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ECOLOGICAL STUDIES OF BOTTLENOSE AND HUMPBACK DOLPHINS IN MAPUTO BAY, SOUTHERN MOZAMBIQUE

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ECOLOGICAL STUDIES OF BOTTLENOSE AND HUMPBACK DOLPHINS IN MAPUTO BAY, SOUTHERN MOZAMBIQUE

by

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ABSTRACT

The ecology and population biology of bottlenose and humpback dolphins inhabiting the Maputo Bay, Southern Mozambique were studied through boat based photo-identification surveys and behavioural methods between December 1995 and December 1997. Data from preliminary surveys carried out in 1992 are also included.

Bottlenose dolphins occurred throughout the year in Maputo Bay, but were sighted infrequently (36% of surveys). Their occurrence and group size were significantly larger during winter. Group size of bottlenose dolphins not differ significantly between months, daylight hours, semi-lunar tidal cycles and depth.

Most identifiable bottlenose dolphin individuals had low site fidelity, but nursing females had relatively high site fidelity, implying that Maputo Bay is a nursing area. The group dynamics of bottlenose dolphins suggests a fluid (fission-fusion) social organisation. Age and sex appears to influence the degree of association between individuals,. An influx of bottlenose dolphins occurred during winter and influenced group size and occurrence.

Bottlenose dolphins occurred in restricted areas of the Bay, preferring the north eastern area (the pass between the Bay and the Ocean), and along the 3 km strip from the east coast of Inhaca Island. Their distribution here did not vary with depth, although they did not occur in intertidal areas.

Feeding dominated both frequency and proportion of time of bottlenose dolphin behaviour. Social behaviour accounted for a small proportion of time (10%) and was greater in open unsheltered areas. Neither season, nor depth, nor daylight, nor tides

influenced the proportion of time allocated to the types of behaviours. Non directional movement occurred on most of the sightings of bottlenose dolphins, but smaller groups of dolphins moved inshore at high tide late in the afternoon.

Few bottlenose dolphin births were observed and the numbers of animals born varied between years. Recruitment rates at six months and one year were low and mortality rates of calves appeared high, but were probably inaccurate because the fate of mother-calf pairs that left the area could not be established. Population estimates of the bottlenose dolphins varied between 170 and 526 individuals. The precision of these estimates was poor, because of high proportion of transient individuals which almost certainly violated some model assumptions.

Humpback dolphins occurred throughout the year in Maputo Bay, but were sighted infrequently (21% of surveys). The occurrence and group size of humpback dolphins were not influenced by season, months, daylight, semi-lunar tidal cycles and depth. Groups of humpback dolphins in Maputo Bay were the largest observed along the east coast of Southern Africa.

Most identified humpback dolphin individuals showed low site fidelity, but a relatively high proportion of individuals (including nursing females) had high site fidelity. Humpback dolphin groups had a fluid (fission- fusion) social organisation, but there was a large proportion of stable associations between resident individuals. Age and sex appears to influence the degree of association between individuals. An influx of humpback dolphin individuals occurred during summer but did not change group size or occurrence, suggesting the occurrence of an outflux of other individuals.

Humpback dolphins in the Bay ranged between the deep north eastern Maputo Bay to the southern intertidal areas. Most sightings occurred within 1 km from shore along the eastern coast of Inhaca Island, at variable depth.

Humpback dolphins spent more time feeding (57%) and travelling (30%) than socializing and resting, because of their movements between extensive intertidal areas and deep channels. Social behaviour contributed a small proportion of time (10%), but increased when humpback dolphins moved towards and within shallow sheltered areas. Neither season, nor depth, nor daylight, nor tides influenced the proportion of time allocated to the types of behaviours of this species. Non directional movement occurred on most of the sightings of humpback dolphins, thought this was significantly influenced by diurnal tides.

Few humpback dolphin births were observed and their numbers varied between years. Recruitment rates at six months and one year were low and mortality rates appeared high, but were probably inaccurate because the fate of mother-calf pairs that left the area could not be established. Population estimates of humpback dolphins varied between 105 and 308 individuals, but their precision was poor, because of a high proportion of transient individuals which almost certainly violated some model assumptions.

Maputo Bay is a feeding, breeding and nursing area for bottlenose and humpback dolphins. These species are threatened by intense fishing activity, habitat degradation, coastal development and disturbance by powerboats and other activities (tourism, port) carried out in and around Maputo Bay.

Their low estimated growth rates imply the implementation of precautionary conservation measures . The actual distribution of these species may reflect the deterioration of the habitats in the western part of the Bay. A coastal zone management plan to address environmental problems affecting the dolphin species need to be formulated and implemented.

PREFACE

This study was carried out in Maputo Bay, Mozambique between December 1996 and December 1997 under supervision of Dr. Vic Cockcroft and Prof. Mike Perrin. The study also includes unpublished data obtained by the author of this Thesis between January and March 1992. It was funded by SIDA- SAREC (Swedish Agency for Research and Education in Developing Countries) within the support program called, The Development of the Biological Research Capacity at the Department of Biological Sciences, Universidade Eduardo Mondlane. The Centre for Dolphin Studies, Plettenberg Bay had an important role in this project, through provision of valuable scientific and logistic assistance.

DECLARATION

This study represents the author's own original ideas and work and has not been submitted before in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text. One peer-reviewed paper resulting from this thesis was published and is presented in the Appendix 12.

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I also dedicate this work to my daughter Naira, who was born in this troublesome period of my life!

The African Women and culture:

About 100 years ago, men of African tribes in Southern Africa spent most time fighting with other tribes for the best land! Because man were always involved in war and most died, the African woman had an additional responsibility, apart from the household keeping and caring of children, of transmitting to the her children, their father's lineage, since birth. Every time her baby cried, the mother had to tell the whole husband's lineage. My mother taught me my lineage in the same manner:

Bambo
wa
Bambo Guissamulo
Guissamulo wa Macumbana
Macumbana wa Macandra
Macandra wa Bango
Bango wa Nhaguibila
Nhaguibila wa Libarra
Libarra wa Ndzadzi Madzindzela Kule.
Ndrau!

According to my lineage, I must not fear of the lightings, rain & storms!

CHAPTER 2. MATERIALS AND METHODS

INTRODUCTION

Maputo Bay is located in southern Mozambique between latitudes 25°35'S and 26°15'S and longitudes 32°35'E and 33°00'E (Figure 2.1) and its surface is 1100 km^2, excluding estuaries (Anonymous 1998). It lies in the transition zone between temperate and tropical climate with hot, but not very wet summers and dry winters (Kalk, 1995).

The study was carried out in the whole Maputo Bay area, but most survey effort (about 80%) was confined to an 18km wide strip of the Bay between Maputo and Inhaca Island, located at the north of latitude 26°07'S, where depth allowed surveys to be carried out regardless of the tidal height. However, within this area, effort was also unequally distributed: most surveys were carried out toward the eastern portion of the strip (Fig. 2.6). Occasionally, the southwestern part of the Bay was surveyed during high tide because of its shallowness that is less than 1 m deep). Surveys were not carried out at estuaries because shallow banks barred their mouths.

STUDY AREA

Depth, Sediments, Currents and Tides

The Bay is shallow, depth varies from 1 to 20 m (Sousa, 1982). The depth decreases from north to the south, but the 10 meters isobath is indented, forming channels surrounded by long sandbanks which run in the north-south direction (Figure 2.2). The intertidal area comprises 27.3 % of the surface, sand banks 2.2% and the subtidal area about 66.4% (Fig. 2.3 and Hydrographic chart no. 46659, 1995, INAHINA). Sandbanks emerge during low spring low tides (Chart 46659-M, INAHINA), giving the Bay a riverine appearance. The 20 m isobath is located at the northern part of the Bay and represents < 20% of the whole Bay area. 380 km^2 are less than 5 m and 171 km^2 are less than 10 m deep (Anonymous 1998).

The texture of the sediments in the subtidal area of the Bay varies from clay-silt (phi = 3.67) to medium size sand (phi = 1.73). The amount of clay-silt in the sediments varies from 0.09 to 32.02%. Medium and fine grain sands dominate the sediments of Maputo Bay, the finest mean grain size particles (phi>4) is most abundant in the west and southwest area of the Bay. Areas with grain size between 1-3 phi are dominant to the east and northeast of the Bay (Achimo 2000). There are small spots of coarse sediments in the central part of the Bay, along the shoal and sandbank edge (Achimo 2000). The sediment within an area deeper than 10 m consists of very fine sands with low silt content (<3%), (Cossa 1996). Medium-sized sand occurs in the channels located off the west coat of Inhaca Island, while fine sands occur in the southern part of Maputo Bay, within the 5 m isobath (Cossa, 1996).

An intertidal area ranging from 0.5 to 1.5 km wide surrounds Maputo Bay. Most of it is colonised by seagrass meadows. The few seagrass meadows which occur off Maputo city are composed of Nano*zostera capensis* (Martins, 2002), though most of the intertidal area off Maputo City is bare. About 140 km^2 of Maputo Bay is covered by seagrass meadows (Anonymous 1998). The most extensive meadows and large seagrass species diversity occur at Inhaca Island. Seagrass species of the western coast of Inhaca Island and inshore sandbanks are *Thalassodendrum ciliatum, Cymodocea rotundata, Halodule sp.* and *Zostera capensis* (Bandeira, 1991). Mangrove swamps and trees surround > 80% of the coastline of the Bay (Kalk 1995) and cover an area of 143 km^2 (Anonymous 1998).

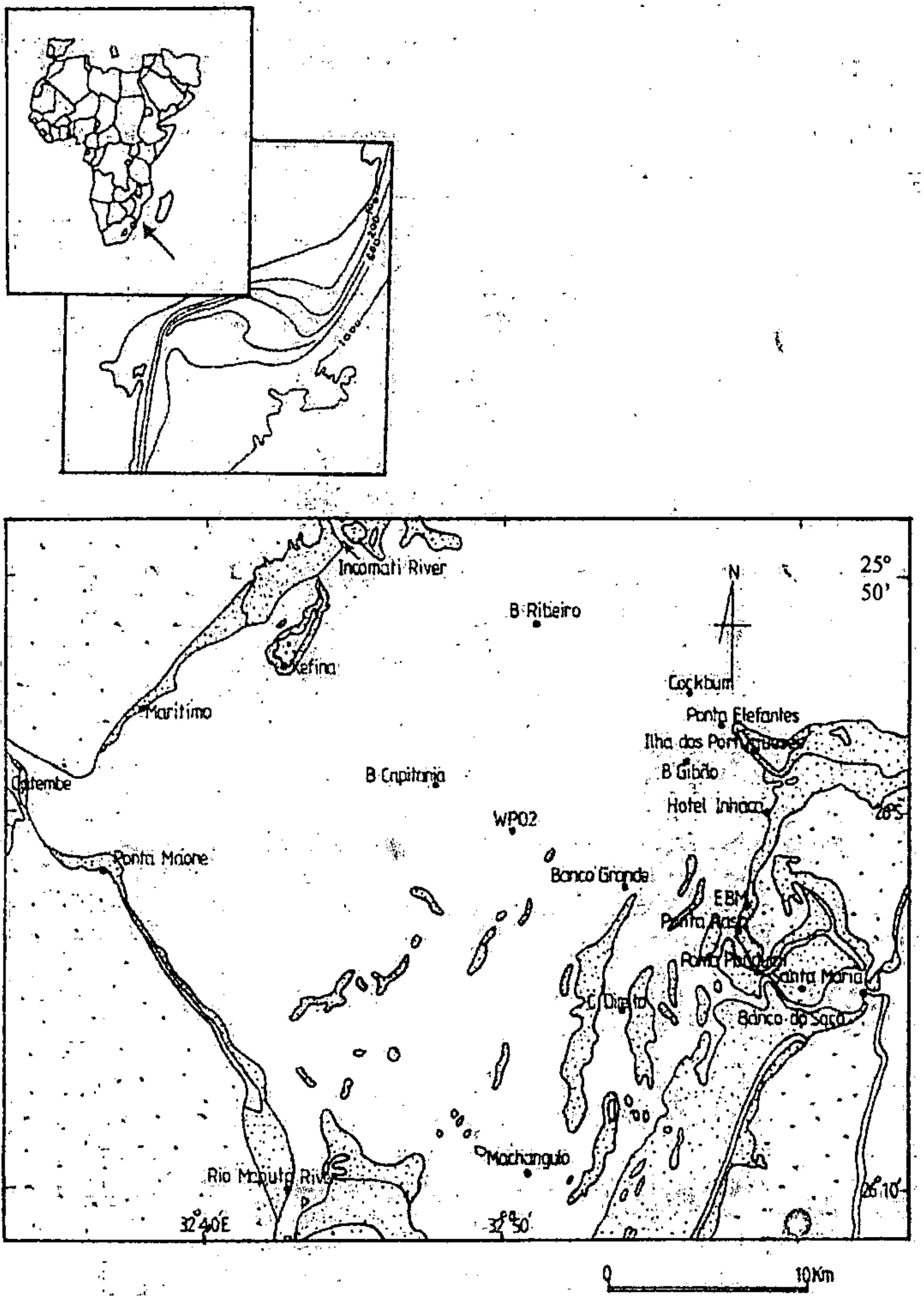


Figure 2. 1. Maputo Bay, location, of reference sites, rivers and waypoints of the survey routes and depth contour lines outside Maputo Bay. Sparsely dotted area represents land, and dense dotted area represents intertidal areas

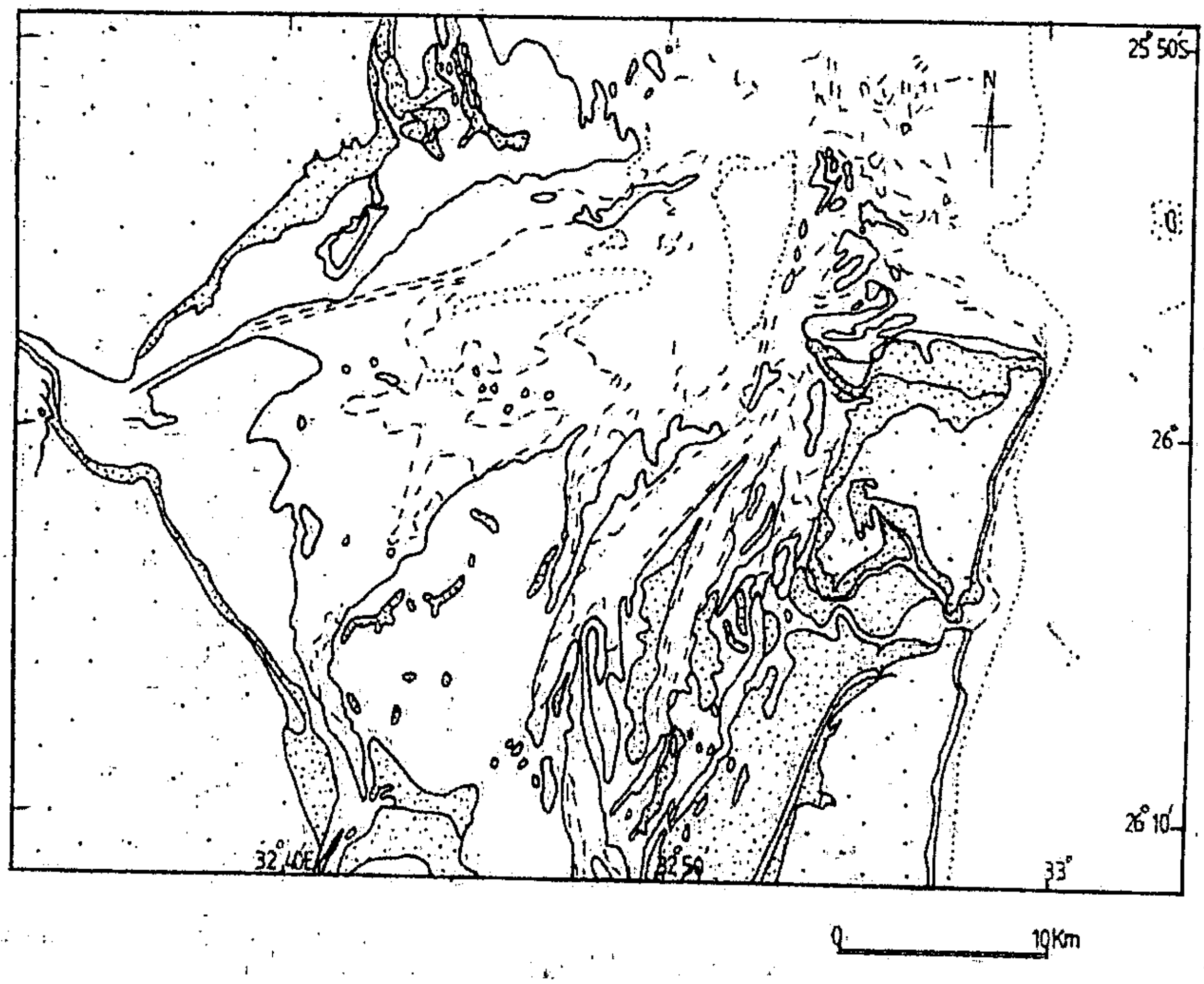


Figure 2.2. Maputo Bay: intertidal areas (dense dotted area) depth countor lines of 5 m (solid line), 10 m (dashed line) and 20 m (points). Sparsed dotted area represents the mainland and islands (From Chart 46659-M, INAHINA, 1986)

