg, s.d. = 2.9, n = 15) calculated from the mean length and mass of captive born or stranded neonates in which the umbilicus was unhealed.

In both males and females most growth occurred during the first 10 to 12 years of life and thereafter reached a plateau (Figs. 2 & 3). A plot of mean length and mass at age shows that, in females, both mass and length increase in a smooth, continuous process with no evidence of any discontinuity (Fig. 3). In males, length increase follows a similar pattern whereas mass increase shows a clear discontinuity between 10 and 13 years of age (Fig. 2) and indicates that a two stage growth curve would better fit these data.

The mean length and mass of the first five year classes, calculated from calves displaying whole, completed GLGs only, showed that growth rate during the first year far exceeded that in

Figure 4: Relationship between mass and length for male (closed squares) and female (open squares) bottlenose dolphins. Power curves of the form (males  $-\log Y = -5.1 + 3.06 \log X$ , females  $-\log Y = -4.7 + 2.9 \log X$ ) are fitted to these data.

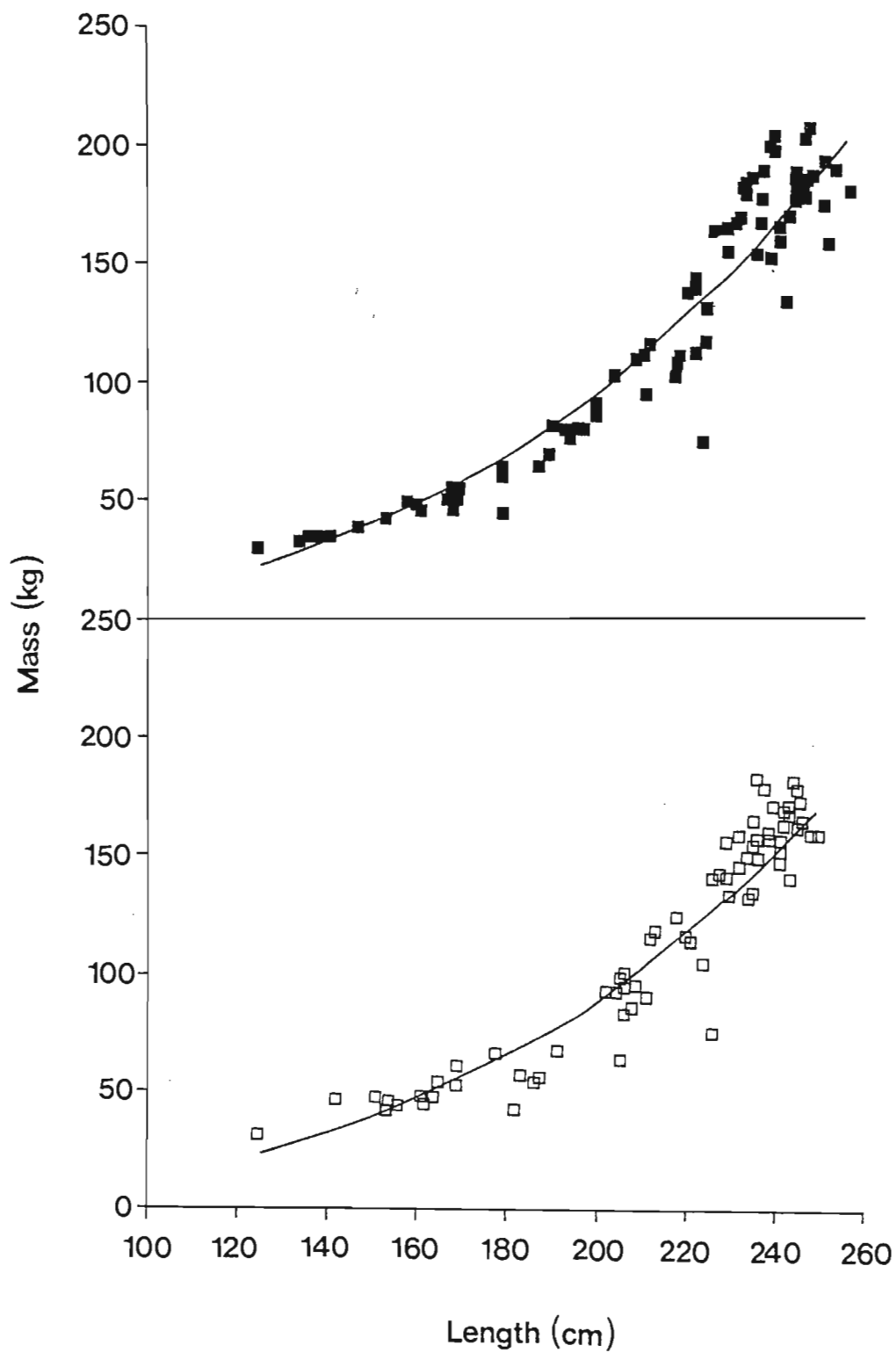




Table 2: The range in age (GLG counts) at which the vertebral epiphyses of male and female bottlenose dolphins were unfused, fusing and fused.

	Age (GLG counts)		
	Unfused	Fusing	Fused
Males	0 to 8	4 to 14	> 12
Females	0 to 6	4 to 13	> 12

Figure 5: Foetal growth in length and mass and a regression of the form ( $Y = 23.914 + 0.006 \times X$ ) drawn through these data.

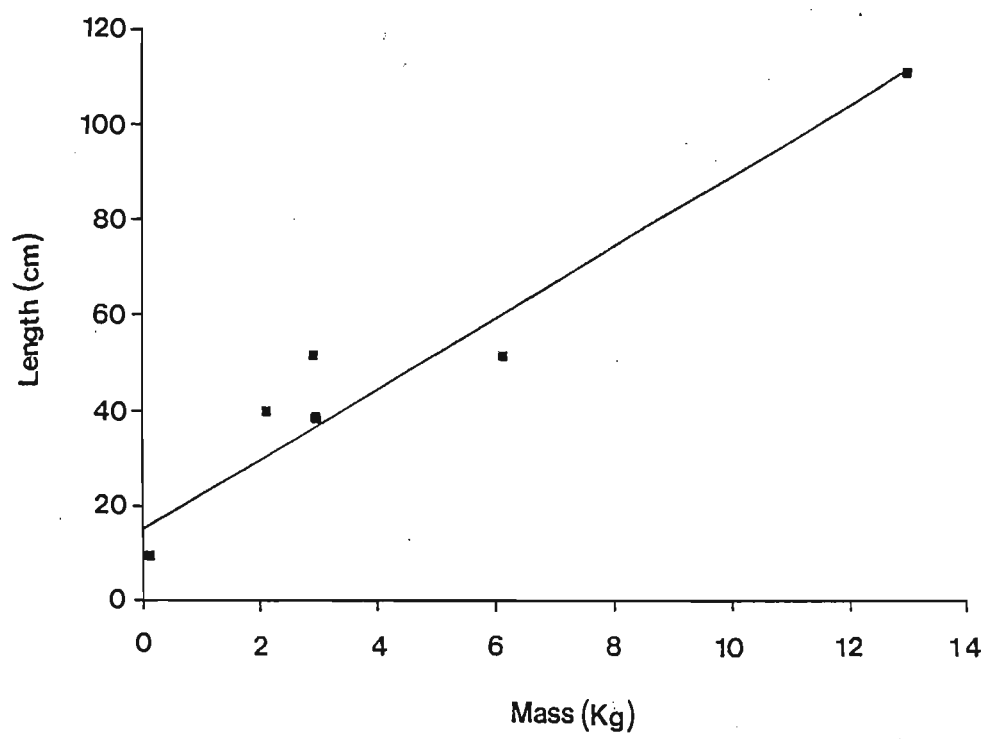


Figure 6: The Increase In brain volume with age in bottlenose dolphins.

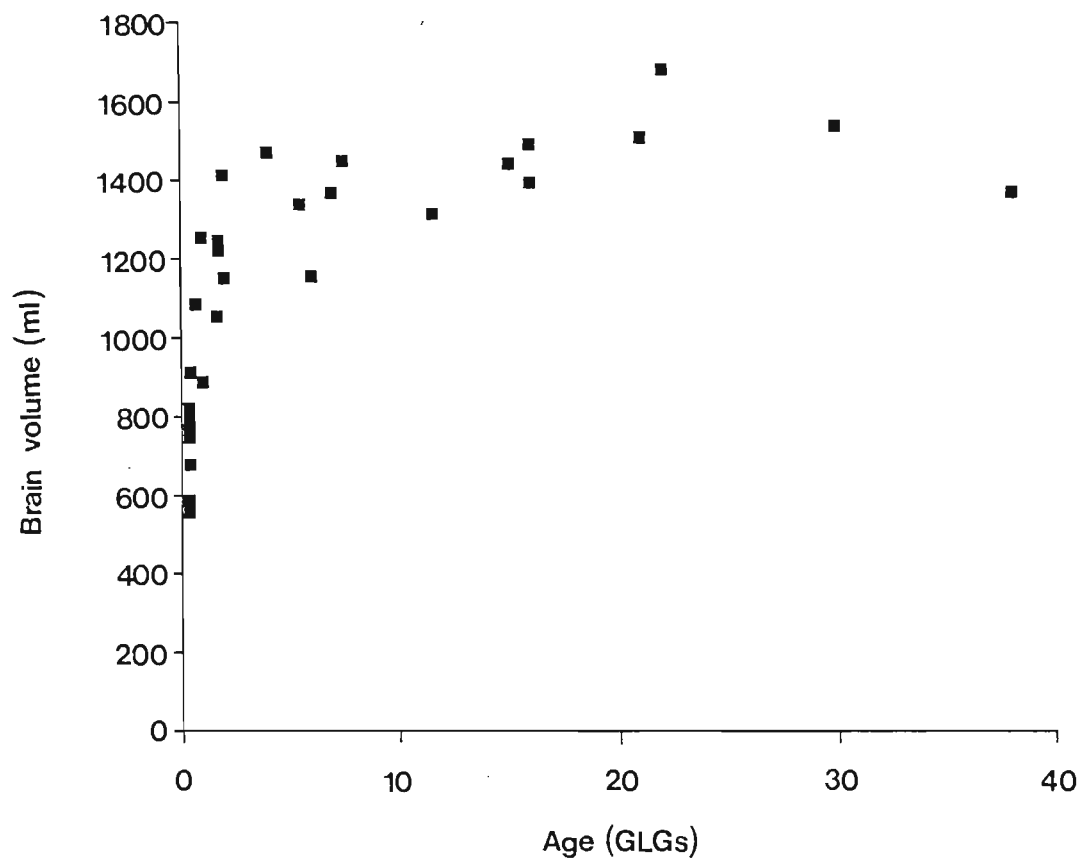


Table 3: The length, mass and brain mass of six stranded or captive born neonate bottlenose dolphins.

	Length (cm)	Mass (kg)	Brain Mass (g)
	100	12.4	562
	105	17.7	680
	106	14.8	738
	106		595
	108	13.0	635
	109	13.4	625
Mean	106	14.3	639

any other. In the first year mass increases by some 255 % of mean birth mass but increases over the subsequent four years slow to 49 %, 13.5 %, 10.6 % and 3.8 %, respectively. In contrast, length increase is much less rapid over this same period and is approximately 57 %, 15.2 %, 3.7 %, 4 % and 5.5 %, respectively. In both males and females the relationship between mass and length, up to asymptotic values, is well defined by power curves (males;  $\text{Log mass} = -5.1 + 3.06 \times \text{Log length}$ ,  $r=0.97$ ; females;  $\text{Log mass} = -4.7 + 2.9 \times \text{Log length}$ ,  $r=0.95$ ) (Fig. 4).

Both male and female bottlenose dolphins appear to reach physical maturity between 12 and 15 years of age (Table 2). The youngest physically mature animal was 12 years old while the oldest non-physically mature animal was 14 years old (Table 2). The mean age of physically mature males and females was 23 and 24.4 years, respectively.

#### Female reproduction:

Only six (2.8 % of the total catch and 12 % of mature females) of the captured females were pregnant and the growth of the six foetuses, length (cm) against mass (kg), was well defined by a linear regression ( $Y = 23.914 + 0.0065 \times X$ ) (Fig. 5) but no estimate of gestation period was possible from these data. An estimate of gestation period was obtained from the relationship between neonatal and adult brain mass (Sacher & Staffeldt, 1974, in Perrin *et al.*, 1977) (Fig. 6). A neonatal brain mass of 639 g was estimated from the mean brain mass of six stranded or captive born neonates in which the umbilicus was unhealed (Table 3). An asymptotic brain mass of 1460 g was calculated from the mean brain volume of females older than 10 years. The variation in maximum size of females would obviously affect this calculation. However, application of the Sacher & Staffeldt equation:

$$\log G = 0.274 \log E_n + 0.144 \log A_e + 0.173 \log N + 1.853$$

Figure 7: The birth month of 25 bottlenose dolphin calves back-calculated from the width of the first dentinal growth layer group.



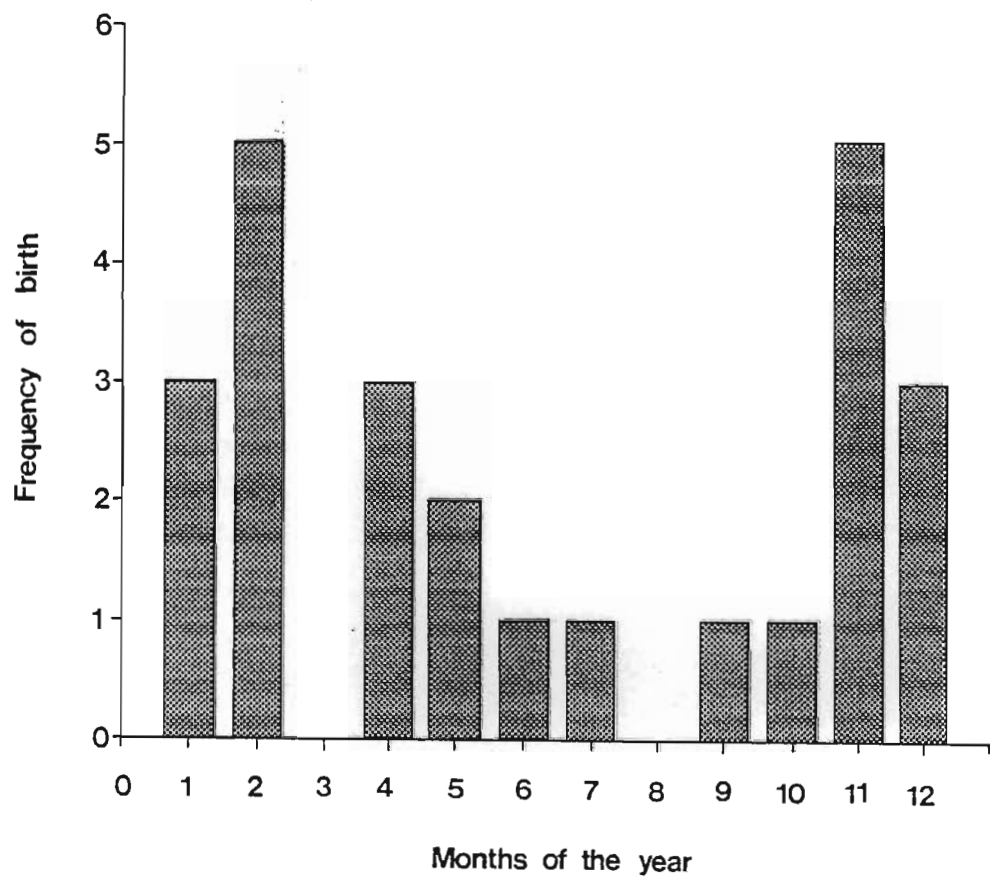


Figure 8: The relationship between combined ovary mass and the total number of ovarian scars.

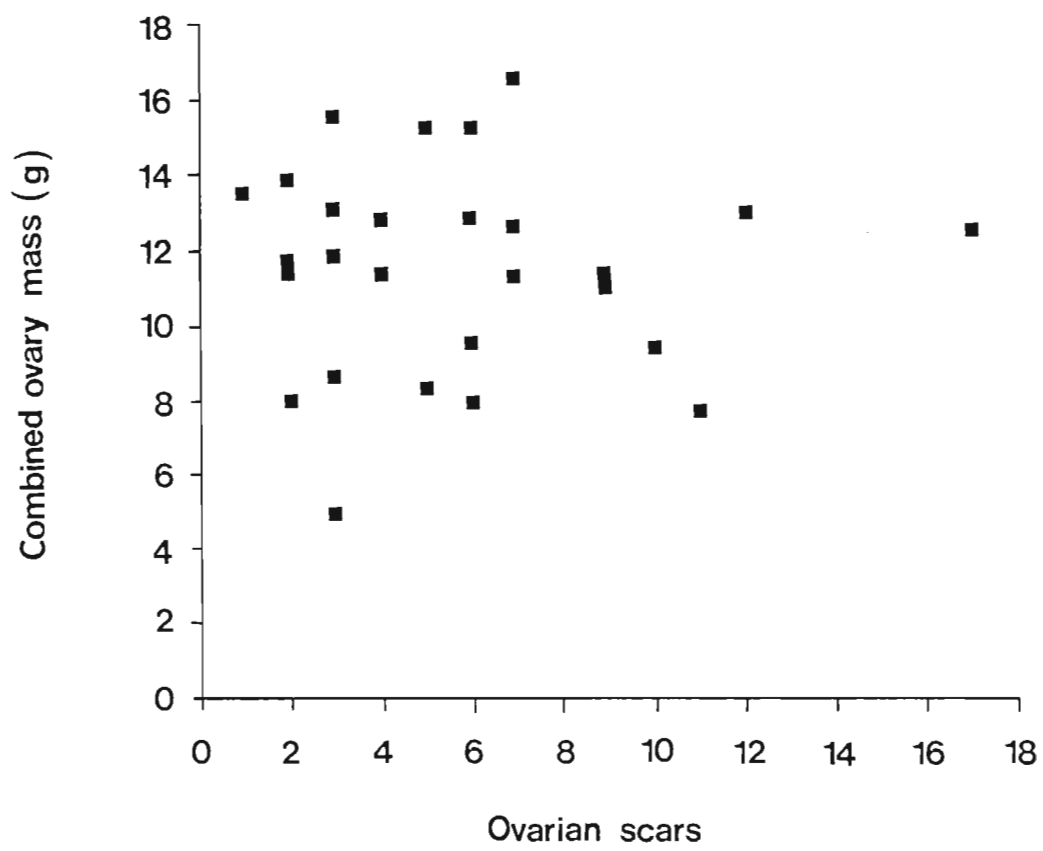


Figure 9: The increase in the number of ovarian scars with mass, age and length of female bottlenose dolphins. A linear regression ( $Y = 0.8 - 0.32 \times X$ ) fitted to this relationship in post-pubertal females is shown.

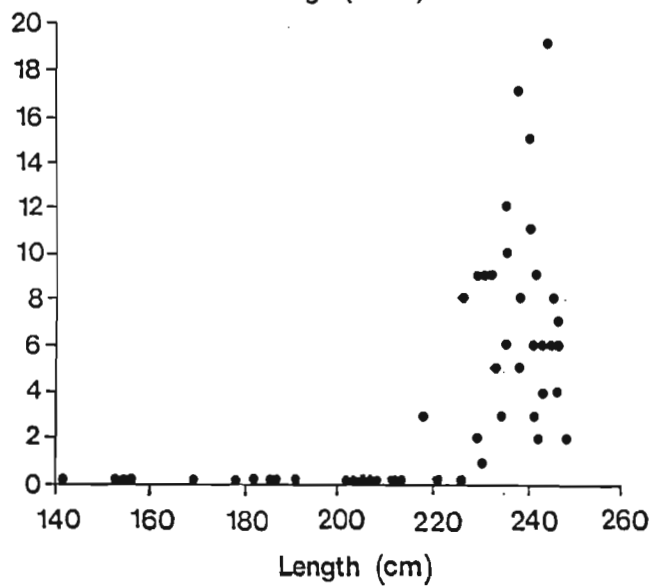
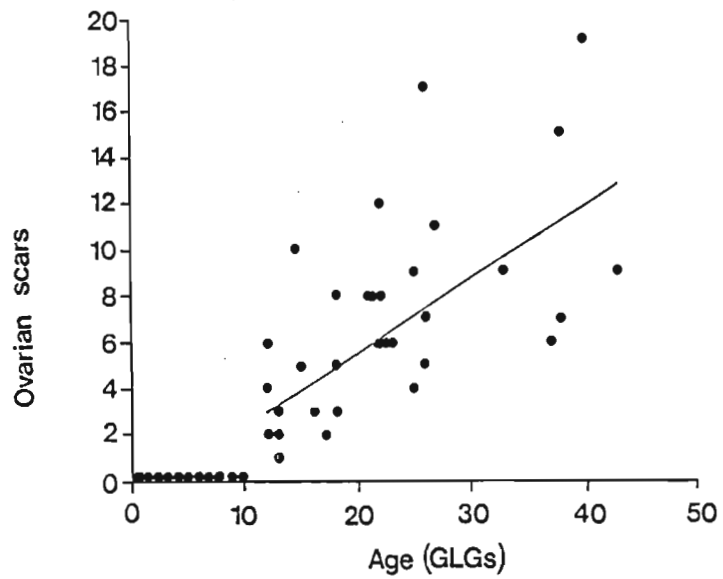
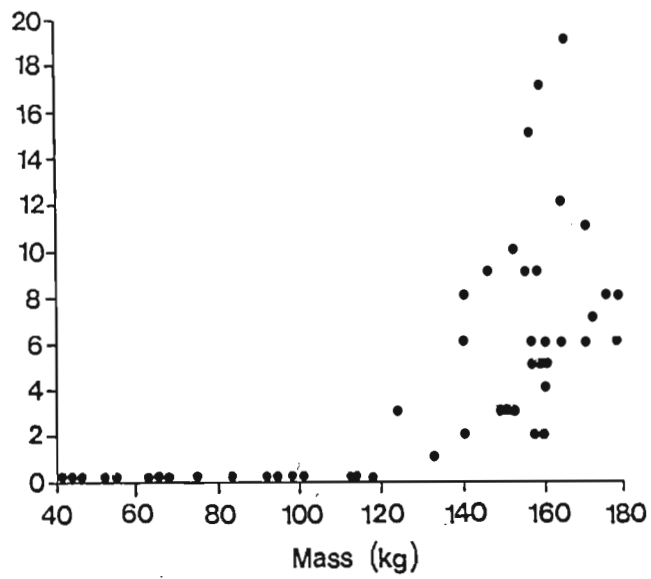
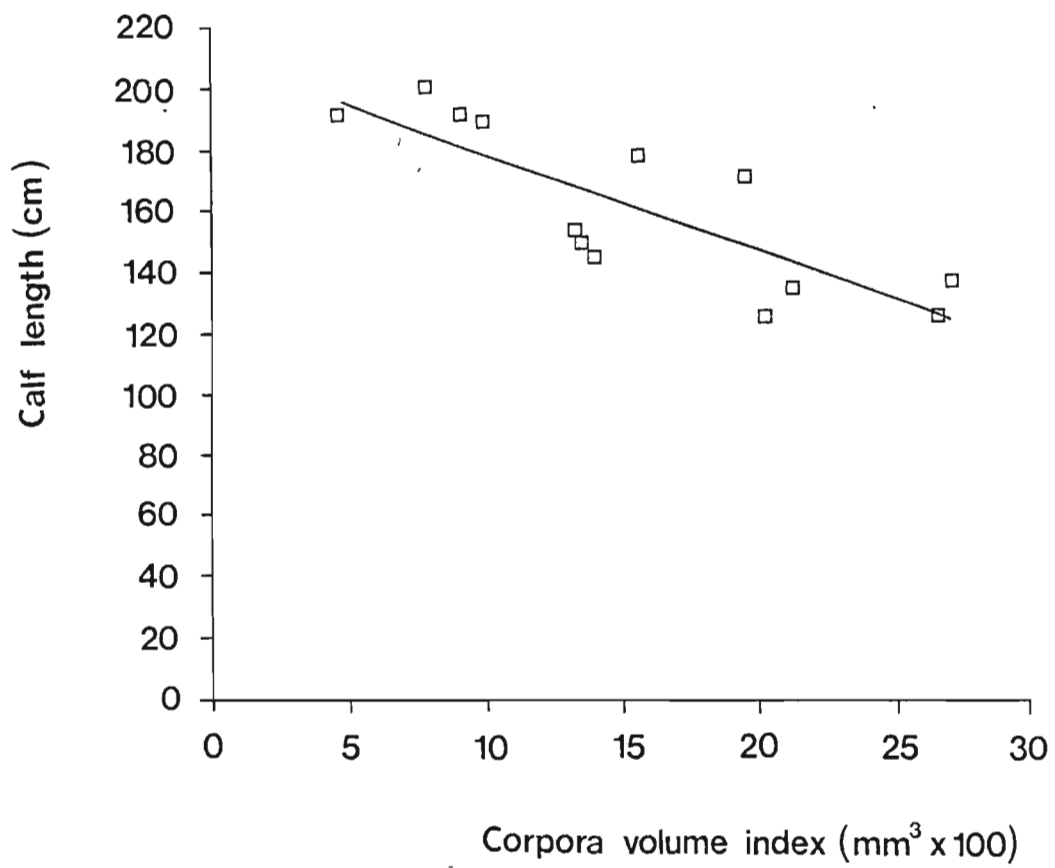


Figure 10: The relationship between the length of a calf and an index of the volume of the most recent or largest corpus in the mother. The fit of a linear regression ( $Y = 209.61 - 0.032 \times X$ ) to these data is shown.



(in Perrin *et al.*, 1977) ( $G$ =gestation time in days,  $E_n$ = neonatal brain mass in grams,  $A_e$ =ratio of neonatal to adult brain mass,  $N$ =litter size) suggests a gestation period of approximately 372 days.

An alternative method of estimating gestation period based on the relationship between birth length and gestation period (Perrin *et al.*, 1977) where:

$$\text{Log(gestation period)} = 0.4586 \times \text{log(birth length)} + 0.1659$$

yielded an estimate of 12.3 months or 374 days, assuming a birth length of 103 cm.

There was no relationship between the size of a foetus and the month in which the mother was captured. However, an estimate of birth time/season was provided by back calculation of birth date on 25 captured calves less than one year old (Fig. 7). For these calves, the proportional growth of the first GLG was estimated to the nearest month in relation to fully formed GLGs of one year olds. The mean width of the formed GLG layer of one year olds was 279  $\mu\text{m}$  ( $n=29$ , range 229 - 331  $\mu\text{m}$ ) with a 95 % C.I. of 10  $\mu\text{m}$ , suggesting a maximum back calculation error of about 13 days.

In all females the majority of ovarian scars (80 %) occurred in the left ovary. The maximum number of scars in any one ovary was 11 and there was no indication that ovary mass decreased with the number of ovarian scars (Fig. 8). Age, mass and length related ovulation rates appear extremely varied in bottlenose dolphins (Fig. 9). In only one female was there one ovulation so calculation of mean age at first ovulation was impossible. This 13 year old female had a corpus lutea measuring 10x8x8 mm (index volume 640  $\text{mm}^3$ ) and was lactating, indicating she probably had a suckling calf. Extrapolation from a regression of calf length on an index of the most recent or largest corpus volume, for mother and calf pairs (Fig. 10), suggests that her calf would have been some 184 cm in length or approximately 18 months old (Fig. 2 & 3), suggesting that her



Figure 11: The relationship between the mass of a calf and an index of the volume of the mother's mammary glands.

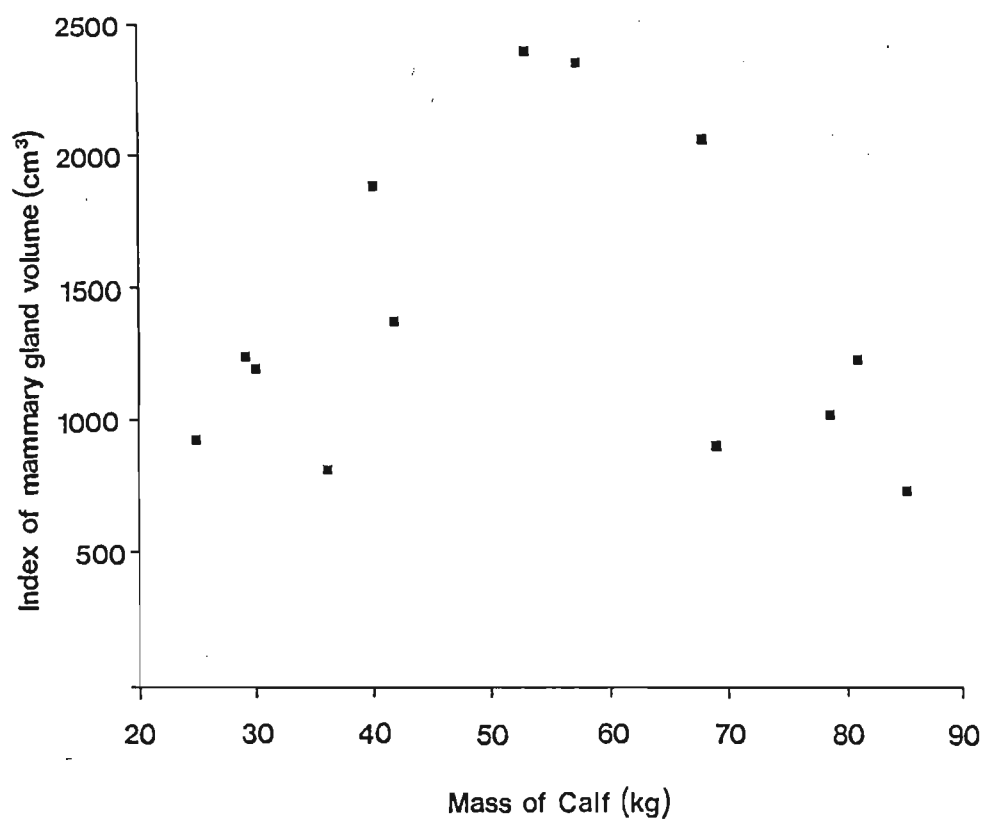
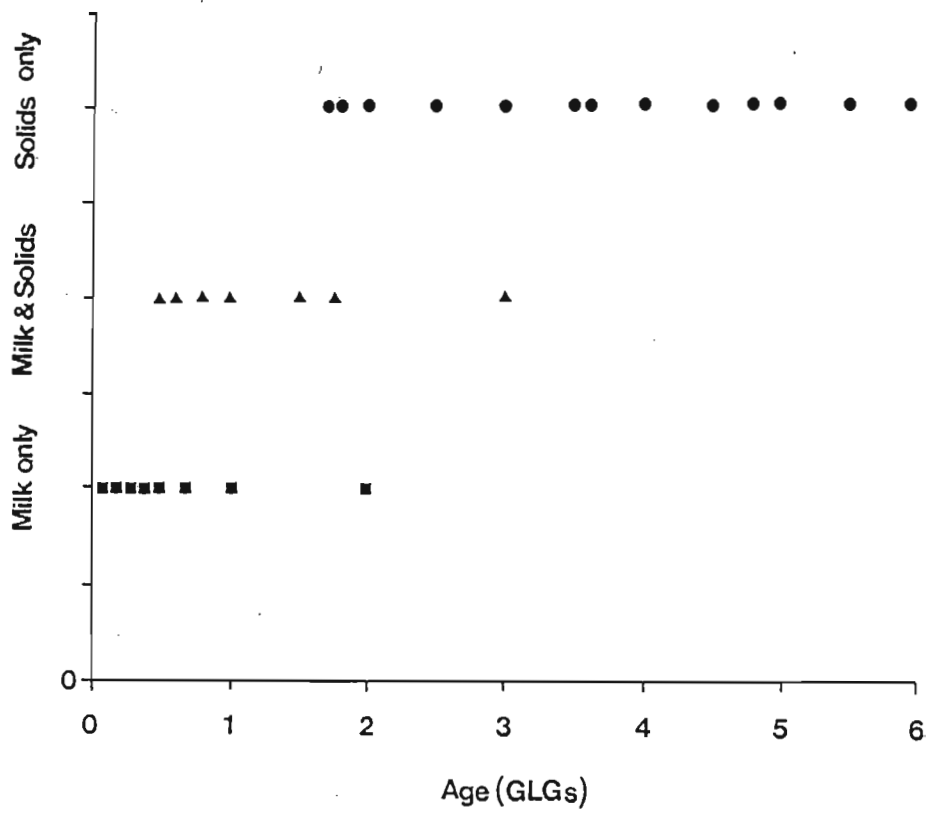


Figure 12: The age range of calves in which milk (squares), both milk and solids (triangles) and solids only (circles) were found in the stomach.



first ovulation and conception occurred when she was approximately 10.5 years old.

Two other females, 12 and 13 years old, which had each undergone two ovulations (Fig. 9), were lactating and had corpus lutea index volumes of  $900 \text{ mm}^3$  and  $2100 \text{ mm}^3$ , respectively.

Extrapolation from the regression in Figure 10 suggests that the calves of these females were approximately 181 cm or 18 months old and 143 cm or 6 months old, respectively. These data suggest that at conception of the calves, these two females were about 10.5 and 9.5 years old, respectively. The above data and the presence of 10 year old females that had not ovulated imply that first ovulation occurs between 9.5 and 11 years of age. One 17 year old female had undergone two ovulations, was lactating and had a 170 cm calf of approximately one year old. This suggests that this female was 15 years old at the time of conception of this calf, although she may have undergone a previous pregnancy.

A regression fitted to the number of ovarian scars on age ( $Y = -0.8 + 0.32 \times X$ ) has a slope of 0.32. This implies that mature females, in general, ovulate every third year (Fig. 9). A regression of the log of age and log of number of ovulations, for all females with more than one ovulation, was linear ( $Y = -0.61 + 1.03X$ ,  $r=0.62$ ) indicating no decrease in ovulation rate with age.

No direct estimate of lactation period was possible from the available data. However, the relationship between calf mass and an index of mammary gland volume (length \* height \* depth), in 13 mother and calf pairs, suggests that the mammary glands increase in size during lactation, until the calf's mass is approximately 60 kg, after which the mammary volume decreases (Fig. 11). Extrapolation from the growth curves suggests that calves of this mass are about 18 months old. An examination of the stomach contents of captured calves and juveniles shows that solids appear in stomachs at about six months of age, although, suckling may continue up to two or three years of age (Fig. 12).

Figure 13: The increase of mean seminiferous tubule diameter (squares) and combined testis mass (circles) with age in male bottlenose dolphins.

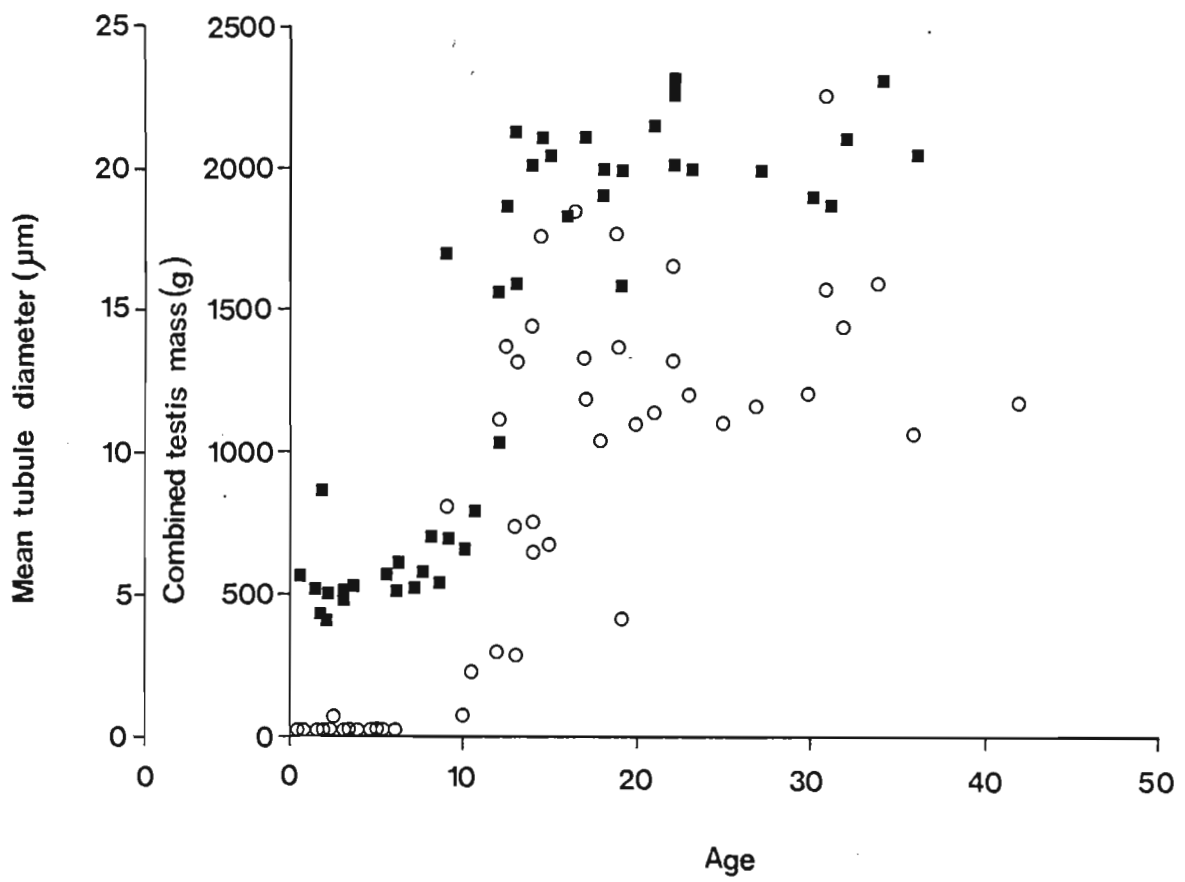


Figure 14: The increase in combined testis mass with mass and length in male bottlenose dolphins.



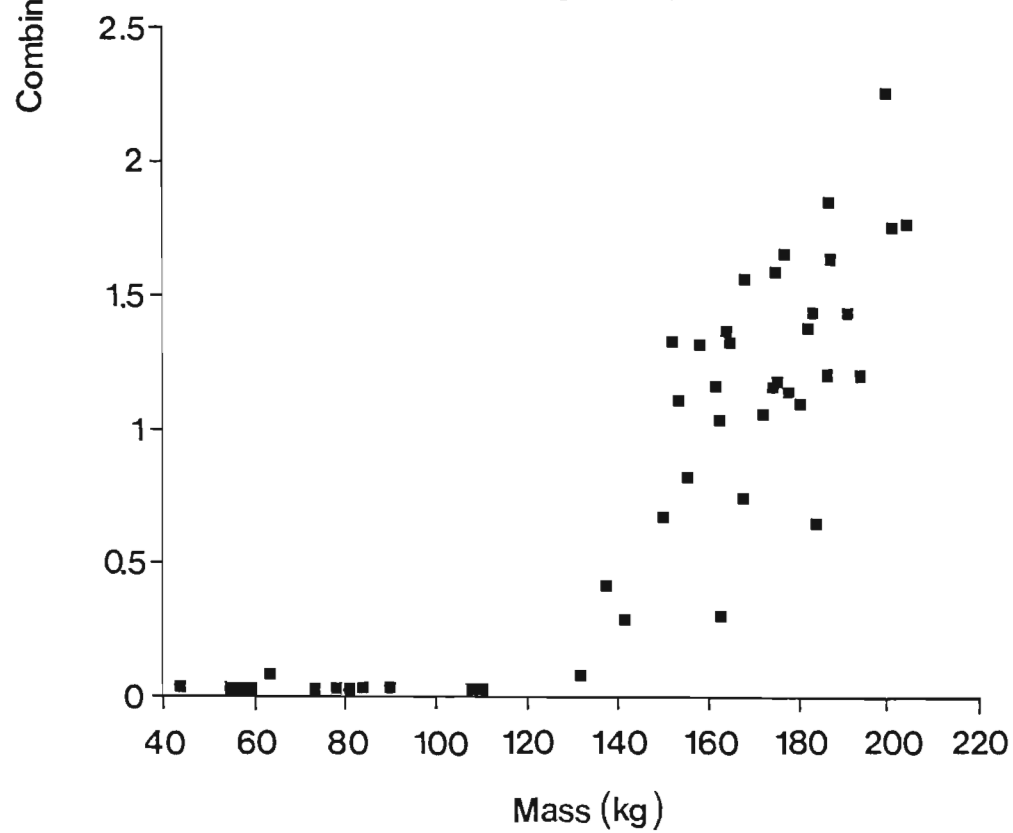
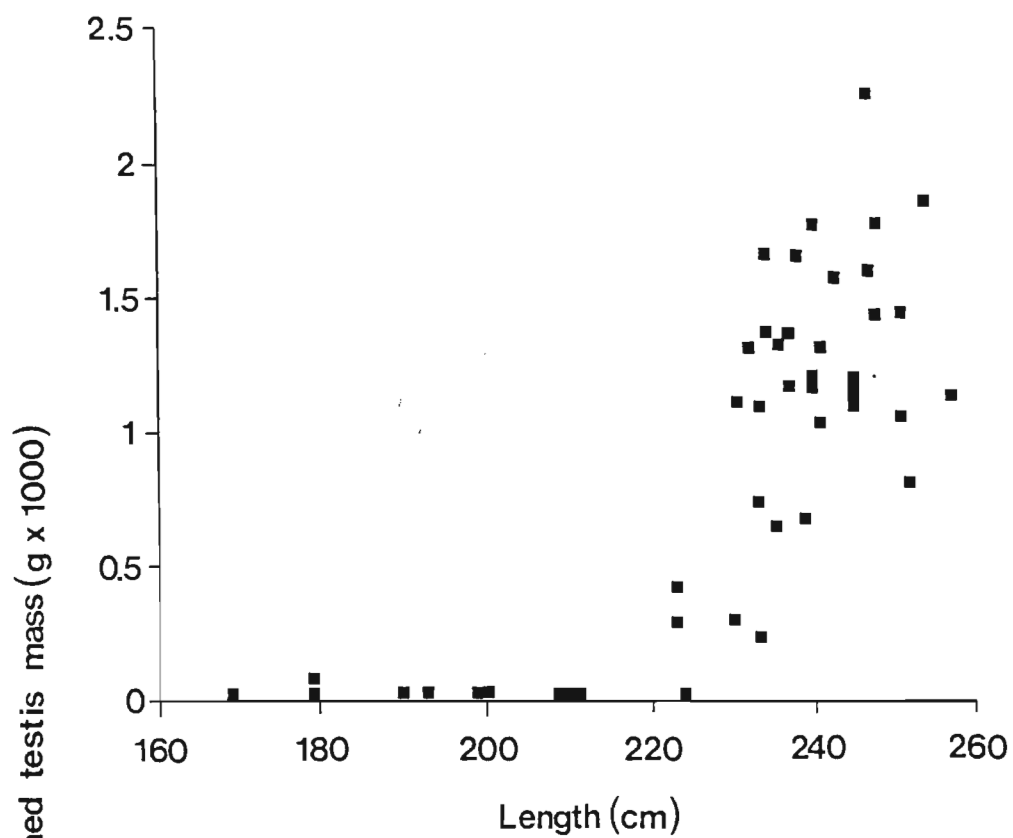
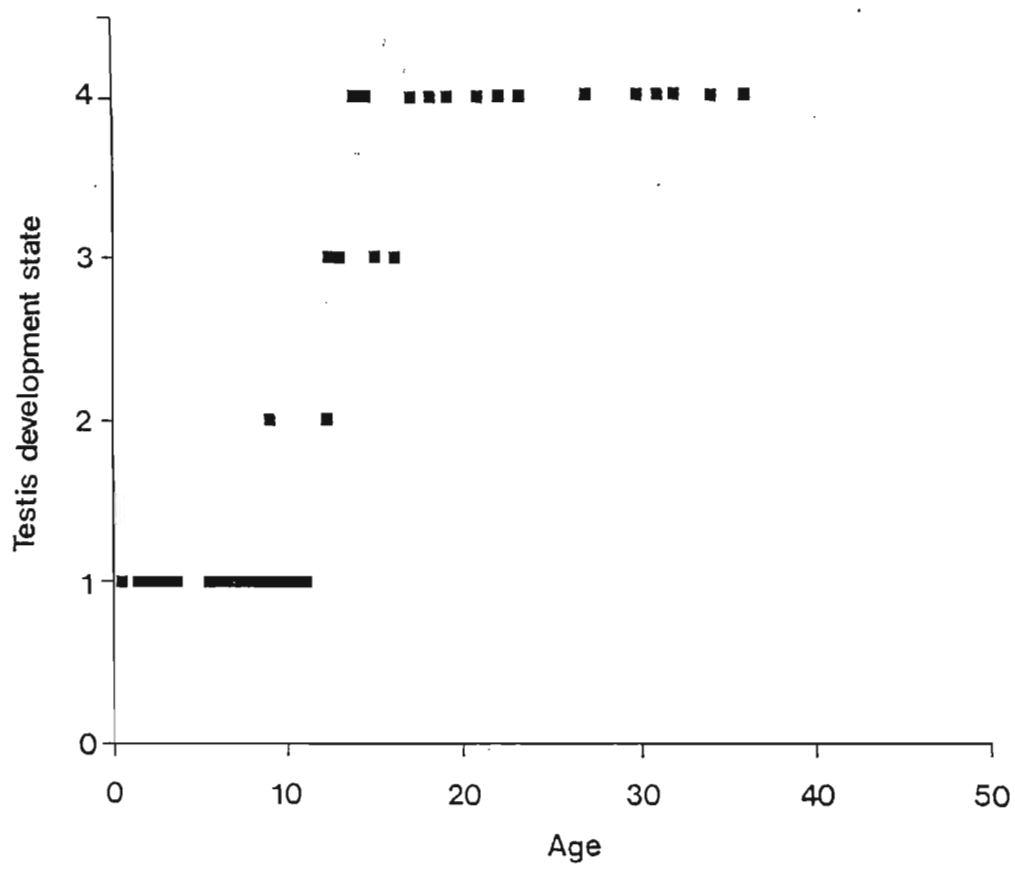


Figure 15: Relationship between testis development state (1 = no mature seminiferous tubules, 2 = <50 % mature seminiferous tubules, 3 = >50 % but <100 % mature seminiferous tubules, 4 = All seminiferous tubules mature) and age of bottlenose dolphins.



Length of lactation calculated from the catch statistics of animals on the Natal coast (Cockcroft & Ross, in press) (proportion of females lactating (27 %) / proportion pregnant (5.2 %) = lactation time in years - Perrin & Reilly, 1984) gave an estimate of 5.2 years. This figure is obviously exaggerated by the overabundance of lactating and dearth of pregnant females and indicates that alternative means of estimating lactation period are required.

Of the 20 known mother calf pairs, 10 calves were one year old or less, five were between one and two years old and a further five were greater than two years old, the mother of one of the latter was pregnant with a foetus of only 38.5 g. Although only solids were found in the stomach of her 69 kg calf, she was still lactating, the only one of six pregnant females lactating simultaneously. These facts imply a mother and calf association of up to three years before a subsequent pregnancy. The youngest lactating female was 12 years old while the oldest 43 years old. The youngest lactating female caught with a calf was 13 years old and the oldest 38 years old and there was no relationship between the age of a calf and the age of the mother, in mother calf pairs.

Female resting period (Rest period = Gestation period \* (% females resting {5.8 %}) / % females pregnant - Perrin & Reilly, 1984) calculated from the catch statistics of Natal bottlenose dolphins (Cockcroft & Ross, in press) yielded an estimate of about one year.

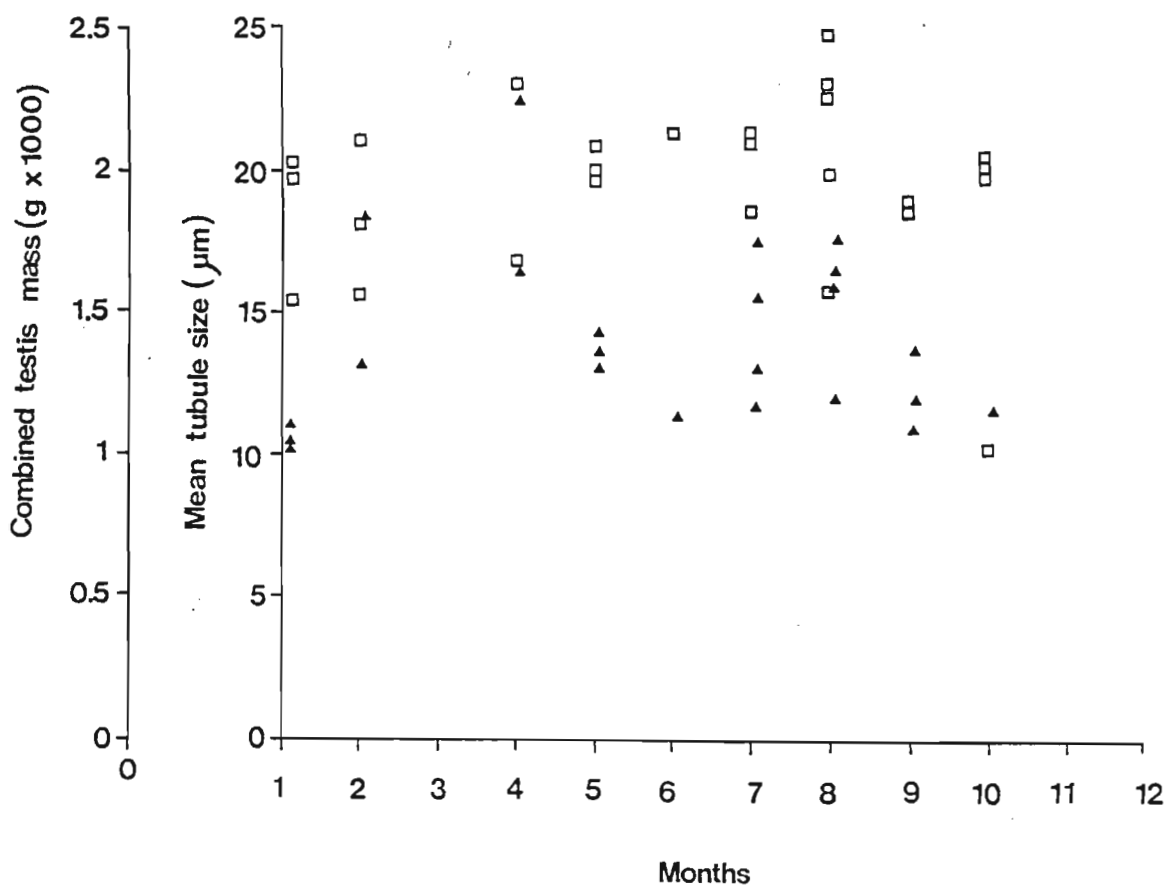
#### Male reproduction:

No consistent differences were found between mean tubule diameter of samples taken from the outer, middle and inner sections of testes. In general, left and right testes were of similar mass ( $r=0.95$ ). Combined testis mass remained low (less than 100 g) up to approximately 10 years of age, approximately 140 kg body mass and a length of 225 cm, but thereafter increased rapidly (Figs. 13 & 14). Tubule diameter growth and state of testes development (Mitchell & Kozicki, 1984) showed a similar pattern of growth with age, mass and length (Figs. 13 & 15), although

Table 4: The mean age, mass and length of male bottlenose dolphins with testes showing no mature tubule development (stage 1), some mature tubule development (stage 2 - approximately half of tubules mature) and 75 % to 100 % of tubules mature (stage 3/4).

	TESTIS DEVELOPMENT STAGE		
	1	2	3/4
AGE	4.68	14.3	20.6
MASS (kg)	90.8	151	174
LENGTH (cm)	201	228	241
n	22	6	25

Figure 16: The Influence of season (month) on combined testis mass (triangles) and mean testis seminiferous tubule diameter (squares) in male bottlenose dolphins.



development of tubules appeared to occur earlier than did the increase in testis mass. The maximum mature testis (stage 4) mass of any male was 1160 g and the largest apparently immature testis (stage 1) was 130 g. The smallest testis at stages 2, 3 and 4 were 140 g, 320 g and 310 g, respectively. Mean age, mass and length of males according to testis development stage are given in table 4. Puberty in male *Tursiops* from the Indian Ocean may begin as early as nine years of age but primarily between 10 and 12 years (Fig. 13). However, sexual maturity (50 % each of stages 2/3 and 4) occurs only at about 14.5 years of age, a length of 240 cm and a mass of 165 kg.

There was no evidence of a seasonal pattern in either combined testis mass and tubule size (Fig. 16) or the presence of sperm in the epididymis.

## DISCUSSION

The similarity of dentinal GLG counts to 'Dolfie's' actual age indicate an annual deposition of dentinal GLGs for at least the first six years. Ross (1984) superimposed the growth rate of 'Dolfie' on a length versus age (dentinal GLGs) relationship in bottlenose dolphins from Natal and the Eastern Cape and concluded that "the best fit of the points to the curve is reached when the accumulation rate of dentine layers is equal to one per year". Similarly, if the growth rate of another captive animal from this region (Cockcroft & Ross, 1989b), is fitted to the curve in Figure 2, the relationship is best explained by an annual deposition of dentinal GLGs. An annual deposition of dentinal GLGs has been proposed for *Tursiops* in other areas (Sergeant *et al.*, 1973; Hui, 1980).

In contrast to apparently continuously deposited dentinal GLGs, cemental GLGs appear to be rapidly deposited and only accumulate as whole layers in the teeth of *Tursiops*. Nevertheless, the strong correlation between dentinal and cemental age estimates up to occlusion of the pulp cavity and the similarity of dentinal and cemental GLG counts in 'Dolfie's' teeth suggest that



cemental GLGs also accumulate annually and are reliable estimators of age in bottlenose dolphins from the Indian Ocean, at least up to an age of 12 years. Despite the lack of direct evidence, it seems likely that cemental GLGs are deposited annually even after 12 years.

Male and female Indian Ocean bottlenose dolphins may attain an age greater than 40 years (cf. Ross, 1977), with little difference in the apparent maximum ages of the sexes. In excess of 20 % of the Natal net catch were older than 20 years indicating a long lived species. Few data are available on the longevity of *Tursiops* elsewhere and most existing studies have used dentinal age estimates. Sergeant *et al.* (1973) estimated the longevity of *Tursiops* from northeast Florida to be about 25 years, with no apparent differences in the life expectancy of males and females. Hohn (1980), in a study of *Tursiops* from the south east coast of the United States, found animals with up to 27 dentinal GLGs, males and females reaching similar ages. In contrast, the maximum age of spotted dolphins, estimated from cemental GLGs, is in excess of 45 years (Kasuya, 1976). Thus, the use of cemental GLG age estimates in future studies of bottlenose dolphins may yield greater estimates of maximum age.

The estimated mass and length at birth of Indian Ocean bottlenose dolphins in this study are comparable to those calculated by Ross (1984). Subsequent to birth, growth is rapid, particularly in terms of mass, but decreases gradually with age. The proportional length increase is similar to that previously recorded for bottlenose dolphins from Natal and the eastern Cape (Ross, 1977; Ross, 1984; Cockcroft & Ross, in 1989b), from northeast Florida (Sergeant *et al.*, 1973) and from the western North Atlantic (Hohn, 1980). An enormous increase in mass during the first (suckling) year is well known in seals and balaenopterid whales but has not been often recorded for delphinids. Presumably, a large, initial mass increase reflects the rapid development of the calf and its need to reach thermoregulatory equilibrium as well as some social and motor independence from its mother (Cockcroft & Ross, 1989b), before the females involvement with the next pregnancy and calf.

The asymptotic length and mass values obtained in this study and those of Ross (1977; 1984) are less than those for bottlenose dolphins from the western North Atlantic (Hohn, 1980) and Florida (Sergeant *et al.*, 1973). It is unclear why bottlenose dolphins from different areas have varying asymptotic sizes, although, Ross & Cockcroft (1989) have suggested that such differences may have been in response to environmental conditions, particularly temperature.

The asymptotic lengths of male and female Indian Ocean bottlenose dolphins are only slightly different (243 cm and 238 cm, respectively). In the western North Atlantic Hohn (1980) found no difference in the maximum lengths of males and females. These results support the findings of Sergeant *et al.* (1973) that the total lengths of male and female delphinids, in general, do not appear to be different, although, they found that the asymptotic length of male *Tursiops* from Florida was 20 cm greater than that of females.

In contrast, fully grown male Indian Ocean bottlenose dolphins are considerably heavier (9 %) and more robust than females (176 kg and 160 kg, respectively). Lactating and non-lactating females had a similar mean mass indicating that this mass difference cannot be attributed to stress and blubber mass loss through lactation (Cockcroft & Ross, 1989a; 1989b). Some of this mass difference between the sexes may be a direct consequence of the male mass growth spurt between 10 and 12 years of age. It is unclear why this growth spurt is not reflected in the length of males, it may be that robusticity and not length is important in male and female interaction.

Despite this, the male growth spurt at the onset of puberty may be similar to the two stage growth that Perrin *et al.* (1976; 1977) described for male and female spotted and spinner dolphins in the eastern tropical Pacific where growth showed a pubertal secondary growth spurt. In male bottlenose dolphins this spurt occurs four to five years later than in spotted or spinner dolphins but also at the onset of puberty, suggesting that such growth spurts may be directly related to the attainment of sexual maturity. It is possible that this growth spurt may

also be evident in females bottlenose dolphins but is not discernable owing to the small sample size.

Females mature sexually some two or three years prior to the attainment of physical maturity in contrast to males, where sexual maturity is attained just before physical maturity. In both sexes, however, physical maturity occurs almost in concert with the occlusion of the tooth pulp cavity supporting previous suggestions that animals with occluded pulp cavities are sexually and physically mature (Ross, 1977; 1984). Females attain sexual maturity at least two years earlier and at a lesser length and mass than do males, although the reduced number of first time ovulators and high occurrence of females with multiple ovulations will have biased this upwards. It is not unusual for female delphinids to attain sexual maturity sometime before and at a smaller size than males. Female *Tursiops* in the western north Atlantic also appear to follow this pattern (Sergeant *et al.*, 1973). Female spotted and spinner dolphins reach sexual maturity about three or three to four years, respectively, before males and both are smaller than their male counterparts (Perrin *et al.*, 1976; 1977). It has been proposed that this disparity ensures more sexually mature females than males in the population (Bryden, 1972). Intensive behavioural field work is needed before this suggestion can be confirmed.

Although no direct estimate of gestation period was available from the foetal growth data, both derived estimates were in excellent agreement, about 373 days. A 373 day gestation period is slightly longer than previous estimates for *Tursiops* from this area which range from minimum estimates of 342 and 341 days (Saayman & Tayler, 1977) to maximum estimates of 364 and 368 days (Ross, 1984) in captive bottlenose dolphins. Similar estimates of the gestation period in captive *Tursiops* from other areas have been given by Tavalga & Essapian (1957) and McBride & Kritzler (1951) and Kasuya (1985).

Although the sample was too small for an assessment of the age at first ovulation, the onset of ovulation in females is apparently rapid. Thereafter, there was considerable variability in the

ovulation rates of both pubertal and sexually mature females. Some 12 or 13 year old females had particularly high ovulation rates, possibly a result of several initial infertile ovulations (Harrison *et al.*, 1972). Others of the same age had low corpora counts, were all lactating and one was pregnant, indicating that fertilisation occurred on the first or second ovulation. Indirect evidence, which shows that lactational transfer of organochlorines in female bottlenose dolphins occurred after one or two ovulations (Cockcroft *et al.*, 1989), supports the view that the majority of females conceive after one or two ovulations. The variation in ovulation rates of older females may be due, in part, to the same factors which apply to pubertal females and to additional reasons such as calf mortality or aborted pregnancies.

Overall, the calculated annual ovulation rate for female bottlenose dolphins was 0.32, a substantially lower rate than that observed for *Tursiops* from north east Florida (Sergeant *et al.*, 1973). There was little sign of reproductive senescence in females from Natal as ovulation rate did not appear to decline with age and there was no reduction in ovary mass with an increasing number of ovarian scars. Also, the oldest captured female was lactating and a number of older females were captured with calves and had enlarged corpus lutea in their ovaries. Results from organochlorine residue studies in these females also indicate that older females do not become senescent (Cockcroft *et al.*, 1989). These data imply that older females do not act as 'wet nurses' and is contrary to suggestions that several species of odontocete manifest age related declines in fecundity producing senescent females which invest more in quality (calf-rearing), with a longer lactational commitment, than in quantity (calf-bearing) as their reproductive potential falls (Kasuya & Marsh, 1984; Marsh & Kasuya, 1986). However, sample numbers in this study were small and certain female and calf pairs showed an extended relationship, although there was no indication that this was restricted to older females.

Taken in combination, these facts indicate that some Indian Ocean bottlenose dolphin females are probably reproductively active until an advanced age. A similar conclusion was reached by Kasuya (in Marsh & Kasuya, 1986) who found that although the annual pregnancy rate and the number of

resting females in a sample of *Tursiops* from the Pacific declined with age, pregnant and lactating females were present in all age groups, presenting no conclusive evidence of senescence.

Although births apparently occur throughout the year, there is a peak in summer, between November and February, when over 60 % of births occur. However, as birth dates were back-calculated, they may reflect the greater catch of dolphins in these months and the bias of the net catch for larger calves (Cockcroft & Ross, in press), although previous work in this region noted that births occurred predominantly in late spring and summer (Ross, 1977). No seasonal cycle of either testis mass, tubule diameter or occurrence of sperm was evident in mature males. These data also imply no distinct mating or breeding season in Indian Ocean *Tursiops*. In Florida waters, the main mating and calving season is apparently from February to May (Essapian, 1963), or from spring to early fall (Irvine *et al.*, 1981), which is similar to that found in the present study. In contrast, bottlenose dolphins off Argentina show a distinct summer calving and mating season (Wursig, 1978). These geographical variations, however slight, indicate the adaptability of coastal *Tursiops* to local conditions.

Although, it has been suggested that suckling as a nutritional source probably only lasts one year (Kasuya & Marsh, 1984; Cockcroft & Ross, 1989b), there is evidence that this may be nearly two years in *Tursiops* and that non-nutritional suckling may continue for as long as three years for some mother and calf pairs. An estimate of the duration of lactation is difficult, where suckling extends over long periods and may serve a non-nutritional purpose such as enhancing the cow calf bond (Brodie, 1969). Of the calves from lactating female and calf pairs, 25 % were over one year old and a further 25 % were over two years old and some of the two year olds had both milk and solids in their stomachs. The mammary glands from these lactating females, only one of which was pregnant, increased in size with calf size, until calves were approximately two years old. In combination, these data indicate that lactation in Indian Ocean bottlenose dolphins lasts more than one year and in some instances may extend to more than two years,

suggesting an 18 month to two year lactation period.