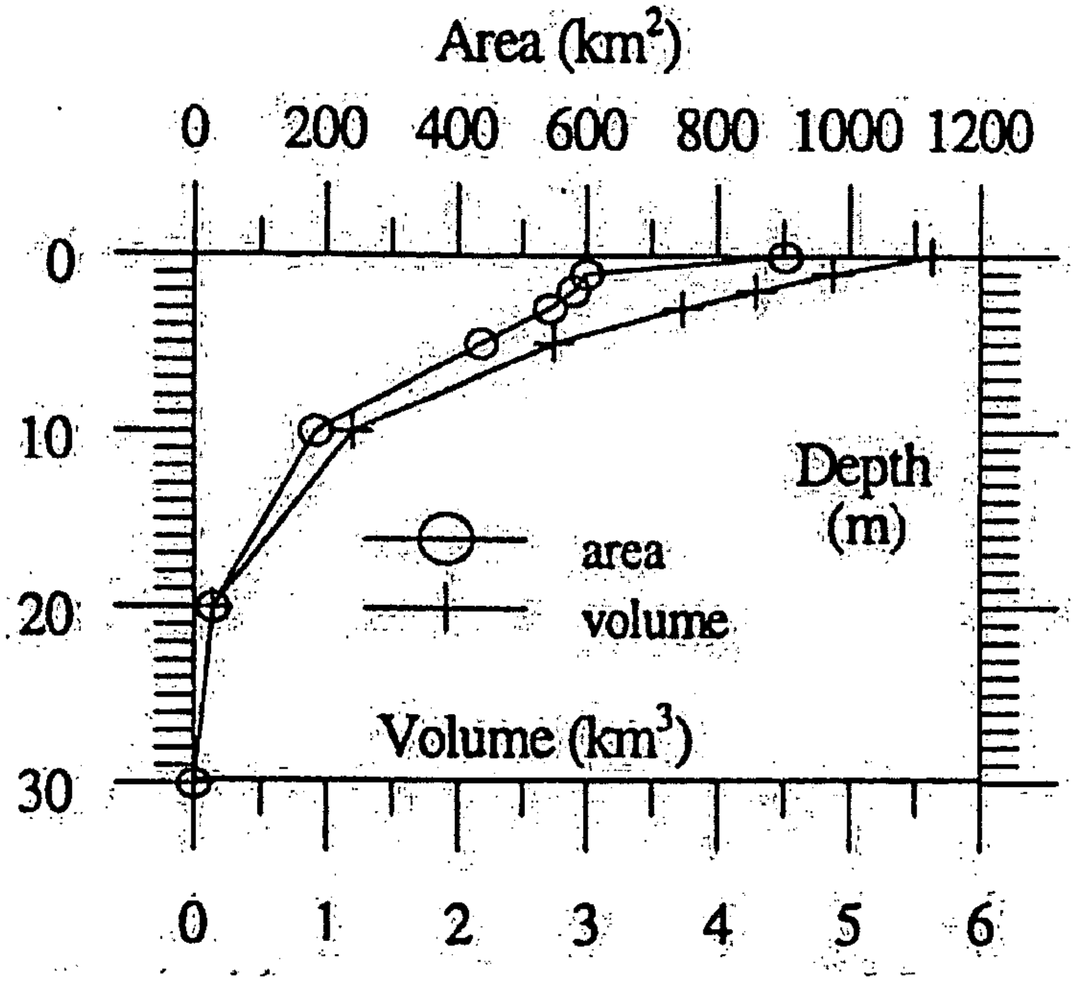


Figure 2.3. Hypsographic curve of Maputo Bay, showing the relation between depth, surface and volume (From Saide 2000)

Maputo Bay has two hydrodynamic regions: (i) a zone consisting of mixing waves of currents and tides at its west and southwest areas and (ii) a zone dominated by tidal current at the east and northeast areas of the Bay. The littoral drift in the Bay has two directions: (i) a major anticlockwise direction shore drift from north to south at the west and southwestern portions of the Bay which is driven by the northeast winds, and (ii) a clockwise shore drift from south to north at northern part of Maputo Bay (Achimo 2000). The velocity of tidal currents varies spatially, but attains the maximum speed range of 1.3 to 1.5 m/s during the dry season (Moura, 1973). In the open areas of the Bay, the currents are weaker, whereas in narrow, confined areas such as channels, a tidal prism predominates and the currents are very strong (Achimo 2000).

Daily tides are semi-diurnal and the mean tide range is 2 m; in good weather, waves in the Bay are low, < 0.5 m high, usually about 0.25 m, but occasional storms create waves of over 1 m high (Kalk, 1995). Tidal currents at the west shore of Inhaca have minimal velocity during mid-tide level (Kalk, 1995). Net water flow off the western coast of Inhaca Island is southward and is under tidal influence (Gove & Cuamba, 1989). Moon cycles influence the tidal ranges in the Bay, because it is shallow. There is a cycle of seven days of low daily tidal range (≤ 1.9 m between high and low tide marks) known as neap tides and seven days of high tidal range (from 2.0 m to 3.1 m), known as spring tides (Kalk, 1995).

Rainfall, river discharge and water transparency

Rainfall occurs throughout the year, for over 80 days in summer and about 30 days in winter, but is rarely heavy and the mean annual average is 900 mm; January and February are the wettest months (Fig. 2.4) with an average of 145 mm monthly rainfall and August is the month with the lowest rainfall (25 mm) (Kalk 1995). Winds blow gently from the north-east or from south west, but there are occasionally severe storms, lasting a few hours in the afternoon during summer months (Kalk, 1995). In addition , the area is affected by frontal systems in winter (Kalk 1995)

Rivers affect the marine environment off the western coast of Maputo Bay. Five rivers discharge into the Bay: The N'komati River in the north and the Maputo River in the south. The remaining three rivers - Umbeluzi, Matola and Tembe - form the Espírito Santo Estuary at the western Maputo Bay (Sousa, 1982). The N'komati, Umbeluzi and Maputo rivers have the largest flow, discharging into the Bay 6000 million m^3 of water per year (about 16.5 million m^3 /day). The largest discharge takes place during summer (rainy season), while in the winter (dry season) the water flowing into the Bay is 800 000 m^3/day (Anonymous 1998). Therefore river flow dilutes strongly the seawater during the rainy season, at the north-west around the mouth of N'komati River and in south-west of the Bay, in the Maputo estuary (Anonymous 1998). River flow recorded at the most downstream stations (during 1995 and 1997 is shown in Figure 2.5 (Unpublished data from National Directorate of Water Affairs, Mozambique).

Water transparency, off the western coast of Inhaca Island, measured as Secchi depth has a mean of 3 m, but over the coral reef it attains 5 m on calm days (Kalk, 1995). In December, a gradient of water transparency, caused by river run-off; is observed in Maputo Bay, ranging from less than 1 m in the western coast of Maputo Bay to about 10 m towards Portuguese Island, north-eastern Maputo Bay (Anonymous 1998).

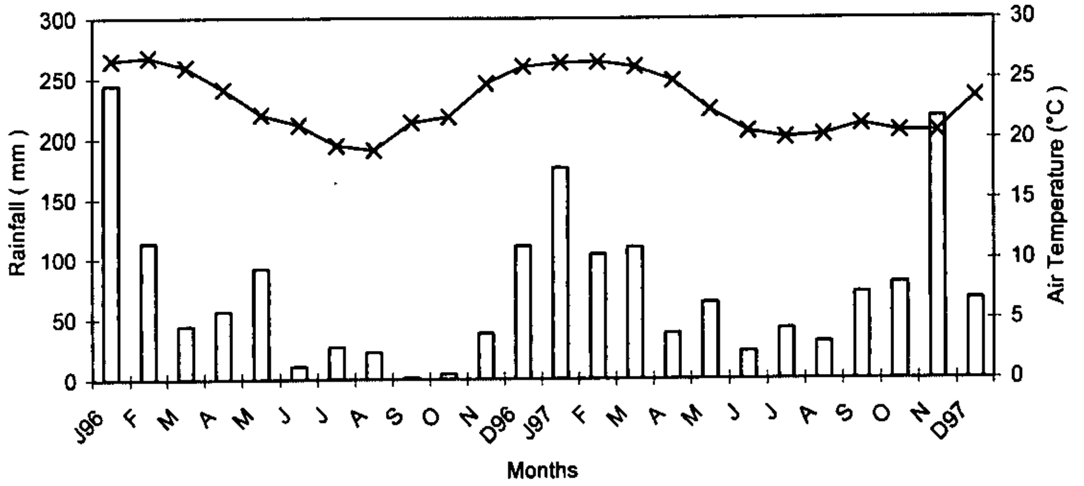


Figure 2.4 Mean monthly rainfall (bars) and mean monthly air temperature (line) measured for Maputo Bay between January 1996 and December 1997 (Unpublished Data from the Weather National Institute of Mozambique).

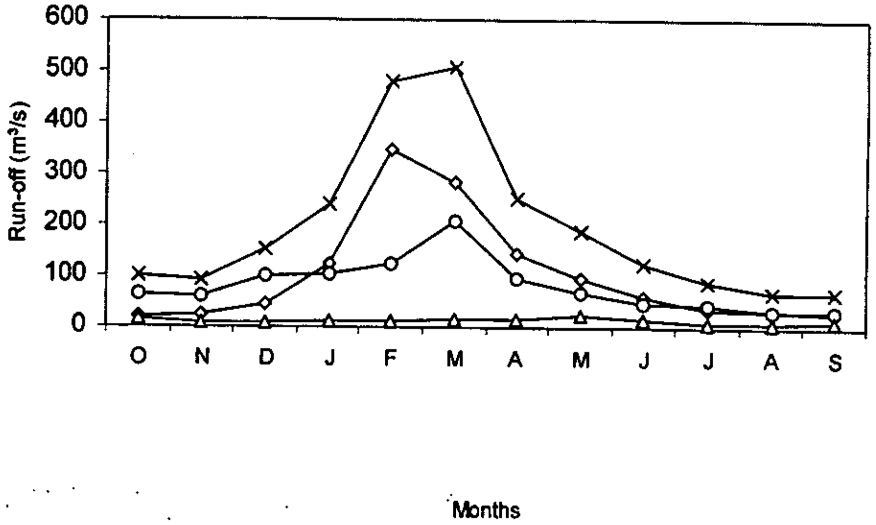


Figure 2. 5. Mean monthly river run-off (m^3/s) which entered Maputo Bay between December 1995 and December 1997 (Unpublished data from National Directorate of Water) (x= total river run-off,◊ = Maputo River Run-off ,o = N'Komati River run-off ,Δ = Unbeluzi River Run-off),

Salinity and water temperature.

The oceanography of the Bay is not well known, except for some fragments such as the Espírito Santo estuary (at the western part of the Bay) and the west coast off Inhaca island (at the eastern part of the Bay). At the Espirito Santo estuary (in a river mouth located western Maputo Bay), data from 1969 (Martins & Costa 1972) report high salinity during winter, peaking in September, and decreased salinity during summer, when river run-off increases. Water temperature varied between 19.5°C in July to 26.7°C in December (Sousa, 1982). At the eastern part of the Bay, mean water salinity is 34 ppm (Kalk, 1995), varying between 33.33 to 35.03 ppm (Gove & Cuamba, 1989; Saide, 2000). Minimum water temperature was 18° C in July. Surface water temperatures measured between August 1995 to January, 1996 increased steadily from 21°C to 37°C (Pinto, 1996). Water surface salinity off the west coast of Inhaca Island was lower in August (32ppm), but was around 42ppm from September to January during low tide (Pinto, 1996). No stratification occurred in the water column off the eastern part of Maputo Bay (Gove & Cuamba, 1989).

During April, 2000, an horizontal gradient of water temperature was observed from west to eastern Maputo Bay: the lower temperatures (21ºC) are found at the channels in the middle of the Bay, and higher temperatures near the east and west coasts (26ºC). This pattern was similar to that observed in May, 1993. On the other hand, water salinity increased, during April 2000, from west (32ppm) to east (33.0 to 34.5ppm) and from the surface, downwards. However, during May 1993, there was also an horizontal gradient of salinity, which was 32.0ppm at the west coast, that increased to 36.2ppm towards the east coast of the Bay (Hoguane & Dove 2001). Higher variations of water density occur at the western part of the Bay (Nhampulo 2001; Hoguane & Dove 2001). In general, the higher density of salt water at the east coast of the Bay, forces the propagation of the marine water toward the western part of the Bay (Hoguane & Dove 2001).

The oceanography of areas surrounding Maputo Bay (The Delagoa Bay)

The oceanography of Maputo Bay is influenced by the river run-off of Maputo Bay and the surrounding water masses. Maputo Bay is part of Delagoa Bay (Fig 2.1), located between 25° and 27°S and between the mainland and the latitude 35°E (Jorge da Silva 1983). Delagoa Bay has a wide shelf between 24° and 25°, but is narrow elsewhere, and a hook-shaped terrace between the 300 m and the 700 m isobaths, in the latitude range of 25°15' and 26°40' S (Jorge da Silva 1983). This terrace has a minimum slope between 500m and 400 m isobaths (1.2 m/km), but at the shoreward side there is a steep escarpment up to the 100 m isobath with the maximum slope of 31 m/km (Jorge da Silva 1983). The Delagoa Bight receives water masses driven southward driven by intermitent anticyclonic gyres generated in the north of the Mozambique channel (at Davies Ridge, 17º S) (Schouten *et al*, 2003; Quarlty & Srokosz, 2004).

The upper layers of the Mozambique coastal waters between latitudes 21ºS and 27º S consist of the following waters masses: equatorial surface waters and subtropical water, interacting at the surface level (upper 100 m), subtropical water, at subsurface level, with a salinity maximum centred at approximately 150-200 m, and the central water (below 300 m) with the oxygen maximum centred at 400-500 m (Brinca *et al.* 1983, Gründlingh *et al.* 1991).

Off Delagoa Bay, the modified equatorial surface waters (temperature above 27°C and salinity below 35.3 ppm) are distributed parallel to the1000 m isobath and occupy the upper 30 m (Jorge da Silva 1983, Gründlingh *et al.* 1991). The cooler and more saline subtropical water, entering the area from the east, cuts the warmer tongue into two parts and water mixing takes place in the surface layer in the upper 100 m (Jorge da Silva 1983, Gründlingh *et al.* 1991). The third water mass is the Antarctic intermediate water below 500 m (Jorge da Silva 1983, Gründlingh *et al.* 1991).

The hook-shaped terrace in the Delagoa Bay (described above) influences the circulation pattern of the area, creating a permanent lee cyclonic eddy (Schouten *et al.* 2003, Quartly & Srokosz, 2004). It is centred at 26°15'S and 33°30'E, which influences an area of 150 km x 80 km at least from 300 m depth, upwards (Jorge da Silva 1983, Gründlingh *et al.* 1991). It promotes vertical movements of water masses, lifting the Intermediate Antarctic waters from the depth of 900 m to 500-600m depth, and the core of central water (11°C isotherm and 35.0 isohaline) from 500 m to 200 m deep. The cyclonic eddy is stronger during part of the southern summer (Jorge da Silva 1983), reaching a depression of about 100 cm in October and reducing its intensity in December (Gründlingh *et al.*, 1991). During August-September, it apparently moves toward the coast because of the existence of an anti-cyclonic eddy between the latitudes 21°S and 26°S (Jorge da Silva 1983, Schouten *et al.* 2003). Such seasonal oscillations in the intensity of the cyclonic eddy are apparently caused by vertical changes in the baroclinic structure, (Jorge da Silva 1983) and the influence of southwest movements of eddies generated off Madagascar ridge (Gründlingh *et al.* 1991, Quartly & Srokosz, 2004). This permanent cyclonic eddy off eastern Inhaca Island creates a dynamic upwelling that affects the subsurface and intermediate layers (Brinca *et al.* 1983), generating high levels of chlorophyll (Quartly & Srokosz, 2004). Possibly, tydes may then drive surface waters under the effect of the upwelling into the north-western part of Inhaca Island, within the surveyed area.

River run-off from Maputo Bay is transported northward offshore close to the coast, reducing water salinity to below 35.3 ppm.

Boat movements and fishing activity

Several types of boats utilize Maputo Bay for various purposes (fishing, dredging, transport and tourism). Fishing boats comprise the bulk of the fleet using the Bay. The western and southeastern area of the Bay is utilized by semi-industrial fishing trawlers, targeting shrimps (Guissamulo, 1993). These boats operate daily from March to December and fish from 04:00 to 18:00 (Guissamulo, 1993). About 18 trawlers operate in Maputo Bay (Massinga & Hatton 1996). Most activities are carried out between the 5 and 10 m isobaths.

Several artisanal fisheries are active in the Bay:
Seine netting for pelagic fishes is carried out off the west coast of Inhaca Island, the Catembe area (south of Maputo city) and off Xefina Island. The number of boats off Inhaca Island involved on this fishery decreased from 20 in 1995 to 12 in 1996 (Premegi, 1995; Massinga & Hatton 1996).

The drift gillnet fishery is carried out during the whole year but most effort is spent during December to May and targets the keele shad *Hilsa keele*. Most effort is concentrated off Xefina Island and just off Maputo City, although the fishing zones are extensive (Abdula, 1995). From 1992 to 1995 the registered fishing boats decreased from 438 to 216 (Premegi, 1995), a further decrease to 135 boats occurred in 1996 (Tomás, 1996) and in 1997 the number of boats was 152 (Loureiro 2001), mostly because fishermen experienced increased operational costs and low revenues, high operational costs (Abdula 1995).

Bottom set gill nets are used within the Bay, mainly along the coast of Maputo city and the west and south coasts of Inhaca Island (Guissamulo, 1993). Most nets have small mesh size targeting mullets, but a shark fishery also uses this fishing gear. Shark nets are laid in the Polana Channel, the area south of Portuguese Island, and at the Inhaca channel, south of Inhaca Island (pers. obs.). These nets are permanently set during neap tides. Mesh size for sharks varies from 10 to 20 cm. Fishing effort in 1987 was 120000 fishing days per year which decreased to 11800 fishing days during 1996 and 1997 (Loureiro 2001).