This is slightly longer than previous estimates of lactation length and age at weaning based on studies of captive and captured free-ranging bottlenose dolphins (McBride & Kritzler, 1951; Gurevich, 1977; Saayman & Tayler, 1977; Kasuya, 1985; Cockcroft & Ross, 1989b) and suggests a prolonged mother and calf association which may extend in free-ranging bottlenose dolphins for at least 15 months (Irvine *et al.*, 1981). Such extended mother and calf interaction may indicate a stable school structure, such as that postulated for short-finned pilot whales off the Pacific coast of Japan, which may be indicative of late maturing, long lived animals (Kasuya & Marsh, 1984). This may equally apply to *Tursiops* where a lengthy mother calf bond may be important in the calf's development and be a reflection of the smaller school size and inshore habitat, mastery of which may require greater maternal care and a longer learning period (Cockcroft & Ross, 1989b).

During a study captive bottlenose dolphin mother and calf association Cockcroft & Ross (1989b) have shown that the calf's suckling rate decreased with age, although its energy requirements probably grow with its level of independence and activity. As there was no evidence of energy changes in delphinid milk during lactation (Arvy, 1974) to compensate for this, the authors proposed that the quantity of milk ingested may increase as the calf's stomach volume increased (Cockcroft & Ross, 1989b). This explanation is supported by the present findings that a females mammary glands increase in size, probably increasing the volume of milk produced, during lactation.

In view of the extended lactation period of female bottlenose dolphins and the early and probably increasing intake of solid food by the calf, it is unlikely that females require a substantial interval between the end of lactation and the next pregnancy. A one year resting period, estimated from the catch statistics data, is almost certainly an overestimate due to catch bias. Kasuya (1985) estimated a three month resting period for *Tursiops* in the western

north Pacific and it is probable that Indian Ocean *Tursiops* are similar. Considering that gestation lasts about one year and that lactation probably lasts 18 months to two years, a calving interval of around three years can be estimated for Indian Ocean bottlenose dolphins. This estimate is in good agreement with the projected ovulation rate of one every three years, but assumes that all calves survive and ignores the affects of differential calf mortality (Perrin & Reilly, 1984) which would lower the mean calving interval considerably.

Nothing is known of the age and sex structure of the Natal bottlenose dolphin population. The only available information is from the catch of these animals in the Natal shark nets, the sex, size and age structure bias of which have been discussed (Cockcroft & Ross, in press). Given these biases, attempts to calculate reproductive parameters from these data are flawed but provide the only means of calculating the reproductive potential of this population.

The relevant proportions of females, females mature, females lactating, females pregnant and females resting in the net catch are 56 %, 43 %, 27 %, 5.2 % and 5.8 %, respectively (Cockcroft & Ross, in press). Annual Pregnancy Rates (APR) (Perrin & Reilly, 1984) calculated from these catch data and lactation period (either one or two years) range between 5.2 and 27 %. Changes in either the proportion of females lactating or the length of lactation greatly influence this calculation but even the highest estimate is low in comparison with values calculated for *Tursiops* in other areas; 63 % in the Black Sea (Danilevskiy & Tyutyunnikov, 1968, in Perrin & Reilly, 1984) and 43.6 % and 40.4 % for the western north Pacific (Kasuya & Izumisawa, 1981, in Perrin & Reilly, 1984; Kasuya, 1985).

Similarly, Gross Annual Reproduction Rate (GARR) (Perrin & Reilly, 1984) calculated from catch statistics and the range of APR values yields estimates between 0.043 and 0.065. The former GARR estimate is greater than that calculated for an unexploited stock of *Tursiops* from eastern Australian waters, although this was based on an unreliable technique of estimating calf numbers from aerial surveys (Lear & Bryden, 1980, in Perrin & Reilly, 1984). The latter GARR figure,



although probably an overestimate, is some 40 and 500 % lower than those estimated for exploited populations of *Tursiops* off Iki Island, Japan (Kasuya, 1985) and in the Black Sea (Danilevskiy & Tyutyunnikov, 1968, in Perrin & Reilly, 1984), respectively.

An assessment of the theoretical maximum natural rate of increase (ROI) of the Natal bottlenose dolphin population, assuming a calving interval of 2 to 3 years, age at first breeding of 10 years and an annual survival rate of less than 0.97, yields an annual population increase between 4 and 6 % (Reilly & Barlow, 1986). The ROI makes allowances for adult and calf mortality not accounted for by a GARR estimate which, therefore, infers that even the greater GARR figure may be an underestimate. Given an annual increase of as much as 6 % of the estimated 900 population, the mean annual mortality of bottlenose dolphins in shark nets, 32 dolphins per year including about four reproductive females, in conjunction with other sources of man induced mortality, such as the probable death of first born neonates through pollutant toxicity (Cockcroft *et al.*, 1989), implies that mortalities may be close to or exceed the likely replacement rate of this population. However, this conclusion should be viewed with some caution as it is based on an estimated population of only some 900 dolphins, although biases during aerial counts suggest that numbers may be greater (Ross *et al.*, in press). Additionally, other factors may also influence the understanding of the reproductive capacity of this population. If bottlenose dolphins on the Natal coast are geographically separated for long periods (Cockcroft *et al.*, 1989) with little mixing even of adjacent groups (Ross *et al.*, 1987), then reproductive parameters for females in different areas may vary and have a profound affect on calculated replacement potentials.

The incidental mortality and probable depletion of long lived dolphins which invest many years in the care and socialisation of their young and are resident in areas with which they are familiar is of concern. The future management of the Natal bottlenose dolphin population requires accurate population figures and an unbiased estimate of age and sex structure. Regular aerial, boat and shore based surveys along the Natal coast are needed to define the former. The



latter is best obtained through a combination of intensive field observational work on free-ranging dolphins and a continued monitoring of captured animals.

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## CHAPTER FOUR

Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa.

V.G. Cockcroft and G.J.B. Ross,  
Port Elizabeth Museum, P.O. Box 13147,  
Humewood. 6013. Republic of South Africa.



## ABSTRACT

A study of the diet of bottlenose dolphins captured in shark nets along the southern Natal coast, South Africa, was based on stomach contents of 127 dolphins. A total of 5611 prey items, representing at least 72 prey species of teleost fishes, elasmobranchs and cephalopods, were identified from prey remains. Reconstituted prey mass was estimated for each dolphin, using regressions of otolith or beak dimensions on body length and mass for each prey category. The fishes *Pomadasys olivaceum*, *Scomber japonicus*, *Pagellus bellotti*, *Trachurus delagoae*, and the cephalopods *Sepia officinalis* and *Loligo* sp. were the most important prey species, contributing some 60 % by mass of all prey throughout the study period. Some seasonal variation in the proportions of these species was noted. Mean prey length increased with increasing predator length. Stomachs of calves held significantly fewer prey species per stomach than adolescents, adult males and lactating females. Mothers and calves feed close to shore in the nursery grounds of their prey. Differences in the prey spectra of these sex and maturity categories suggest intraspecific partitioning in feeding activity or selection for certain species. Comparisons of stomach volumes with estimates of prey mass and nutritional requirements suggest that calves and lactating females may need to feed more often than other sex and maturity categories. The significance of this difference concerning home range useage and the development of social structure is discussed.

## INTRODUCTION

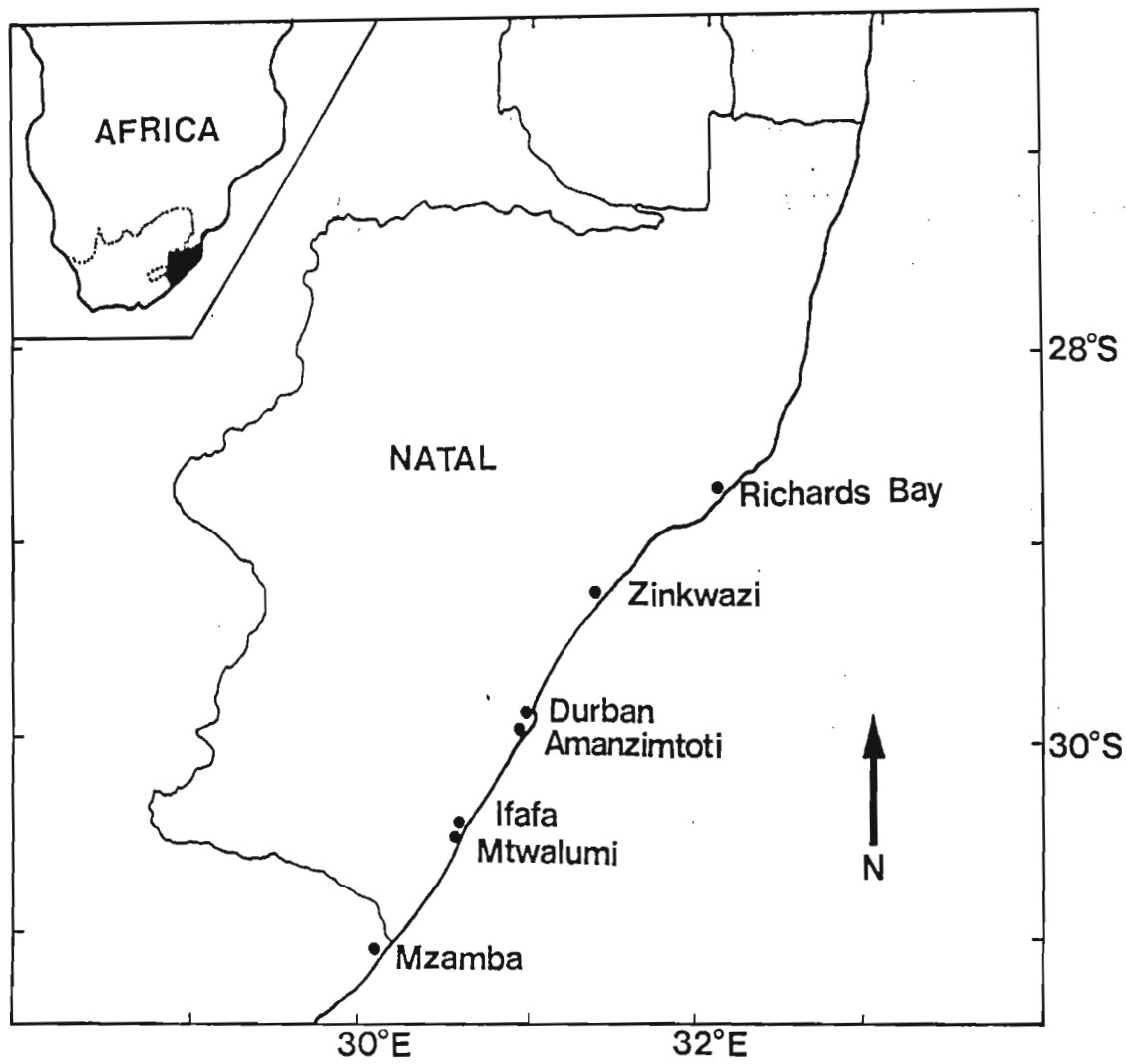
Small cetaceans, living in marine waters, can be divided, crudely, into two broad groups based on their feeding strategies. Pelagic dolphins, by and large, traverse large areas of ocean in search of food, their movements probably related to the availability of food resources (Norris and Dohl, 1980; Wells, Irvine and Scott, 1980). In contrast, some offshore dolphins and particularly most coastal species appear to range far less widely. Although, some of their movements may be related to the movements of their prey, they probably exert considerably more pressure on local food resources than do highly mobile pelagic species (Irvine, Scott, Wells, Kaufmann and Evans, 1979; Irvine, Scott, Wells and Kaufmann, 1981). The authors cited above suggested that this dichotomy in feeding strategies would have a profound effect on our understanding of cetacean ecology, indicating the necessity for comparative studies.

The Indian Ocean bottlenose dolphin (*Tursiops truncatus*) is widely distributed in coastal waters of the Indian Ocean (Ross, 1984). On the east coast of southern Africa it inhabits shallow, inshore water, rarely venturing beyond the 30 m isobath (Ross, Cockcroft and Butterworth, 1986). Off the Natal coast this species, the Indo-Pacific humpbacked dolphin (*Sousa chinensis*) and the common dolphin (*Delphinus delphis*) are killed sporadically in gill nets. These nets are located at 44 prime bathing beaches along this coast and are set to catch and reduce the numbers of sharks potentially dangerous to bathers.

Stomach contents from bottlenose dolphins caught in the shark nets form the basis of this study and provide a quantitative analysis of the diet of this species. Further, the relationship of diet to movements and social structure in this population is valuable in providing a better understanding of the ecology of coastal species, particularly those exploited by man or caught incidentally during coastal fishing.

## STUDY AREA

Figure 1: Natal, on the east coast of southern Africa. Shark net installations are positioned at 44 bathing beaches between Mzamba and the Tugela River. The area north of Durban is known as the North Coast. The area between Durban and Mzamba is equally divided between the Upper and Lower South Coasts.



The Natal coast of southern Africa is oriented north-south between about 27°S and 31°S (Fig. 1). The climate is mild. Monthly air temperatures range between 15°C and 27°C, and sea temperatures, warmed by the Agulhas Current, range between approximately 17°C and 27°C. The southern half of this coast between the Tugela River (29° 13' S) and Mzamba (31° 05' S) is heavily populated and supports an extensive tourist industry. Almost all of this coastline slopes steeply offshore, reaching depths of 30 m within 1 km of the beach. The surf zone is highly energetic, extending 100-200 m offshore.

## MATERIALS AND METHODS

Animals caught in shark nets were frozen as soon as possible after death. After thawing the animals were weighed, measured and dissected. Stomachs were removed whole, after tying and cutting the oesophagus anterior to the forestomach and the intestine posterior to the pylorus. On occasion the oesophagus was cut directly posterior to the larynx. On removal, stomachs were frozen until processing.

Thawed stomachs were weighed whole to the nearest gram and the contents washed into a plastic dish. Loose tissue was removed by agitating the contents of the dish and allowing water and loose tissue to flow gently over the lip. This was repeated until all light, loose tissue was removed. Loose cephalopod beaks and shells were removed and stored in 10 % buffered formalin. Remaining material, such as bones, otoliths and larger pieces of tissue, were sorted by hand. Beaks still encased in the buccal mass were removed and added to the formalin. All otoliths were removed from whole fish and skulls. Otoliths and any bones deemed important were stored dry. Whole fish were identified, measured and weighed where possible. Empty stomachs were then weighed, for calculation of content mass, and discarded.

Where the stomach and entire oesophagus were excised, both were weighed while containing food.

With the oesophagus held upright, both were filled with water until the oesophagus overflowed. On all occasions the aspect of the stomach was kept the same and it was not allowed to become over-distended. The oesophagus was tied off and the stomach, plus contents and water were weighed. After removal of the contents the empty stomach was again weighed. This gave an estimate of the maximum volume of the stomach.

Squid beaks and otoliths were identified using the prey-identification collection established for this purpose at the Port Elizabeth Museum. This collection includes over 15,000 specimens from which regressions for fish and cephalopods relating otolith or beak dimensions, respectively, to prey length and mass have been determined. Nomenclature for fish species follows Smith and Heemstra (1986).

Otoliths were measured to the nearest 0.1 mm across their greatest dimension. Some species with fragile points prone to breakage (e.g. *Scomber japonicus*) were measured across the shoulder. Beak lower rostral length was measured for all cephalopods, except octopods and sepiids, for which beak lower crest length was taken (Clarke, 1986a). The length and mass of prey species represented in each stomach were calculated from the otolith or beak measurements using the appropriate regression. Otoliths that were visibly badly eroded were excluded from these calculations. The calculated weights of all fish and cephalopod remains found in each stomach were summed to give a reconstituted mass of prey for that stomach.

For species for which the collection contained insufficient numbers of specimens to calculate a regression, length and mass were indirectly estimated either from similar species in the same genus or from the few mass or length data in the prey reference collection. In those few species for which no information was available, even from closely related species, the mean mass of all species (either fish or cephalopod) for which regressions were available were used to estimate reconstituted mass.

Table 1. Prey of bottlenose dolphins off Natal, expressed by number, frequency of occurrence and reconstituted mass per stomach, and percentage number, frequency of occurrence and reconstituted weight over the whole sample. Derivation of the index of relative importance (IRI) is given in the text.

Prey Species	Number	Freq. of Occurrence	Total Mass	% Number	% Freq. of Occurrence	% Mass	IRI
<b>ELASMOBRANCHS</b>							
<i>Rhinobatos</i> sp.*	1	1	118	0.0	0.8	0.0	<1
unidentified elasmobranch*	9	7	5490	0.2	5.5	1.3	8
<b>FISH</b>							
<i>Anguilla mossambica</i>	1	1	1660	0.0	0.8	0.4	<1
<i>Conger cinereus</i> *	24	12	24190	0.4	9.4	5.8	59
<i>Conger wilsoni</i>	23	6	1097	0.4	4.7	0.3	3
unidentified congrid sp 1*	94	18	6307	1.7	14.2	1.5	45
<i>Etrumeus whiteheadi</i>	30	4	594	0.5	3.1	0.1	2
<i>Hilsa kaley</i> *	12	1	805	0.2	0.8	0.2	<1
<i>Sardinops ocellatus</i>	80	7	4416	1.4	5.5	1.1	14
<i>Thyssa vitreostriis</i> *	21	5	215	0.4	3.9	0.1	2
unidentified clupeid*	1	1	67	0.0	0.8	0.0	<1
<i>Galeichthys feliceps</i>	4	2	1528	0.1	1.6	0.4	1
<i>Saurida undosquamis</i> *	22	8	1615	0.4	6.3	0.4	5
<i>Synodus indicus</i> *	1	1	67	0.0	0.8	0.0	<1
<i>Trachinocephalus myops</i> *	2	2	134	0.0	1.6	0.0	<1
<i>Merluccius capensis</i>	2	2	134	0.0	1.6	0.0	<1
<i>Petalichthys capensis</i> *	1	1	67	0.0	0.8	0.0	<1
<i>Chellopogon furcatus</i> *	29	9	5014	0.5	7.1	1.2	12
<i>Scorpaenodes variegatus</i> *	1	1	67	0.0	0.8	0.0	<1
<i>Sorsogona prionata</i> *	1	1	67	0.0	0.8	0.0	<1
<i>Cheilodanichthys capensis</i>	10	4	56	0.2	3.1	0.0	1
<i>Cheilodanichthys queketti</i>	1	1	67	0.0	0.8	0.0	<1
<i>Ambassis natalensis</i> *	1	1	67	0.0	0.8	0.0	<1
<i>Kuhlia mugil</i>	6	1	402	0.1	0.8	0.1	<1
<i>Epinaphalus andersoni</i>	1	1	1500	0.0	0.8	0.4	<1
<i>Epinaphalus</i> sp.*	1	1	1500	0.0	0.8	0.4	<1
<i>Prilacanthus</i> sp.*	54	3	11234	1.0	2.4	2.7	9
unidentified apogonid sp 1*	7	3	469	0.1	2.4	0.1	1
<i>Pomatomus saltatrix</i>	60	21	8516	1.1	16.5	2.0	51
<i>Pomadasys commersonni</i>	10	6	7617	0.2	4.7	1.8	9
<i>Pomadasys olivaceum</i>	2330	86	46773	41.5	67.7	11.2	3569
<i>Pomadasys striatus</i>	154	21	3039	2.7	16.5	0.7	57
<i>Lutjanus argentimaculatus</i> *	5	1	336	0.1	0.8	0.1	<1
<i>Dinoperca petersi</i>	2	2	201	0.0	1.6	0.0	<1
<i>Chelmerius nufar</i>	4	1	400	0.1	0.8	0.1	<1
<i>Chrysoblephus puniceus</i>	5	2	924	0.1	1.6	0.2	<1
<i>Crenidens crenidens</i> *	2	1	134	0.0	0.8	0.0	<1
<i>Diplodus cervinus</i>	1	1	991	0.0	0.8	0.2	<1
<i>Diplodus sargus</i>	135	26	11444	2.4	20.5	2.7	105
<i>Lithognathus mormyrus</i>	1	1	67	0.0	0.8	0.0	<1
<i>Pagellus bellotti</i>	493	44	10274	8.8	34.6	2.5	389
<i>Rhabdosargus sarba</i> *	13	2	1216	0.2	1.6	0.3	1
<i>Rhabdosargus thorpei</i>	32	14	1618	0.6	11.0	0.4	11
<i>Sarpa salpa</i>	105	21	10606	1.9	16.5	2.5	73
<i>Monodactylus falciformis</i>	17	6	745	0.3	4.7	0.2	2
<i>Argyrosomus hololepidotus</i>	4	4	268	0.1	3.1	0.1	<1
<i>Upeneus vittatus</i> *	18	1	583	0.3	0.8	0.1	<1
<i>Argyrosomus thorpei</i>	45	4	2661	0.8	3.1	0.6	5
<i>Otolithes ruber</i>	8	3	2032	0.1	2.4	0.5	1
<i>Umbrina canariensis</i>	28	17	771	0.5	13.4	0.2	9
<i>Gazza minuta</i> *	1	1	67	0.0	0.8	0.0	<1
<i>Secutor insidiator</i>	2	1	151	0.0	0.8	0.0	<1
<i>Trachurus delagoae</i>	322	34	20555	5.7	26.8	4.9	285
<i>Caranx williamsi</i>	1	1	67	0.0	0.8	0.0	<1
<i>Liza dumerilii</i>	12	6	2005	0.2	4.7	0.5	3
<i>Liza macrolepis</i> *	7	2	1134	0.1	1.6	0.3	1
<i>Liza tricuspidens</i>	1	1	162	0.0	0.8	0.0	<1
<i>Mugil cephalus</i>	49	6	10977	0.9	4.7	2.6	17
unidentified mugilid*	6	5	972	0.1	3.9	0.2	1
<i>Sphyræna acutipinnis</i>	33	17	980	0.6	13.4	0.2	11
<i>Parapercis</i> sp.	3	2	201	0.1	1.6	0.0	<1
unidentified gobiid*	1	1	1	0.0	0.8	0.0	<1
<i>Trichlurus lepturus</i>	83	6	3016	1.5	4.7	0.7	10
<i>Scomber japonicus</i>	184	66	21648	3.3	52.0	5.2	439
unidentified bothid*	52	5	3487	0.9	3.9	0.8	7
<i>Cynoglossus zanzibarensis</i>	3	3	201	0.1	2.4	0.0	<1
unidentified cynoglossid*	2	2	134	0.0	1.6	0.0	<1
unidentified fish	228	52	15299	4.1	40.9	3.7	316
<b>CEPHALOPODS</b>							
<i>Sepia officinalis</i>	415	66	136837	7.4	52.0	32.7	2082
<i>Loligo</i> sp.	241	43	14573	4.3	33.9	3.5	263
<i>Octopus</i> sp 1	38	13	4184	0.7	10.2	1.0	17
<i>Octopus</i> sp 2*	10	4	1101	0.2	3.1	0.3	1
unidentified ommastrephid*	4	1	895	0.1	0.8	0.2	<1
Totals	5610		418810				

An Index of Relative Importance (IRI) for each prey species was calculated according to Pinkas *et al.* (1971), where:

$$\text{IRI} = (\% \text{ number} + \% \text{ reconstituted mass}) \times \% \text{ frequency of occurrence.}$$

Eight stomachs collected in 1986 were processed using the Modified Volume technique (Bigg and Perez, 1985) of assessing the importance of prey remains in stomachs, for comparison with estimates made using the reconstituted mass method.

## RESULTS

The contents of 165 stomachs, representing bottlenose dolphins caught between 1975 and 1986 were examined during this study. Unfortunately, date and locality of capture, length, mass and sex information were not available for all animals caught. Thirty four of the stomachs examined were from suckling calves, between 129 cm and 170 cm in length, and contained only a milky substance or this substance in addition to a few crustaceans, squid and/or fish. Stomachs containing only the milky substance were excluded from calculations. Four of the remaining 131 stomachs were completely empty.

More than 72 species of prey representing 5610 prey items were found in the stomachs containing solid remains (Table 1). Of the fish prey categories, 56 were identifiable to species level. A further four and six were identifiable only to genus and family, respectively. All unidentified fish were pooled into a single category. Five cephalopod categories were identified, including three decapods and two octopods. Almost all decapod beaks were from the cuttlefish *Sepia officinalis* and an inshore squid *Loligo reynaudi*. However, the latter may have included a few specimens of a similar, smaller species *Loligo dauvercelli*. Of a number of elasmobranchs found, only one was identified to genus. In addition to the above, three near-intact penaeid prawns, and a few euphausiid exoskeletons were found in three stomachs. These have been ignored in all



Table 2: Index of Relative Importance (IRI) of the six major prey of bottlenose dolphins off Natal. Data were based only on stomachs where information was available.

	1982	1983	1984	1985
<i>Trachurus delagoae</i>	98	361	8	1873
<i>Pomadasys olivaceum</i>	3995	1515	4383	4270
<i>Pagellus bellotti</i>	51	830	140	637
<i>Scomber japonicus</i>	121	547	87	319
<i>Sepia officinalis</i>	1115	2467	1927	924
<i>Loligo</i> sp.	267	740	147	54
No. of stomachs	18	22	23	23

Table 3: Index of Relative Importance (IRI) of the six major prey items of bottlenose dolphins in quarterly periods during the year. Data were based only on stomachs where information was available.

	Jan-Mar	Apr-June	July-Sept	Oct-Dec
<i>Trachurus delagoae</i>	243	149	107	883
<i>Pomadasys olivaceum</i>	3538	8629	2718	2528
<i>Pagellus bellotti</i>	1114	335	65	1181
<i>Scomber japonicus</i>	49	227	85	249
<i>Sepia officinalis</i>	2213	1720	3147	184
<i>Loligo</i> sp.	197	456	250	2076
No. of stomachs	17	12	50	15

Table 4: Index of Relative Importance (IRI) of the six major prey items of bottlenose dolphins in three regions of Natal. Data were based only on stomachs where information was available.

	North Coast	Upper South Coast	Lower South Coast
<i>Trachurus delagoae</i>	590	42	44
<i>Pomadasys olivaceum</i>	1198	2471	6092
<i>Pagellus bellotti</i>	1428	185	63
<i>Scomber japonicus</i>	592	109	<1
<i>Sepia officinalis</i>	653	1741	2017
<i>Loligo</i> sp.	317	826	81
No. of stomachs	33	28	43

calculations because of their scarcity.

Six prey species had IRIs considerably higher than the others (Table 1). These six species contributed approximately 60 % by mass of all prey taken. The estimated IRI of unidentified fish was also relatively high (316) and their estimated mass contribution was 3.7%. This group is made up of a number of unidentified species which individually would probably not be important.

Between 1982 and 1985, the four years for which sufficient data were available, the proportions of the six species were similar by number, frequency of occurrence and mass but variations in their IRI's were evident (Table 2). The greatest species variety was in 1982 (40) with 29, 35 and 28 taken in 1983, 1984 and 1985, respectively. The number of unidentified fish species was similar in all years (10 -15).

Some seasonal patterns were evident when all data were stratified into quarters (Table 3), though inferences are limited due the small numbers. Between October and December the IRI of both *Loligo* sp. and *T.delagoae* increased while that of *S.officinalis* decreased. An increased IRI of *P.olivaceum* between April and June was not concurrent with a decreased IRI in any other species.

The same six prey were dominant throughout the study area, although, some variations between the north coast, upper south coast and lower south coast were evident (Table 4). On the lower south coast only *P.olivaceum* and *S.officinalis* appeared of prime importance (Table 4). Conversely, the north coast showed a greater parity of IRI values, while on the upper south coast the IRI values of these prey were intermediate between those of the north and lower south coasts, except for an apparent greater importance of *Loligo* sp.

Both area and season were poorly correlated with the mean length of prey in stomachs, the variety of prey consumed and the number of prey items in stomachs (all r values <0.31). A poor

Figure 2. The relationship between the length of bottlenose dolphins and the mean length of their prey.

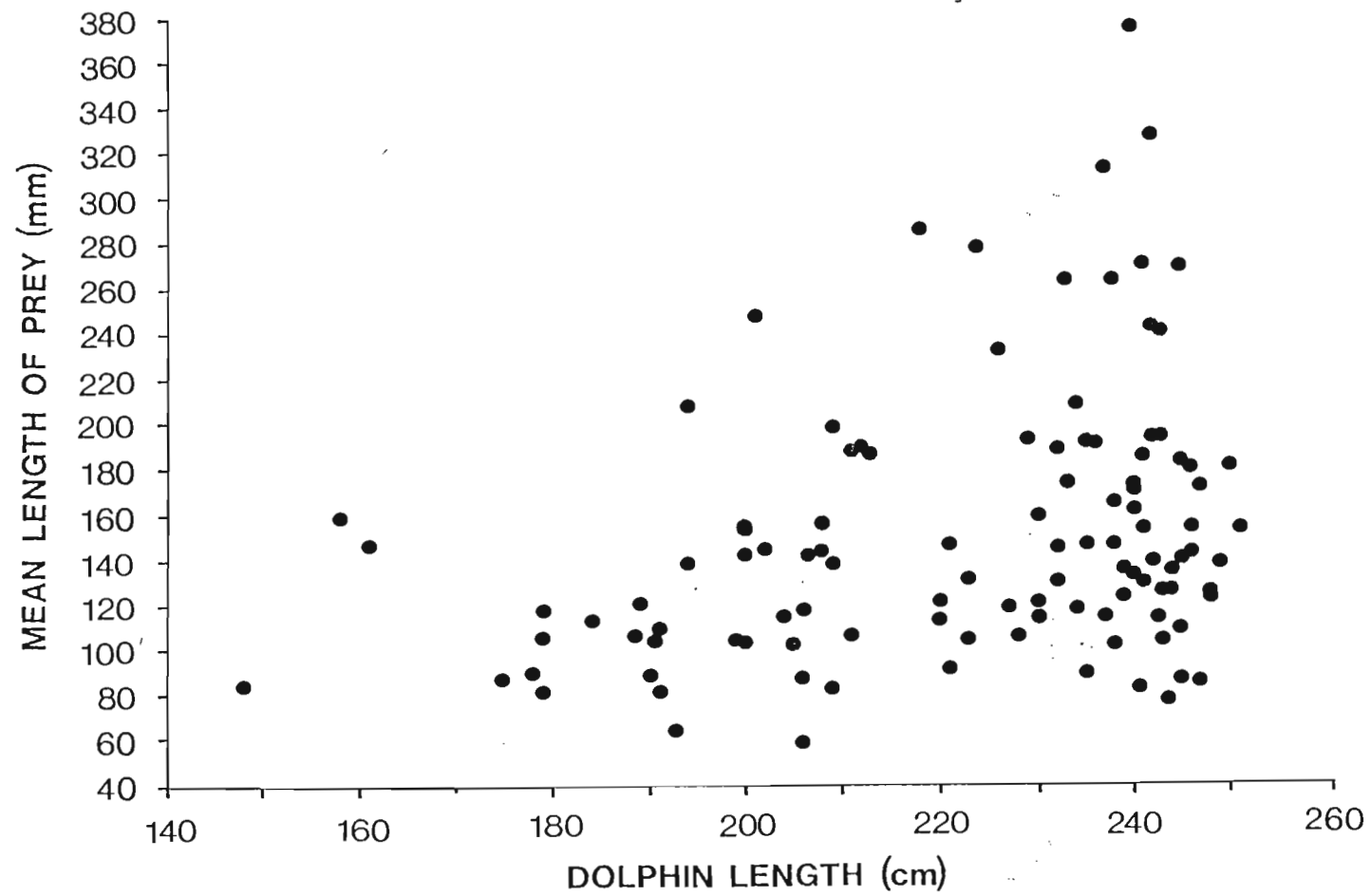


Table 5: The index of relative importance (IRI) rank of importance and mean length of the eight major prey items from each of five maturity size classes (calves < 200 cm in length, adolescents > 200 cm but < 230 cm in length, lactating females, resting females and mature males) of bottlenose dolphins.

Species	Calves			Adolescents			Lactating Females			Resting Females			Mature Males		
	IRI	(rank)	$\bar{X}$ Length	IRI	(rank)	$\bar{X}$ Length	IRI	(rank)	$\bar{X}$ Length	IRI	(rank)	$\bar{X}$ Length	IRI	(rank)	$\bar{X}$ Length
<i>Pomadasys olivaceum</i>	7109	(1)	85	3990	(2)	106	2428	(2)	107	3885	(1)	103	3630	(2)	113
<i>Sepla officinalis</i> *	196	(3)	79	9769	(1)	129	3155	(1)	141	2371	(2)	136	5957	(1)	142
<i>Pagellus bellotti</i>	467	(2)	109	509	(3)	120							393	(4)	109
<i>Sarpa salpa</i>	181	(4)	162	135	(8)	158				91	(7)	165			
<i>Conger cinereus</i>	142	(5)	+				570	(3)	+	196	(5)	+			
<i>Sardinops ocellatus</i>	120	(6)	207				110	(8)	175						
<i>Loligo</i> sp.*	108	(7)	109	155	(7)	123	498	(4)	128				319	(5)	125
<i>Diplodus sargus</i>	104	(8)	108				176	(7)	162	1417	(3)	172			
<i>Pomadasys striatus</i>							194	(5)	195						
<i>Trachurus delagoae</i>				232	(5)	163	187	(6)	141	546	(4)	154	442	(3)	171
<i>Mugil cephalus</i>				272	(4)	306									
<i>Scomber japonicus</i>				174	(6)	215							234	(6)	259
<i>Prilacanthus</i> sp.													90	(7)	208
<i>Octopus</i> sp.1*													68	(8)	66
<i>Sphyræna acutipinnis</i>										107	(6)	198			
<i>Monodactylus falciformis</i>										87	(8)		+		
Total % Mass	70.4			76.3			67.3			70.5			70.3		
Total No. of species recorded	15			39			47			24			48		
No. of Stomachs	16			32			18			7			32		

\* Mantle Length.

+ Estimated, no regressions available.

Figure 3: The relationship between bottlenose dolphin mass and the estimated maximum volume of the stomach. A power curve ( $\text{Log } Y = a + b \text{ Log } X$ ,  $a = 0.2143$ ,  $b = 1.596$ ) is fitted to these data ( $r^2 = 0.723$ ).



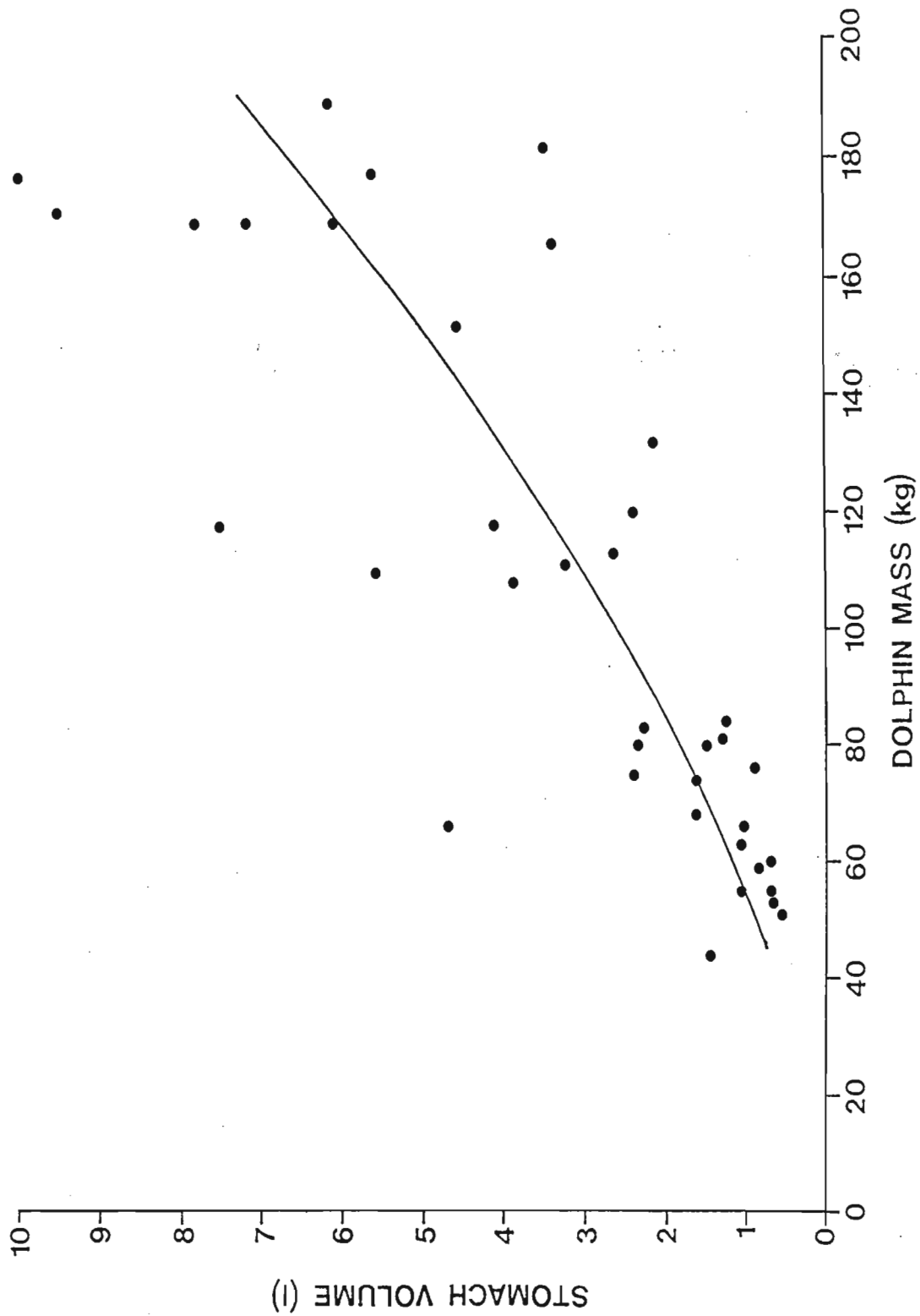
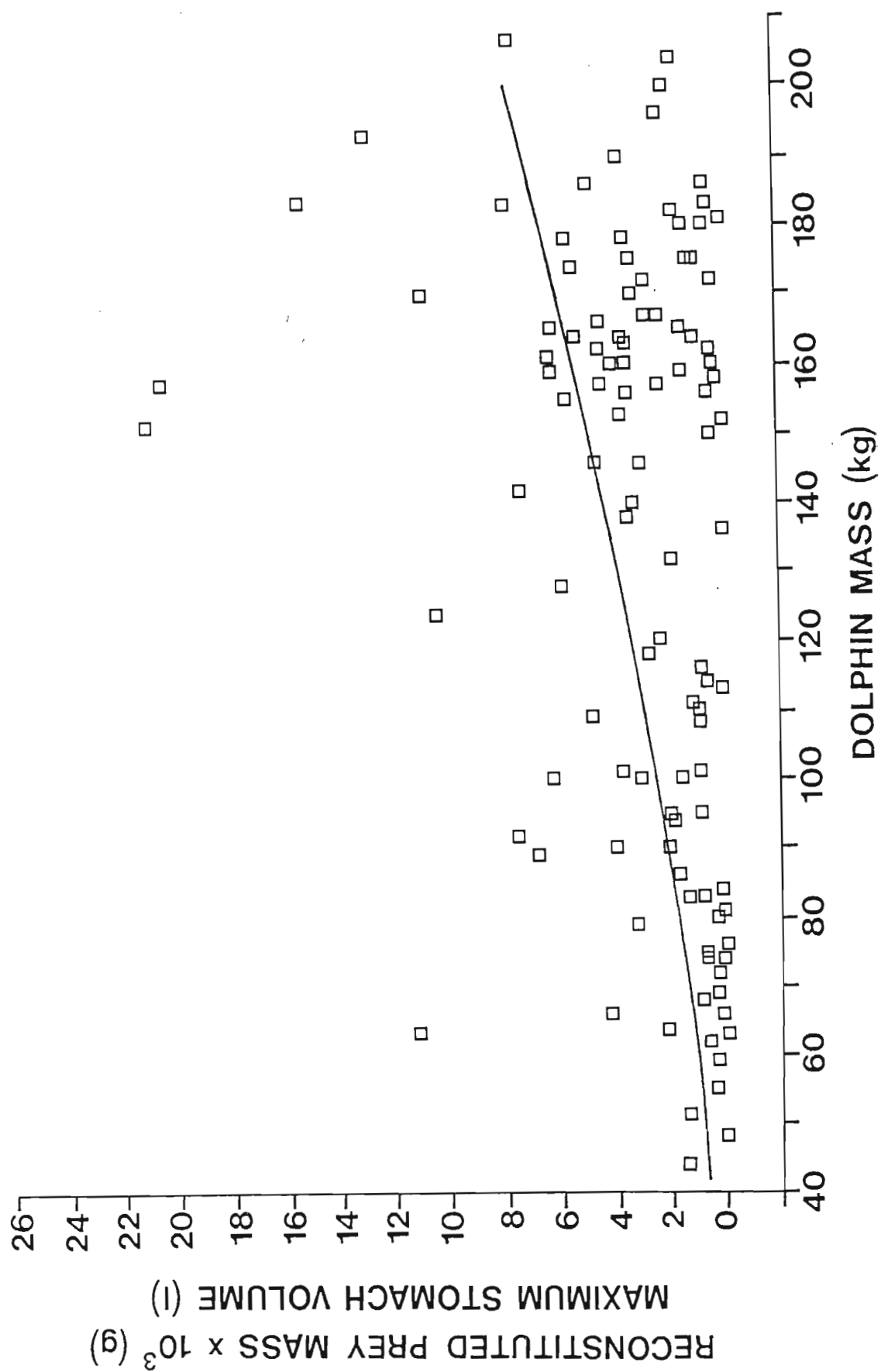


Figure 4: The relationship between bottlenose dolphin mass and the reconstituted mass of the stomach contents. The power curve from Figure 3 is superimposed on these data.



correlation ( $r < 0.3$ ) was found between dolphin length and mean length of prey consumed.

However, the maximum length of prey consumed increased with dolphin length (Fig. 2). Comparison of the mean prey length for each of five length, sex and maturity classes showed a significant increase with predator size (Table 5). The mean length of prey found in calves was significantly less than those in all other groups ( $P < 0.01$ , Student's 't' test). The mean prey length of adolescents was significantly less than that found in all adult groups ( $P < 0.01$ , Student's 't' test). There were no significant differences between the mean prey lengths taken by any of the adults.

A plot of dolphin mass against maximum stomach volume is presented in Figure 3. A power curve of the form:

$$\log Y = 0.2143 + 1.596 \log X \quad (r^2 = 0.72)$$

was fitted to these data.

Stomach content weights ranged from practically zero to a maximum of almost five kilograms. A poor correlation ( $r = 0.37$ ) was found between dolphin mass and stomach content mass, suggesting that dolphins were caught in all stages of repletion. Additionally, a low correlation was found between dolphin mass and the reconstituted mass of items contained in the stomach ( $r = 0.26$ ) (Fig. 4). This suggests that many dolphins either voided the stomach of otoliths and/or beaks prior to capture or, in some instances, these remains may have been retained from an earlier feed. The former would tend to underestimate the meal size and the latter to overestimate it.

Approximately 75 % of the reconstituted mass estimates lie below the plot of the relationship between maximum stomach volume and dolphin mass (Fig. 4), assuming that prey volume and prey mass are equivalent. This suggests that 25 % of stomachs may have contained otoliths and/or beaks from a previous meal. Four of the seven stomachs showing the highest reconstituted mass

Figure 5: The relationship between bottlenose dolphin length and the number of prey items contained in the stomach.

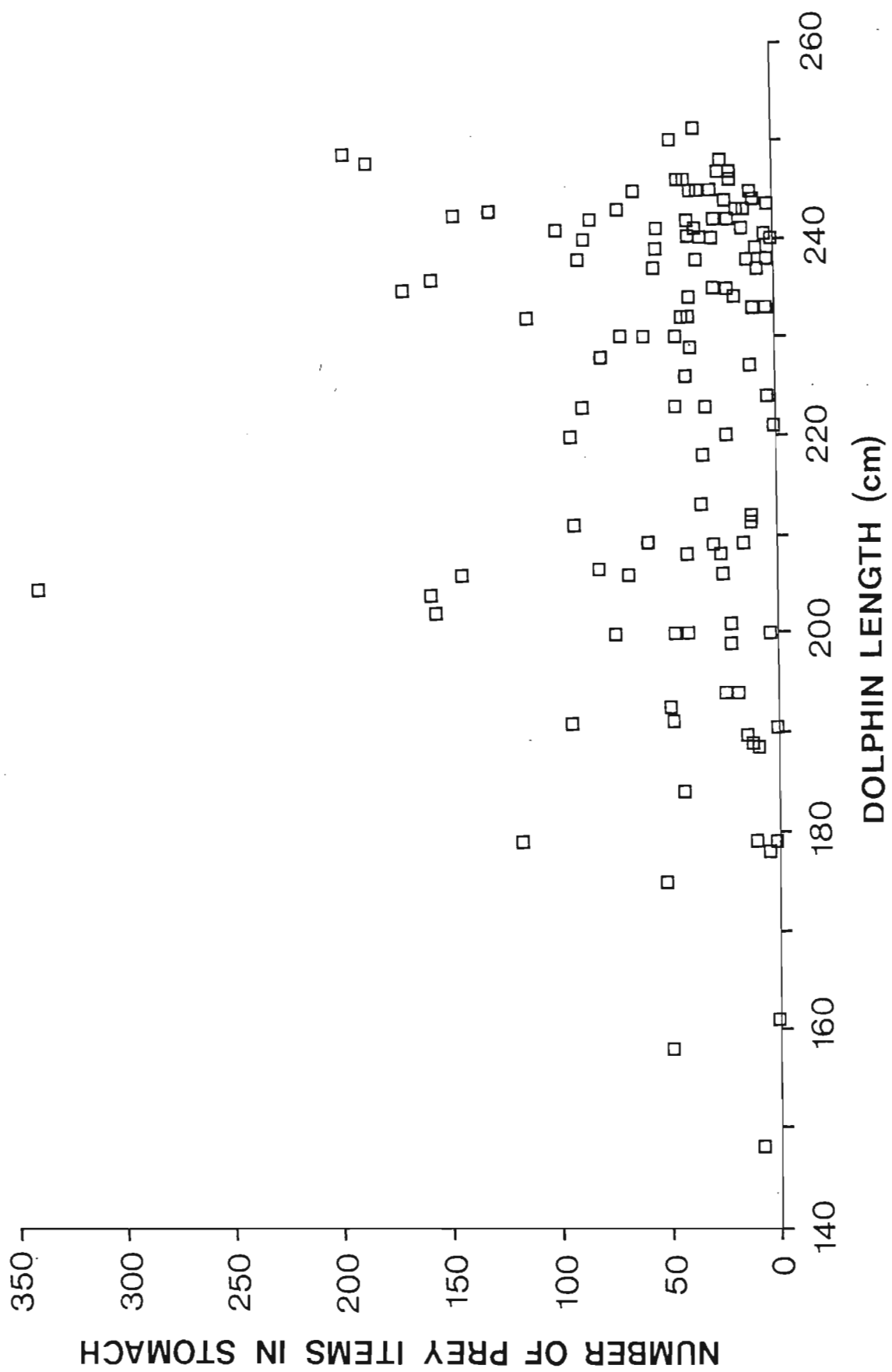
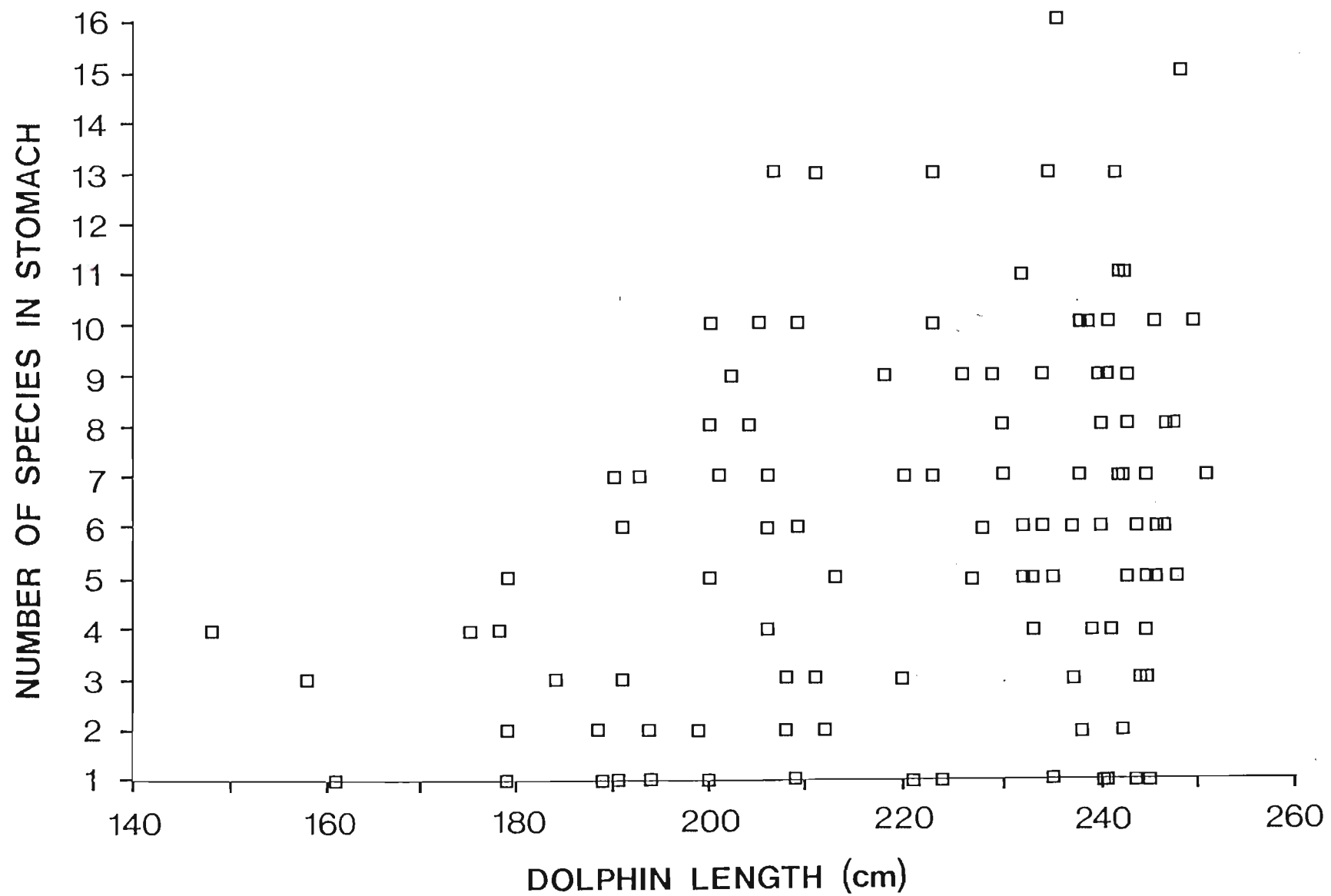


Figure 6: The relationship between bottlenose dolphin length and the number of prey species consumed.





estimates contained large numbers of *S.officinalis* beaks. The indigestibility of cephalopod beaks and their subsequent retention is well documented (Clarke, 1986b). A further two stomachs contained otoliths of the eel *Conger cinereus* and a third contained a pair of otoliths of a species of *Epinephalus*. The mass estimates of both *C.cinereus* and *Epinephalus* sp. were made from smaller species of the same genus and may well be overestimates.

The mean number of prey items per stomach deduced from the number of otoliths and/or beaks remaining in the stomach, was 48.5 (range 1-340). There was little correlation between the number of prey items found in stomachs and the length of dolphin ( $r = <0.1$ ) (Fig. 5). However, the maximum number of prey items consumed increased with dolphin length and stomach volume. In general, the number of species present in any stomach was low (mean 6, range 1-15) but tended to increase with dolphin length (Fig. 6), although, there was little correlation ( $r=0.03$ ) between the two.

However, calves (mean=2.9) contained significantly fewer prey species than adolescents (mean=6), mature males (mean=6.5) and lactating females (mean=8.4) (Kruskal-Wallis test  $H=22.325$ ,  $P<0.01$  and Dunn's Multiple Contrast method, Zar, 1984). Numbers of prey species in non-lactating females (mean 5.5) did not differ from those in any other group. Supporting evidence that mothers' stomachs contained more species than their respective calves is shown by the proportions of species in four known mother and calf pairs (15:1, 6:1, 9:3 and 4:1). In all four cases all species in the calf's stomach were also present in the mother's stomach. No differences in mean prey length and numbers of prey taken were found between calves caught with or without their mothers or between mothers caught with or without calves.

In each of the five length, sex and maturity classes of bottlenose dolphins, eight prey species contributed approximately 70% by mass of all prey consumed (Table 5). *P.olivaceum* and *S.officinalis* were important to all classes, although their individual importance to each class varied. The importance of the remaining prey species varied between classes.

The sizes of *P.olivaceum*, *S.officinalis*, *Loligo* sp. and *D.sargus* taken by adolescents were significantly smaller ( $P < 0.01$ , Student's 't' test) than those taken by any other class. No significant differences were found between the mean sizes of individual prey species taken by adolescents and adults. However, there was a significant difference between the mean length of all prey taken by adolescents and that of the adults ( $P < 0.01$ , Student's 't' test).

No significant differences were found between the seasonal or overall geographic distribution of bottlenose dolphin size/maturity classes throughout the year. This suggests that the dietary differences observed are not due to sample variation.

The overall contribution of fish and squid to the diet of bottlenose dolphins were calculated as 69.9 % and 30.1 %, respectively, using the technique of Bigg and Perez (1985). In comparison, calculation of fish and squid contributions in this study yielded figures of 74.8 % and 25.2 %, respectively.

## DISCUSSION

The number of stomachs used to assess the similarity of methods used in this study and that of Bigg and Perez (1985) was small. Despite this, there was a close agreement between the results of the two methods, suggesting that the approach used in the present study was valid.

The four fish and two cephalopod species which constitute the major portion of prey of bottlenose dolphins off Natal, are all common inshore. Of the four fish species, two can be considered as benthic. *P.olivaceum* inhabits inshore reef areas and *P.bellotti* prefers inshore sandy bottom areas (van der Elst, 1981). The two remaining fish species, *T.delagoae* and *S.japonicus*, are both pelagic shoaling fish occurring in inshore waters in this area, particularly as juveniles (van der Elst, 1981). The two cephalopods *Loligo* sp. and *S.officinalis*

are also common in the Natal inshore environment and are regularly seen around the shark nets (Natal Sharks Board personnel, pers. comm.). Of the 16 most important prey species (Table 5), all but *Priacanthus* sp. are known to be common inshore (van der Elst, 1981; Smith and Heemstra, 1986). *Priacanthus* inhabit deeper coastal waters (>50 m depth) (Smith and Heemstra, 1986) and were found in stomachs of mature males only. *Sardinops ocellatus* is a pelagic shoaling species occurring in Natal inshore regions only from July through September. *Conger cinereus* and *Sphyræna acutipinnis* are both predators of inshore reef fish and occur either singly or in small groups close inshore while *Mugil cephalus* and *P. bellotti* occur predominantly above sandy bottoms (van der Elst, 1981).

This information suggests that bottlenose dolphins off Natal use a variety of food resources. These include benthic reef and sandy-bottom prey and their associated predators, pelagic shoaling fish and cephalopods, and deeper water fish. The variety of prey consumed by bottlenose dolphins off Natal is one of the most extensive yet reported for any cetacean, superficially supporting the usual interpretation that these dolphins are opportunistic feeders. Such conclusions have been drawn about other bottlenose dolphin populations. Gunter (1942) reported that the diet of bottlenose dolphins off the coast of Texas was catholic but dominated by mullet (*M. cephalus*), one of the four most abundant benthic fish in the area. In British waters these animals often feed on inshore herring and salmon shoals but were still considered as benthic feeders (Evans, 1980). Tomilin (1957) described bottlenose dolphins from the Black Sea as benthic feeders, only feeding on pelagic schooling fish when they formed dense aggregations. Walker (1981) noted that the prey of inshore bottlenose dolphins off southern California inhabited littoral and sublittoral zones.

Considering that only six species accounted for 60 % by mass of the diet of bottlenose dolphins off Natal, it seems inappropriate to consider this species an opportunistic predator. Though there is some indication of annual, seasonal and geographical variation in the proportions of the six major prey species, their continued importance throughout this study, for all age and

sex classes, is particularly significant. The causes of these variations are uncertain, though they may reflect changes in the relative availability of each species.

The daily food requirement (as a percentage of body mass) of a captive, weaned bottlenose dolphin calf has been estimated at between 5 % and 6.7 %; the requirements for a lactating female and two non-lactating females were 8.3 %, and 3.9 % and 5 % respectively (Ross, 1984; Cockcroft and Ross, 1989). The daily requirement of mature males is probably similar to that of non-lactating females and comparable to the 4.2 % given for captive animals by Sergeant (1969).

If maximum stomach volume is equated to the amount of food in a full stomach a number of assumptions can be made (Figs. 3 and 4). Mature males and mature quiescent (neither pregnant nor lactating) females would obtain their daily food requirements from about two stomachs full.

However, a lactating female of 130 kg must consume the equivalent of between three and four stomachs full per day. Similarly, a weaned calf of about 75 kg must fill its stomach four or five times per day. These assumptions are based on biomass estimates and make no allowance for the nutritional value of the different prey species consumed by size/sex classes. Although the use of energy values is preferable in comparisons (Innes *et al.*, 1987), the energy values for most of the prey species are not available. Where available, the energy values of prey species are similar (Ross and Cockcroft, 1989) and although there are apparent differences in the diet of size/sex classes, they share many common species, particularly *P.olivaceum* and *S.officinalis*. This suggests that the use of energy values rather than biomass would not greatly alter the above pattern.

Saayman *et al.* (1973) observed two feeding peaks in free-ranging bottlenose dolphins, early morning and late evening, which is in keeping with the projected needs of adult males, quiescent females and adolescents. In contrast, the present results suggest that calves and lactating females have to feed more often, perhaps almost continuously. The low numbers of mothers and calves would make such activities inconspicuous within the overall activity of mixed schools.

The energetic cost of lactation is an obvious and important component of the lactating female's increased nutritional requirements, particularly during the calf's early suckling. A second component is maternal care, which increases in importance during the weaning and post-weaning periods (Cockcroft and Ross, 1989). These increased costs may be reflected in the trend towards greater numbers of prey species observed in stomachs of lactating females. Time spent in maternal care may restrict the mother's foraging time and make it beneficial for her to cooperate with other female and calf pairs (subgroups) and to take any prey presenting itself. In contrast, the prey species diversity in the stomachs of calves is low. Calves clearly feed with their mothers. In each of the four known mother and calf pairs the prey species consumed by the calf were also present in the mother. This implies that mothers assist the calves in foraging, possibly by herding prey and that therefore the energetic cost of maternal care may be substantial.

The evidence that each class of dolphins prefers different prey sizes and, to some degree, different species (Table 5) suggests that subgroups within schools are likely to employ different feeding strategies. The partitioning of bottlenose dolphin populations into distinct size or sex subgroups and the postulated importance of these subgroups has been well documented in recent literature (Mead, 1975; Irvine and Wells, 1972; Irvine *et al.*, 1981; Wells *et al.*, 1980) and has been reviewed for cetaceans in general by Norris and Dohl (1980). Nursery groups of mothers and calves have been reported by Leatherwood (1977), Wursig (1978), Irvine *et al.* (1981) and Wells *et al.* (1980).

The implication that mothers and calves may need to feed more than other dolphins is of interest in view of the findings of Wells *et al.*, (1980) who reported that this subgroup has the most extensive range of any within the school. The present study also indicates that calves used both reef and sand dwelling prey, perhaps maximising their usage of the inshore area. Taken together these results suggest that foraging by nursery groups is an important determinant of the extent of their movements and may be a major factor in the delimitation of apparent home range.

Shallow inshore reefs constitute the nursery areas for several fish species off Natal, including *P. olivaceum* (Joubert, 1981) which predominate in the diet of calves. Juveniles of this species are present inshore for at least nine months of the year, indicating that calves are assured of a consistent food source by feeding in shallow water throughout the year. The seasonally occurring *S. ocellatus* was the only pelagic fish found in the stomachs of calves. In contrast, the stomachs of other age/sex classes contained other pelagic shoaling fish. The reasons for this difference are unclear. Calves may be too inexperienced to participate in cooperative feeding on pelagic fish, except in shallow water where *S. ocellatus* is at times packed tightly close to the surf zone by sea conditions and other predators. Though there was no significant difference between the mean lengths of their prey, adult male bottlenose dolphins consumed a greater proportion of larger fish than did adult females (Table 5). Additionally, males took species either not consumed at all (eg. *Priacanthus* sp.) or consumed only in low numbers by other dolphins. Exclusively male subgroups within schools (Irvine *et al.*, 1981; Wells *et al.*, 1980) may facilitate this. The diet of females not under the stress of lactation or pregnancy differed from that of adult males only in the spectrum of species taken, suggesting that female subgroups may exist, though these have not been identified elsewhere.

Bottlenose dolphin schools off the Natal coast have been observed more frequently along particular regions, termed preferred areas (Ross, Cockcroft, Cliff and Richards, in press). There is some evidence that dolphins reside in these areas for relatively long periods. Consequently, they probably exert continuous pressure on available food resources in these areas. Under these circumstances inshore dolphins may have adapted socially and behaviorally to alleviate intraspecific competition for food. These behavioral adaptations may include partitioning of the school into subgroups and the use of different foraging ranges or different prey sizes and species by these subgroups. The present results support the conclusions of Irvine *et al.* (1979), who suggested that relatively mobile, wide-ranging pelagic dolphins may not exert the same pressure on their food resources, and that management and conservation

strategies for each species need to be defined separately, particularly for those which are part of the more complex coastal ecosystems.

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## CHAPTER FIVE

Bottlenose dolphins in the Natal shark nets, 1980 to 1987:

Catch rates and associated contributing factors.

V.G. Cockcroft and G.J.B. Ross

Port Elizabeth Museum, P.O. Box 13147, Humewood. 6013.

Republic of South Africa.