METHODS

Surveys were carried out between December 1995 to December 1997 using two types of boats: a 10 m boat with an 50 Hp inboard engine and a 5.5 m rubber duck with two 30 horsepower engines. A survey consisted of any individual boat trip dedicated to search for dolphins, that had varying number of legs, length and duration. The surveys were performed at varying directions in the Bay. Survey were carried out in the daylight period between 06:00 and18: 00, at Beaufort scale sea state not exceeding 3. If seastate deteriorated, the surveys were terminated. Survey routes covered most of the Bay area , but almost 80 % of the surveys were carried at the eastern portion of the Bay, off the western and southern coasts of Inhaca and Portuguese Islands (Fig. 2.6).

The survey routes were systematic, and run between some of the 17 landmarks selected in the Bay (Fig. 2.6). The selection of these landmarks considered that:
(i) the depth profile of the Bay is uneven and large shallow area in the south was not accessible to the boat at all diurnal tidal stages (depth less than 2 m),
(ii) the Bay has North-South oriented sand banks are not navigable during neap tides and certain daily tidal stages during spring tides. Between these sand banks there are navigable channels (>5 deep) regardless of the diurnal tidal stages.
(iii) dolphin density was higher in the east of the Bay.
(iv) moderate wind speed had different influence on the sea state of the Bay. Therefore, the direction of survey route in these days was selected in a way to increase dolphin sightability (when south wind blowed, the survey routes selected were those directing to the Northeast of the Inhaca Island, but when northward wind blowed, the surveys could be conducted in the sheltered areas of the South of the Bay.
(v) fuel resources were limited to allow for long transit trips to begin the surveys at any random locations. Therefore, the majority of surveys were commenced at Inhaca Marine Biology Station, In adition, the return trip to the Marine Biology Station was included in the survey to increase probablility of detecting dolphins.

During the survey, a single observer, standed in the bow of the boat and searched for dolphins ahead of the route, with a visual field of 180 degrees. Surveys were conducted at the average speed of 10 knots (15 km/h). If a sighting of dolphins occurred, the survey was interrupted and the boat initiated a dolphin follow procedure.

The dolphin follow procedure

The boat approached the sighted dolphins, at a low speed (around 5 knots), maintaining a steady engine rotation. The dolphins were approached to a distance varying between 5 -10 m and then followed parallel to their route, maintaining the boat abeam. Approach of dolphins from behind were avoided. The duration of the dolphin follow varied and was influenced by the group size, the speed of the dolphins and the time needed to take photographic pictures of the dorsal fin for photo-identification of recognizable individuals and to record their behaviours. During the dolphin follow, the

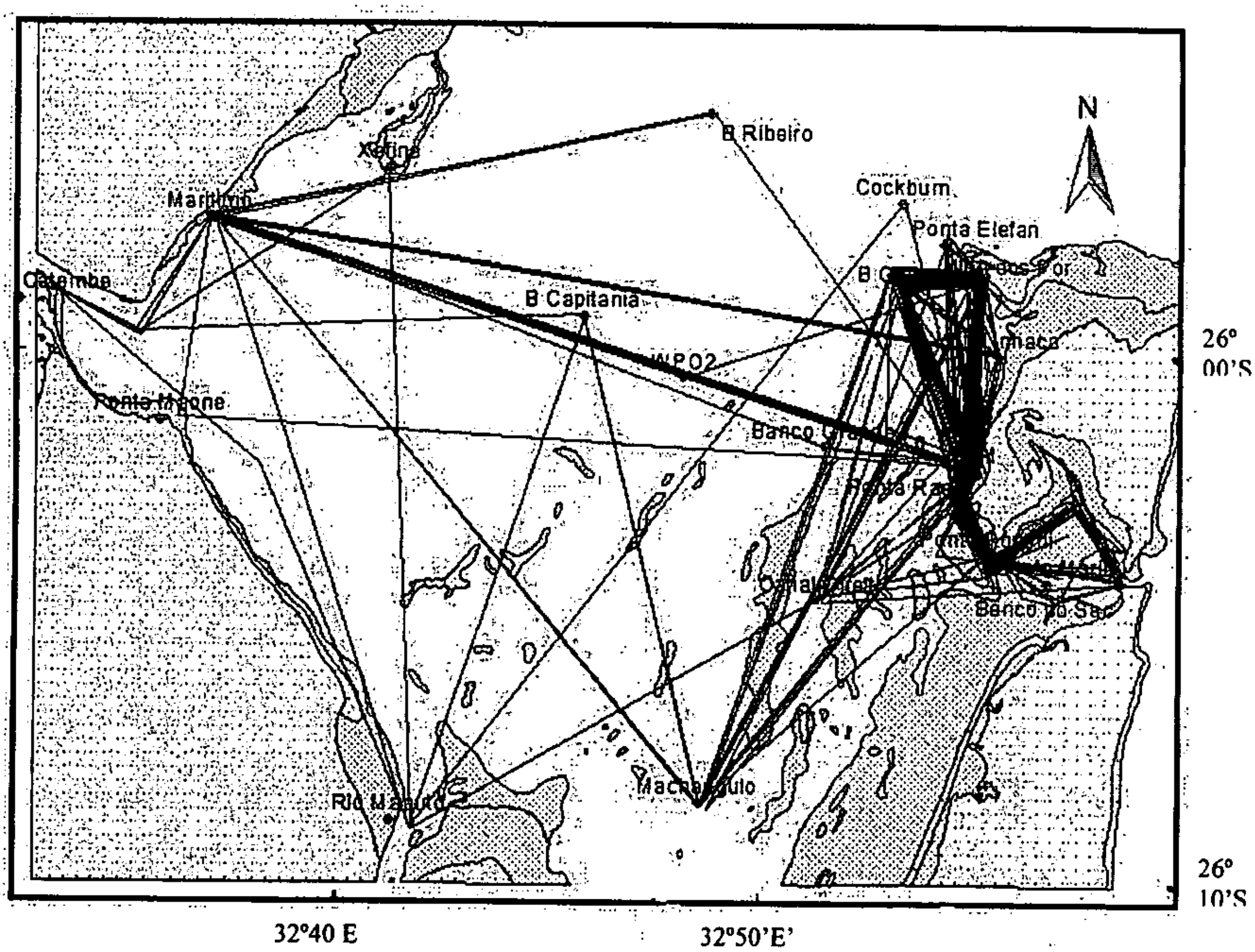


Figure 2. 6 The spatial distribution of survey effort (solid lines) conducted in Maputo Bay between December 1995 an December 1997. Names indicate locations of beginning, end and turnpoints of the surveys in the Bay.

position of boat, while moving parallel to the dolphins was recorded at regular time interval (varying between 5 ans 10 minutes) using a GPS Magellan Trailblazer.

After the dolphin follow procedure the survey was resumed at the place where dolphins were abandoned and the planned survey route was completed. If weather and time permitted permited multiple surveys were carried out during the same day, at varying diurnal tide stages (high, receeding, low or rising tides) and varying cloud cover conditions (from clear sky (0) to full cloud cover (8)), Sea state and cloud cover were measured at the beginning of the survey and monitored every hour of the survey.

The list of surveys, the survey legs and their initial and end geographic coordinates is shown in the Appendix 1. The sea state, cloud cover, diurnal tide phase and tidal range during each survey is presented in the Appendix 2.

Observed dolphins were identified to species, and the size of groups was estimated by multiple counts of number of the individuals surfacing within the visual field of the observer. The number of calves, juveniles and adults were counted to assess group structure. The age class of dolphins was assigned comparing their length relative to the length of the adult dolphin (Karczmarski 1996). Calf age was estimated from several features, like the first time a known (photographically identified) adult dolphin was sighted in a persistent company of a small calf, the calf size, the shape of dorsal fin, the pattern surfacing during breathing and the positioning on the central side of an adult dolphin.

Water transparency was only measured using a Secchi disk at the sites where dolphins were sighted. The Secchi disk was lowered in the water until it became invisible and this depth was recorded. If the Secchi disk hit the bottom while visible, this information was also recorded. The location of sightings of the dolphins was obtained from a GPS receiver Magellan Trailblazer (precision 100 m).

Photographying dolphin dorsal fins

Subsequently, dolphins were followed and their dorsal fins photographed for identification of naturally marked individuals. Photographs of dolphin fins were taken using Minolta X-300s and X-700 cameras equipped with lenses of variable length (80 mm to 250 mm), and colour positive films of sensitivity ranging between 100 ASA and 400 ASA. Dolphin dorsal fins were photographed randomly and an effort was made to take photographs of all surfacing individuals, regardless of the presence of any visible marking. To photograph the dolphins, the boat was positioned between the sun and the dolphins, to improve clarity of the pictures taken. Photographying dolphins in a sun reflection (dolphins between the sun and the boat) was avoided because it produced out of focus pictures,

Selection of photographs for photo-identification

Individuals were then identified and catalogued using marks, scars and pigmentation pattern on the dorsal fin and back, using the procedure developed by Karczmarski & Cockcroft (1998), This procedure included the record for each identified dolphin, the number, position and shapes of nicks in the dorsal fin (front, top and trailing edge, position and number of the persistent scars on the dorsal fin and on the back of the dolphin, the estimated stage of the dolphin (adult, subadults, juvenile, and calf), the sex of the dolphin , females were idenfitied based on the persistent sighting and surfacing with a newborn calf, Few dolphins were identified as males after observation with a penis erected during social behaviours.

The spools of developed film were initially mounted in slide flims and using a slide projector projected in a wall, such that the dorsal fin filled an A4 white paper. the first selection of slides was based on the focus, clarity, parallax and sharpness of the image. Images that were not clear and out of focus and these showing dorsal fin profiles in positions that were not parallel were discarded. Then, a second screening of the above selected slides was performed and photographs that were too small to notice identification features were also removed and tagged an 'unable to indentify". In the third screening, the remaining slide films that had with fins with features visible for idenfification were grouped by the position and the number of nicks and scars and those without features for identification were separated and grouped together, and their number recorded. The screening was repeated until all photographs were grouped for different idenfied individual. These slides of the same individual were matched with fins traced in the previously selected picture on the catalog of traced fins. If none was recognized, the fin was recorded as a new addition to the catalog and considered a new identified individual, and assigned a code. The code consisted of the species (BD – for bottlnose dolphin, or HB for humpback dolphin, the number of notches in the front, top and trailing edges and the sex (f for females, m for males and U for undetermined sex) If a match of the dolphin was found, its occurrence in the day of survey was added for the capture history.

To determine the use of the area by dolphins off the eastern Maputo Bay, the area at the west coasts of Inhaca and Portuguese Islands were partitioned into 28, 500 m wide sectors (Fig 2.7), whose features are presented in Table 2.1. During the dolphin follow the occurrence of the main behavioural categories and the proportion of time dolphins performed each behaviour (feeding, travelling, socialising and resting) were recorded using focal group sampling methods (Altmann 1974). This consisted on recording predominant behaviour, which was performed by the majority of dolphins in a group, at regular intervals of five minutes throughout the observation time. The duration of predominant behaviours was estimated at the end of the observation period of each dolphin follow (Altmann 1974).

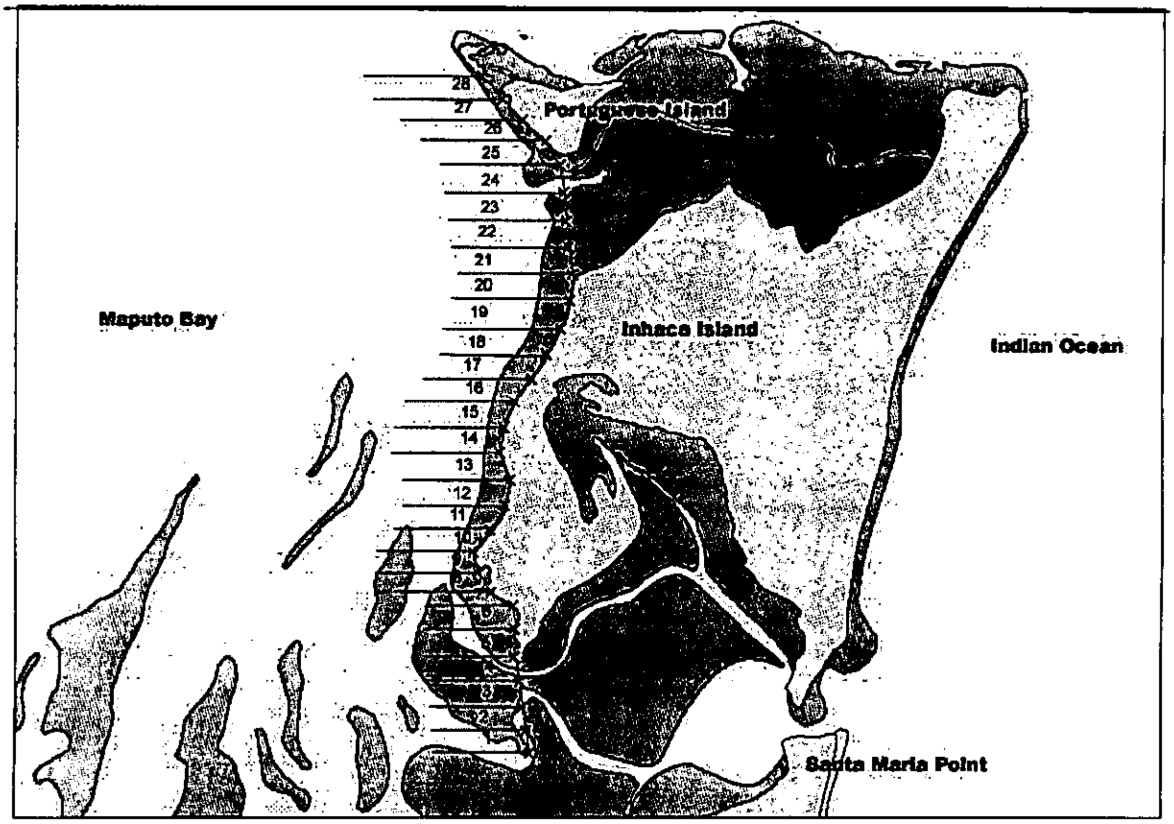


Figure 2. 7 Each of 28, 500m sectors along the west coast of Inhaca Island, in which area use by bottlenose and humpback dolphins was studied (see text for details).

Table 2.1 Depth and width of the channel, the presence (- = low abundance, + = high abundance) or absence (0) of seagrass, corals, rocks, sand and mangrove, and level of shelter from open sea wave action (0 = absence, - = low, + = good) in each of 28, 500m sectors of the west coast of Inhaca and Portuguese Islands, eastern Maputo Bay (cf Fig. 2.7). See definitions in the text below for description of a Channel.

	Depth range	Channel width	Coastline					Level of shelter
Sector	(m)	(m)	Seagrass	Coral	Rocky	Sandy	Mangrove	
1	0-1	150	-	-	-	-	-	-
2	0-1	100	-	-	-	-	-	-
3	0-1	50	-	-	-	-	-	-
4	0-2	200	-	-	-	-	-	-
5	0-3	250	-	-	-	-	-	-
6	0-2	400	-	-	-	-	-	-
7	0-8	600	-	-	-	-	-	-
8	0-10	600	0	0	0	+	0	+
9	0-17	1900	+	+	+	+	+	+
10	0-17	2100	+	+	+	+	+	+
11	0-10	2100	+	+	+	+	+	+
12	0-10	2200	+	+	+	+	+	+
13	0-12	1800	+	+	+	+	+	+
14	0-14	1800	-	-	-	-	-	-
15	0-14	1800	-	-	-	-	-	-
16	0-14	2200	-	-	-	-	-	-
17	0-14	2300	+	+	+	+	+	+
18	0-14	2400	+	+	+	+	+	+
19	0-10	2200	+	+	+	+	+	+
20	0-10	2800	+	+	+	+	+	+
21	0-10	2800	+	+	+	+	+	+
22	0-22	2800	+	+	+	+	+	+
23	0-15	800	-	-	-	-	-	-
24	0-19	400	0	0	0	0	0	0
25	0-15	400	0	0	0	0	0	0
26	0-10	2000	0	0	0	0	0	0
27	1-15	2000	0	0	0	0	0	0
28	1-21	2000	0	0	0	0	0	0

Occurrence of movement and types of movements (directional or not directional) were compared between the tides (rising tide and ebb tide). Movements were considered directional when the majority of individuals moved in the same direction, which resulted in general displacement from the initial location. The movement was considered non-directional when dolphins performed random or circular movements that resulted in maintenance of the same positions as at the beginning of their observation. The direction of movement, if directional was classified as southward or northward, which was similar to those exhibited by the daily tidal direction. East and westward movements were not considered because dolphins moved along the north south oriented channels, and were not observed.

During the study, to overcame practical difficulties, and reduce subjectivity or improve interpretation of results, the following definitions were applied:

Group: Any aggregations of more than one dolphin, within the visual range of the researcher, and separated by not more than 300 m. All individuals were considered to be in a group if they maintained contact during the observation period and followed the same general movement pattern. This definition has the same meaning as group used by Karczmarski (1996), Felix (1994) and Bräger (1994), and included the party definition of Smolker *et al.* (1992). **Sighting** refers to any observation of separated groups or single dolphins. **Population** refers to a statistical population, but does not refer to any genetically isolated population. **Summer**: the period between October and March, with a mean air temperature of 28° C and high rainfall. **Winter**: the period between April and September, with low air temperature (mean 22°C) and low rainfall. **Spring tide** is defined as the period of days when the daily tidal range was higher than 2.0 m, between two consecutive low and high tide marks, while **neap tide,** refers to the period of days when daily tide amplitude was lower than 2.0 m (Kalk, 1995). **Channel** is defined as any marine water mass of the Bay, of any width and depth, which has currents, that is navigable in the Bay regardless of the tidal phase. It is is bordered either by sandbanks on their margins, or by the island or mainland coastline and a sandbank.