## ABSTRACT

A minimum of 212 bottlenose dolphins, *Tursiops truncatus*, were caught in anti-shark nets off Natal, South Africa between January 1980 and December 1987. Catches from January 1982 onwards showed significant interannual and seasonal variations in numbers and mass/sex composition. Males and females constituted 44 % and 56 % of the catch, respectively. Sexually mature males and females constituted 16.7 % and 23 % of the total catch, respectively. Of the latter 63 % were lactating and a further 12 % were pregnant. Adolescents 90 kg - 130 kg in mass and eight GLGs or less in the dentine contributed 14.8 % of the catch. The majority of the catch, almost 45 %, consisted of calves of less than 90 kg mass and less than two GLGs in the dentine. Of these 69.5 % were either weaned or weaning at capture. Analysis of the biological, environmental and physiographic data for each capture suggests a number of reasons for the catch of bottlenose dolphins. The longshore distribution of catches was random but catch rates were proportional to the number of nets. The stomachs of most dolphins were more than 69 % full at the time of capture suggesting that enmeshing occurred either during or subsequent to feeding. Most captures were of single animals but lactating females with calves constituted more than 20 % of catches. The direction of the prevailing current was significantly related to captures. These data are examined in relation to existing knowledge of bottlenose dolphins in this area and possible methods of reducing captures are proposed.

## INTRODUCTION

The incidental death of marine mammals in fishing gear is a recurring problem wherever marine mammals and fisheries interact. These interactions are diverse (Beddington, Beverton & Lavigne, 1985; Gulland, 1986) and involve a variety of marine mammals including large whales (Whitehead & Carscadden, 1985), sea lions and fur seals (Shaughnessy & Payne, 1979; Fowler, 1982; Loughlin & Nelson, 1986), freshwater dolphins in both South America and Asia (Pei-Xun, 1981; Best & da Silva, 1984; Northridge & Pilleri, 1986) and inshore and oceanic small cetaceans (Perrin, 1970; Bannister, 1977; Best & Ross, 1977).

The mortality of marine mammals associated with fishing operations is recognised as a major threat to many of their populations (Beverton, 1985; Northridge & Pilleri, 1986). Currently, fishing activities have become so wide spread and in many areas so intensive, that they probably account for the major portion of small cetaceans killed (Meith, 1984). Mitchell (1975) reviewed fisheries for and incidental catches of small cetaceans in a species by species account. More recently, the interactions of small cetaceans with fishing enterprises has been reviewed by Northridge & Pilleri (1986) and Meith (1984).

On the east coast of southern Africa, numbers of small cetaceans are caught incidentally in non-commercial gill nets set off those Natal beaches frequented by tourists. These nets are set to catch and reduce the population of sharks, reducing the probability of contact between bathers and sharks. Although nets were first installed off Durban in 1952 and subsequently at other localities, most were maintained and serviced by private tenders until the mid 1970's. Little regulation of these contractors made the assessment of numbers and identity of cetacean catches difficult. Since early in the 1980's the entire shark netting operation has been administered by a parastatal body, the Natal Sharks Board, which maintains these nets using trained staff. Cooperation with these staff and an increased effort in collecting meshed cetaceans has enabled a better assessment of catch rates since this time, particularly since January 1982 when

collection procedures were defined.

Incidental catches of cetaceans in the shark nets include three species of dolphin, the common dolphin (*Delphinus delphis*), the humpback dolphin (*Sousa plumbea*) and the bottlenose dolphin (*Tursiops truncatus*) (Best & Ross, 1977). Recent concern at the level of the catches of bottlenose and humpback dolphins has prompted assessments of the population numbers of these two species in Natal (Ross, 1982; Ross *et al.*, 1987b). The results of the latter work suggest that the continuing mortality of bottlenose dolphins in the nets may lead to a decline in their numbers in the Natal region. This, and the apparent similar plight of the humpback dolphin in Natal, lead to the initiation of an experimental programme to test the effect of various net attached deterrents on captures of these two species (Peddemors, Cockcroft & Wilson, in press).

## STUDY AREA, MATERIALS AND METHODS

Nets are installed at 44 beaches along the southern half of the Natal coast, between Richards Bay and Mzamba (Peddemors *et al.*, this volume). In all, some 416 nets are set along this coastline. At most installations nets are approximately 110 m long by 10 m in depth. The number of nets positioned at each beach is dependent on beach use by bathers and ranges between two and 63. Nets are set in a constant fixed position, in a staggered fashion, 400 - 500 m offshore and approximately 100 m seaward of the surf. Weather permitting, the nets are examined daily and any catch, shark or dolphin, is removed and taken to shore where it is frozen to await processing. The beach, net number and date of all catches are recorded.

Routine necropsies were performed on all dolphins retrieved from the nets between January 1980 and December 1987. Biological and morphological parameters (*sensu* Ross, 1984) including length, mass, sex and reproductive state were recorded. Age was determined from the number of growth layer groups (GLGs; *sensu* Perrin & Myrick, 1980) counted in thin sections of the dentine of teeth. For data interpretation dolphins were divided into the following mass classes; juveniles



Table 1: Variables included in the matrix of biological, environmental and physiographic parameters examined to determine factors contributing to the catch of bottlenose dolphins off Natal.

- 1 Locality of capture
- 2 Year of capture
- 3 Month of capture
- 4 Day of capture
- 5 Sex (male or female)
- 6 Sex/mass class (1 = <90 kg, 2 = males >90 kg < 130 kg, 3 = females >90 kg < 130 kg, 4 = quiescent females > 130 kg, 5 = lactating females, 6 = pregnant females, 7 = mature males > 130 kg)
- 7 Mass (kg)
- 8 Length (cm)
- 9 Age (GLGs)
- 10 Net in which caught (locality specific)
- 11 Number of animals caught simultaneously
- 12 Percentage fullness of stomach
- 13 State of the tide (two days either side of spring tide = 1, two days either side of neap tide = 2, mid tide = 3)
- 14 Water visibility on day of capture (m)
- 15 Water visibility on day after of capture (m)
- 16 Difference between 14 and 15
- 17 Temperature on the day of capture (°C)
- 18 Temperature on the day after of capture (°C)
- 19 Difference between 17 and 18
- 20 Current direction (northerly = 1, southerly = 2, offshore = 3)
- 21 Swell Height (m)
- 22 Channel at the net (yes = 1, no = 2)
- 23 Reef under the net (yes = 1, no = 2)
- 24 Reef in the net area other than under net (yes = 1, no = 2)
- 25 Type of reef (bare rock = 1, flora covered = 2)
- 26 Substratum type (rock = 1, rock + algae = 2, rock + sand = 3, sand = 4, mud = 5)
- 27 Distance of net from shore (m)
- 28 Depth of water at net (m)

(< 90 kg), adolescent males and females (between 90 kg and 130 kg) and adult males and females (> 130 kg), adult females were further divided into lactating, pregnant or quiescent (neither lactating nor pregnant adult females). The partition of adolescents and adults at 130 kg corresponds to the approximate mass at which females first appear to ovulate (Cockcroft, unpublished data). Statistical analyses were performed on data for biological and one derived biological parameters for each dolphin and also for environmental factors and physiographic characteristics of the capture installation pertaining to each capture (Table 1). The derived biological character was the 'proportional fullness of the stomach' and was estimated from the mass of the remains in the stomach as a percentage of the stomachs estimated maximum volume (sensu Cockcroft & Ross, 1989b). Environmental factors were taken from daily records of sea temperature, water visibility, wave height and current direction routinely made by officers while meshing the nets. The physiography of each net installation was obtained from underwater surveys undertaken by staff of the Natal Sharks Board.

The biological, environmental and physiographic matrix resulting from all captures was, by definition, a serial matrix containing data from captured animals only. Additionally, the matrix consisted of both ordinal and nominal data, of different measurements and scales, and was therefore unsuitable for multivariate analysis.

Bottlenose dolphin catches and data gathered between January 1980 and December 1987 are examined in this work. However, catches for 1980 and 1981 reflect only those dolphins worked after freezing and not the total catch. In some circumstances during these two years dolphins were not retrieved from nets or were retrieved in a condition too decayed to warrant transport ashore. Analysis of annual catch statistics has therefore been limited to those between January 1982 and December 1987 only, when all dolphins captured were recovered. All other analyses include dolphins throughout the study period for which the relevant information was available.

## RESULTS

Table 2: The numbers of each bottlenosed dolphin mass/sex class caught between January 1980 and December 1987. The total catch for each year and the total catch of each mass/sex class is also given.

Maturity class	1980	1981	1982	1983	1984	1985	1986	1987	Total
Males > 130 kg	1	1	4	13	3	7	2	4	35
Males >90 kg < 130 kg	0	2	1	1	3	0	0	6	13
Females < 130 kg	0	1	1	4	1	2	1	2	12
Females >90 kg < 130 kg	2	4	2	2	0	5	3	2	20
Calves <90 kg	9	4	7	7	22	23	8	15	95
Lactating females	1	1	5	4	5	4	3	8	31
Pregnant females	0	0	0	0	0	1	3	2	6
Total catch	13	13	20	31	34	42	20	39	212

Figure 1: The mass/sex composition of the annual catch of bottlenose dolphins from the Natal shark nets between January 1980 and December 1987. (■ - sexually mature males > 130 kg, ▲▲ - adolescent males > 90 kg < 130 kg, □□ - adolescent females > 90 kg < 130 kg, 1 - resting sexually mature females > 130 kg, □ - pregnant females, ●● - lactating females, 2 - calves < 90 kg).

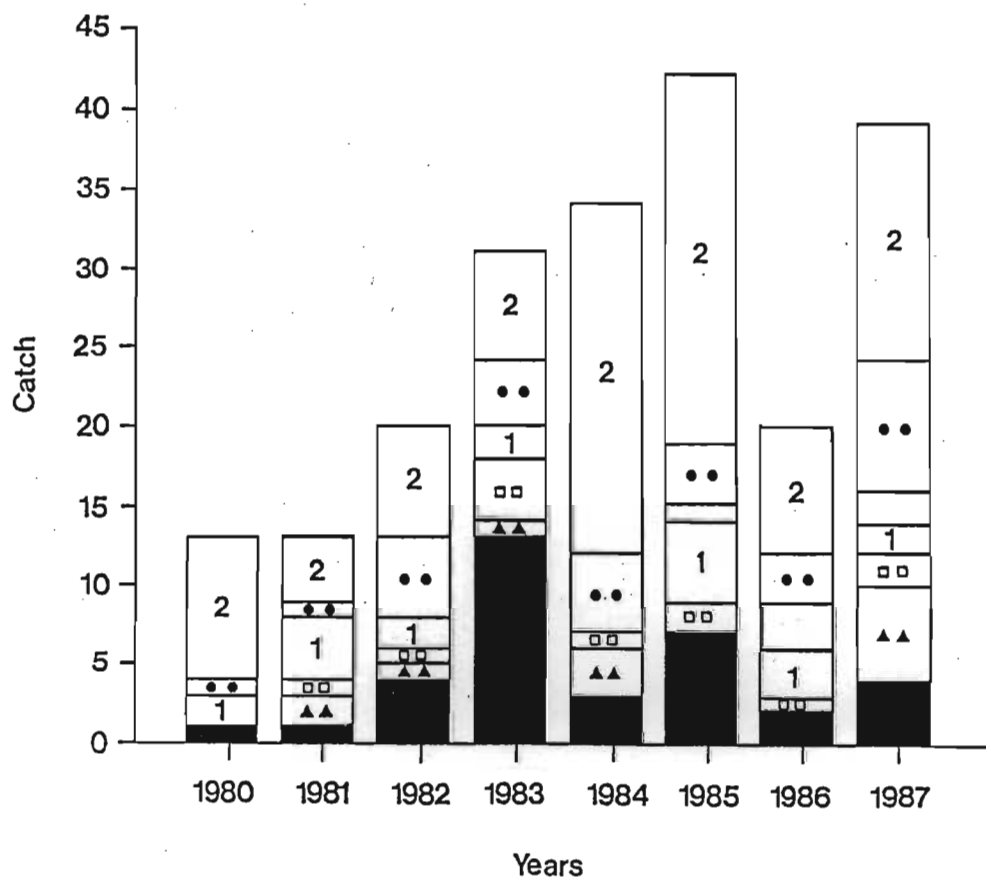
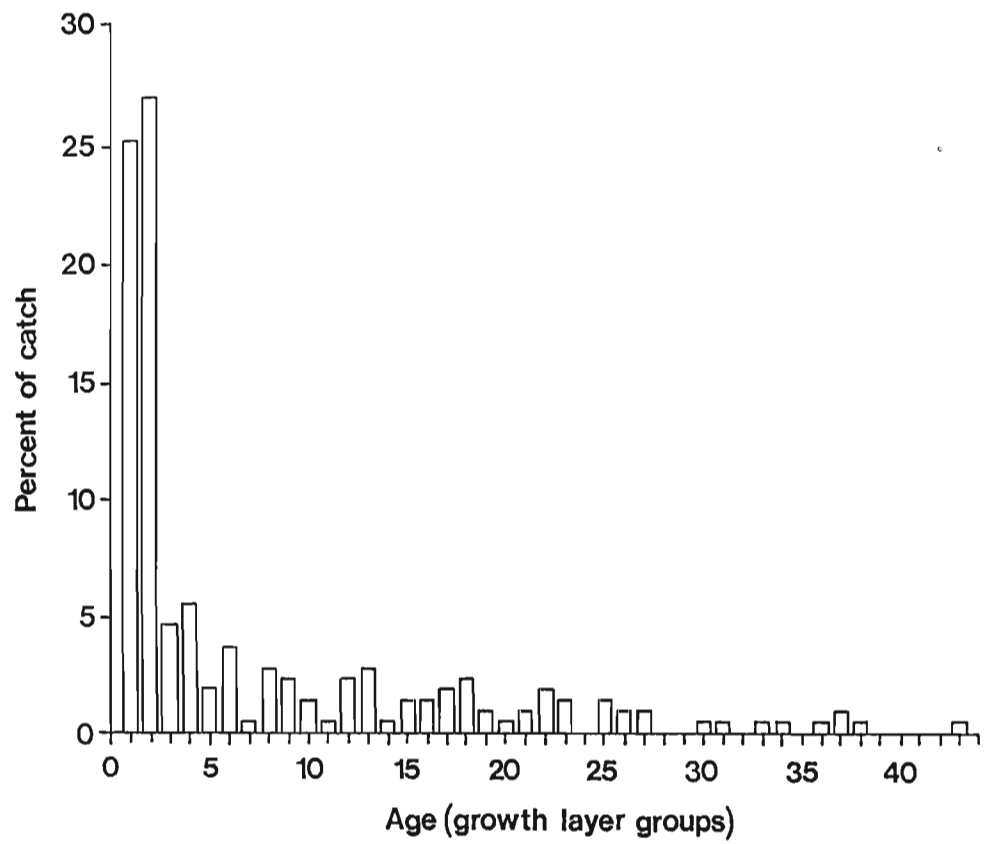


Figure 2: The age (number of growth layer groups in dentine) composition of the bottlenose dolphin catch in the Natal shark nets between January 1982 and December 1987.



Between January 1980 and December 1987, 212 bottlenose dolphins were recovered from the shark nets. Recoveries for 1980 and 1981 were both 13 dolphins. There was significant interannual variation between catches for 1982 to 1987 ( $X^2 = 14.1$ ,  $df=5$ ,  $P < 0.05$ ) (Table 2). There were no differences between years if catches for either 1982 or 1986 were excluded from the analyses.

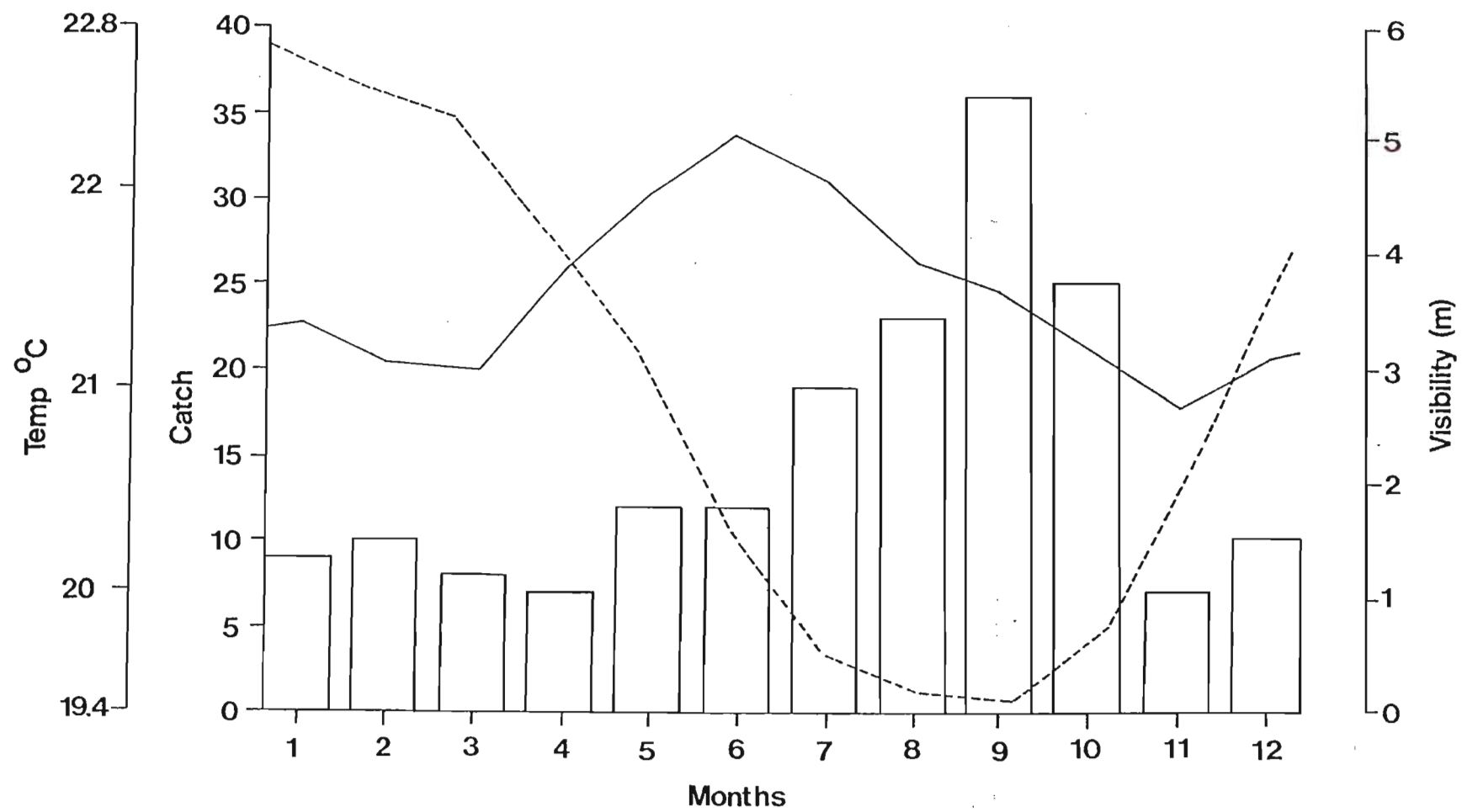
There was also significant interannual variation in the proportions of each of the seven mass/sexual state classes (juveniles; adolescent males and females, adult females, lactating females, pregnant females and adult males) caught (Fig. 1;  $X^2 = 56.2$ ,  $df=30$ ,  $P < 0.01$ ). If the entire catch for 1983 was excluded, the resultant interannual variations were not significant ( $X^2 = 32.44$ ,  $df=24$ ,  $P > 0.05$ ). Similarly, if the males captured during 1983 were excluded from analyses the differences between the mass/sex class composition of the annual catches were no longer significant ( $X^2 = 43.3$ ,  $df=30$ ,  $p > 0.05$ ).

The total numbers of female and male bottlenose dolphins caught were similar ( $X^2 = 2.14$ ,  $P > 0.05$ ,  $n=91$  and  $n=116$ , respectively). Capture rates of mature males and females and adolescent males and females, respectively, were also similar ( $X^2 = 2.01$ ,  $P > 0.05$  and  $X^2 = 0.3$ ,  $P > 0.05$ , respectively). However, fewer adolescent dolphins ( $n=31$ ) were caught than either adults ( $n=84$ ,  $X^2 = 24.6$ ,  $P < 0.01$ ) or calves ( $n=95$ ,  $X^2 = 32.8$ ,  $P < 0.01$ ) if sexes were combined. Mature males constituted 16.7 % of the total catch while mature females made up 23 % of the catch. Sixty three percent of the sexually mature females were lactating and a further 12 % were pregnant. Some 14.8 % of the catch were adolescents of mass between 90 kg and 130 kg and having eight GLGs or less in the dentine (Fig. 2). The majority of the catch, almost 45 %, consisted of calves of less than 90 kg mass and less than two GLGs in the dentine (Fig. 2). The stomachs of 30.5 % of these calves contained milk only, another 8.5 % milk plus solids while the remaining 61 % had no traces of milk, only solids.

The catch was clearly seasonal showing a clumped, non-random distribution (Mean square



Figure 3: Monthly catch of bottlenose dolphins, monthly mean water visibility (—) and monthly mean water temperature (-----) on the Natal coast between January 1982 and December 1987.



successive difference test,  $C=0.58$ ,  $P<0.05$ ), the majority of captures (74%) occurring between May and October (Fig. 3). No significant variation was found between the combined monthly captures of the seven mass/sexual state classes throughout the study period ( $\chi^2=60.27$ ,  $df=66$ ,  $P>0.05$ ). This seasonal capture pattern was significantly correlated with mean monthly temperatures ( $r=-0.776$ ,  $n=12$ ,  $p<0.01$ ) over the study period (Fig. 3). In contrast, monthly catches were not significantly correlated with mean monthly water visibility ( $r=0.205$ ,  $n=12$ ,  $p>0.05$ ) (Fig. 3) and catches occurred over the entire range of water visibility from 0 m to 10 m.

No bottlenose dolphins were captured in the northern most installation at Richards Bay where the mean annual water visibility was less than 1 m but the mean annual water temperature was similar to other installations. The muddy substratum at this installation was also unlike any other along the coast. Catches per net occurred at random along the remainder of the Natal coast (runs test,  $n_1=25$ ,  $n_2=20$ ,  $u=24$ ), although, there was a strong relationship between the number of nets in an installation and the number of dolphins caught ( $r=0.774$ ), dolphin catch increasing with the number of nets set (Spearman's rank order correlation,  $p=0.97$ ,  $P<0.01$ ). There was no significant difference between the proportions of any of the seven mass/sex classes caught on the north Natal coast (Zinkwazi -Durban), upper south Natal coast (Amanzimtoti - Ifafa) and lower south Natal coast (Mtwalumi -Mzamba) ( $\chi^2=15.15$ ,  $df=12$ ,  $P>0.05$ ).

Of the environmental and physiographic variables only the distribution of current direction in the capture matrix differed significantly from its expected frequency of occurrence gauged from the collected data ( $\chi^2=34.006$ ,  $df=2$ ,  $P<0.01$ ). The majority of captures occurred when the current direction was northerly (59.3 %), while a lesser proportion occurred when the current ran south (39.3 %) or offshore (1.5 %). The proportions of these currents in the environmental data were 35.7 %, 63.5 % and 0.8 %, respectively.

The frequency distribution of the number of animals in the net in any instance was significantly

Figure 4: Frequency distribution of the proportional fullness (stomach content mass/estimated stomach maximum volume) of the stomachs of bottlenose dolphins caught in the Natal shark nets.

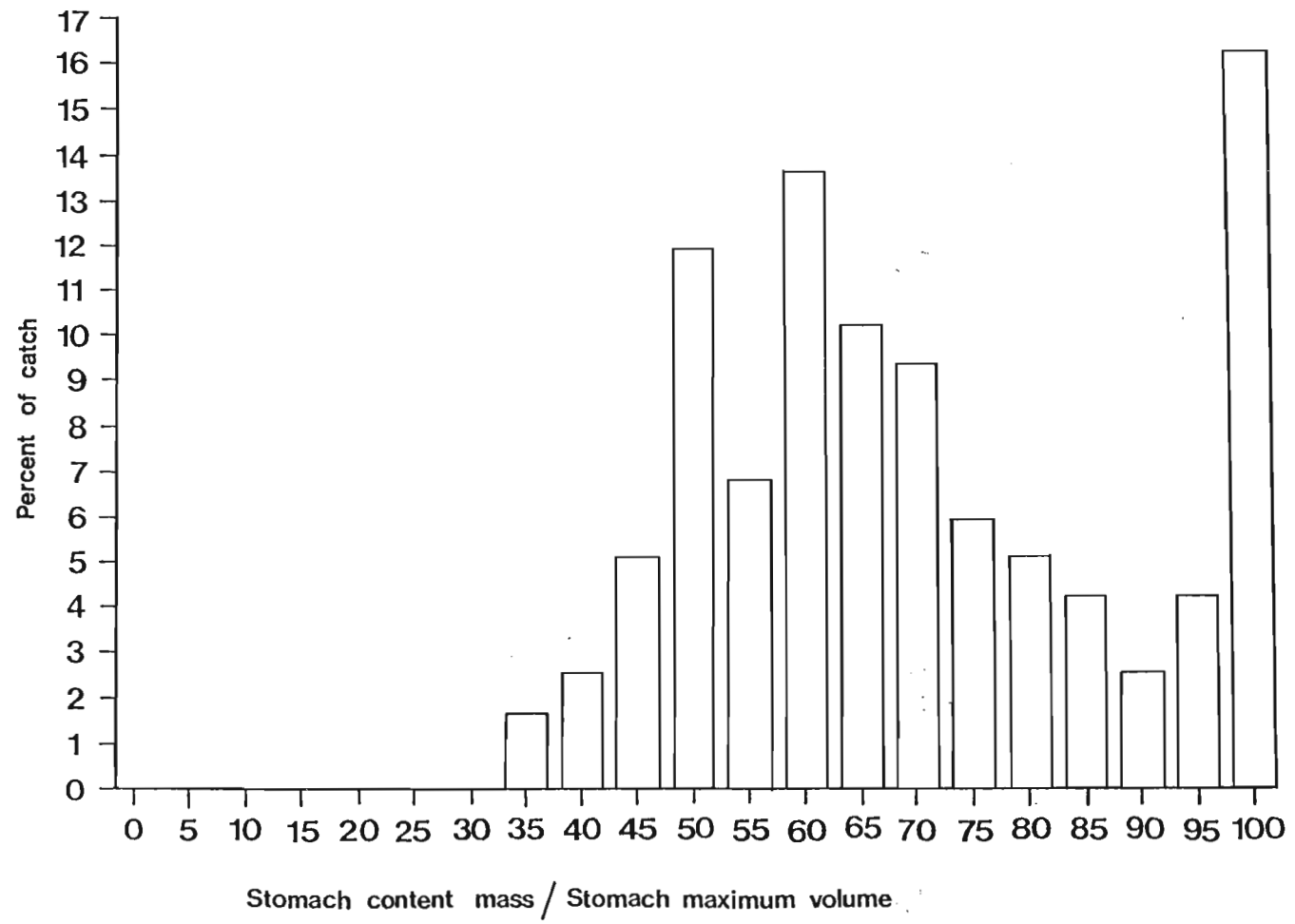
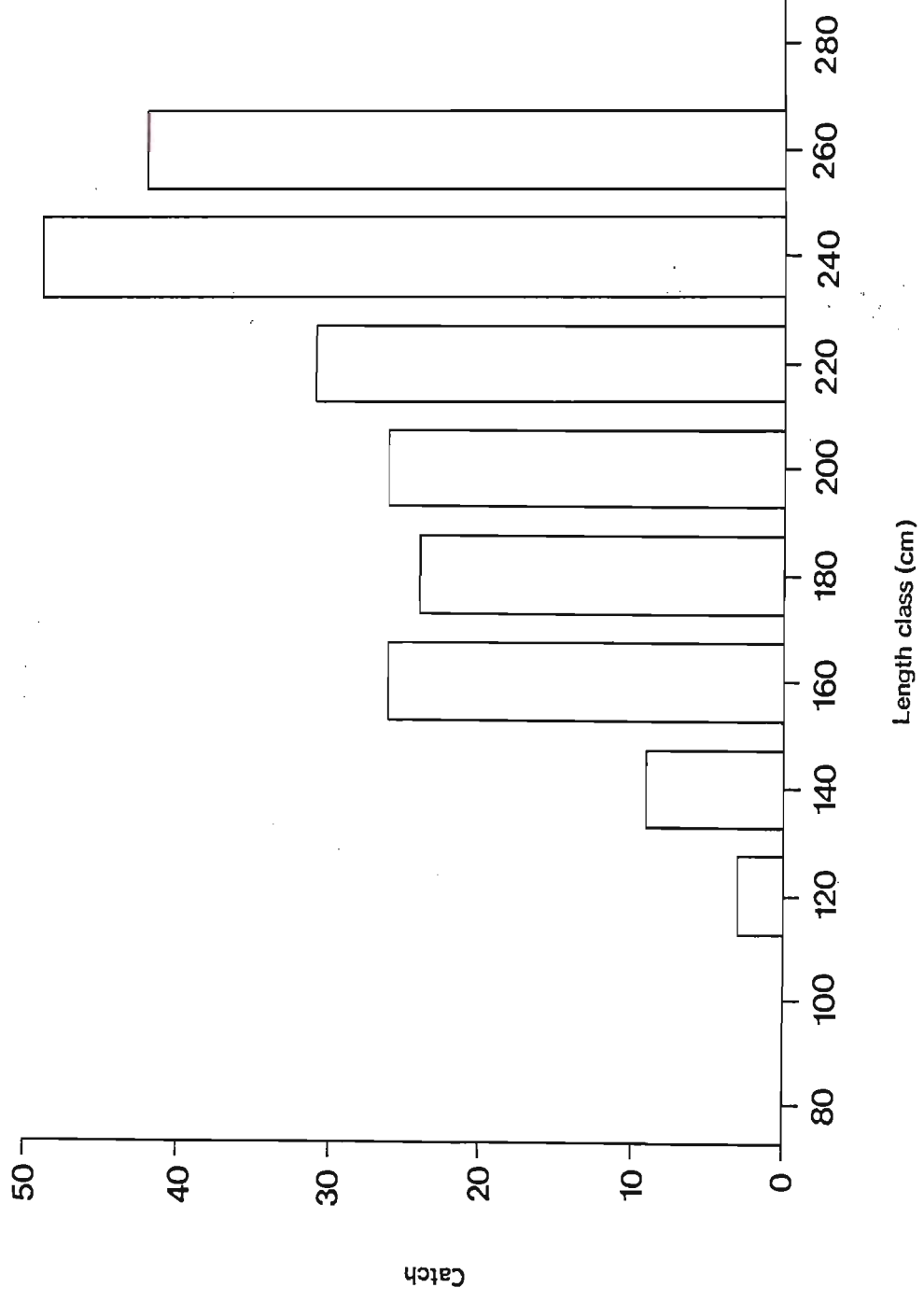


Figure 5: The length composition of bottlenose dolphins caught in the Natal shark nets between January 1982 and December 1987.



non normal (Kolmogorov-Smirnov test,  $D=0.4618$ ,  $n=212$ ,  $p<0.01$ ). One hundred and fifty seven captures were single events. On 27 occasions two animals were caught together, including 20 lactating female/calf pairs and seven calves caught with either adult males, non lactating females or juveniles.

The average fullness of stomachs was 63.9 % and the distribution of proportional fullness of stomachs was significantly skewed from the normal ( $D=0.1821$ ,  $n=117$ ,  $p<0.01$ ) (Fig. 4).

At only three localities, Umhlanga Rocks, Durban and North Amanzimtoti, were catches sufficient (more than 10) to allow statistical analyses on a single locality basis. One locality specific variable, the net in which the animals were caught, was included in these analyses. An examination of this variable showed that animals were randomly caught in nets at each locality (runs test, Durban:  $Z=-1.01905$ ,  $n=18$ , Umhlanga:  $Z=0.13815$ ,  $n=11$ , North Amanzimtoti:  $Z=0.138$ ,  $n=12$ ).

An analysis of the length distribution of catches shows only four catches of dolphins less than 140 cm in length (Fig. 5). Estimates from regressions of length on maximum body height ( $X=aY+b$ ,  $a=0.271805$ ,  $b=-0.50425$ ,  $r=0.973$ ) suggest that lengths of 130 cm and 140 cm correspond with maximum body heights of 34.8 cm and 37.6 cm, respectively.

## DISCUSSION

An examination of the catch statistics of bottlenose dolphins off Natal provides some clues to the reasons for their capture. In an analysis of bottlenose dolphins killed during fishing operations off Iki Island, Japan, Kasuya (1985) showed that 42.7 % of the catch consisted of males. Of females 40.1 % were immature, 20.6 % pregnant, 3.6 % pregnant and lactating and 28.6 % lactating. If similar proportions of sexes and size/sex classes are assumed to characterise the Natal bottlenose dolphin population it suggests that the overall proportions of the sexes in the



two catches are similar. However, the proportions of immatures (totalling 60 % of catch) and lactating females (63 % of females) are over represented in the Natal catch while that of pregnant females (12 % of females) is slightly under represented.

Skewed age or size catches of marine mammals in commercial fishing nets are not unusual. Ferrero & Jones (1986) reported on the predominance of immature Dall's porpoise caught during salmon fishing in the western north Pacific Ocean. Loughlin & Nelson (1986) reported that mature females constituted the majority of northern sea lions caught during walleye pollock fishery off Alaska. Read (1987) has suggested that reproductive female harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada, are caught preferentially in groundfish gill nets. Smith *et al.* (1983) found that 52 % of harbour porpoises trapped in herring wiers in the Bay of Fundy, were one year old animals.

Cockcroft & Ross (1989b) have suggested that different mass/sex classes of bottlenose dolphins off Natal feed in different areas of the inshore zone, on differing sizes and types of prey. Mature males feed further from shore, on larger prey and on a different prey spectrum than do other subgroups. Lactating females and calves feed close inshore, the former taking a wider variety of prey than other subgroups while the latter, feeding with their mothers, take a limited variety of small prey. Segregation of small cetacean sex and size classes over limited (Wells *et al.*, 1980) and large areas (Ferrero & Jones, 1986) is well documented and may directly influence the catch of these animals (Kasuya & Jones, 1984).

Distributional segregation of bottlenose dolphins along the Natal coast may contribute to the apparent selectivity of the shark nets. The majority of captured calves displayed less than two GLGs in the teeth and were probably less than eighteen months old and still subject to maternal care (Cockcroft & Ross, 1989a). Evidence from stomach contents indicates that most were either weaned or weaning at capture and Cockcroft & Ross (1989b) showed that prey species found in the stomachs of calves had also been taken by their mothers. These data suggest that feeding plays

an important role in predisposing calves to capture and may explain why they constitute the majority of captures. It is possible that calves may not be adept at perceiving the nets, either visually or acoustically, and are caught as a consequence. The attainment and perfection of behavioural and social skills which is apparent during the long period of maternal care of bottlenose dolphin calves (Cockcroft & Ross, 1989a) suggests that this hypothesis may be valid. Feeding behaviour in the inshore area with calves may also predispose lactating females to capture but it is unclear why fewer lactating females than calves are caught.

Mature males and adolescents, which appear to feed in different areas than lactating females and calves, may only frequent the near shore area occasionally and are therefore only infrequently subject to capture. Ross *et al.* (1987a) have shown that bottlenose dolphins along the Natal coast appeared to frequent 'preferred areas', each some 33–40 km long. This occurred even though captures along the coast occurred at random and were proportional to the number of nets only. They suggested that as captures did not coincide with 'preferred areas' of occurrence, they may result from unfamiliarity with an area. Personal observations (VGC) and those of Natal Sharks Board staff suggest that when swimming at the nets, bottlenose dolphins are aware of the presence of nets and often feed while in their vicinity. That the majority of dolphins had almost full stomachs also suggests that they feed in the net vicinity just prior to capture and may not perceive the nets because of a preoccupation with feeding. Similar conclusions were suggested by Goodson *et al.* (1988) who proposed that bottlenose dolphins may suppress sound echoes which do not match those of their targets which may lead to their entanglement in nets. Detailed behavioural studies of free ranging dolphins are required, however, to provide answers to these questions.

Seasonal variations in the distribution and catch of bottlenose dolphins may result from environmental fluctuations and associated prey abundance and distribution differences which affect feeding. Locally, bottlenose dolphins are known to avoid turbid water (Ross, 1977) and Ross *et al.*, (1987a) linked seasonal decreases in sighting rates of bottlenose dolphins on the

Natal coast to seasonal increases in inshore turbidity. This suggests that the high river runoff in summer resulting in an increase in inshore turbidity may reduce the presence of dolphins in the inshore region, thus decreasing the probability of their capture. Although no direct link between captures and water visibility were evident from this study, the relationship between captures and seasonal temperature variations was clear. These data suggest a strong seasonal component in the lives of Natal bottlenose dolphins which may be related to prey movement and availability. Although there appeared to be no seasonal change in the abundance of the major prey of bottlenose dolphins in Natal (Cockcroft & Ross, 1989b), the spawning of many of these prey and their distribution close inshore is known to occur during peak dolphin capture times (Joubert, 1981). Prey related seasonal distribution patterns have been suggested for bottlenose dolphins off Sarasota, Florida (Irvine *et al.*, 1981) and for the harbour porpoise (*Phocoena phocoena*) and common dolphin (*D. delphis*) in British waters (Evans, 1980).

Alternative reasons for seasonal distribution patterns of dolphins, such as changes in the abundance of sharks, have also been proposed (Wells *et al.*, 1980). However, there is no evidence for this in Natal where shark and bottlenose dolphin peak capture periods coincide (Cockcroft *et al.*, in press). Also, despite the relatively high level of shark predation on bottlenose dolphins in both Australian (Corkeron *et al.*, 1987) and South African waters there was no indication of any involvement of sharks in dolphin capture in Natal (Cockcroft *et al.*, in press).

Factors contributing to the seasonality of the bottlenose dolphin catch off Natal may also be implicated in the interannual catch variation. The annual catch varied quite markedly despite the number of nets remaining constant. Additionally, the mass/sex class composition of the catch also varied annually, although the results suggest that the catch of mature males only was the cause of this. Annual variations in the capture of cetaceans are not unusual. Paterson (1979) has shown an annual variation in the catch of dolphins in shark nets off southern Queensland. Although, the reasons for such variations are unknown, studies of humpback whale

(*Megaptera novaeangliae*) incidental mortality off Newfoundland, suggest that increased captures in the late 1970's were probably a result of changes of the status of the food resource (Whitehead & Carscadden, 1985). In this context it seems likely that annual fluctuations in environmental conditions off Natal may result in differences in the local distribution and abundance of particular prey. This, in turn, may influence the inshore distribution of bottlenose dolphins, particularly that of mature males, and be reflected in the total annual catch rate and that of the various mass/sex classes.

The similarity of the physical conditions at each of the netted beaches, the fact that sightings (Ross *et al.*, 1987a) and captures occur along most of this coast, suggests that the Natal coast provides a suitable, favourable habitat for bottlenose dolphins. The exception is Richards Bay where captures and sightings do not occur, probably because the low mean annual water visibility and muddy substratum makes the area unsuitable. However, the randomness of the catches along the Natal coast, the indication that catch rates are dependant only on the number of nets present and the similarity of the mass/sex composition of catches throughout, all suggest that small variations in physiographic conditions do not contribute to the capture of dolphins. This is further supported by the evidence that bottlenose dolphins off Natal appear not to follow typical travel routes and are captured apparently at random within an installation, their movements dictated by factors other than physiography.

In contrast, a number of environmental factors appear directly linked to the capture of bottlenose dolphins in Natal. Seasonal variations in temperature show a correlation with peak capture times during the year and although no connection was apparent in this study, Ross *et al.*, (1987a) linked the onshore occurrence and distribution of bottlenose dolphins to water clarity. In addition, dolphins were caught under significantly different current regimes than was suggested by the daily environmental data collected. Although no relationship was found between capture and state of the tide, a number of authors have suggested that bottlenose dolphin movements occur in relation to tidal flow (Wursig & Wursig, 1979; Shane, 1980). It is

possible that the prevailing current may be a reflection of this phenomenon and, as suggested earlier, that there is a relationship between this, other environmental fluctuations, and the short term movements of prey species which form the food of bottlenose dolphins along the Natal coast. However, Irvine *et al.* (1981) found that the movement and activity patterns of bottlenose dolphins off Florida were not influenced by environmental conditions, other than tide, in any recognisable way.

A number of biological factors also showed biases which suggest that they are directly related to the causes of capture. Despite the crudeness of the method, the assessment that the stomachs of most animals were relatively full at the time of capture implies that the animals were feeding when captured. The size/sex class bias in the catch statistics indicate that weaned calves, and to a lesser degree lactating females, are at a greater risk of capture than other size/sex classes. The results also indicate that the majority of captures are single events but that when double captures do occur they are likely to be of calves and lactating females. The interpretation of catch statistics must therefore be viewed in light of these facts.

The implications of continuing mortality in the shark nets appear severe for the Natal population of the bottlenose dolphin. Ross *et al.*, (1987b) estimated that the population of these dolphins in the netted areas of Natal totalled approximately 900 animals. The capture and death of 212 of these in the nets between 1980 and 1987 represents a 3.5 % annual mortality. An assessment of the impact of this mortality is not possible without unbiased data of the sex and age structure of bottlenose dolphins in this population. However, the high proportion of reproductively active females caught is of concern (19 % of catch between 1980 and 1987 and 0.7 % of the estimated total population annually) as the replacement potential of the population may be impaired. Dolphin populations are particularly sensitive to depletion through exploitation and once exploitation has ceased recover only very slowly (Estes, 1979). Recovery is more difficult for populations which continue to be exploited, particularly if this involves reproductive females. The exploitation of bottlenose dolphins in Natal has not ceased, mortality

continues in the shark nets and they may suffer deleterious effects from the accumulation of comparatively high levels of chlorinated hydrocarbons (Gardner, Connell, Eagle, Moldan, Oliff, Orren & Watling, 1983).

The results of this study indicate some potential methods for preventing dolphin captures in the shark nets. The obvious approach would be the removal of some or all nets, at least for the period of peak capture, between May and November. Unfortunately, peak shark captures coincide with peak dolphin captures (Cockcroft *et al.*, in press) and consequently, economic realities suggest that the tourist industry on the Natal coast may suffer huge losses from this approach. An alternative would be to increase the mesh size of the shark nets. The existing mesh has a 25 cm bar, resulting in a triangular height and width mesh dimension of 35.4 cm when the net is set and taut. This measurement coincides almost exactly with the minimum size of dolphin caught (34.8 cm maximum height and 130 cm length) even though birth occurs at a length ranging between 838 cm and 1120 cm (Ross, 1977). Although there are a number of possible reasons for this coincidence, including the mother protecting the neonate from coming into contact with nets, it nevertheless implies that an increase in the bar size may increase the minimum size of dolphin captured.

An increase of the mesh bar to 32 cm would increase the diagonal height and width, on a fully taut net, to 45.2 cm. Extrapolation, using the given regression, suggests that a mesh of this size may allow dolphins of 170 cm length or less to pass through the net reducing the mean annual catch by some 27 %. However, some problems may result from such an increase in mesh size. The range of sharks caught would obviously change, many of the smaller sharks presently caught may escape. Additionally, an increase in the mesh size may increase the capture rate of larger dolphins, particularly the mothers of those calves that may pass through the nets. Experimental evaluation of these hypotheses and alternate methods of reducing bottlenose dolphin mortality in the nets are urgently needed.

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## CHAPTER SIX

Shark predation on Indian Ocean bottlenose dolphins  
(*Tursiops truncatus*) off Natal, South Africa.

V.G. Cockcroft, G. Cliff\* and G.J.B. Ross.

Port Elizabeth Museum, P.O. Box 13147, Humewood, 6013. Republic of South Africa.

\* Natal Sharks Board, Private Bag 2, Umhlanga Rocks, 4320.

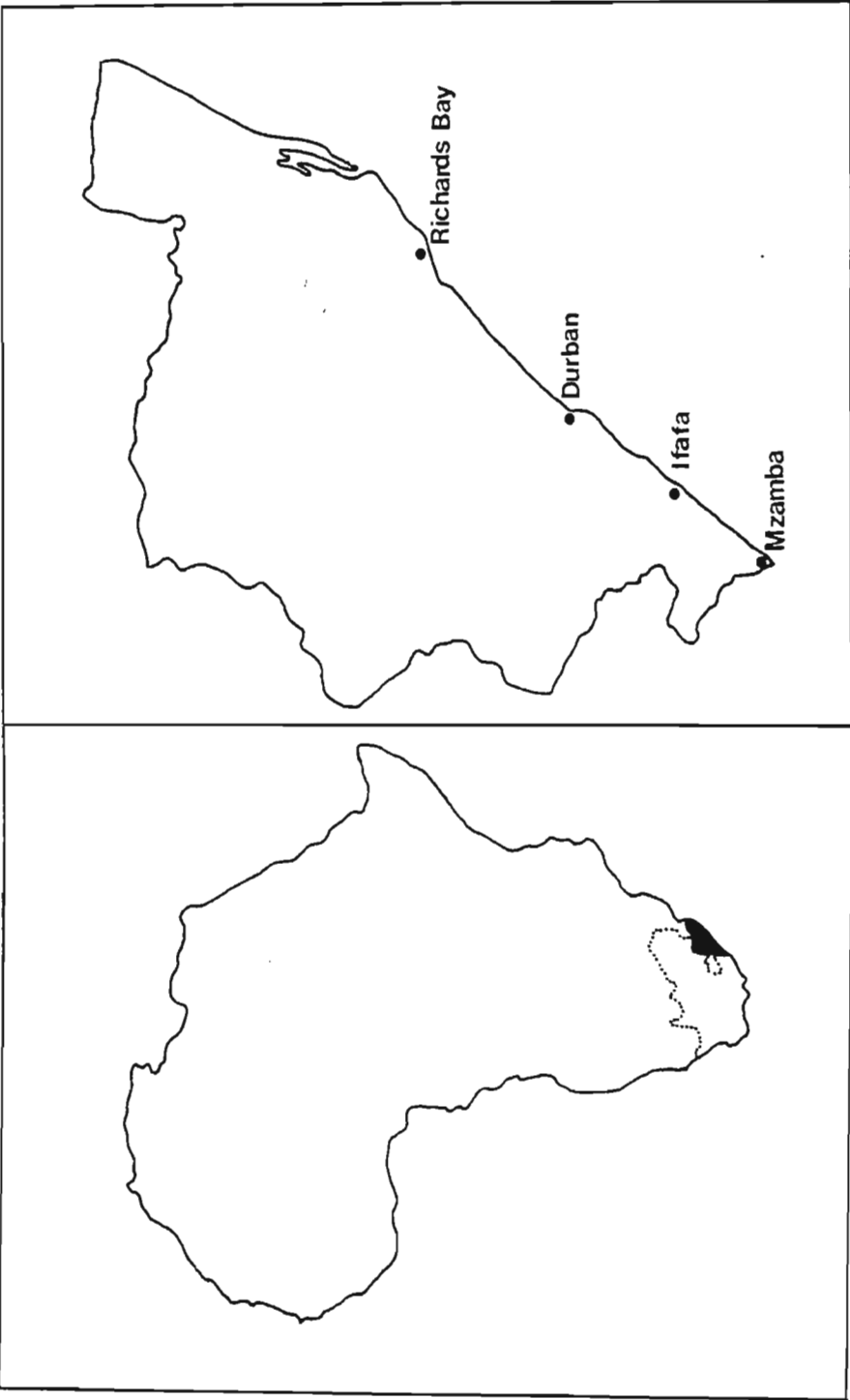
Republic of South Africa.

## ABSTRACT

The incidence of shark induced scars on Indian Ocean bottlenose dolphins caught in gill nets off Natal, on the south east coast of southern Africa, was monitored between January 1983 and June 1987. The occurrence of dolphin remains in sharks caught in these nets between January 1980 and December 1985 was also recorded. 10,3 % of the dolphins caught exhibited scars or wounds consistent with shark bites. Only 1,2 % of over 6000 sharks caught contained cetacean remains. Four species of shark, the Zambesi (*Carcharhinus leucas*), the tiger (*Galeocerdo cuvieri*), the great white (*Carcharodon carcharias*) and the dusky shark (*Carcharhinus obscurus*) were implicated as dolphin predators. Estimates from the number of these four species caught annually and the frequency of occurrence of dolphin flukes and vertebrae in their stomachs suggest that a minimum of 20 bottlenose dolphins or 2,2 % of the estimated population in southern Natal coastal waters are killed each year by sharks.



Figure 1: Natal, on the east coast of southern Africa between 27°S and 31°S. Gill nets to catch sharks are set at 44 prime bathing beaches between Richards Bay and Mzamba.



## INTRODUCTION

An assessment of the extent, causes and sources of natural mortality in marine mammal populations presents some formidable problems (Gaskin, 1982). One source of natural mortality is that from predation by killer whales and sharks. Shark predation on seals is well documented and mortality resulting from this source may be significant in the population dynamics of certain seal populations such as the Hawaiian monk seal (Kenyon, 1981) and the grey seal in eastern Canada (Brodie and Beck, 1983). Furthermore, Ainley *et al.* (1985) propose that the abnormal timing of the breeding season of the northern elephant seal on the Farallon Islands may, in part, be a response to white shark predation pressure on newly weaned pups. They further speculate that the timing of breeding seasons of other seals may be, partially, an evolutionary response to shark predation.

Although the predatory interactions between sharks and cetaceans have been observed or inferred on numerous occasions (Wood *et al.*, 1970; Ross and Bass, 1971; Leatherwood *et al.*, 1972; Arnold, 1972; Ross, 1977; Saayman and Tayler, 1979; Norris and Dohl, 1980; Stevens, 1984; Corkeron *et al.*, 1987), little is known concerning the frequency of shark attack on cetaceans or their influence on dolphin populations. Norris and Dohl (1980) reported that spinner dolphins off Hawaii were apparently attacked with some frequency. Corkeron *et al.* (1987) found that 36,6 % of identified bottlenose dolphins in Moreton Bay, Queensland, Australia showed definite evidence of shark attack. In South African waters, Ross (1977) noted that although the level of shark predation on bottlenose dolphins was unknown it appeared to be low based on the number of animals displaying shark bite scars.

On the Natal coast (Fig. 1) 44 prime bathing beaches are protected by inshore gill nets, set to catch and reduce the number of sharks off these beaches. Currently, some 1400 sharks are caught in these nets annually. In addition, three species of dolphin, the Indian Ocean bottlenose dolphin (*Tursiops truncatus*), the Indo-Pacific humpback dolphin (*Sousa plumbea*) and the common

dolphin (*Delphinus delphis*), are captured and killed incidentally in these nets. Common dolphins frequent Natal only during mid winter, from June to September, when they migrate northwards in association with a winter migration of pilchards (*Sardinops ocellatus*). In contrast, humpback and bottlenose dolphins occur in the Natal inshore region throughout the year and there is concern that the continued mortality of these species in the nets may deplete their respective Natal populations.

Access to both net captured dolphins and sharks provided a unique opportunity to gain an insight into shark predation on bottlenose dolphins. The incidence of shark attack on humpback dolphins is reported elsewhere (Cockcroft, in press).

## MATERIALS AND METHODS

Over the period January 1980 to December 1985, 6878 sharks of 16 species were necropsied. During these necropsies the contents of the stomachs were removed and washed. Vertebrate remains other than fishes were closely examined. Amongst these remains ingested flippers, flukes and vertebrae were relatively easily identified. Blubber was also easily identifiable, and classified as whale or dolphin blubber on its thickness, that of dolphins being thin in comparison to that of whales. Certain skeletal material and muscle were often not identifiable with any certainty, and were excluded for the purposes of this study.

Bottlenose dolphins caught between January 1983 and June 1987 were inspected, during routine dissections, for the presence of old scars or recent wounds. The decomposed condition of some dolphins made it difficult to determine the presence of scars and, due to time constraints, not all animals were examined with equal effort. Only scars or fresh wounds forming single or double arcs on the body, similar to type 1, 2 and 5 injuries observed on penguins by Randall *et al.* (1988), were classed as shark bites and were included in this study. The number and

Table 1: The number of bottlenose dolphins, showing evidence of shark bite, caught in the Natal shark nets between January 1983 and June 1987.

	No.	%
Single scars	4	2.8
Multiple scars	7	4.8
Recent wounds	4	2.8
Total	15	10.4
Total No. of dolphins examined	145	

Plate 1: PEM N1058, an adult female *Tursiops truncatus* showing a 21 cm x 35 cm semi-healed shark bite probably inflicted sometime in June or July 1984.



position of scars or recent wounds was noted and photographs taken. Measurements were taken across the axes of recent wounds. Fresh wounds obviously inflicted subsequent to capture in the nets were excluded.

## RESULTS

Twenty eight of the 145 bottlenose dolphins captured showed scars or wounds that may have resulted from shark attack. Of these only 15 exhibited single or multiple scars or wounds that fulfilled the criteria set for shark bite (Table 1). Recent bite wounds (Plate 1) were observed in June and July only, in four different years. The width of all four recent bites were measured (20 cm, 23 cm, 25 cm and 35 cm). The identity of the shark or sharks responsible for any of the scars or recent wounds was not established.

Only two of the 15 dolphins were calves less than 200 cm in length while all others were subadults or adults greater than 220 cm in length. Only three (20 %) of the 15 were caught north of Durban (north coast), two (13 %) between Ifafa and Durban (upper south coast) and the remainder (67 %) between Mzamba and Ifafa (lower south coast). The majority of bite scars were posteriorly situated and generally on the ventral, paler portions of the body, slightly anterodorsal to the genital area.

Ten (7 %) of the 145 bottlenose dolphins caught showed signs of having been scavenged in the nets subsequent to capture. The most commonly scavenged areas of the body were the soft underbelly and posterior flanks. In only one instance were the flippers removed but in no instances were the flukes or any vertebrae removed. Consequently, the presence of flukes or vertebrae in shark stomachs was considered a more reliable indicator of dolphin mortality due to predation than the presence of blubber or unidentified small cetacean (dolphin) pieces.

Only 89 sharks (1,2 %), covering nine species, contained dolphin remains. In only three shark



Table 2: The frequency of occurrence of flukes and vertebrae in great white sharks >180 cm SL, dusky sharks >170 cm SL, tiger sharks >190 cm SL and Zambesi sharks >140 cm SL, caught between November and May.

	great white	dusky	tiger	Zambesi
Frequency of occurrence, between November and May, of flukes and vertebrae in shark stomachs.	1	0.2	1.9	2.2

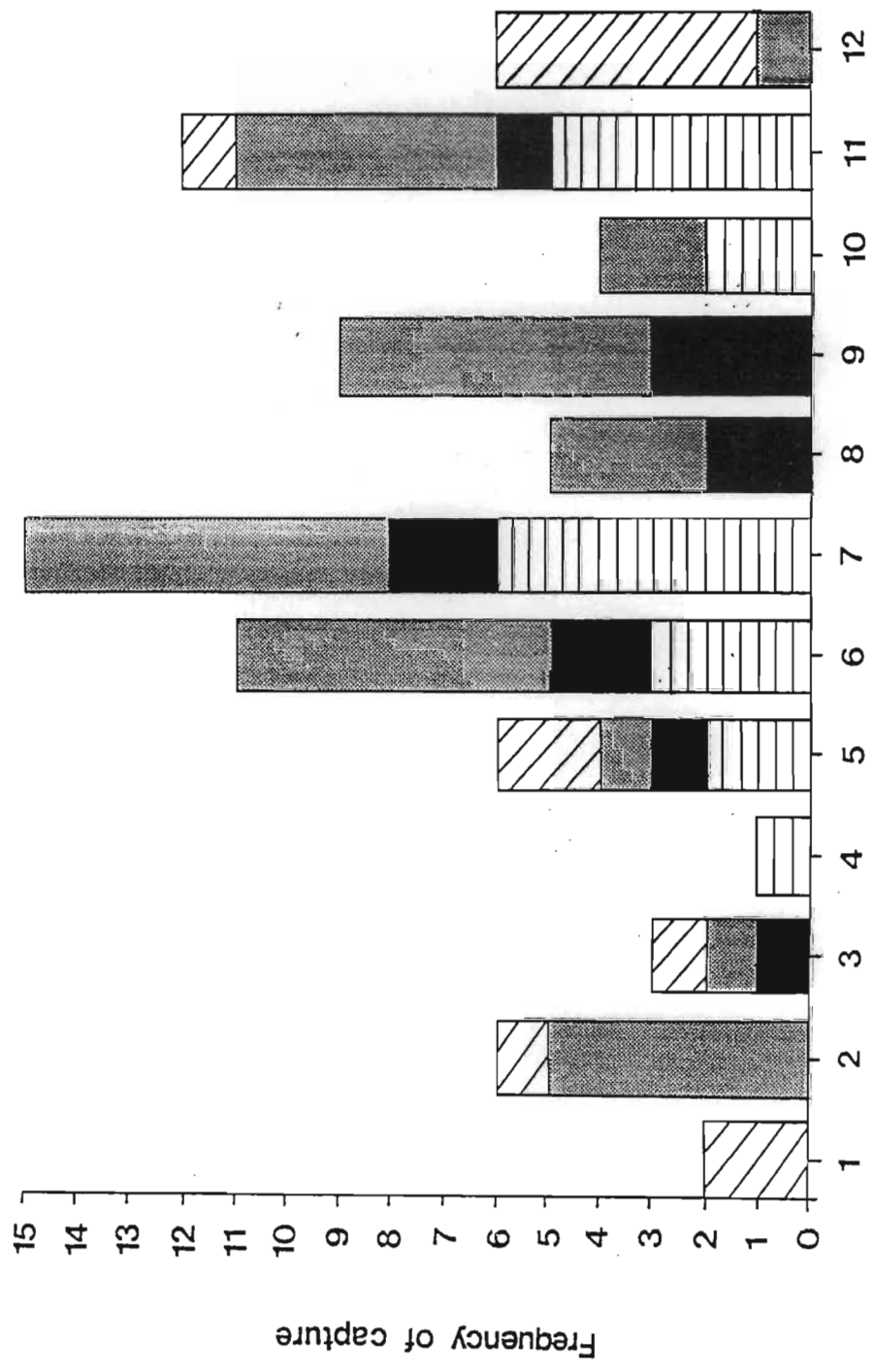
Plate 2: The remains of a young dolphin found in the stomach of a 290 cm, female great white shark caught in the Natal shark nets.



Table 3: Estimated total lengths (TL) and standard lengths (SL) of four species of shark inflicting 20 cm and 35 cm width bites on bottlenosed dolphins. The percentage catch of these sharks estimated to have a bite width exceeding 20 cm is also given. (TL to SL conversions after Bass et al., 1973, 1975a and 1975b).

	Estimated length from bite width				% of catch > col. 1
	TL	20 cm SL	30 cm TL	SL	
<i>Carcharhinus leucas</i>	180	140	304	236	89.5
<i>Galeocerdo cuvieri</i>	260	190	470	343	43.9
<i>Carcharodon carcharias</i>	220	180	390	320	88.5
<i>Carcharhinus obscurus</i>	200	170	350	280	49.2

Figure 2: The monthly frequency of capture of great white (horizontal bars), tiger (hatched), dusky (black) and Zambesi (inclined bars) sharks containing dolphin remains over the period January 1980 through December 1985.



species, the Zambesi (*Carcharhinus leucas*), the tiger (*Galeocerdo cuvieri*) and the great white (*Carcharodon carcharias*), was the frequency of dolphin remains in stomachs more than 1 % (Table 2). Additionally, the remains of dolphin flukes and vertebrae occur only in these three species and the dusky shark (*Carcharhinus obscurus*) (Table 2).

Notes kept on flukes and vertebrae recovered from the stomachs of sharks were unidentifiable to species but indicated that the majority were from young dolphins (Plate 2). This was determined by the relative size of the flukes and the degree of fusion of the epiphyses to the centra of vertebrae. Unfortunately, most of this material was discarded and further assessment of age was not possible.

The total lengths of Zambesi, tiger, great white and dusky sharks capable of delivering the smallest and largest of the recent wounds were calculated using figures given by Bass *et al.* (1973, 1975a, 1975b) (jaw width 11,5 %, 9 %, 7,8 % and 10 % of total length, respectively) (Table 3). The percentage of total catch of each species larger than that predicted by the smallest bite width is also shown. Catches of these four shark species containing dolphin remains occurred throughout the year, although catches in June, July and November were marginally greater (Fig. 2).

Five sharks were caught together with bottlenose dolphins. In only one instance did the shark contain cetacean remains suggesting it had been scavenging. The majority (42 %) of sharks containing small cetacean remains were caught south of Ifafa (lower south coast); 32 % and 26 % were caught between Ifafa and Amanzimtoti (upper south coast) and between Durban and Richards Bay (north coast), respectively. Varying proportions of sharks captured had everted stomachs and therefore no stomach remains. The percentage of examined Zambesi, great white, dusky and tiger sharks with everted stomachs was 2,7 %, 11,6 %, 1,5 % and 13,2 %, respectively.

## DISCUSSION

There is circumstantial evidence that Natal bottlenose dolphins actively avoid encounters with large sharks. They consistently avoid dirty, discoloured water (Ross, 1977). This behaviour may be an attempt to minimize confrontations with some species of big sharks, large numbers of which have been seen just inside and on the borders of discoloured water (pers. obs. VGC and GJBR) during aerial surveys conducted along the Natal coast. Most shark attacks on humans, on the Natal coast, also occur when the water is turbid (Wallett, 1973). There is also evidence that Natal bottlenose dolphins move offshore in the evening and only return to nearshore waters at first light (N.S.B. personnel, pers. com. and Cockcroft, unpubl. data). This movement may be evidence of a diurnal rhythm (Klinowska, 1986) in response to the inshore movement of some species of shark at dusk, apparently to feed overnight (Wallett, 1973).

This study provides evidence that a minimum of 10,3 % of bottlenose dolphins captured in Natal showed some sign of shark attack, although this may be an underestimate of shark, bottlenose dolphin interaction in this area. In Moreton Bay, Queensland, Australia, Corkeron *et al.* (1987) found 36,6 % of bottlenose dolphins showed signs of attack by sharks, particularly great white and tiger sharks. The discrepancy between the former and latter estimates may result from the biased sex and size composition of the net sample (Cockcroft & Ross, 1989a). As both studies deal with dolphins surviving shark attack, it is impossible to relate the incidence of scars and wounds on surviving dolphins to the extent of attack or resulting mortality. Nevertheless, the presence of shark induced scars and wounds on dolphins in relation to other data provide some interesting information.

Multiple scarring on dolphins suggests that shark attack is relatively common, although often unsuccessful. The position of most scars and wounds observed in this study suggests that most attacks are aimed at the posterior, ventral surface of dolphins. This is in agreement with other studies on porpoises and seals which have suggested that attacks almost invariably occur from the rear and below (Arnold, 1972; Tricas and McCosker, 1984; McCosker, 1985; Ainley *et al.*,



1985).