CHAPTER 3. SEASONAL OCCURRENCE, GROUP SIZE, GROUP DYNAMICS AND HABITAT USE OF BOTTLENOSE DOLPHINS IN MAPUTO BAY, MOZAMBIQUE

INTRODUCTION

Delphinids inhabiting inshore areas change their occurrences, numbers and group sizes to respond to seasonal changes of the environment (Wursig 1978; Pilleri & Pilleri 1979; Ross & Cockcroft 1990; Kenney 1990; Mead & Potter 1990; Felix 1995). However, this is not exclusive of inshore dolphins, because pelagic dolphins, although influenced more by large-scale factors such as El Ninõ (Anganuzzi 1991; Weller 1991), also respond to seasonal events. One example is the response of common and bottlenose dolphins to the "sardine run" off the coast of South Africa (Ross *et al.* 1987).

Temperate and sub-tropical seas change seasonally their temperature and/or salinity, influencing the primary production and, subsequently impact on the local distribution and abundance of fish and cephalopods (Longhurst & Pauly 1987), that constitute the major prey species of dolphins (Berta & Sumich 1999). Despite this, the animals' requirements are not only limited to food, since other needs of animal life, such as mating, nursing and safety also determine their occurrence, numbers and group size. In the animal world, mating and parturition usually occur at places where and when prey abundance is high and predictable, to ensure the survival of calves (Berta & Sumich, 1999).

The group sizes of delphinids vary widely between species and location (Berta & Sumich, 1999), appearing at large scale that they are correlated with depth. The sizes decrease from pelagic areas, where large sizes are observed, toward inshore and river dwellers (Wells *et al.*1980; Johnson & Norris 1986; Jefferson *et al.*1993). Within a species, the group size vary as a result of the temporal and spatial abundance, distribution, accessibility of prey species and foraging methods, (Jefferson *et al.* 1993, Würsig 1986) availability of mates and safety (Berta & Sumich 1999).

Examining the species' group dynamics provides insight into the understanding of the social structure of dolphin populations. In some studied dolphin communities it was observed that age, sex, reproductive condition and familiar relationship play a role in their social organisation (Wells 1991; Smolker *et al.* 1992), by influencing the degree of association between individuals (Berta & Sumich 1999). A number of functions are discussed regarding the role of groups, which range from formation of signalling system for transmission of information (Würsig 1986), co-operation for nurturing, care, defence and access to mates (Berta & Sumich, 1999). The social structure among odontocents range from the highly stable family pods of killer whales (Jefferson *et al.* 1993; Baird 2000; Connor 2000) to the fission-fusion societies observed in dusky and bottlenose dolphins (Würsig & Würsig 1979; Würsig & Batista 1986) and Hawaiian spinner dolphins (Norris & Dohl 1980a). However, a relatively high level of group stability has been observed for small communities of bottlenose dolphins (Wursig 1978; Ballance 1990). Within a species, the degree of association among individuals varies between locations and habitat type and size, but it may also be influenced by the degree of mixing with adjacent dolphin communities.

The social structure of dolphins appear to influence the by-catch of dolphins interacting with trawlers in several species of cetaceans (Fertl & Leatherwood 1997). In Australian waters, a bottlenose dolphins community feeding behind trawlers formed large groups and interacted less with another community that shared part of their range (Chilvers & Corkeron 2001)

The utilization of the area and site fidelity provide insight into the role of the habitats for dolphin communities and it is important for formulation of management measures. The degree of site fidelity and habitat use appears to be related to the size of suitable habitats, food supply and breeding needs (Weigle 1990; Defran & Weller 1993; Freitas *et al.* 1995; Arnold & Mayer 1995; Lechuga *et al.* 1995; Lynn 1995). However, site fidelity and area use are influenced by the balance between the amount and spatial distribution of food, the predation level (Norris & Dohl 1980a and Shane *et al.* 1986) and intraspecific competition (Wrangham & Rubestein 1986).

Seasonal changes of occurrence and group size have been observed for bottlenose dolphins elsewhere (Connor *et al.* 2000, Peddemors 1995). Bottlenose dolphins off Kwazulu- Natal waters, some 600 km south of Maputo Bay, are caught in shark nets at levels above their natural replacement rate and also suffer from pollution by organochlorines which levels may depress their reproduction (Cockcroft *et al.* 1989a, 1989b). The bottlenose dolphin also inhabits the coastal waters of Mozambique (Saetre & Paula e Silva 1979; Guissamulo 1993, Guissamulo & Cockcroft 1998), but the factors affecting the occurrence, group size and dynamics have not been documented. These features (occurrence and group size and dynamics) change spatially in relation to the habitat type, climate and other factors. Therefore an understanding of the influence of these factors on bottlenose dolphins is essential for the a proper management of the impact of human activities on dolphins.

The bottlenose dolphin population off the east coast of South Africa has low genetic variability and appears to be isolated from those of Mozambique (Goodwin 1997). This fact, may represent a constraint for the survival of the dolphin community inhabiting Maputo Bay, which interacts with fisheries (Guissamulo 1993, Guissamulo & Cockcroft 1998) and it is exposed to domestic pollution (Fernandes 1996). In southern Mozambique, dolphins are also used in recently established tourism, which may disturb their normal behavior and pattern of area use.

This chapter analyses the seasonal changes of occurrence and group size, the group dynamics, site fidelity and the area utilization by bottlenose dolphins in Maputo Bay with the aim to evaluate their ecological needs and evaluate the effect of fishing activity on their survival in Maputo Bay.

METHODS

The surveys were carried out in Maputo Bay (Fig.2.6) between December 1995 and December 1997. The survey procedure for the determination of occurrence and group size is described in Chapter 2. Occurrence was measured using relative measures (sightings per unit effort – SPUE- and number of dolphins per unit effort - NPUE), and effort was measured as time spent searching for dolphins during the survey.

During the dolphin follow procedure (Chapter 2), the initial and the final locations of each sighting were recorded using a GPS Magellan Trailblazer. Dolphins were followed for as much time as possible to collect the photographs of individuals and behaviour. The maximum duration to follow and observe a sighted group of dolphins was 2 hours. However, some observations were terminated if the dolphin groups disappeared from the observation field of the researcher for more than 15 minutes. The time spent observing dolphins was also recorded. It consisted of the time of approach and follow the dolphins until the group disappeared of was abandoned.

The stability and dynamics of groups of dolphins is analysed through the use of indices of associations between each pair of photographically identified dolphins. These indices of each pair are then used to produce association matrices of individuals (Cairns & Schwager 1987). In this study, the association was measured through the half weight index (HWI), (Ginsber & Young 1992; Cairns & Schwager 1987). The half weight index (referred to as Coefficient of Association - CA) was calculated using the formula:

$$CA = 2J/(A+B),$$

Where: CA = coefficient of association, J - number of times that individuals A and B were seen together, A - total number of sightings of individual A, and B - total number of sightings of individual B. This Coefficient of association varies between 0 and 1. Zero indicates that the pair was never seen forming the part of the same group, and 1 that the animals were always present in the same group.

The HWI was chosen to account for the low numbers of identified dolphins in groups, and for the avoidance of some dolphin individuals to the boat during photo-identification. These two reasons reduced the probability of photographing two individuals present in the same group and the HWI becomes a more accurate estimator of association under these conditions (Cairns & Schwager 1987).

Affiliates are defined as any identified dolphins that occurred in the same group/or sighting with any other identified dolphin. As dolphins are social animals which have a fluid association pattern (fission-fusion), individuals seen once also have affiliates, that can be either other transient individuals arriving and leaving at the same time or other individuals which meet varying time periods (Whitehead & Default 1999). The number of affiliates of any individual and the number of sightings were compared between adults of undetermined sex, adult females and for juveniles. The seasonal occurrence of all photographically identified individuals was also examined.

The number of sightings, number of affiliates and days between re-sightings were compared between age and sex categories using the Kruskal Wallis non-parametric test.

Grouping into larger social units and associations was analysed using group average cluster analysis (UPGMA) employing the software PRIMER (Clarck & Warwick 1994). Only dolphins sighted four or more times were included in the analysis. Coefficient of associations for different age and sex categories were compared using one-way ANOVA and subsequently, multiple comparison tests (least square difference - LSD at 5% significance intervals).

The distribution of sightings was plotted on a Maputo Bay chart using the Geographic Information System ArcView 3.2. version 2000 (NCC RS & IFPRI 2004).

To examine the daylight pattern of occurrence and preferred depths, sightings were partitioned into six time intervals (06:00 - 08:00, >08:00 - 10:00, >10:00 - 12:00, >12:00 - 14:00, >14:00 - 16:00 and >16:00 - 18:00) and four water depth intervals (>0-2 m, >2-5 m, >5-10 m and >10-20 m). The depth intervals were obtained by plotting the initial location of the sightings on Hydrographical Chart No. 46659-M (National Institute of Hydrography and Navigation 1986). Comparison of frequency of sightings was carried out using Chi-square test. The distance from shore of each sighting was determined using the initial location of each sighting provided by the GPS.

The distribution of sightings along the coast between Portuguese and Inhaca Islands and the mainland at Machangulo Peninsula was examined using sightings observed within 3 km off the coast (Fig. 2.5), because their distribution was skewed towards the shoreline. This area is 14 km long, divided into 500m long sectors (after Karczmarski, 1996). The following features of each sector were also described: the type of the bottom substrate (sand, seagrass, reef, rocks), depth range, width of the channels and the type of coastline (sandy, mangrove, rocks or sand). At each sector the number of groups sighted passing the area was plotted. The number of sighted groups that passed each sector and time spent observing dolphins at each sectors varied because it depended on the speed of the dolphins followed. Therefore, a coefficient of area utilisation (AU) was calculated for each sector to compare the importance of each sector for the dolphins:

$$AU = D/T$$

Where: AU = coefficient of area utilisation
D= total time spent by dolphins in a particular sector
T= total observation time during any one day

The Activity Index (AI) was also calculated separately for feeding, travelling and social behaviours, using the formula:

$$AI = B/T$$

B= Time dolphins were engaged in a particular activity within a sector
T= Time spent by dolphins in any one sector

The mean values of the area utilisation index (AU) and activity index (AI) between sectors were compared for statistical significance using the Kruskal-Wallis ANOVA.

The types of dolphin movements and the direction of the movements were examined in relation to the semi-diurnal tides (see Chapter 2 for details). The frequencies of the types of movement and the movement direction between tidal phases (rising/ebbing) were compared for significant differences using the Chi-Square Test, based on the Contingency Tables.

RESULTS

Effort and Sightings

146 surveys were conducted during 101 days from December 1995 to December 1997, but no surveys were carried out during January, October and December 1996 and July - August 1997 (Figure 3.1A), because of logistic constraints. The number of surveys and the total duration of surveys varied between months (Figure 3.1). The duration of each survey varied between 0.42 to 4.73 hours, and the mean was 2.08 hours (S.D. = 1.20 hours). These variations occurred because of differences in the size of surveys and the duration of adequate weather (seastate) for surveys. A total of 302 hours was spent surveying for dolphins. The minimum mean surveying time was in October 1997 (mean = 0.83 hours/day) and August 1997(mean = 3.05 hours/day) had the maximum mean survey time.

Mean duration of a survey in summer (1.99 hours; S.D. = 1.01, n = 96) did not differ significantly from the mean duration of a survey during winter (2.26 hours; S.D. = 1.48, n = 49), (Mann Whitney, U= 2241.5 n = 96 and 49; p = 0.643).

During spring tide, the mean duration of a survey (1.94 hours; S.D. = 1.22 hours, n = 82) was small and significantly different from the duration during neap tides (2.25

hours, S.D. = 1.15 hours, n = 63), (Mann Whitney, U = 2079.5, n = 82 and 63, p = 0.044).

There were 61 sightings in 53 surveys (36% of total surveys) during which 1562 bottlenose dolphins were counted. Single sightings occurred during 45 surveys and duplicate sightings occurred during eight surveys.

Occurrence

The monthly distributions of mean SPUE and NPUE of bottlenose dolphins were variable (Figure 3.2 A) and significantly different between months (Kruskal Wallis, H = 28.36, n = 107, p = 0.0004 and H = 31.35, n = 107, p = 0.0001 respectively). Higher values occurred between April and July and the lowest between January and February (Fig 3.2B). Table 3.1 presents values of sightings per hour of survey and number of dolphins per hour of survey between spring and neap tides. The sightings per hour and number of dolphins per hour were significantly larger during winter compared to summer (Table 3.1) and these differences were also significant between seasons (Mann - Whitney, U = 814.5, n = 94 and 49, p = 0.0000 and Mann Whitney, U = 1236, n = 94 and 49, p = 0.0000 respectively). However, the sightings per hour and number of dolphins per hour did not differ significantly between neap and spring tides (Mann Whitney; U= 2110; n = 81 and 62; p = 0.059 and Mann Whitney, U= 2209, n = 81 and 62, p = 0.149 respectively).

The overall mean Secchi-depth measured was 6.30 m (S.D. = 3.47, n = 53). The mean water clarity measured when bottlenose dolphins were sighted was 7.89 m (S.D. = 3.03, n = 35) and ranged between 2.6 and 12 m. The mean tidal range when bottlenose dolphins were sighted was 2.00 m (S.D. = 0.87), ranging from 0.7 to 3.3 m.

Group size and structure

The mean group size of bottlenose dolphins was 27.47 (S.D. = 32.19) individuals and ranged from 2 to 150 individuals (Fig. 3.3). The mean monthly group size varied throughout the months as the mean number of dolphins observed on surveys when sighting occurred (Figure 3.4).

Group size did not differ significantly between months (Kruskal Wallis, H = 9.599, n= 56, p = 0.2944), daylight periods (Kruskal Wallis, H = 5.907, n = 56 p = 0.3154), tides (Mann-Whitney U=379, n=31 and 25, p=0.8919) depth intervals (Kruskal Wallis, H = 9.949, n = 54 p = 0.0767), semi-lunar tidal cycle tides (Mann-Whitney U=379, n=31 and 25, p=0.8919), but was significantly different between seasons (Mann - Whitney; U = 300, n = 20 and 36, p = 0.0240). Bottlenose dolphin groups were smaller during summer compared to winter (Table 3.1). Group sizes of bottlenose dolphins did not significantly differ with Secchi-depth (Spearman, r_s = - 0.1306, n = 27, p = 0.516).

The age structure of groups is shown in Figure 3.5. Adults comprised more than half of the groups (54 %), Juveniles comprised 35% of groups. The mean number adults was 15.22, S.D=19.57 individuals. The mean number of juveniles was 9.55 (S.D. = 13.31) individuals and ranged from 0 to 60 individuals. Five per cent of groups had only one juvenile and 27 % (n = 16) of groups had no juveniles.