The low number of calves and juveniles (<200 cm in length) with bite scars is interesting considering that this size group constitute over 40 % of the annual bottlenose dolphin catch (Cockcroft & Ross, 1989a). This disparity suggests that either calves and juveniles may not be attacked, that they are protected from attack by their mothers, or that attacks on young dolphins may almost always prove fatal. Corkeron *et al.*, (1987) found that a large proportion of nursing female bottlenose dolphins in Moreton Bay displayed fresh bites and that mothers with calves showed shark avoidance behaviour, suggesting that females and their calves may be more prone to attack. The predominance of young dolphin remains found in the stomachs of sharks in Natal, supports this view and suggests that young animals may be particularly vulnerable to attack.

It is difficult to determine whether sharks contained small cetacean remains as a result of predation or scavenging. It is also uncertain whether dolphin capture in the nets occurs during avoidance of shark attack, scavenging occurring subsequent to this. However, the low association between scavenged netted dolphins and sharks containing dolphin remains and the small numbers of sharks and dolphins caught together suggest that captures of both occurred independently and that dolphin captures were not a result of harassment by sharks.

Four shark species are apparently involved in predation on dolphins off Natal - the Zambesi (*Carcharhinus leucas*), the tiger (*Galeocerdo cuvieri*) and the great white (*Carcharodon carcharias*) and the dusky (*Carcharhinus obscurus*) - all of which have previously been implicated in marine mammal predation (Wood *et al.*, 1970; Compagno, 1984; McCosker, 1985; Stewart & Yochem, 1985; Alcorn & Kam, 1986; Corkeron *et al.*, 1987). A minimum dolphin mortality can be estimated from the frequency of occurrence of flukes and vertebrae in the stomachs of these four shark species, assuming, as seems justifiable from the scavenging data, that the presence of either of these represents one dolphin killed. Further, bottlenose dolphin mortality can be estimated if

mortality of other dolphin species can be excluded. Thus, if sharks smaller than those indicated by the smallest bite (Table 3), those caught at Richards Bay, where the majority of humpback dolphin catches occur (Cockcroft, unpubl. data), and those captured during the Natal 'sardine run' (June to October), during which common dolphins are present in Natal, are excluded, an estimate of bottlenose dolphin mortality can be derived.

The annual catch of the four shark species, with the above exclusions, is about 327 animals (Cliff, unpubl. data) and nearly 0,7 % (2,3 sharks per annum) of these contained either dolphin flukes or vertebrae. Carey *et al.*, (1982) have suggested that large great white sharks may only need to feed once in six weeks, assuming they fill their stomachs at each feed. Although an assumption of equal metabolic and feeding rates for the other large sharks is speculative, these data suggest a predation mortality of some 20 bottlenose dolphins annually.

This figure is a gross estimate and includes a number of sources of error. Shark abundance is greater in June and July (Wallett, 1978) and the presence of fresh wounds during these months only, suggests that predation on dolphins may be greater during this period. Sharks with everted or empty stomachs were included in calculations and would tend to reduce mortality estimates. Other shark species probably capable of killing a dolphin calf, have been ignored. In combination, the above factors suggest that a mortality of 20 bottlenose dolphins annually is a minimum estimate. However, the estimate is directly related to the assumed feeding and metabolic rates of sharks and would vary considerably according to these parameters.

Ross *et al.*, (1987) have estimated the Natal population of bottlenose dolphins to approximate 900 animals. Although the derived estimate of annual bottlenose dolphin mortality can not be related to overall annual mortality as the population levels of sharks off Natal are unknown, it represents some 2,2 % of the population estimate and is approximately half the mortality due to net captures (Cockcroft & Ross, 1989a). This suggests that predation by sharks may account for significant numbers of bottlenose dolphins and possibly other inshore dolphins. Bottlenose

dolphins are likely to have adapted both behaviourally and physiologically to this predation pressure to minimise its effect on the population. The avoidance of turbid water and the efficient camouflaging of the young calf (Cockcroft and Ross, 1989b) are possible examples of these adaptations.

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CHAPTER SEVEN



Organochlorines in bottlenose dolphins from the  
east coast of southern Africa.

V.G. Cockcroft, A.C. De Kock<sup>\*</sup>, D.A. Lord<sup>\*</sup> & G.J.B. Ross

Port Elizabeth Museum, P.O. Box 13147, Humewood. 6013. Republic of South Africa.

<sup>\*</sup>Department of Oceanography, University of

Port Elizabeth, Box 1600, Port Elizabeth. 6000. Republic of South Africa

## ABSTRACT

The concentrations of polychlorinated biphenyls (PCBs), t-DDT (DDT + DDE + DDD) and dieldrin were determined in blubber samples of 108 bottlenose dolphins inhabiting the coastal waters of the south east coast of southern Africa. Residue concentrations increased with age in males and reached levels that may impair testosterone production. In females, a decline in concentrations of all three residues was evident between eight and 10 dentinal growth layer groups. A significant difference was found between residue levels in females before and subsequent to their first or second ovulation suggesting that first born calves received the majority of the mother's load through lactation. Evidence is presented indicating that primiparous females impart the majority of their load within seven weeks post partum. Levels of PCBs, t-DDT and dieldrin differed significantly in different geographical areas, suggesting a degree of isolation of sections of the population.

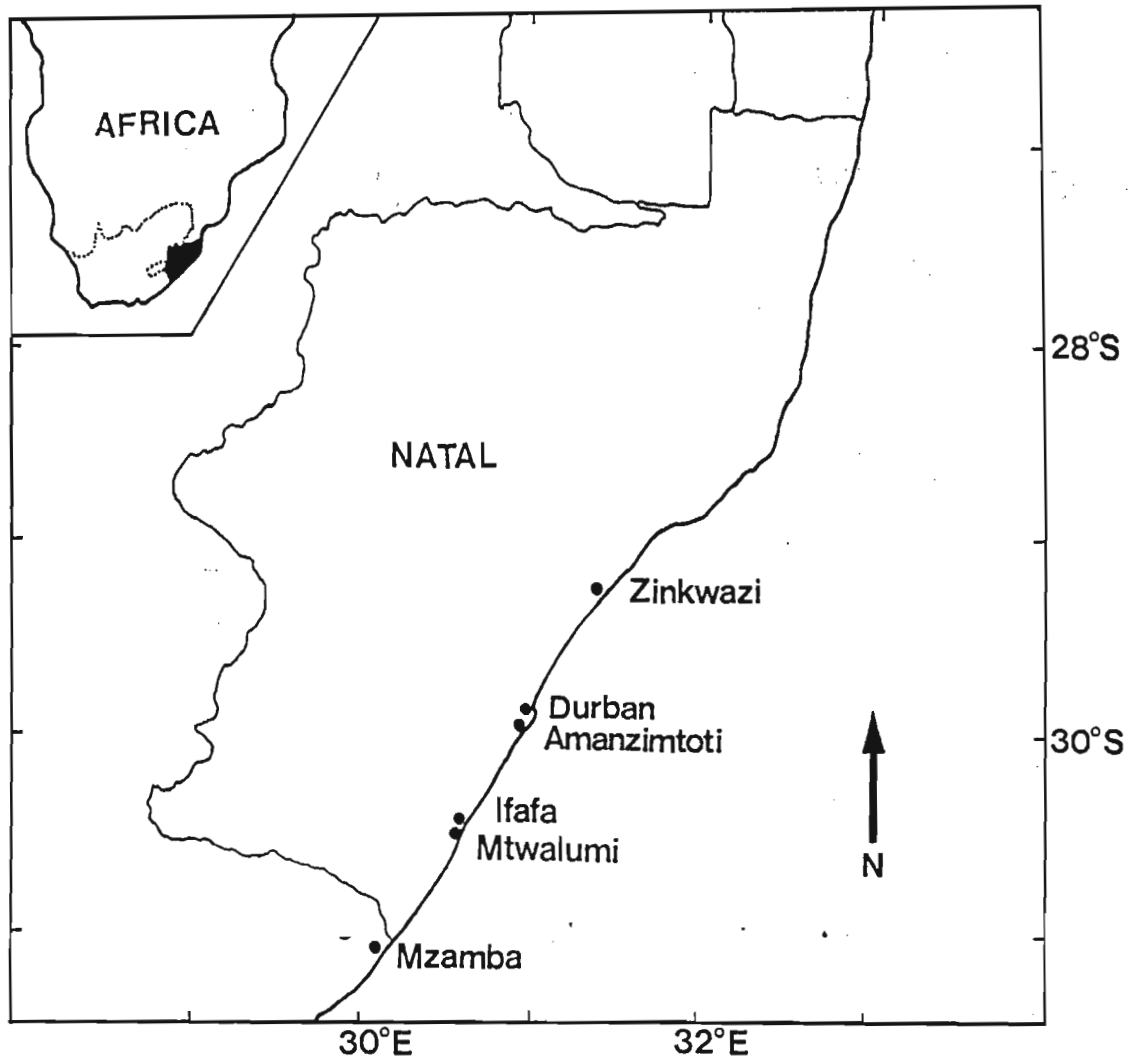
## INTRODUCTION

Chlorinated hydrocarbon residues, particularly the synthetic PCBs, DDT and its derivatives and dieldrin, have been recorded from marine mammals in a variety of geographical areas (Holden, 1978; Risebrough, 1978; Gaskin, 1982; Wagemann & Muir, 1984). Although the toxic effects of these compounds are difficult to assess, their effect on marine mammals has come under increasing scrutiny. Marine mammals may accumulate chlorinated hydrocarbons to a greater degree than other mammals, because they lack many of the enzymes necessary for their metabolism, implying an increased susceptibility to the deposition of these compounds in the environment (Tanabe, 1988; Tanabe *et al.*, 1988).

A number of studies have suggested that chlorinated hydrocarbon toxicity may be a significant and often critical factor in the survival of marine mammal populations. High concentrations of PCBs and DDTs have been implicated in reproductive abnormalities in female harbour seals in the Wadden Sea and, also, in the reduced survival of seal populations in this area (Duinker *et al.*, 1979; Reijnders, 1986). Similarly, Martineau *et al.* (1987) have suggested that high tissue PCB concentrations may prevent the recovery of the St. Lawrence estuary stock of beluga whales. Subramanian *et al.* (1987) have shown that high levels of PCBs and DDE are negatively correlated with testosterone levels in Dall's porpoise.

There are few published data on the occurrence of chlorinated hydrocarbon residues in cetaceans inhabiting the coastal waters of southern Africa (Gardner, *et al.*, 1983; Henry & Best, 1983; Ross, 1984). Preliminary data for the coastal dwelling humpback dolphin (*Sousa plumbea*) and bottlenose dolphin (*Tursiops truncatus*), show that these species contain levels that warrant investigation (Gardner, *et al.*, 1983). The Natal populations of both these species are subject to a number of pressures including accidental capture in nets set to catch and reduce the number of sharks off bathing beaches (Fig. 1) (Cockcroft & Ross, in press). In all, some 416 nets are set along 45 prime bathing beaches on this coastline (Peddemors *et al.*, in press) and are

Figure 1. Natal, on the south east coast of southern Africa.



involved in catches of these two species (Cockcroft & Ross, in press). Population estimates of bottlenose and humpback dolphins suggest totals of 900 and, possibly, 200 animals, respectively, prompting concern that both may be at considerable risk of depletion in Natal region (Ross, 1982; Ross *et al.*, in press; Cockcroft & Ross, in press).

## MATERIALS AND METHODS

Netted animals were routinely dissected to evaluate biological characteristics. Blubber samples of approximately 30 g were removed from the flank, in the neck region anteriodorsal to the flipper insertion where the greatest blubber thickness was consistently found. Samples were immediately wrapped in aluminium foil and frozen to await analysis. All blubber from the neck to the caudal peduncle was removed to obtain blubber weights. Ovaries of females were sectioned serially and the number of corpora lutea and albicantia in both ovaries was counted and summed. Age is expressed as the number of growth layer groups (GLGs; *sen su* Perrin & Myrick, 1980) counted in thin sections of the dentine of teeth taken from relevant animals.

For data interpretation animals were grouped into age classes; calves (<2 GLGs), immatures (2 to <10 GLGs), mature males (>10 GLGs) and mature females (>10 GLGs). The latter were further divided into lactating, pregnant and resting. Additionally, samples were grouped according to geographic area (south Natal coast -Mzamba north to Mtwalumi, mid Natal coast -Ifafa to Amanzimtoti and north Natal coast -Durban to Zinkwazi) (Fig. 1).

### Sample analysis:

Thawed samples (5 g) were mixed with approximately 100 g anhydrous sulphate and subjected to soxhlet extraction with hexane for four hours. The solvent was removed by rotary evaporation at 40°C and lipid volume determined gravimetrically. Extracted solutions (400 mg) of fat in hexane

were cleaned in 25 mm x 200 mm glass columns packed with 20 g alumina, deactivated with 10 % water (m/m). Two hexane fractions of 75 ml each were collected and, suitably diluted, injected into the gas chromatograph. For each series of samples the clean-up procedure was tested for efficiency, blanks and recoveries. High resolution capillary gas chromatograms were obtained with a Carlo Erba Vega 6180 gas chromatograph equipped with an electron capture detector and cold-on column injector. The fused silica capillary column was coated with DB-5 to a thickness of 0,25 mm. The oven temperature was programmed at a rate of 5°C/min from 80°C (2 min) to 180°C (1 min), then at 2°C/min to 220°C and at 4°C/min to 260°C. The detector temperature was 320°C.

Quantification and confirmation of analytical results:

PCBs were quantified by comparing the total area of PCB peaks in the sample chromatograms with total peak area of Aroclor 1260 external standard. Other compounds were quantified by frequent calibration (every three sample runs) of the GC/ECD with an external standard mixture. The presence of PCBs was confirmed by alkali dehydrochlorination (Young & Burke, 1972) and perchlorination (Steinwandter & Brune, 1983).

## RESULTS

Between 1980 and 1987 blubber samples from 108 bottlenose dolphins were assessed for the presence of chlorinated hydrocarbon residues. Significant differences in the age distributions of animals sampled from 1980-1983 and 1984-1987 ( $\chi^2 = 17,2$ ,  $df = 5$ ,  $P < 0,01$ ) precluded comparison of overall differences with time. However, there were no differences in the mean PCB, t-DDT, DDT/t-DDT ratio and dieldrin levels of either calves or immatures sampled over the two time periods. No difference was found between the age distributions of dolphins sampled from the three geographic areas ( $\chi^2 = 10,49$ ,  $df = 10$ ,  $P > 0,05$ ). Comparison of PCB, t-DDT, dieldrin levels and PCB/t-DDT ratios from all sexually immature animals and mature males only, thus excluding any effects of female reproductive history, showed significant differences between geographic areas

Table 1: The mean concentrations of PCBs, t-DDT and dieldrin and PCB/t-DDT ratio found in the blubber of combined samples of calves, adolescents and mature male bottlenose dolphins taken from three geographic locations along the coast of Natal (North Natal coast - Durban to Zinkwazi - South Natal coast - Ifafa to Amanzimtoti - and the south Natal coast - Mzamba to Mtwalumi). The F value obtained from two way ANOVAs between geographic areas and the relevant significance levels are shown ( $P > 0.05^*$ ,  $P < 0.05^{**}$  and  $P < 0.01^{***}$ ).

Area	X PCB Conc.		ANOVA F value	
	$\mu\text{g/g}$	n	Mid Natal coast	South Natal coast
North Natal coast	20	28	2.37*	16.59***
Mid Natal coast	13	18		3.17*
South Natal coast	8.4	31		
	X t-DDT Conc.			
	$\mu\text{g/g}$	n		
North Natal coast	24	29	2.17*	11.27***
Mid Natal coast	14	15		2.11*
South Natal coast	8.7	31		
	X Dieldrin Conc.			
	$\mu\text{g/g}$	n		
North Natal coast	0.7	27	7.28**	9.52***
Mid Natal coast	0.1	14		0.87*
South Natal coast	0.2	27		
	PCB/t-DDT ratio			
		n		
North Natal coast	1.3	28	0.98*	8.09**
Mid Natal coast	1.3	15		4.07*
South Natal coast	1.4	31		



Figure 2. The relationship between PCB concentration and age (expressed as the number of growth layer groups - GLGs) in the blubber of bottlenose dolphins from Natal.

○ Females  
● Males

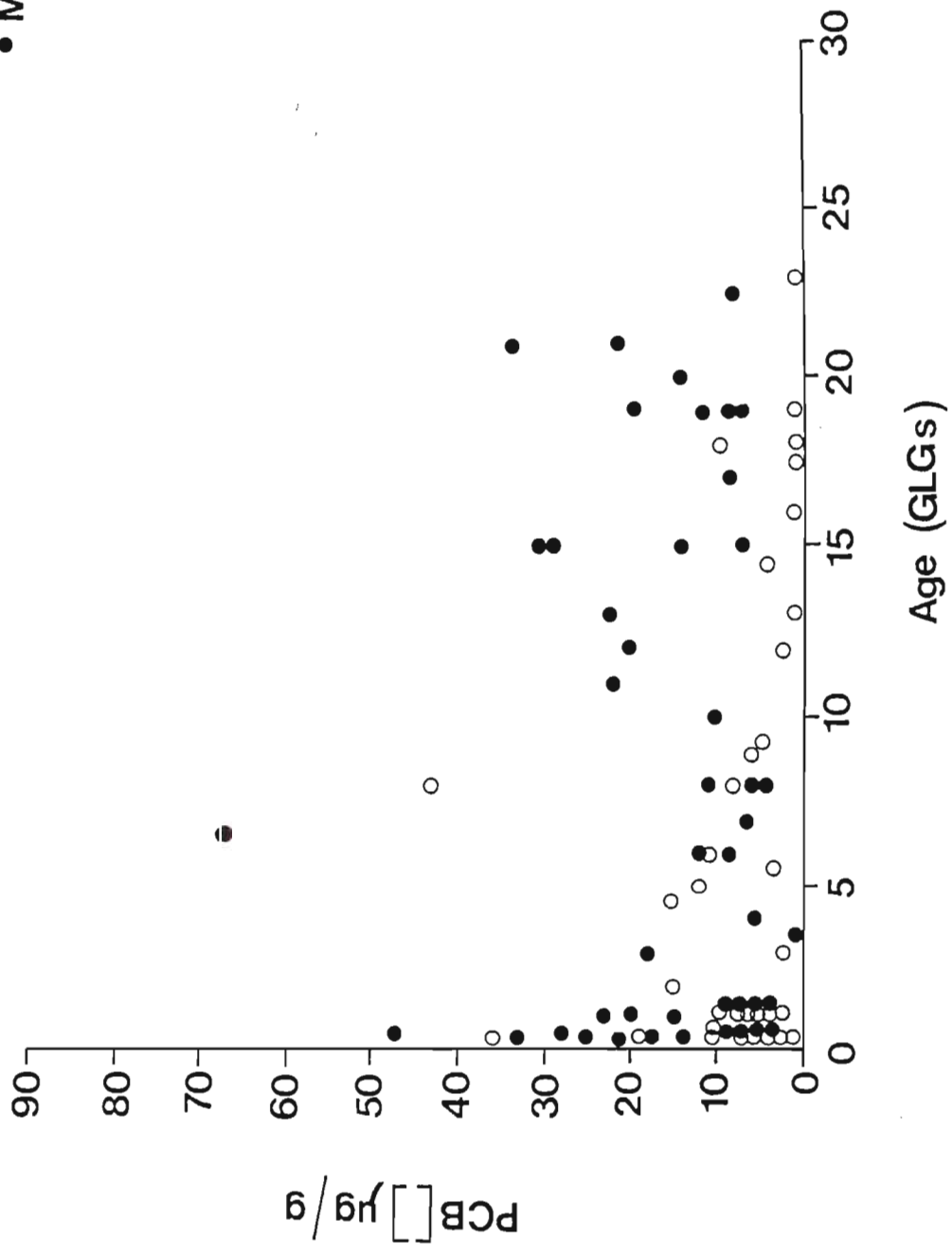


Figure 3. The relationship between t-DDT concentration and age (expressed as the number of growth layer groups - GLGs) in the blubber of bottlenose dolphins from Natal.

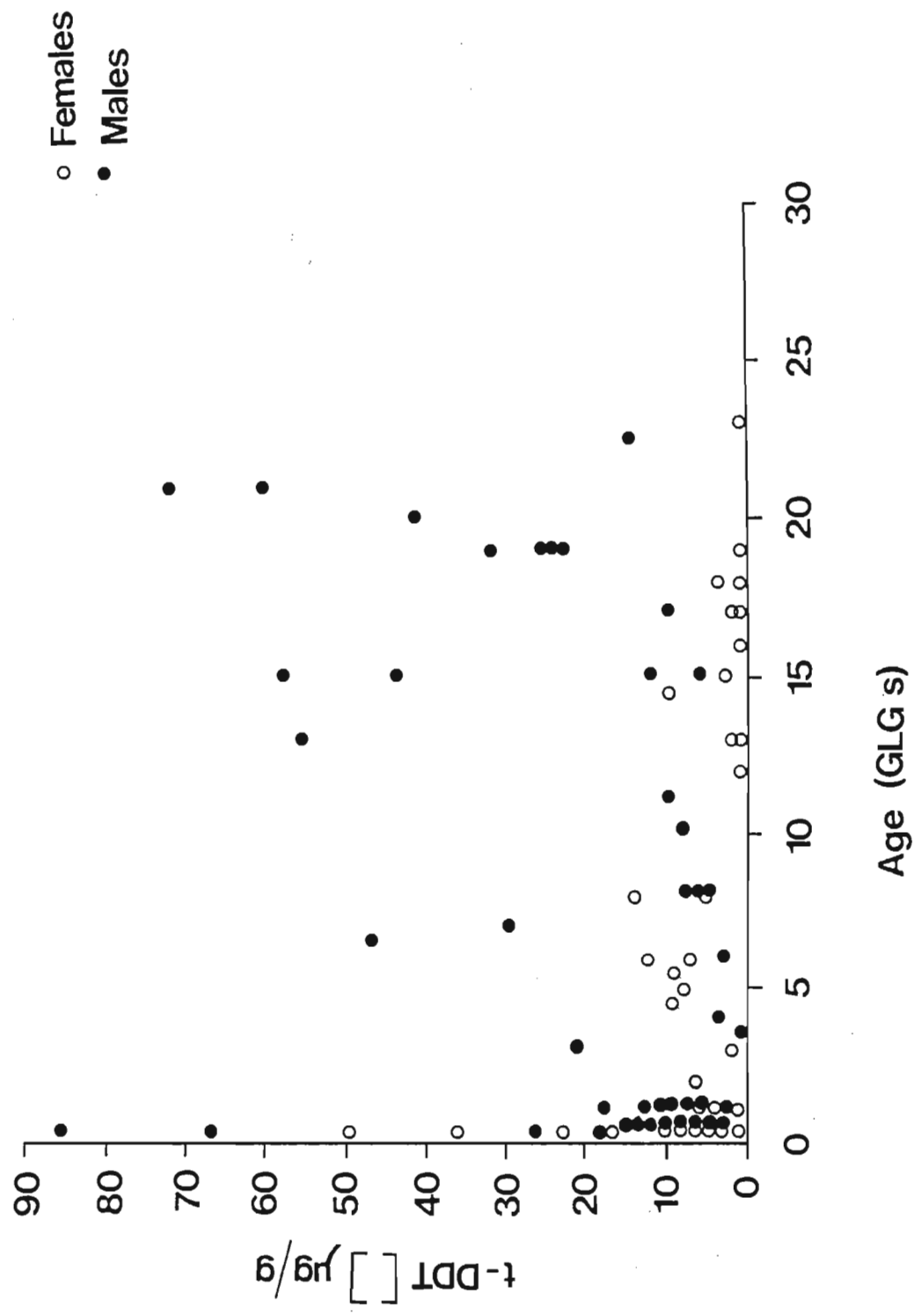


Table 2: The mean concentrations of PCBs, t-DDT, dieldrin in the blubber of four bottlenose dolphin age categories (calves <2 GLGs, adolescents >2 GLGs to <10 GLGs, mature males >10 GLGs and lactating females >10 GLGs). The F value obtained from two way ANOVAs between age categories and the relevant significance levels are shown ( $P>0.05^*$ ,  $P<0.05^{**}$  and  $P<0.01^{***}$ ).

Age Category	X PCB Conc.		ANOVA F value		
	$\mu\text{g/g}$	n	Adolescents	Mature males	Lactating females
Calves	10	38	0.97*	5.75**	10.09***
Adolescents	14	18		0.41**	5.93**
Mature males	16	17			27.99***
Lactating females	2.5	14			
	X t-DDT Conc.				
	$\mu\text{g/g}$	n			
Calves	10	37	0.05*	55.44***	4.14**
Adolescents	11	18		160.8***	9.26**
Mature males	38	16			273.41***
Lactating females	1.3	13			
	X Dieldrin Conc.				
	$\mu\text{g/g}$	n			
Calves	0.5	33	0.34*	2.2*	2.84*
Adolescents	0.4	15		1.59*	3.28*
Mature males	0.2	15			42.5***
Lactating females	0	8			

Figure 4. The relationship between total blubber t-DDT load and age (expressed as the number of growth layer groups -GLGs) of bottlenose dolphin calves, adolescents and mature males from the north Natal (triangles), mid Natal (closed circles) and south Natal coasts (squares) and lactating females (open circles).

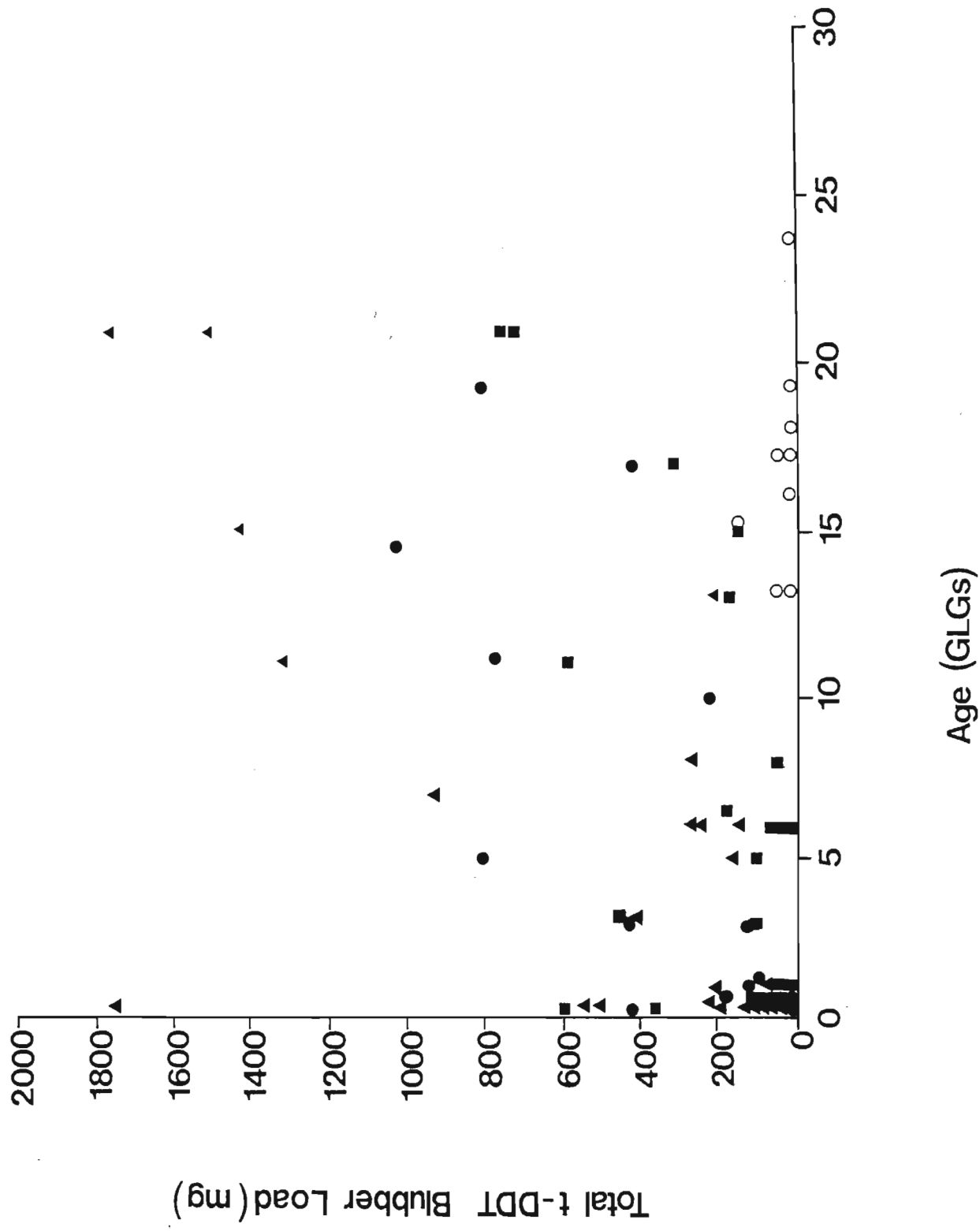


Table 3: The calculated mean total blubber load of PCBs, t-DDT and dieldrin in four age categories of bottlenose dolphins (calves <2 GLGs, adolescents >2 GLGs to <10 GLGs, mature males >10 GLGs and lactating females >10 GLGs). Loads were calculated from the estimated total blubber mass x blubber residue concentration in ug/g (blubber mass was estimated from a regression of blubber mass on length,  $Y=aX+b$ ,  $a=0.1886$ ,  $b=-20.208$ ,  $r=0.9$ ).

Age category	Total blubber load (mg)		
	PCBs	t-DDT	Dieldrin
Calves	102	94	5.3
Adolescents	265	226	7.4
Mature males	423	814	4.0
Lactating females	67	33	0.9



Figure 5. The relationship between blubber PCB, dieldrin and t-DDT concentrations and the number of ovarian scars in female bottlenose dolphins from Natal.

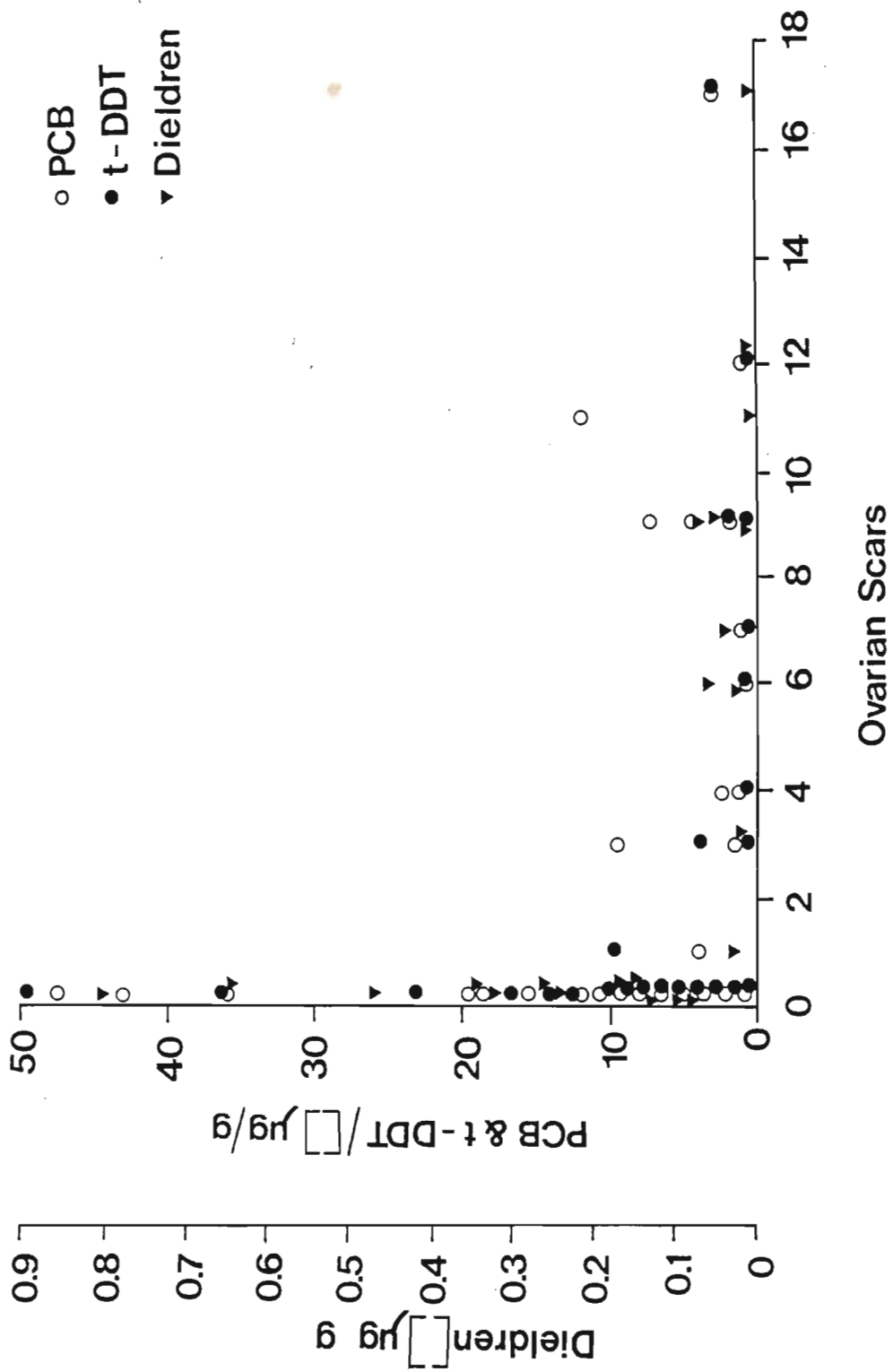
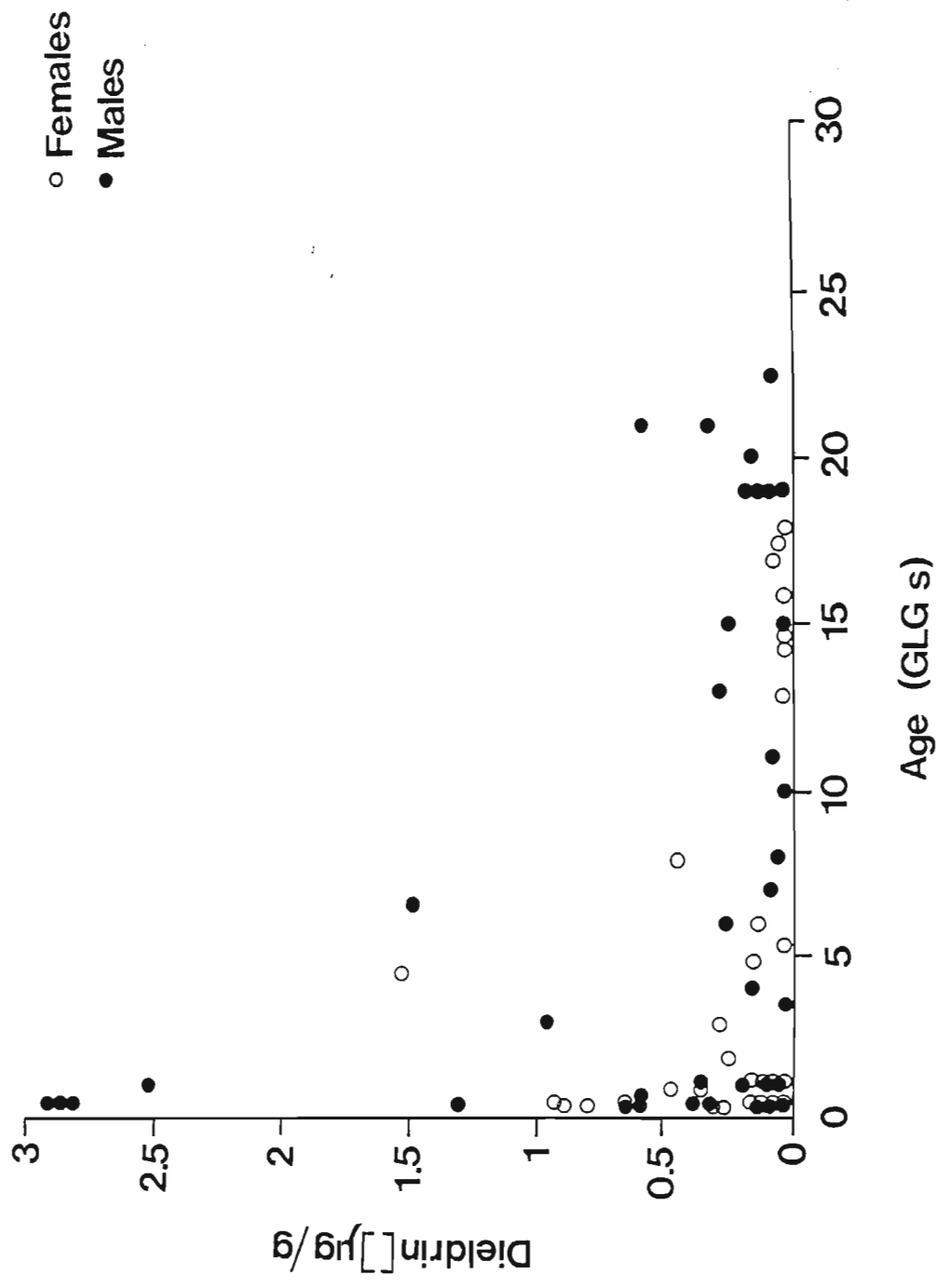


Figure 6. The relationship between dieldrin concentration and age (expressed as the number of growth layer groups -GLGs) in the blubber of bottlenose dolphins from Natal.



(Table 1). The mean DDE to t-DDT ratio of all samples was 0,726 and no significant differences were found between the mean ratios of the three geographic areas (ANOVA,  $F=0,33$ ,  $P>0,05$ ).

Despite these area differences, insufficient sample numbers necessitated the pooling of all samples for further analysis. Too few resting and pregnant females (only three of each) were sampled to warrant statistical comparison with other age classes. There is a wide scatter of PCB and t-DDT concentrations in calves and young juveniles (<3 GLGs) (Figs. 2 & 3). In general, the concentrations of both residues in males appears to decrease between two or three GLGs and five or six GLGs (Figs. 2 & 3). Thereafter, concentrations for both PCBs and t-DDT seem to increase (Figs. 2 & 3, Table 2). Females display a similar pattern up to an age of some eight GLGs (Figs. 2 & 3, Table 2). However, the levels of PCBs and t-DDT in the blubber of females greater than 12 GLGs in age are distinctly lower than those of males at a corresponding age (Figs. 2 & 3, Table 2).

Age related patterns and geographic area differences are even more evident if the total blubber load of residues is considered, as shown for t-DDT in Figure 4. Total blubber burdens (minimum body burden) for each age class were calculated from total blubber weight, assuming an equal residue level throughout the blubber (Table 3).

The decline in the blubber residue concentrations of females occurs at the age at which females reach sexual maturity and is subsequent to their first or second ovulation (Fig. 5). Mean PCB and t-DDT levels of females pre and post one or two ovulations were significantly different (10,2 ug/g and 3,04 ug/g, ANOVA,  $F=9,96$ ,  $df=27$ ,  $P<0,01$  and 6,95 ug/g and 1,49 ug/g, ANOVA,  $F=78,63$ ,  $df=26$ ,  $P<0,01$ , respectively) and were reduced by 70,2 % and 78,6 %, respectively.

In contrast to the pattern for PCB and t-DDT residues, dieldrin levels in males do not appear to increase significantly with age although females again show a reduction of levels between eight and 13 GLGs (Fig. 6), after the first or second ovulation (Fig. 5). Mean dieldrin

concentrations before (0,29 ug/g) and after (0,04 ug/g) one or two ovulations were significantly different (ANOVA,  $F=9,18$ ,  $df=18$ ,  $P<0,01$ ) the reduction being some 87,1 %.

## DISCUSSION

The residual profile of PCBs and t-DDT in the bottlenose dolphin is similar to that described for all other small cetaceans in which the presence of these organochlorines has been studied (Gaskin *et al.*, 1971, 1983; Gaskin, 1982; Fukushima & Kawai, 1980; Tanabe, *et al.*, 1980; Martineau *et al.*, 1987; Subramanian *et al.*, 1987). In the bottlenose dolphin, and all other species so far examined, the concentration of these residues is closely correlated with age until animals reach sexual maturity. Thereafter, females experience a marked drop in residue concentrations while males continue to accumulate residues throughout their lives. The reduction in female residue load has been ascribed to offloading by the female during pregnancy and lactation (Fukushima & Kawai, 1980; Tanabe *et al.*, 1980; Gaskin *et al.*, 1983; Martineau *et al.*, 1987).

Despite the obvious scatter, a product of the area differences in residue levels, mature male bottlenose dolphins show relatively high levels of both PCBs and t-DDT but low dieldrin contamination. The toxicity of dieldrin to cetaceans is unknown, however, the health of rats and dogs given daily oral doses of 10 ppm dieldrin was not impaired (Walker *et al.*, 1969).

Bottlenose dolphins on the north Natal coast accumulate mean levels of PCBs in excess of 19 ug/g while the most southerly animals have mean levels half this (Table 2). Residue concentrations at these levels may not be deleterious. Alzieu & Duguy (1979) consider that liver PCB levels in excess of 20 ug/g (lyophilised tissue), corresponding to blubber levels of between 50 ug/g and 200 ug/g (Wagemann & Muir, 1984), are levels at which the health of a dolphin may be at risk. However, Subramanian *et al.* (1987) have shown that increased blubber PCB and DDE concentrations

in Dall's porpoise from the northwestern north Pacific were correlated with decreased blood testosterone levels. Interestingly, the mean level of PCBs in these porpoises was less than half of that found in bottlenose dolphins in the current study, particularly on the north Natal coast, although DDE levels were similar. This implies that male bottlenose dolphins off Natal, especially the northern areas, may be subject to a reduced reproductive capacity.

The effect of PCBs, t-DDT and dieldrin on female marine mammals is unknown, although reproductive abnormalities in seals have been correlated with high concentrations of the former two residues (Helle *et al.*, 1976; Reijnders, 1986). Correlations between residue levels and reproductive abnormalities in cetaceans have been more difficult to establish. No ovarian abnormalities were observed in beluga whale females from the St. Lawrence estuary, Canada, in which the PCB and t-DDT levels were considerably higher than those observed in the present study (Martineau *et al.*, 1987).

The depuration of a females residues through lactation and the effect of this on the calf needs further investigation. Fukushima and Kawai (1980) have proposed that first born dolphin calves receive a fourfold higher initial burden of PCBs and t-DDT than subsequent calves and that in excess of 90 % of this is transferred through lactation. This study provides evidence that almost 80 % of a bottlenose dolphin females residue load is passed to a first born calf. Thus, residue levels of females reaching reproductive age and the rapidity of residue transfer to the calf are of more concern.

Assuming an 80 % transfer of a females PCB and t-DDT load, a 20 % concentration of residues in mothers milk (Kawai and Fukushima, 1980) and a neonatal milk consumption of 4 l daily (Cockcroft & Ross, 1989), a number of calculations can be performed. If females prior to their first ovulation have residue concentrations similar to immatures (13,5 ug/g PCBs, 11,25 ug/g t-DDT and 0,38 ug/g dieldrin), milk residue concentrations of primiparous females would be 2,7 ug/g, 2,25 ug/g and 0,08 ug/g for PCBs, t-DDT and dieldrin, respectively. Milk at these residue

concentrations would load the calf with 10,8 mg/day of PCBs, 9 mg/day of t-DDT and 0,32 mg/day of dieldrin. This represents an estimated transfer of approximately 4 % of the mothers total load per day indicating that transfer of the mothers load would take some seven weeks.

From the total blubber loads in Table 3 it is evident that an 80 % transfer of all residues results in a transfer of 198 mg of PCBs, 192 mg of t-DDT and 6,4 mg of dieldrin to the calf. This would result in two month old calves with residue concentrations of PCBs and t-DDT in excess of 30 ug/g and dieldrin levels of some 1 ug/g (given that mean blubber mass at this age is about 6 kg).

In this study, the few neonates and weaned calves which approached concentrations at these levels may have been first born calves and although these residue concentrations may not be harmful (Alzieu & Duguy, 1979), the initial high dose and rapid transfer may constitute a greater risk than the actual residue levels suggest. Carstens *et al.* (1979) have shown that monkey infants ingesting mothers milk with PCB concentrations between 0,154 ug/g and 0,397 ug/g show signs of PCB intoxication within two months of birth. They suggest that the foetus and neonate have increased susceptibility to PCB intoxication. In view of the recent work suggesting that marine mammals lack certain PCB metabolising enzymes and may therefore be more susceptible to PCB toxicity than terrestrial mammals (Tanabe, 1988; Tanabe *et al.*, 1988), it is likely that dolphin neonates may be particularly susceptible to a heavy, rapid, initial PCB, and perhaps t-DDT and dieldrin transfer. Especially, considering the evidence that PCBs are strong immunosuppressive agents (Safe, 1984).

The value of organochlorine residues as tracers in determining some physiological and ecological aspects of marine mammals is receiving increased attention (Tanabe *et al.*, 1987; Martineau *et al.*, 1987; Subramanian *et al.*, 1988). In the present study it is evident that there are clear differences in PCB and t-DDT levels between bottlenose dolphins, excluding mature females, on the north Natal coast and those on the south Natal coast. Animals on the north Natal coast show



higher levels of PCBs, t-DDT and ratio of the two residues, reflecting the greater agricultural and industrial use of this area. The delineation of geographic areas in this study was arbitrary and we are hesitant to suggest that they correspond to real separations, but unfortunately, the data were too few to analyse for smaller scale distinctions such as home ranges. However, Ross *et al.* (1987), in a study of the long shore distribution of Natal bottlenose dolphins, suggest that these animals frequent 'preferred areas', possibly co-incident with 'home ranges'. This is supported by evidence that dolphins on the south Natal coast take fish from the hooks of fishermen (Garratt, 1980; Ross *et al.*, 1987) a trait not evident in dolphins on the mid or north Natal coasts. The present data and the latter evidence imply little interchange of animals inhabiting the north and south coasts. This has clear implications for our understanding of the dynamics of the Natal population and suggests that sections of the population may be isolated and should be treated as such when estimating population parameters.

Dieldrin levels from bottlenose dolphins, excluding mature females, show an analogous pattern of separation between north and south Natal coasts. Of interest in these data is that levels on the north Natal coast are also significantly higher than those on the mid Natal coast, suggesting, further, a clear geographic separation of sections of the bottlenose dolphin population along this coast. The presence of dieldrin in the blubber of these animals is of concern considering that its use in South Africa was apparently terminated in 1979 (Van Dyk *et al.*, 1982). The relatively high levels in animals from the north of Natal indicate that there may have been recent input in this area, unless, as for PCBs (Tanabe, 1988; Tanabe *et al.*, 1988), marine mammals are deficient in the enzymes necessary to metabolise dieldrin.

There is no evidence in the present results that older, probably post reproductive, females accumulate residues in the same manner as males. This phenomenon has been observed in Dall's porpoise (Subramanian *et al.*, 1988) and short-finned pilot whales (Tanabe *et al.*, 1987). The latter authors attributed this to a probable reduced number of parturitions with increase in age consistent with the findings of Marsh & Kasuya (1984) that female short-finned pilot whales have

a significant post reproductive stage in their life history. Marsh & Kasuya (1986) reviewed the evidence for senescence and change of reproductive role of female cetaceans, but the few data available from the present study suggest that this does not occur in bottlenose dolphins.

Present results also enable an assessment to be made of the DDT inputs into the system. It has been suggested (Aguilar, 1984; Addison *et al.*, 1984; Borrell & Aguilar, 1987) that a DDE/t-DDT ratio which exceeds 0,6 indicates a reduction, or even termination of new DDT into that system. Unfortunately, differences in the age structure of animals sampled over the period of this study prevented a comparison between years. However, for all age/sex groups throughout this study, the average ratio was 0,76 suggesting no recent input of DDT into these coastal waters. Mean ratios on the north Natal coast were also no different from those in the other two geographical areas even though DDT is still being used in northern Natal to combat malaria (Van Dyk *et al.*, 1982).

Mortality of bottlenose dolphins from accidental entanglement in Natal's anti-shark nets accounts for almost 4 % of the estimated population annually (Cockcroft & Ross, in press). Predation by sharks could also account for a significant number of animals, particularly calves, each year (Cockcroft *et al.*, in press). The effects of a possible mortality of first born calves and a possible reduction of male reproductive efficiency on the Natal population are unclear and will probably vary according to area and the residue load of animals in the area. If these effects are real they are likely to be of relevant to a population already stressed by other factors, particularly as sections of the population appear to be relatively discreet. Any attempt at conservation and management of these animals must take cognisance of these facts.

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## CHAPTER EIGHT

## CONCLUSIONS

The two forms of bottlenose dolphin inhabiting Natal waters can be differentiated by size and distribution (Ross, 1984; Ross *et al.*, 1986; Ross & Cockcroft, 1989). The larger form occurs in deeper pelagic waters while the smaller, inshore bottlenose dolphin, the subject of this work, is restricted to coastal waters, approximately within the 30 m isobath (Ross *et al.*, 1986).

Previous work suggests that there are less than 1000 bottlenose dolphins in Natal's coastal waters (Ross *et al.*, in press). Their group size ranges from less than ten to up to several hundred, although the mean group size is between 40 and 50. Groups are sighted more frequently in particular areas of the Natal coastal belt and these localities are separated by similar distances, implying that they represent 'preferred areas' of habitation (Ross *et al.*, 1987). The amount of mixing between adjacent groups is unknown, although the presence of a group specific behaviour -stealing fish from the hooks of fishermen - in the group of dolphins off Margate, suggests that little occurs (Ross *et al.*, 1987).

The contribution of the present work to the understanding of the natural history of bottlenose dolphins is summarised in the following nine paragraphs.

Although bottlenose dolphin calves are born throughout the year, most births occur between spring and summer after a gestation period of one year. This infers that mating also is non-seasonal, but is primarily a summer activity. Calves are born at a length of approximately 103 cm and a mass of nearly 14 kg. The mother attends the neonate closely, the calf swimming in a negative pressure vortex high up on the females flank, its respiration and activities governed by her. The first few weeks *post partem* are characterised by an increase in the independence of the calf, which is evident from the calf's acquisition of swimming skills and its ability to regulate its own respiration rate.

During the following months the calf becomes progressively more independent until, at an age of

between six months and one year, it is able to take solid food. The first year is marked by a rapid increase in mass as the calf develops. Although the calf probably acquires nutritional benefit from the mother's milk only up to about one year of age, suckling may continue for as much as three years, during which time the mother and calf bond is strengthened. This extended suckling period may also provide the calf with the learning and socialisation skills necessary for its eventual independence from the mother.

Juvenile growth is rapid, but slows progressively with the approach to puberty. Females reach sexual maturity at about nine or ten years of age and may undergo a series of rapid ovulations before fertilisation occurs. Subsequently, the mean ovulation rate is about 0.3/year indicating that the interval between calves is about three years. Males reach sexual maturity at least two or three years later than females and at the onset of puberty undergo a growth spurt in mass, which may be significant in male dominance and sexual interaction. Physical maturity and asymptotic size, in both sexes, are attained at approximately 15 years. Both sexes live equally long and may reach ages in excess of 40 years.

There are distinct differences in the size and species selection of prey eaten by the various sex and size classes of dolphins within groups, although some dietary overlap occurs. Mothers and their calves feed close inshore on small benthic sandy-bottom and reef-associated prey, while other sex and size classes feed further from shore. This infers that the sex and size class segregation within schools, may, apart from any social function, effectively partition some of the available food resources. Lactating females and growing calves have a greater energy requirement than other classes of dolphins within the group. It is likely that nearshore food resources are more predictable and the prey more abundant and easily captured than those further from shore. Thus, the use of nearshore resources by lactating females and their calves contributes to their predominance in net catches.

The natural mortality patterns of bottlenose dolphins are unknown, but examination of shark

stomachs indicates that shark predation may be an important component in their natural mortality. An estimated 22 dolphins, 2.4 % of the estimated population, are killed by sharks annually, and although many of these may be a result of scavenging from animals killed through interaction with man, some may be from direct predation. There is evidence that, prior to the introduction of nets, the shark population was fourfold higher than it is at present (Wallet, 1978; Cliff *et al.*, 1988). If this applies to all species, including those implicated in dolphin predation, predation pressure on dolphins may have decreased as shark populations were reduced. Although this is speculative, it suggests that shark predation pressure may have been replaced, to an unknown extent, by net captures.

Incidental capture in shark nets accounts for some 32 bottlenose dolphins annually, about 4 % of the estimated population, and lead to an assessment of the factors implicated in dolphin capture. Although the seasonal distribution of bottlenose dolphins is unknown, the seasonality of capture implies that either conditions or food resources may seasonally limit dolphin distribution in the nearshore area. The majority of enmeshed dolphins had almost full stomachs, implying that capture occurred either during feeding or just after. Analyses showed that capture was significantly related to current direction and sea temperature, both of which may induce short term and seasonal prey movement in the nearshore region. These data indicate that prey distribution and movement are closely associated with capture and infer that nets may act as aggregating devices for prey species.

Captures between 1980 and 1987 occurred at random along the Natal coast but capture rates were found to be directly related to the number of nets in a particular area. This may also relate to nets acting as prey aggregation devices, although greater catch rates with increasing net area are common in fisheries. It is significant that very few dolphins younger than six months of age were captured and that the average girth measurements of captured calves coincides almost exactly with the size of the net mesh. Although there are a number of possible reasons for this coincidence, it nevertheless implies that an increase in mesh may increase the minimum size of

dolphin captured and perhaps reduce the total catch.

Incidental capture in shark nets is probably not the only cause of bottlenose dolphin mortality resulting from interaction with man. Dolphins accumulate industrial and agricultural lipophilic pollutants which are either wind-borne or water-borne into the nearshore environment. In mature males these pollutants accumulate with age and reach levels which may inhibit reproductive efficiency. Females accumulate pollutants up to the age of sexual maturity whereupon primiparous females transfer approximately 90 % of their total load to their offspring through lactation. Circumstantial evidence suggests that the lactational transfer to the first-born calf takes place within about eight weeks of birth, giving the newborn calf a high, possibly fatal, dose of these toxic compounds. Dolphins captured on the North and South Coasts show significantly different levels of pollutants, suggesting little mixing between animals at the extremes of the Natal distribution.

The age and sex structure of the Natal bottlenose dolphin population is unknown and estimates of the replacement rate based on the biased net catch are equivocal. However, the extended calving period (3 years) and the age of females at first birth (probably 10 to 11 years), suggests that recruitment is low and that the annual rate of population increase is probably a maximum of 6 % (Reilly & Barlow, 1986). If the population of bottlenose dolphins in Natal is indeed of the order of 900 animals, then net mortality is close to or exceeds their replacement rate. However, population levels in excess of this level would have much improved chances of survival.

Perhaps the most crucial contribution of this work to the biology of bottlenose dolphins is its identification of aspects of their natural history which require more research. In view of the low estimated numbers of bottlenose dolphins and their apparently low replacement potential, a number of priority research proposals, originating from this present work, have been accepted by the Natal Dolphin Working Group of the Council for Scientific and Industrial Research.

The prime need is to determine how discrete the stock of bottlenose dolphins off Natal is. The depletion of small resident groups, temporally separated from other groups, is of greater significance than mortality to a large homogeneous population. Similarly, if the Natal stock of bottlenose dolphins is genetically distinct from other stocks and there is little or no recruitment from other areas, the significance of any depletion is greatly magnified.

Within the Natal coastal region, existing field studies using photo-identification of naturally marked animals and modified 'mark-and-recapture' techniques, should provide information on the extent and periodicity of movement, residency and individual association of bottlenose dolphins along the Natal coast. A combination of these field studies with the collection of skin samples, for biochemical analysis, may provide additional, more reliable information. (Such a study is planned and only awaits funding). Preliminary studies, using more advanced techniques, are underway. Muscle, liver and heart samples of freshly captured bottlenose dolphins are routinely collected for enzyme analyses in the hope that this will provide further information on group or stock identity.

An extension of these studies to include animals from far northern Natal (north of Richards Bay) and Transkei and Eastern Cape waters is required to determine the extent of mixing of bottlenose dolphins on the east coast of southern Africa and, therefore, to establish how discrete the Natal population is, as a whole. The results from these studies will determine whether proposals to manage and conserve bottlenose dolphins should be structured at either the individual group or stock level.

Ongoing population estimates are needed not only to refine techniques and obtain satisfactory estimates of numbers, but also to monitor population trend. Existing estimates have been based on aerial surveys along the inshore zone, relying implicitly on an inshore distribution of bottlenose dolphins, making no allowance for areas where the coastal shelf is wider and dolphins may occur further offshore. Furthermore, these aerial surveys have been undertaken during

periods of good weather and low water turbidity, usually during May, and assume that numbers and distribution are seasonally constant. To circumvent these shortcomings, a number of aerial and shore-based surveys have been initiated to monitor the abundance and distribution of bottlenose dolphins.

On the Natal South Coast the shallow inshore zone broadens to a maximum of some 8 km in the area between Amanzimtoti and Mzamba. This area is generally subject to high inshore water turbidity, due to river and industrial effluent, which can extend some kilometers out to sea depending on weather conditions. A number of offshore flights across this broad, shallow bank has shown that bottlenose dolphins frequent offshore reefs and banks, although still within the 30 m isobath (Ross, Cockcroft & Peddemors, unpublished data). The original 1985 aerial counts, done from the shoreline, probably missed these animals, which resulted in an underestimate of numbers.

Previous aerial estimates of population numbers have also taken no specific account of undercounting biases. In an effort to gauge the significance of any undercounting bias, a preliminary experiment was undertaken on the North Coast in which two aircraft flew along the shoreline five minutes apart. Two observers in each aircraft made seaward observations. The recorded sightings of both sets of observers were compared after landing to give an indication of undercounting bias. The results from three such flights suggest only a 25 % correlation of sightings between the two sets of observers. This has obvious significance for aerial assessments of populations and indicates that this work needs to be continued.

One way to elucidate further the problem of undercounting bias would be to census total inshore dolphin group numbers using closely spaced shore-based observers on coastal vantage points. During this census, regular shoreline flights would be undertaken for airborne observers to record dolphin groups and the numbers of animals in each group. Simultaneous shore and aerial group sightings would then be compared to assess dolphin group undercounting bias. Total counts of shore sighted dolphin groups, independently counted from the air, would then be compared with



the total number counted and number statistically estimated during the shoreline survey to provide an indication of number, as opposed to group, undercounting bias.

Not only are aerial and shore surveys significant for population assessment, but also for the monitoring of dolphin distribution. Catch and sighting rates of bottlenose dolphins off Natal show a peak from May to November. It is unclear whether dolphins move further offshore during the other months, or move out of Natal. This has clear implications for the understanding of group and population dynamics and work on the seasonal distribution of bottlenose dolphins off Natal is urgently needed. This requires regular, at least monthly, aerial, boat or shore transects. Recorded sightings by Natal Sharks Board meshing officers only partially fulfil this need as the observers are inexperienced and not on dedicated sighting transects. An obvious solution would be to conduct regular coastal flights to determine the presence or absence of dolphins and group sizes throughout the year, under varying environmental conditions. Existing shore or boat-based surveys provide similar information but are limited in the area which can be surveyed at any one time.

Additionally, unbiased estimates are needed of parameters such as the annual birth rate, seasonality of calving, calving interval, calf production per female and age specific mortality rates, to assess the population dynamics of bottlenose dolphins. Given the bias in the age and sex structure of the net catch, the acquisition of this information requires long-term study of free-ranging groups of animals, particularly through photo-identification of identifiable individuals. This work is also of value in defining residency, group size, habitat use, movement and interactions at and with the nets, and the influence of environmental and physiographic conditions on these parameters.

As a consequence of the importance of the above types of approach, two such studies of bottlenose dolphins off the Natal coast were proposed and subsequently initiated. A project on the Natal North Coast is examining aspects of the natural history of free-ranging bottlenose



dolphins, particularly group dynamics, habitat use and group movements. The second project, covering both the Lower North Coast and Upper South Coast, has similar aims but is combined with an investigation of the behavioural, environmental and physiographic factors which influence the capture of bottlenose dolphins in shark nets. It includes investigation of the physical environment around the nets, the acoustic and light properties of the nets and surrounding environment, and the temporal and spatial distribution of prey around the nets. This project, or perhaps an extension of it, should investigate the prevention or reduction of captures and assess such proposals as the removal of certain nets, an increase in mesh size and the use of active and passive acoustic and visual devices to demarcate the nets.

An obvious enhancement of both the above projects, given adequate future funding, would be a combination of present field work with biochemical and genetic work. This would enhance understanding of individual relationships, group dynamics and the sex composition of bottlenose dolphin groups.

Studies on the natural history of bottlenose dolphins in Natal need to be compared with unexploited populations such as those in the Eastern Cape. Eastern Cape bottlenose dolphins are not subject to capture in nets and their pollutant levels are lower than those of animals from Natal (Cockcroft *et al.*, in press). Studies similar to those reported and proposed here on the natural history of Eastern Cape animals could provide unbiased data for comparison with results from Natal. This would provide a factual basis for management and conservation proposals for Natal bottlenose dolphins.

It is important that the dissection of captured animals and the monitoring of environmental and physiographic conditions associated with each capture be continued for the collection of a long-term series of data. Further investigation of females, particularly mothers with calves, should yield better estimates of reproductive data such as ovulation rates, length of lactation, gestation time and calving period. An accumulation of feeding data for bottlenose dolphins

affords an assessment of dietary changes which may result from environmental degradation or competition with fisheries, both recreational and commercial. A larger sample of pollutant residue levels, from both males and females, is important in monitoring variations in the long-term degradation of the inshore environment. This study should be combined with an assessment of dolphin distribution in relation to sources of pollutants, and of the animals' health and reproductive efficiency as an indication of pollutant effects, particularly in males.

Despite the limitations of research on captive dolphins, they provide an ideal opportunity for investigations which complement existing studies on free-ranging animals. The methodology and preliminary results for genetic typing and biochemical analyses can be gained from animals already in captivity. Similarly, experimental evaluation of the responses of trained captive animals to nets could augment studies of the reasons for dolphin capture and could help to identify means and methods of preventing captures.

Lastly, captive studies provide an ideal training ground for prospective researchers. They afford an opportunity to assess growth rates in relation to hard tissue deposition and food intake and to study digestion rates and assimilation efficiency, reproductive cycles (endocrine and exocrine), developmental and behavioural studies, and the feasibility of manipulative techniques such as non-invasive tag attachment.

## INTRODUCTION AND CONCLUSIONS REFERENCES

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