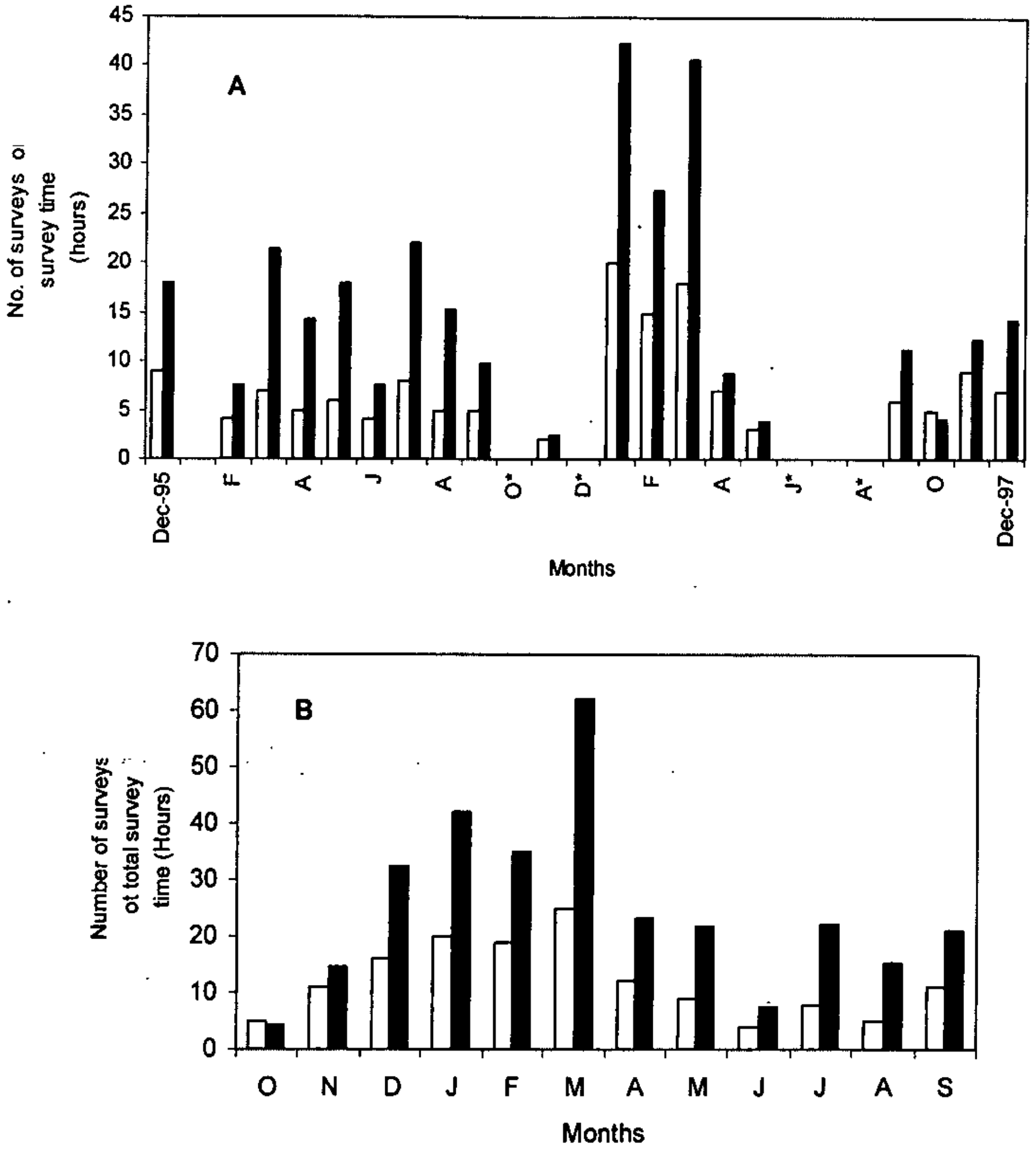
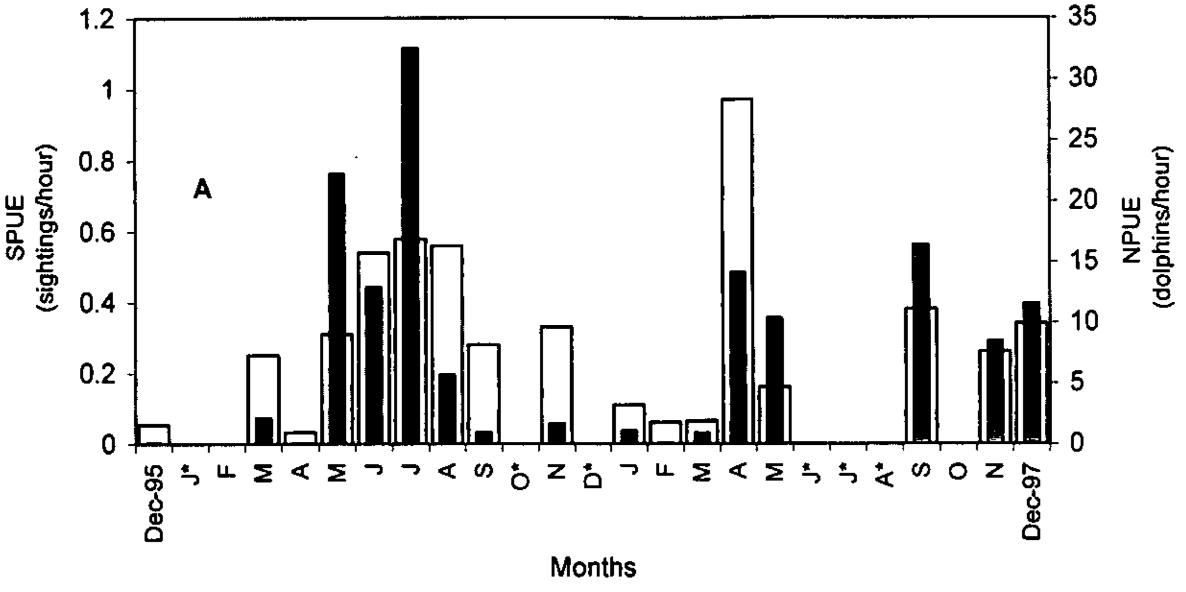


Figure 3.1. (A) Total number of boat surveys (□) and monthly time (■) spent searching for bottlenose and humpback dolphins each month between December 1995 and December 1997. (B) Polled monthly surveys time (■) and number of surveys (□) spent searching for bottlenose and humpback dolphins between December 1995 and December 1997 in Maputo Bay. (* months when surveys were not undertaken).



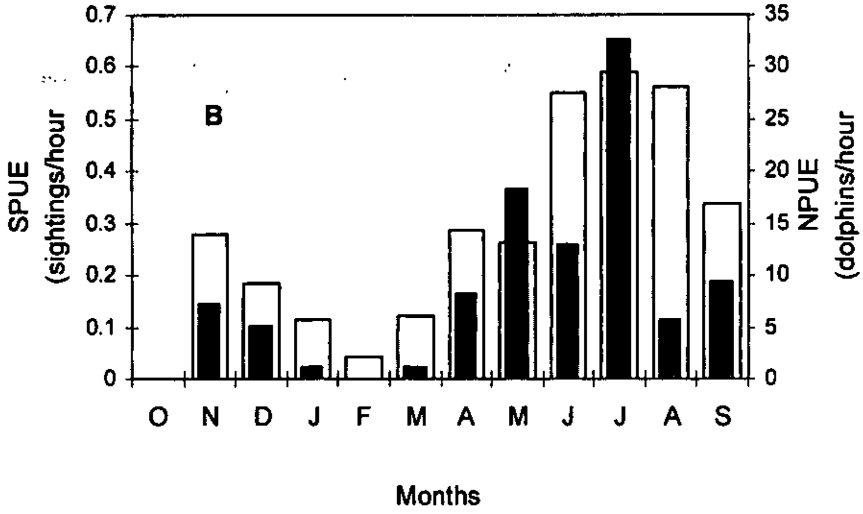


Figure 3.2. Sighting rates of bottlenose dolphins: (A) total monthly number of sightings per hour searched (□) and total monthly number of dolphins sighted per hour searched (■) in Maputo Bay between December 1995 and December 1997. (B) Pooled total monthly number of sightings per hour (□) and pooled monthly number of dolphins sighted per hour (■) in Maputo Bay between December 1995 and December 1996.

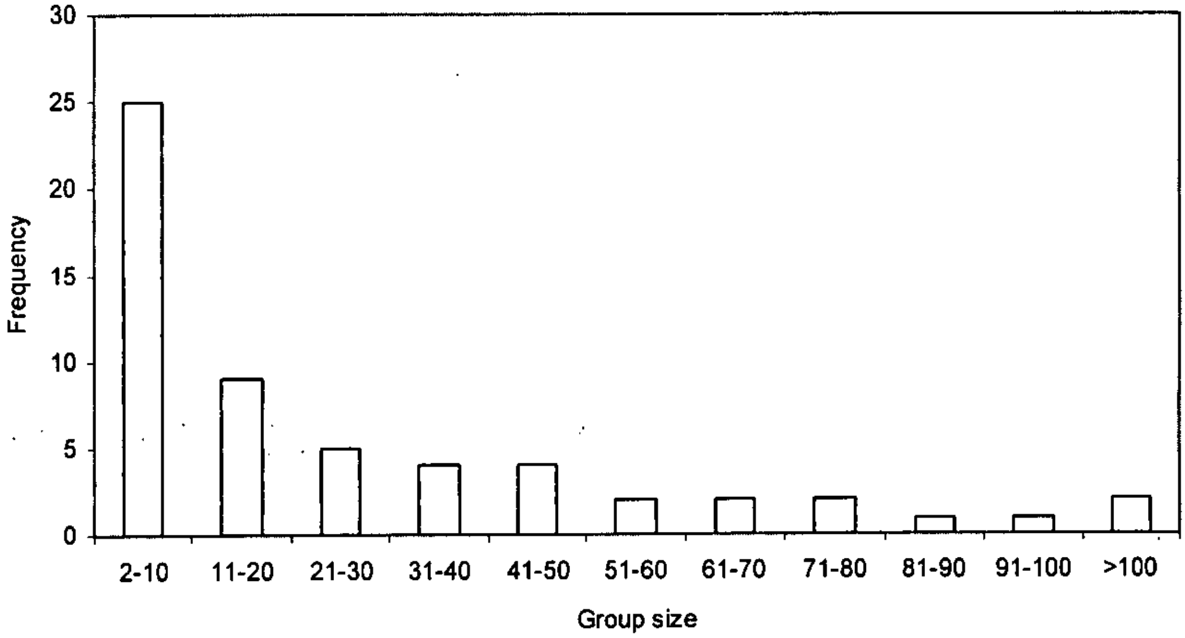


Figure 3.3. The frequency with which the various group sizes of bottlenose dolphins were observed in Maputo Bay between December 1995 and December 1997

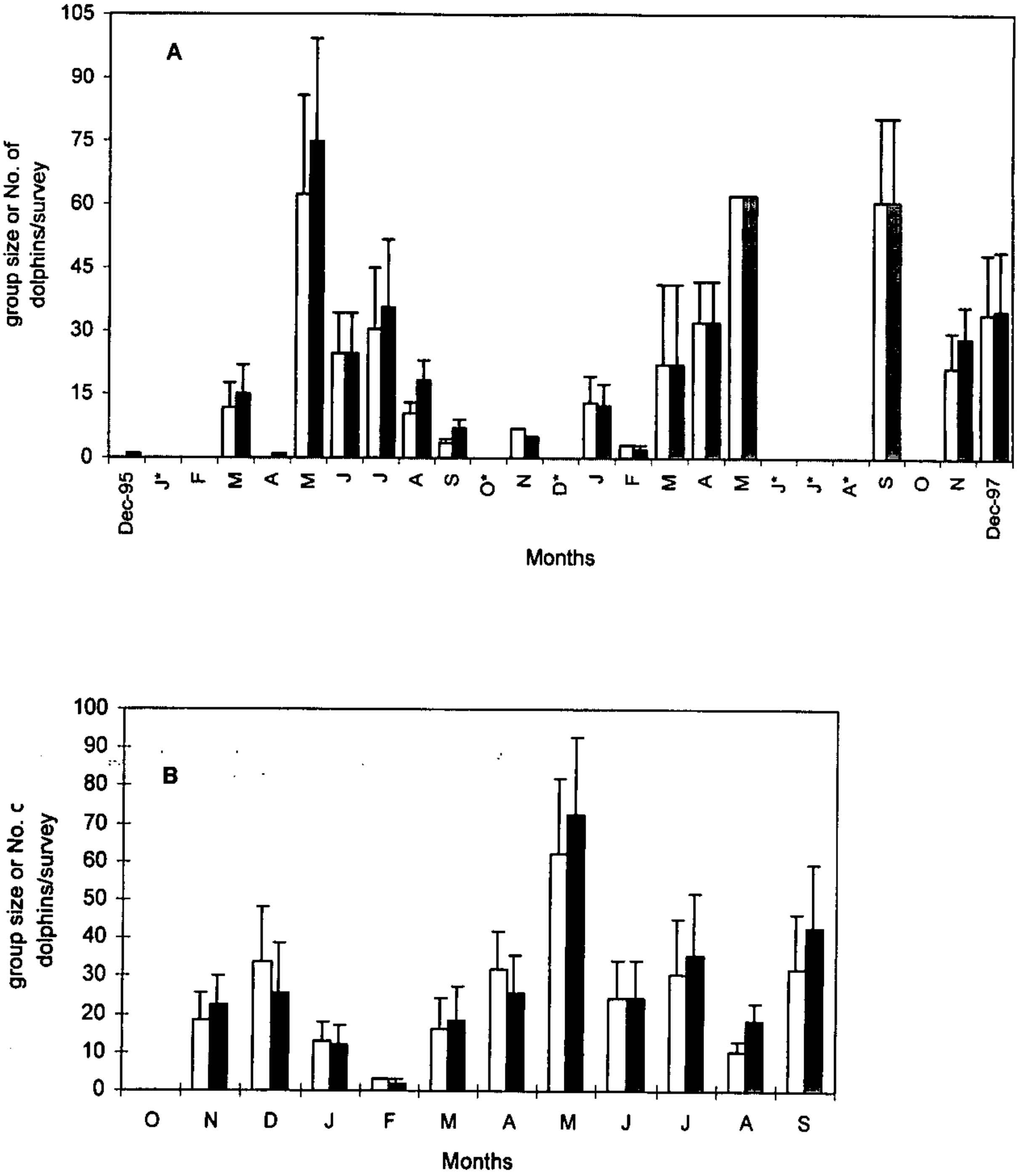


Figure 3.4. (A) Mean monthly group size (□) (and standard errors) of bottlenose dolphins and number of bottlenose dolphins observed per survey (■) in Maputo Bay between December 1995 and December 1997. (B) Pooled mean monthly group size (□) (and standard error) of bottlenose dolphins and pooled number of bottlenose dolphins observed per survey (■) in Maputo Bay between December 1995 and December 1997 (* months when surveys were not undertaken).

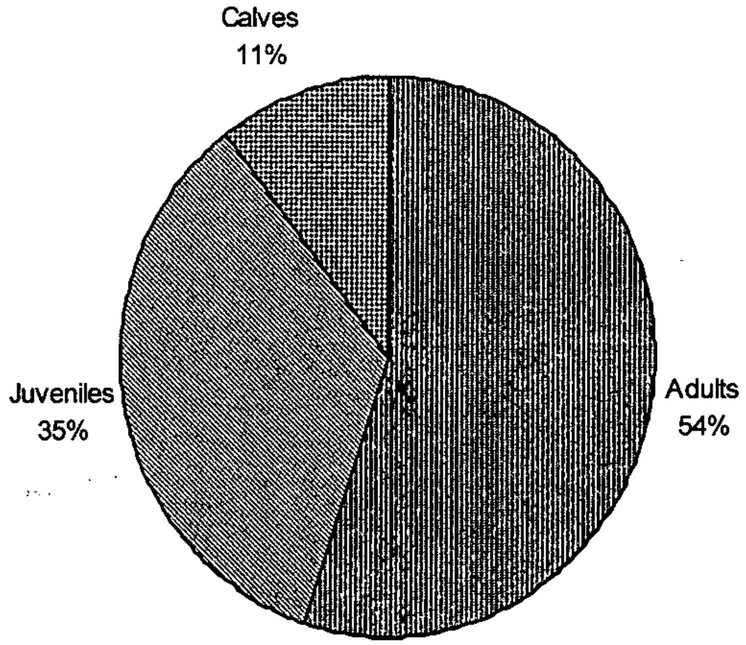


Figure 3.5. Proportion of adults, juveniles and calves in a group of bottlenose dolphins observed in Maputo Bay between December 1995 and December 1997.

Table 3.1. Mean values of group size, sighting rates (sightings per unit effort and number of dolphins per unit effort) of bottlenose dolphins (± standard deviation) estimated for different seasons and semi-lunar tides (spring and neap tides) recorded in Maputo Bay between December 1995 and December 1997. Winter and summer seasons are described in the Chapter 2.

	Winter	Summer	Spring tides	Neap Tides
Group size (No.of individuals)	32.5 (36.9)	17.9 (18.4)	29.0 (31.5)	26.5 (33.8)
Sightings/hour	0.39 (0.41)	0.12 (0.26)	0.16 (0.37)	0.34 (0.63)
Dolphins/hour	14.4 (33.33)	2.28 (7.67)	7.1 (25.5)	5.5 (13.7)

Calves comprised 11% of the groups. The mean group size of calves was = 2.91, S.D. = 2.78 dolphins. The number of calves ranged from 1 to 10 individuals. The most frequent calf number was 1. Groups with calves (mean = 34.8 SD= 33.93) were more frequent (n = 43), and significantly larger than those without calves (mean = 4.85 SD= 3.99), (Mann Whitney: U= 98.5 n = 43 and 14, p = 0.0003).

Group dynamics of bottlenose dolphins

Photographs of bottlenose dolphins were taken during 35 surveys, that occurred during 14 out of 19 months during which all surveys were conducted. In remaining surveys (20 surveys) when dolphins were seen, photographs could not be taken, because dolphins avoided the survey boats or the seastate was rough (not appropriate) to take photographs, as the camera could be damaged by the splash of sea water. A total of 1077 photographs were catalogued resulting in identification of one hundred and forty-nine (149) individuals, from which 108 were adult dolphins and 41 juveniles. Among the adults, 22 bottlenose dolphins were identified as females based on their persistent company with calves. No calves were photographically identified.

i) site fidelity

Among identified individuals the number of sightings of any single animal ranged from 1 to 14 (Fig. 3.6). The most re-sighted individuals were seen during less than half of the photographic surveys. Only a small number of identified individuals (n = 8) were seen frequently throughout the duration of the study. Most of these were adults, including some females with calves. The four most re-sighted individuals were seen during 8 to 11 (56 - 85%) of the 14 months when photographs were taken (Appendix 4). Fifty-nine per cent of individuals were seen infrequently (e.g. ≤ 10% of months surveyed) (Appendix 4). New individuals were identified throughout the sampling periods (Fig. 3.7), but two peaks occurred: a large one in May-July 1996 at the beginning of the study and a small one in March-May 1997 coinciding with the start of winter. Lack of surveys during July- August 1997 possibly reduced the number of new individuals identified in winter 1997 (Fig. 3.1).

About 70% of identified individuals, mostly adults of undetermined sex and juveniles, occurred during only one season (Appendix 5). The occurrence of most adult females and some adults of undetermined sex was similar, but juveniles showed low percentage of residents (e.g. observed more than one season).

Days between the first and last re-sightings ranged from 0 to 405 and about half of the number of individuals identified on any one day were not re-sighted and a small number of individuals were re-sighted after 400 days (Fig. 3.8).

The number of days between re-sightings varied from 0 to 337 (Appendix 6), and the overall mean number of days between re-sightings of any individual was 66. However, the mean number of days between photographic surveys was only 15 days. About 90% of dolphins re-sighted had a mean number of days between re-sightings > 15 days, indicating that individuals were not always been photographed when present or that they visit the area briefly, repeated times. The number of days between re-sightings of an individual decreased as the number of sightings increased, but was largely variable for dolphins sighted 2 to 4 times (range 0-405 days), while individuals sighted > 5 times showed a smaller and less variable number of days between sightings (Fig. 3.9), indicating a varying site fidelity of individuals.

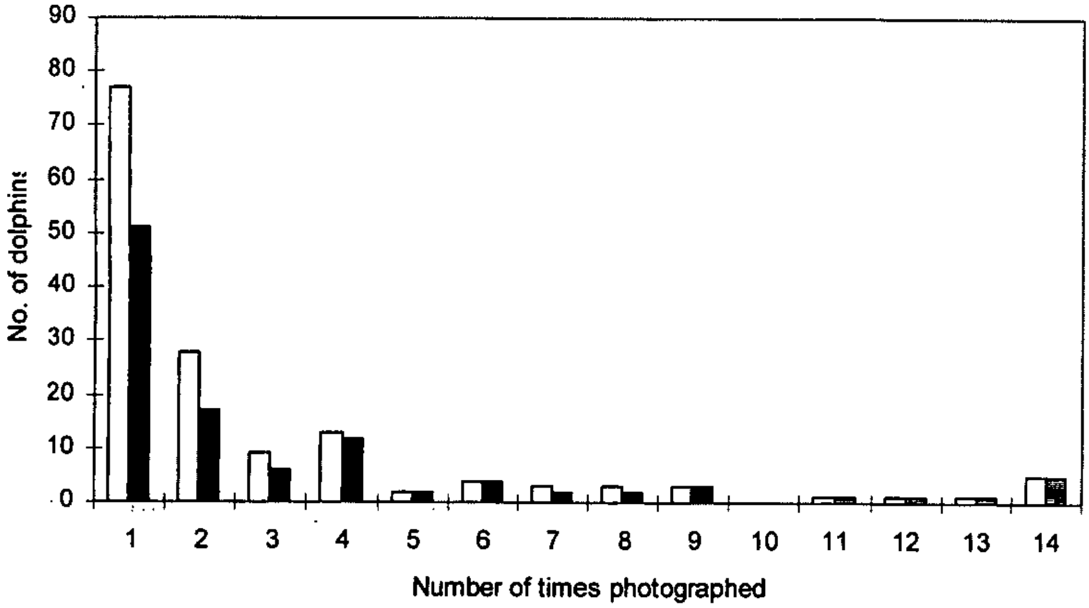


Figure 3.6. The frequency with which identifiable bottlenose dolphins were photographed (□ = all dolphins, ■ = adult dolphins) in Maputo Bay between December 1995 and December 1997.

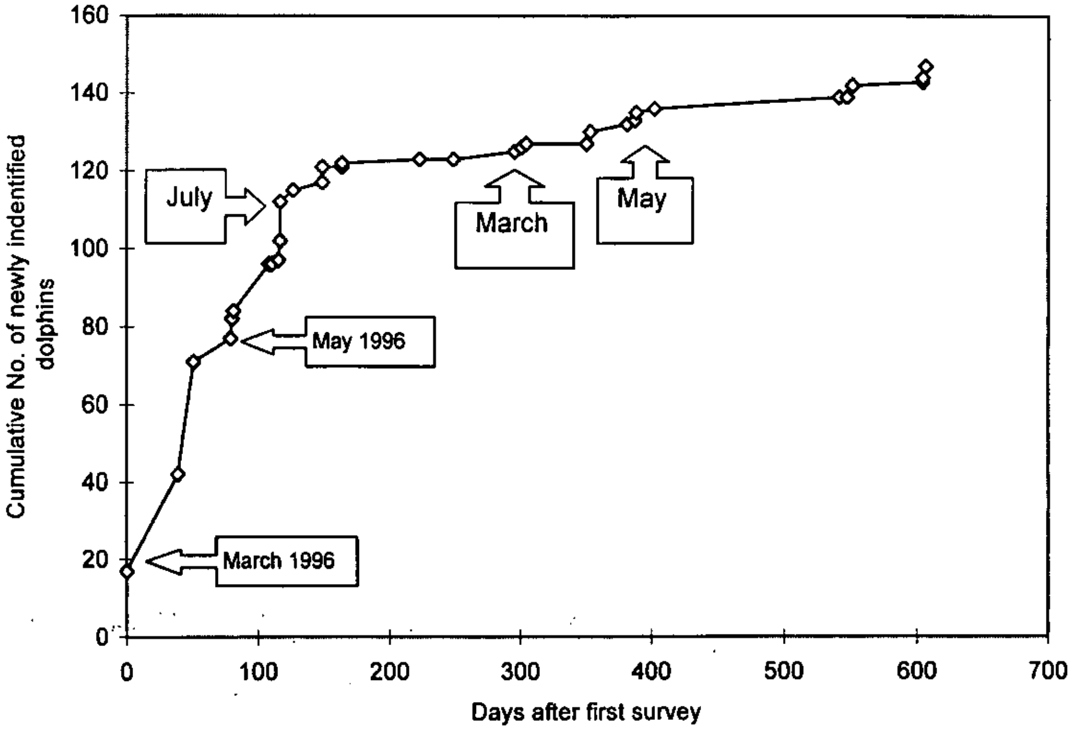


Figure 3.7 Discovery curve: the rate (dolphins/survey) at which new (never photographed and identified before) bottlenose dolphins from Maputo Bay were photographed and identified between December 1995 and December 1997.

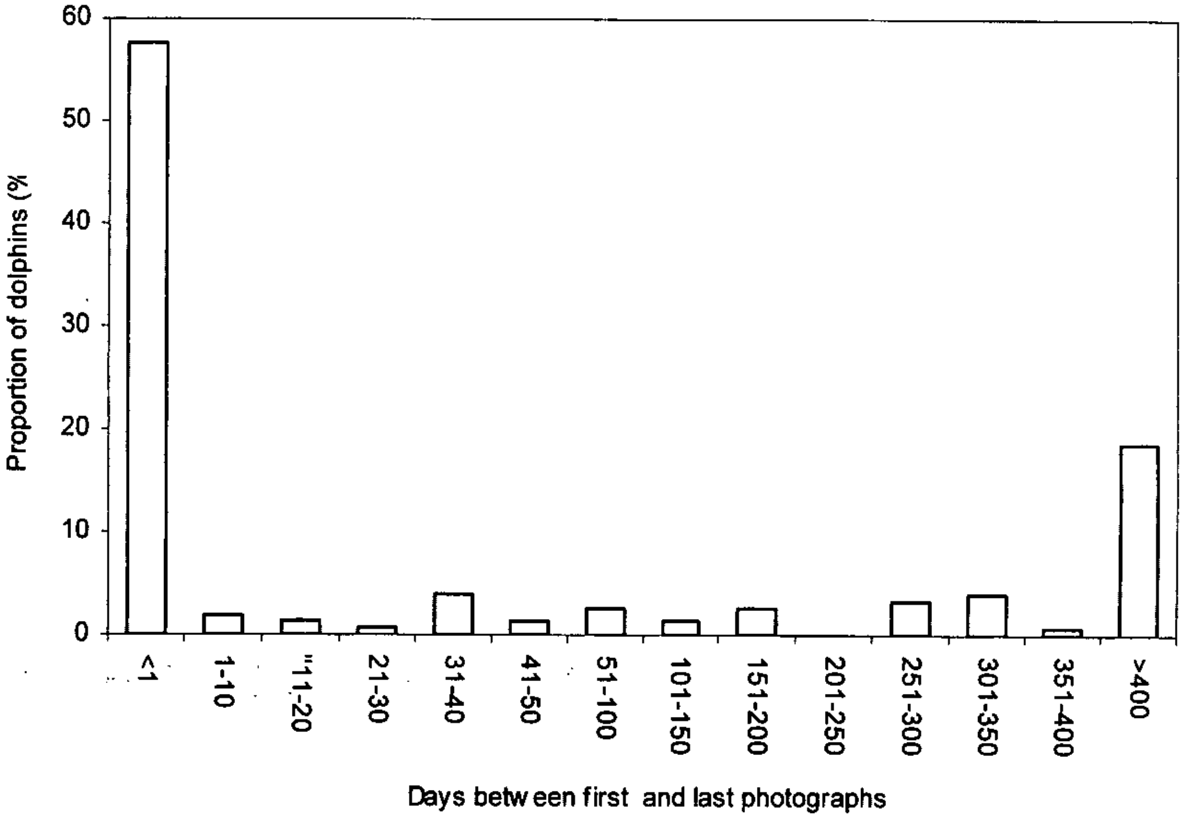


Figure 3.8. The frequency distribution of the number of days between first and last photographs of identifiable bottlenose dolphins observed in Maputo Bay between December 1995 and December 1997.

The analysis of the mean number of sightings and days between re-sightings between individuals of different sexes and age classes (Fig. 3.9) shows that adult females had less variable mean number of days between re-sightings, but adults of undetermined sex and juveniles had highly variable numbers of days between re-sightings. There was a highly significant positive correlation between number of days between first and last re-sightings of any individual and the mean number of days between re sightings (Spearman $r_s = 0.9532$, n=149, $p < 0.001$).

The differences of the number of sightings and the number of days between re-sightings were highly significant between age and sex categories (Kruskal Wallis: H =23.76, n = 149, $p < 0.001$; H =14.53, n = 149, p = 0.007 respectively).

Individuals showed a variable sighting frequency and site fidelity (Fig 3.10). The number of days between re-sightings and the number of days between first and last re-sightings were highly significantly related with the sighting frequency (Spearman r = 0.8349, n = 149, $p < 0.001$; r=0.8349, n = 149, $p < 0.001$ respectively).

ii) social affiliation and association between individuals

Affiliates are defined as identified dolphins occurring in the same group as any other identified dolphin. The mean number of affiliates for dolphins sighted once was 19.6 (13.17% of affiliates), 27.9 (18.2% of affiliates) for dolphins sighted twice and 109 (73.02%) for the most sighted dolphins (14 sightings). The number of affiliates ranged between 1 and 116 dolphins and the overall mean number of affiliates was 33.3 (S.D. = 24.5) individuals per dolphin (Appendix 6).

The number of affiliates increased as the number of re-sightings increased (Fig. 3.11), and this relationship was highly significant (Spearman r=0.7357; n=149; $p< 0.001$). Adult females had the highest mean number of affiliates followed by adults of undetermined sex, while the least number of affiliates was observed among juveniles (Fig. 3.11). Using all photographically identified individuals, the number of affiliates was significantly different between age and sex classes (Kruskal Wallis, H = 12.19, n = 149, p =0.002).

However, when comparing only individuals sighted > 3 times, differences were not significant between adults of undetermined sex, females with calves and juveniles (Kruskal Wallis, H = 0.63, n = 35, p =0.729), implying that prevalence of juveniles and adults of undetermined sex re-sighted with low number of re-sightings (< 4 times) caused these differences.

Of the 595 possible associations (the number of potential associations when each photographically identified dolphin sighted >3 times is matched against any other dolphin also sighted >3 times), only 508 were observed (85%) (Appendix 7). From these, only two (0.4%) had coefficient of association (HWI) > 0.8. The mean HWI was 0.30 (S.D. = 0.20) between all dolphins sighted > 3 times and most associations were below HWI = 0.41 (Fig 3.12). When HWI's were compared between age classes only, the following results were found; adults - adults (mean = 0.35, S.D. = 0.20), adults-juveniles (mean = 0.27, S.D. = 0.15) and juveniles - juveniles (mean = 0.25). No significant differences were found (One-way ANOVA: $F_{2,589} = 0.5990$, p = 0.549).

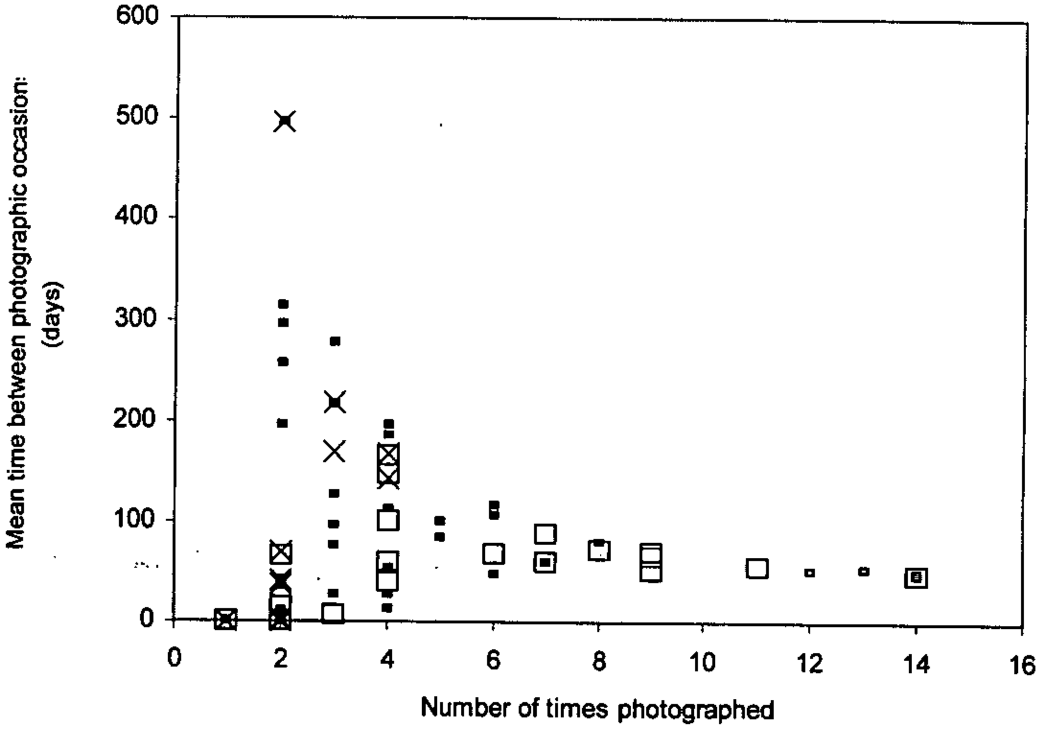


Figure 3.9. The relationship between the number of times a bottlenose dolphin was photographed and identified and the mean number of days between photographic occasions in Maputo Bay between December 1995 and December 1997(▪ = adults of undetermined sex, □ = adult females, × = juveniles).

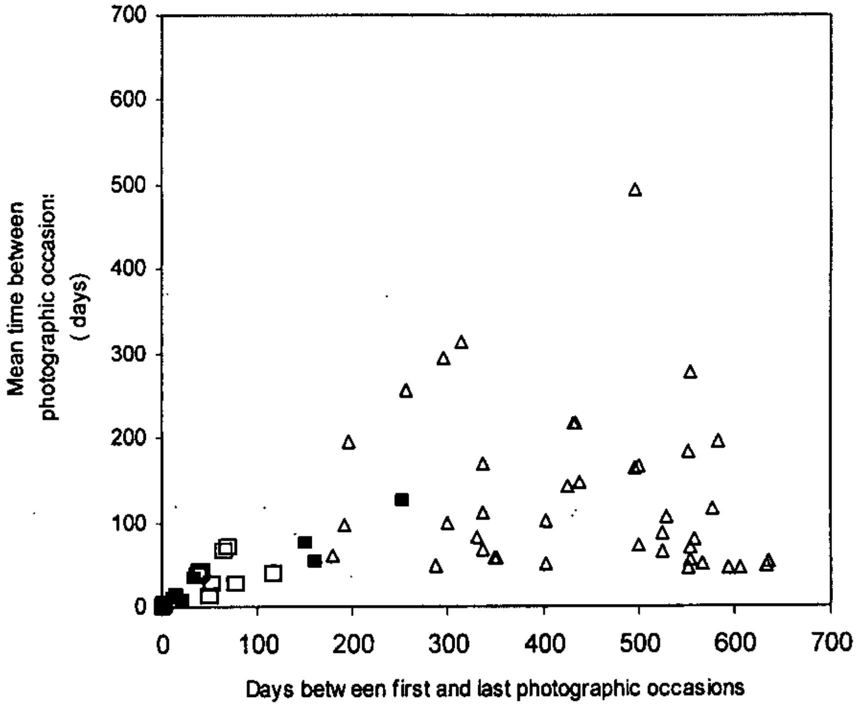


Figure 3.10. The relationship between the time (number of days) an individual was first and last photographed (identified) and the mean time (days) between all re-photograph occasions (re-sightings) of the individual in Maputo Bay between December 1995 and December 1997 (Δ = dolphins photographed in 1995/6 and 1997, □ = dolphins photographed during 1995/6 only, and ■ = dolphins photographed during 1997 only).

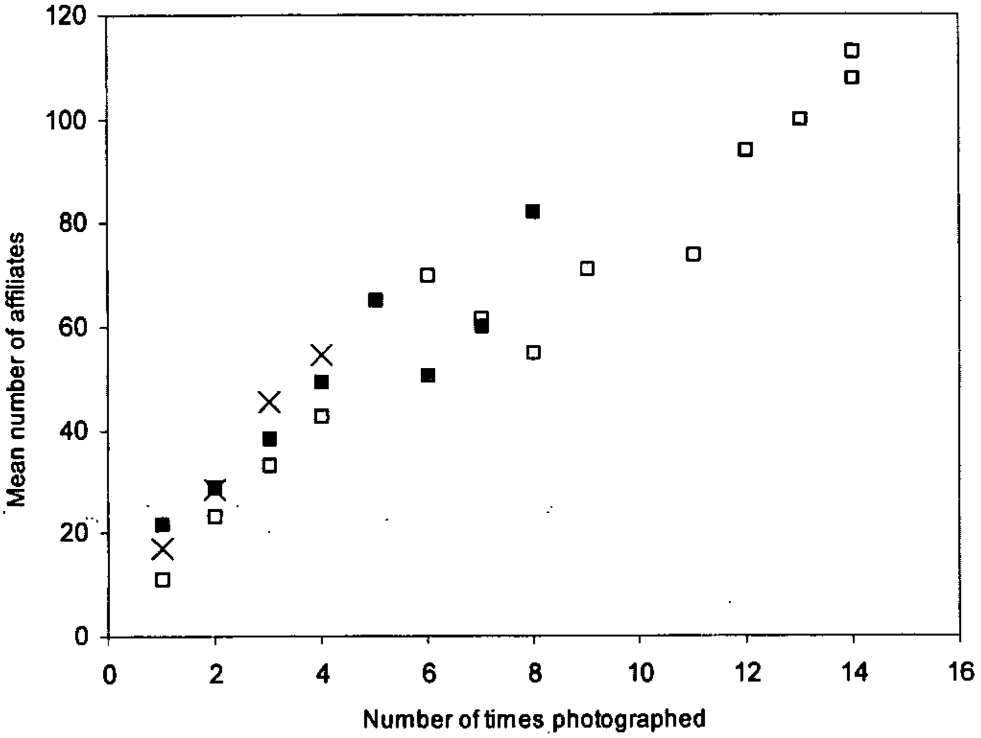


Figure 3.11. The relationship between the number of times a bottlenose dolphin was photographed and the number of affiliates (any other identified dolphin seen in the same group) in Maputo Bay between December 1995 and December 1997 (■ = adults of undetermined sex, □ = adult females, x = juveniles).

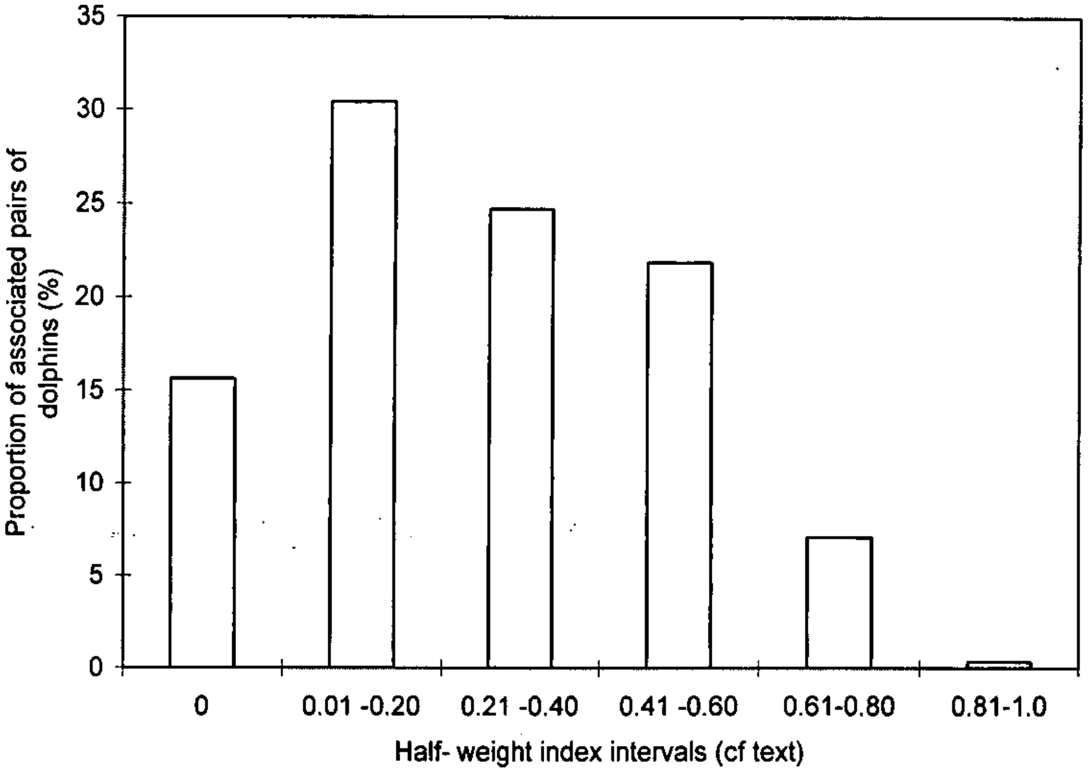


Figure 3.12. The frequency distribution of the proportion of pairs of identified bottlenose dolphins associated at different half weight index intervals in Maputo Bay during the period between December 1995 and December 1997.

However, highly significant differences in the HWI's were found between individuals of different sex and age classes (One way ANOVA: $F_{6,585} = 3.885$, $p = 0.0008$). HWI's between adults of undetermined sex were the highest (Fig 3.13). These value were significantly different from HWI's between adult females, adult females - juveniles, adults of undetermined sex-juveniles and adults- females. In addition, HWI's between adults of undetermined sex and females were higher than between females themselves, which had the lowest HWI's (Fig. 3.13).

In general, the mean HWI between all sex and age categories was below 0.4, which reflects the predominance of weak associations. However, some strong associations between individuals were observed, especially among adults of undetermined sex.

The Bray-Curtis Similarity Index (Fig. 3.14) shows relatively strong associations between dyads of individuals. Dyads consisted of adults of undetermined sex and/or adult females, all with Bray Curtis similarity level > 75%. Two dyads of adult females (B10 & B 27; B23 & B25) were associated at Bray-Curtis similarity levels above 80%. However, few clusters of 4 dolphins including lactating females were associated at high Bray-Curtis similarity levels > 85%). A large cluster comprised of 18 adult dolphins (B+C), all the most re-sighted, was formed at similarity levels > 75% and included 6 females. The cluster B consisted of the 11 most re-sighted adult dolphins, of which 5 were lactating females. This cluster was closely associated with cluster C of 7 individuals, of which one was a lactating female (Fig 3.14).

Area use

i) Distribution of sightings

The distribution of sightings in Maputo Bay is shown in Fig. 3.15. Bottlenose dolphins occurred between 150 m to 19.25 km from the shore (sightings in the middle of the Bay), with a mean distance of 2.67 km (S.D. = 3.86, n = 60). Of the groups (49 sightings), 84% were observed within 5 km from shore, 64% (38 sightings) within 2 km from shore and 35.5% of schools (21 sightings) occurred within 1 km from the shore.

Fifty sightings of bottlenose dolphins occurred within 3 km of the coasts of Inhaca and Portuguese Islands. Eight other sightings occurred in the middle of the Bay at the Machangulo channel which has turbid water while the other two occurred south of Xefina Island, in western Maputo Bay during the winter, when water clarity and salinity were high. The sightings observed off Portuguese Island occurred in areas of strong wave action from the ocean, with bare, medium size sandy sediments close to some shoals, while other sightings occurred close to the reef off the western coast of Inhaca Island.

Though dolphin sightings seemed to increase between 16:00 and 18:00 (Fig. 3.16), the distribution of sightings during the day did not differ significantly ($\chi^2 = 10.08$, d.f. = 5, p =0.07). Dolphins were seen at all depths (Fig 3.17), though more sightings occurred between 5 to 20 meters ($\chi^2 = 22.695$, d.f. = 3, $p < 0.001$).

Only sightings within 3 km from shore were used to calculate the coefficient of area use by dolphins along the west coasts of Inhaca and Portuguese Islands.

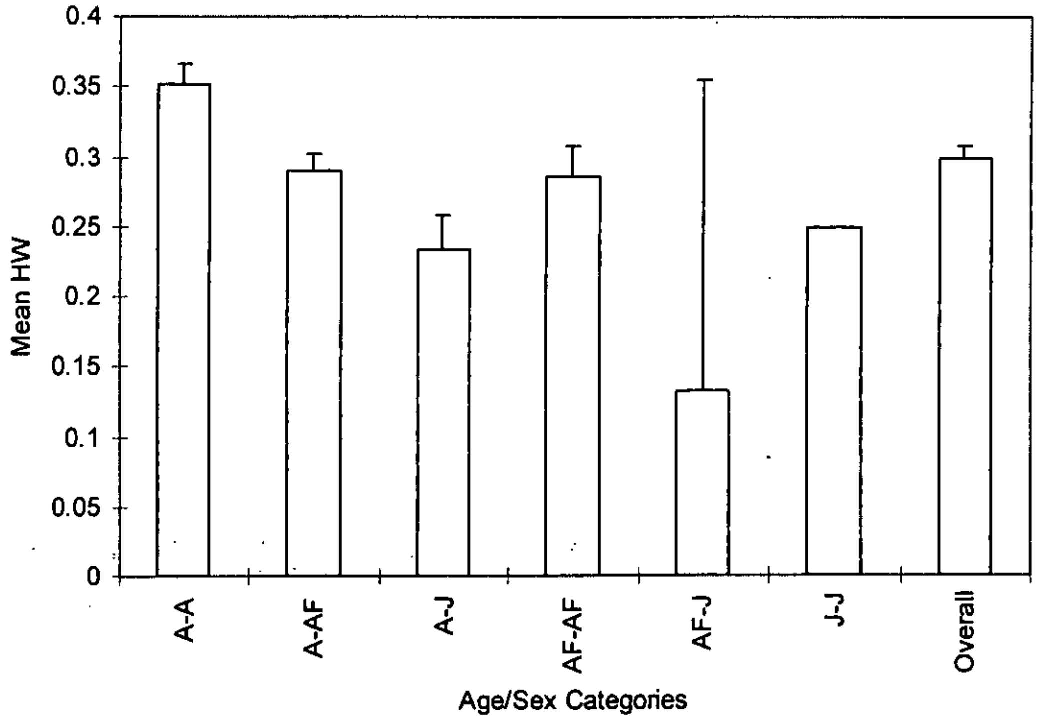


Figure 3.13. Mean values of half weight index (HWI) for age and sex categories of bottlenose dolphins observed in Maputo Bay between December 1995 and December 1997. (A = adults of undetermined sex, AF = adult females, J = juveniles)

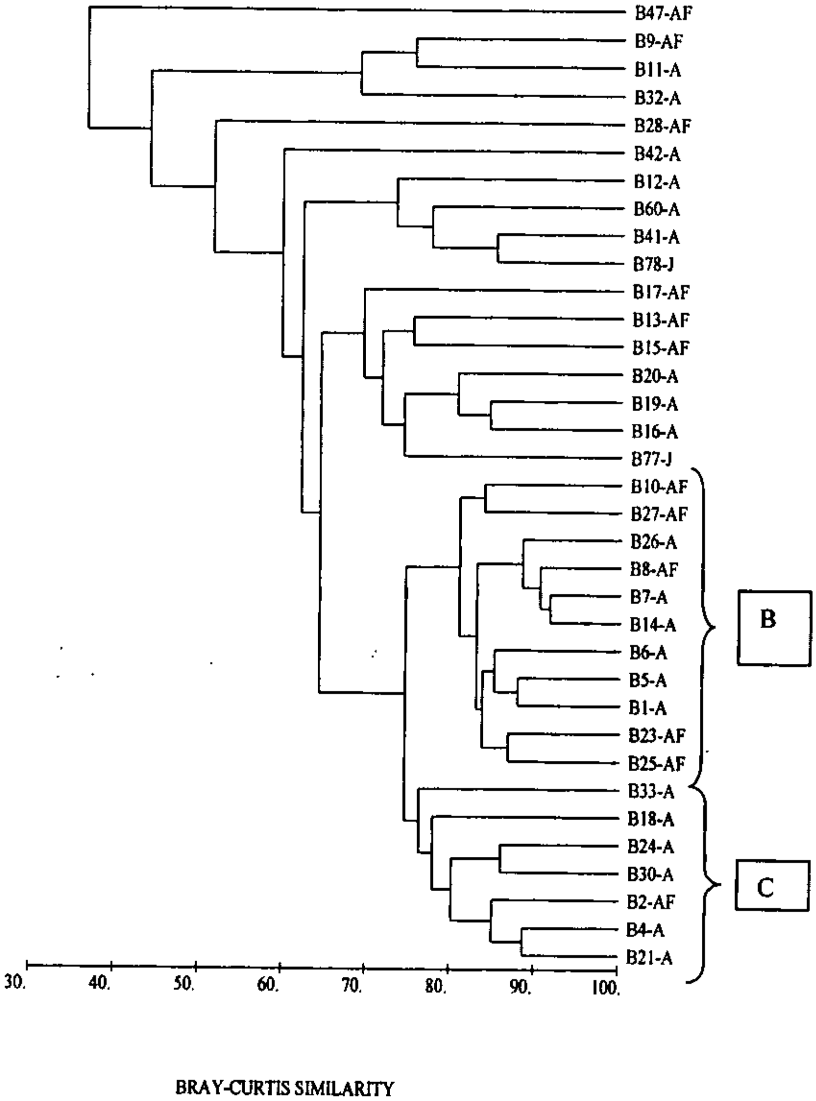


Figure 3. 14 Bray-Curtis Similarity coefficient of association of individually identified bottlenose dolphins photographed in Maputo Bay between December 1995 and December 1997 (AF = adult females, A= adults of undetermined sex, and J= juveniles). B and C denote clusters of dolphins that were most photographed.

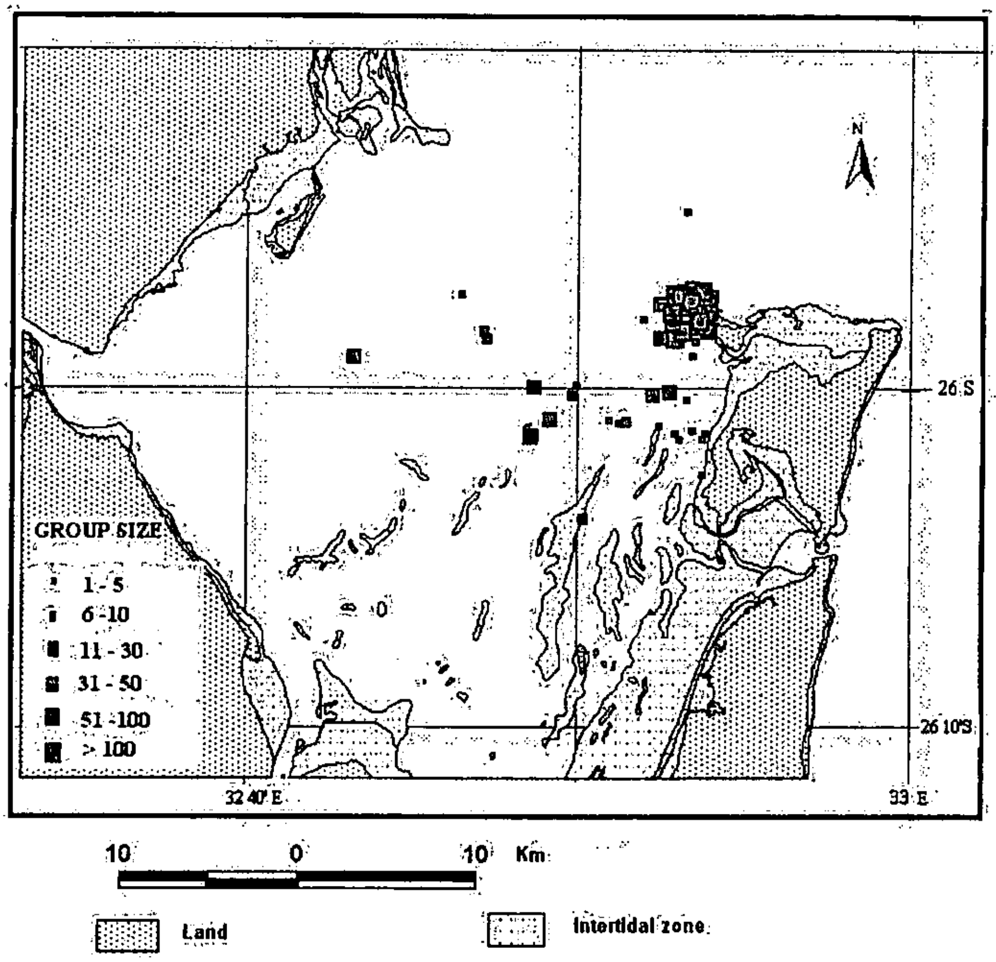


Figure 3.15. The distribution of sightings of bottlenose dolphins in Maputo Bay between December 1995 and December 1997. The squares represent individual sightings and their relative size denotes group size.

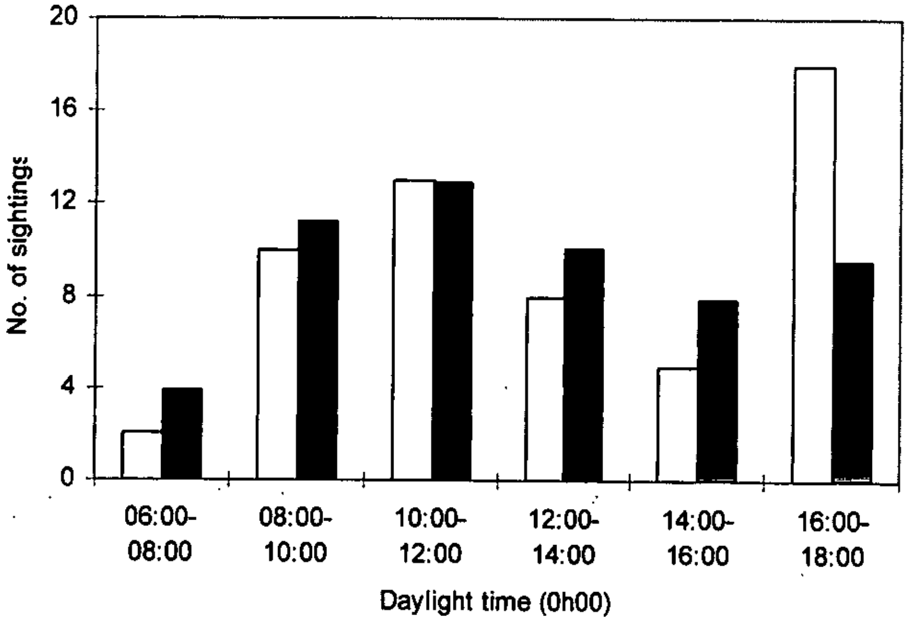


Figure 3.16. Observed (□) and expected (■) frequency distribution of the number of daylight sightings of bottlenose dolphins in Maputo Bay between December 1995 and December 1997. Expected frequencies were obtained multiplying the total number of sightings by the proportion of total effort (total time spent searching for dolphins) conducted at each time interval.

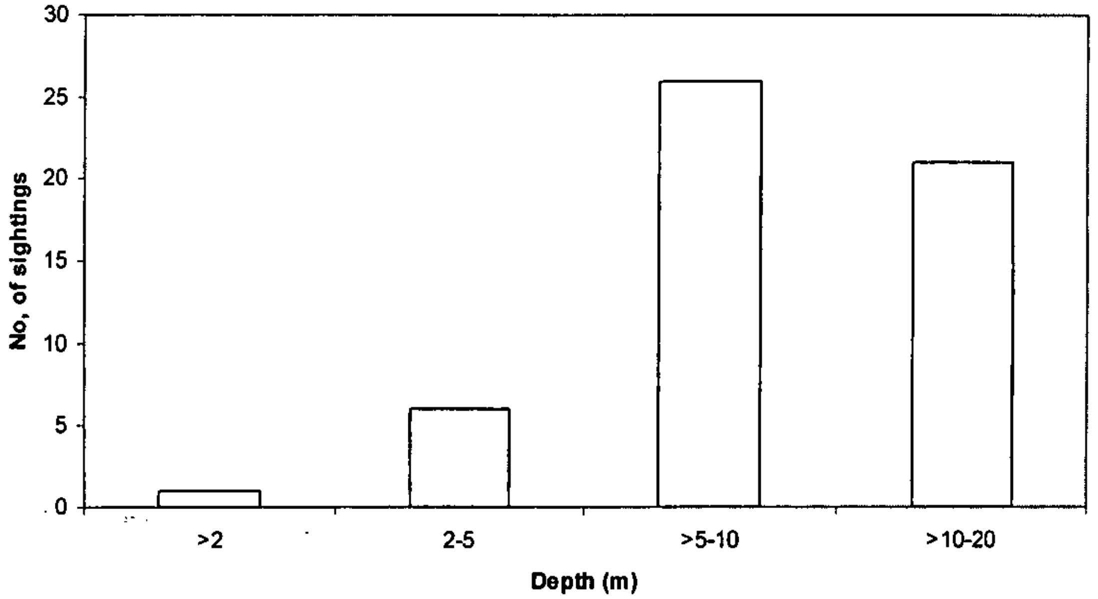


Figure 3.17. Frequency distribution of sightings of bottlenose dolphins in relation with depth, observed in Maputo Bay between December 1995 and December 1997.

Bottlenose dolphins were only observed along 14 sectors (7 km) comprising two sections of 3.5 km of coast (Fig 3.18). The first section (in the south) was the area along the coral reef off the western coast of Inhaca and the second section was the northern limit of the sectors at the pass between the Bay and the open ocean, close to Portuguese Island (Fig 3.15). The coefficient of area utilisation ranged from 0.20 to 1.00 and had a mean of 0.57 (S.D. = 0.32). The statistical differences in area utilisation between sectors were highly significant (Kruskal Wallis, H = 33.93, n=73, p=0.001), suggesting that dolphins had preferred areas along the coast. The number of sightings and the area utilization were higher in sectors 24-28, than between sectors 14-18 (Figs. 3.18 and 3.19).

ii) Activity of bottlenose dolphins in eastern Maputo Bay

The mean and total times spent observing bottlenose dolphins were 0.83 hours per group (S.D. = 0.65) and 48.38 hours respectively. Observation time (effort) in the morning (07:00-11:00), mid day (11:00-14:00) and afternoon (14:00-18:00) was 13.98h, 16.45h and 17.95 h respectively.

The activity index for feeding, travelling and social behaviour along the sectors is presented in the Fig. 3.20.

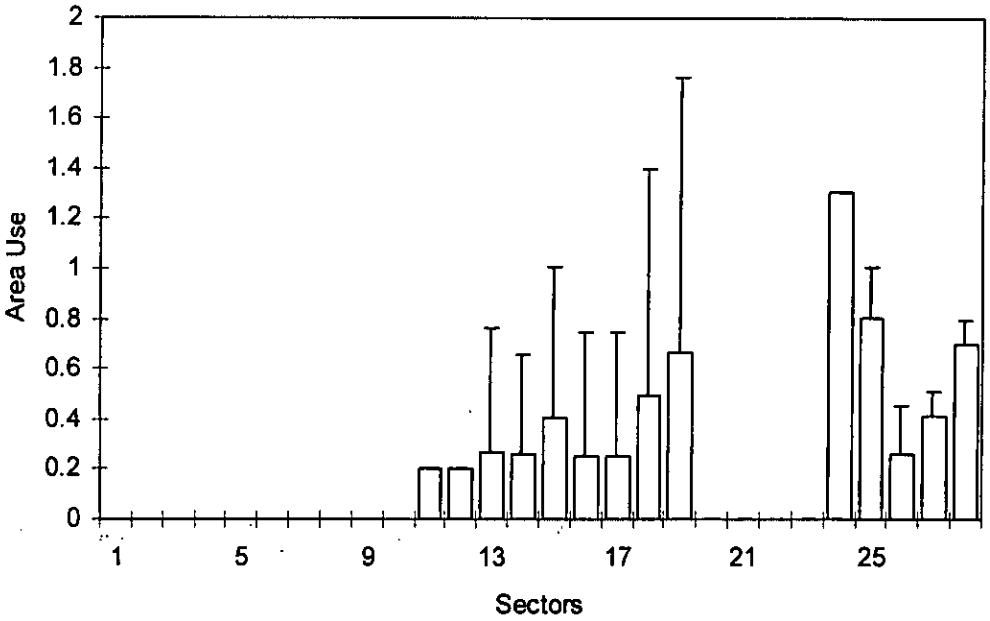


Figure 3.18. The proportion of time spent (Area use = total time spent by dolphins in a particular sector / the total observation time of the dolphins during that day) by bottlenose dolphins in each of the 28, 500 m wide sectors of the west coast of Inhaca and Portuguese Islands , between December 1995 and December 1997. Error bars represent the standard deviations of the area use.

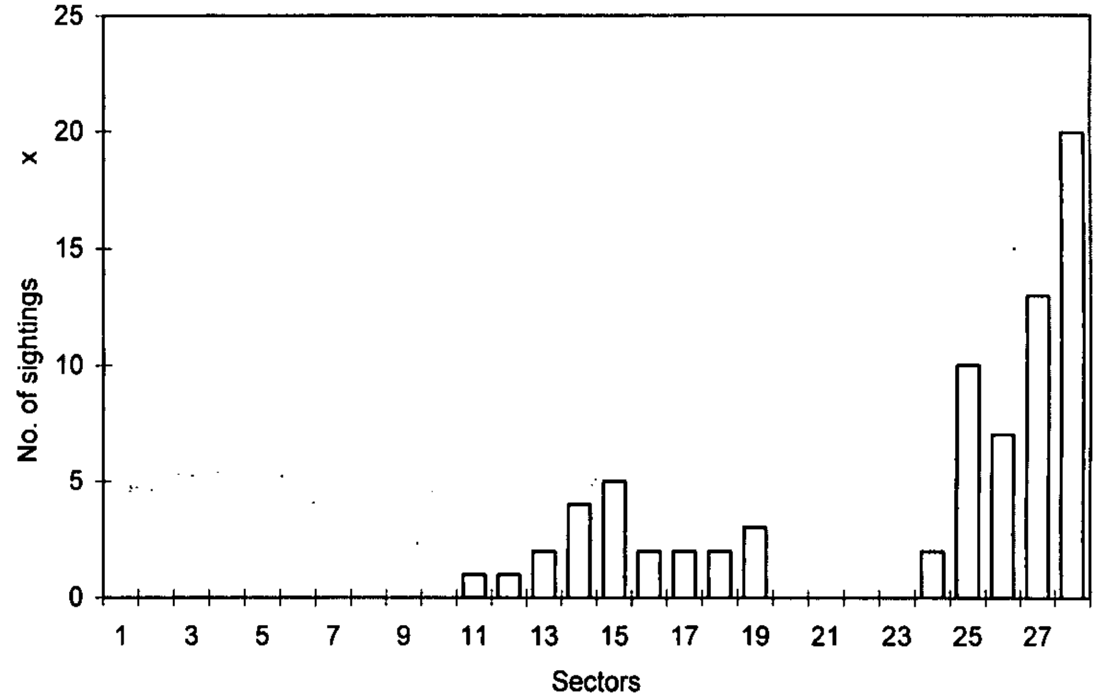


Figure 3.19. The frequency distribution of number of passes of bottlenose dolphins groups in each of the 28, 500 m wide sectors of the west coast of Inhaca and Portuguese Islands, between December 1995 and December 1997, during dolphin follow procedure. The sectors of the coast are described in Chapter 2.

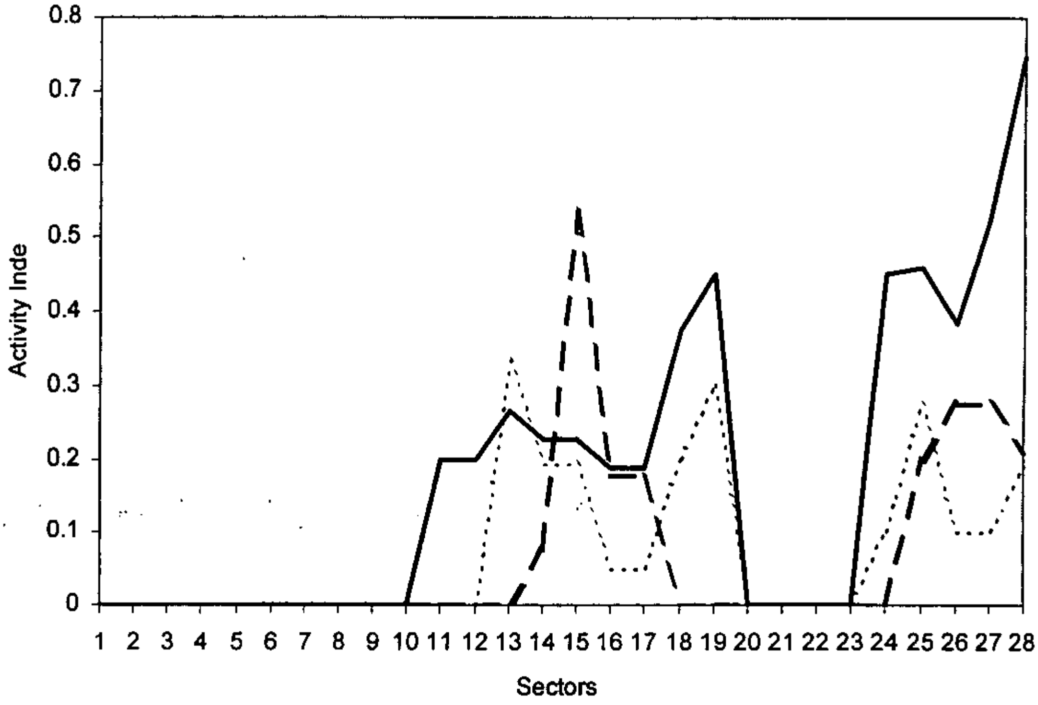


Figure 3.20. The proportion of time bottlenose dolphins spend feeding (——) travelling (– – –) and socializing (.....) (activity index = time dolphins spent performing a certain behaviour / the total observation time any sector) in each of the 28, 500m wide sectors along the coast of Inhaca and Portuguese Islands between December 1995 and December 1997.

The mean activity index did not differ significantly for feeding (Kruskal-Wallis: H = 21.82, n = 71, p = 0.058), travelling (Kruskal-Wallis: H = 7.02, n = 22, p = 0.4278) or socialising (Kruskal-Wallis: H = 10.86, n= 21, p = 0.455) between sectors.

iii) Movements of dolphins.

Bottlenose dolphins exhibited short-range random movements (Table 3.2), despite that the type of movement was not correlated with the tidal stage (Chi-square: $\chi^2 = 1.122$, d.f. =1, p = 0.289). Northward and southward movements (out or into the Bay) were observed infrequently at both tidal stages, but sample size was too small to be tested statistically.

Table 3.2. The influence of tidal stage: the frequency with which bottlenose dolphins in Maputo Bay were observed milling (localised movements) or moving in the northerly or southerly direction between December 1995 and December 1997. Only directional movements were split into southward and northward.

Tides	Ebb tide	Rising tide	Total
Localized	23	27	50
Directional	7	4	11
Southward	2	1	
Northward	5	3	
Total No. of sightings	30	31	61

DISCUSSION

Sighting frequency

Bottlenose dolphins were observed in 36% of the surveys conducted in the Bay. This low sighting frequency may occur because the ranges of the dolphins are larger than the study area. Large ranges may result from patchy distribution of prey and low prey availability in the study area. On the other hand, surveys were restricted to relatively deep areas (navigable, > 2m) preventing the survey of shallow areas (< 2 m), and therefore dolphins occurring in the shallower water were not sighted. The distribution of bottlenose dolphins off the Kwazulu-Natal coast, South Africa ranges from very shallow areas to depth of about 30 m (Ross *et al.* 1989; Peddemors 1995).

The sighting frequency observed in Maputo Bay is consistent with that observed by Durham (1994) off the Kwazulu- Natal coast (38% of surveys), but not with Peddemors (1995) who found higher sighting frequency (58%) on a 43 km stretch between Unhlanga and Umgababa, also off the Kwazulu-Natal coast. Therefore, the high sighting frequency obtained by Peddemors (1995) imply that he carried out his study in a preferred area, while the results of Durham (1994) and of the current study in Maputo Bay represent possibly the mean sighting rate of dolphins over wider areas. Off the coast of Kwazulu-Natal, bottlenose dolphins have been observed to range over , (Peddemors 1995) that is larger than extent of the survey area in Maputo Bay

The low sighting frequency observed can also be expected if most of the inner part of eastern Maputo Bay represented a marginal area of the dolphins range, as most dolphins were only observed at the pass to the Ocean (Fig. 3.15). However, sightings of small groups might also have been overlooked since the sightability may increase for large groups because they often engage in asynchronous surface behaviour.

Variable sighting frequency has been documented worldwide, with dolphins often frequenting reefs and estuaries, and passes to the Ocean. Areas of high prey abundance had high sighting frequencies and are summarised by Shane *et al.* (1986), Klinowska (1991), but also reported by Ballance (1992), Weigle (1990), Wells *et al.* (1990), Felix (1994), dos Santos & Lacerda (1987).

Single sightings per survey predominated over multiple sightings per survey during the surveys. Although many factors might have contributed to this, the relatively short length and duration of most surveys carried out in Maputo Bay could have been important, as an area smaller or equal to the range of only one group may have been covered. Wilson *et al.* (1997) found evidence of seasonal stratified movements and habitat use of dolphins in the Moray Firth, Scotland, suggesting the existence of competition between groups of dolphins. However, this hypothesis requires further investigation in Maputo Bay. Another factor contributing to existence of single sightings in the study area within Maputo Bay may be the patchy distribution of prey that promotes group foraging behaviour of the dolphins, causing coalescence of small groups into larger ones. On the other hand, smaller group sizes might have been overlooked during the surveys due either to their possible elusive behaviour (avoiding the research boat) or unsuitable weather conditions. Usually small groups synchronise their diving/surfacing pattern becoming difficult to locate or follow (Ross *et al.* 1987).

Within preferred areas off the Kwazulu- Natal coast, South Africa, the small long-shore gaps between groups ranged from 0.5 to 6 km, while large gap sizes varied between 10-37 km (Peddemors 1995). These large gaps represent separations between preferred areas. The prevalence of single sightings may mean there are few preferred areas in the Maputo Bay. Possibly, because the Maputo Bay is a very large area of depths < 30 m, dolphin groups may disperse widely (rather than clump themselves to few areas, like off the Kwazulu- Natal coast), resulting in low density. The lack of accessibility to the shallowest areas of the Bay may have further decreased the number of sightings.

Sighting frequency could also be influenced by the mean group size. Mean group size was 27.47 individuals. This relatively large mean group size suggests that prey is scarce and of uneven distribution and dolphins will coalesce to enhance foraging efficiency (Würsig 1986) over wide ranges. This will therefore decrease their sighting frequency in a given location if prey occurrence in the study area is unpredictable.

The occurrence of bottlenose dolphins did not show any relationship with the daily tidal cycle in Maputo Bay. Dolphins often occurred at subtidal areas, less affected by tidal range. However, dolphins may have responded to the effect of ebb tidal currents, which mix nutrient rich water from the Bay with the clear oceanic water boosting the plankton production and subsequently fish aggregation. The importance of tidal currents as sources of nutrients has been documented by Hanson & Defran (1993) off San Diego and Ballance (1992) that refer dolphins to concentrate at the mouths of estuaries which receive high load of nutrients with fresh water run-off off the Gulf of California. The hydrology of eastern Maputo Bay is under strong influence of tidal currents (Achimo 2000). The movements of the dolphins, however, were partially affected by the tides as some dolphins moved into the shallower areas of the Bay during rising and high tides. Possibly, the concentration of survey effort and sightings at areas of depth >2 m masked the relationship between dolphin occurrence and tidal cycle.

In summary, bottlenose dolphin sightings were infrequent, implying that dolphins may disperse widely in the Bay. The restriction of effort to navigable areas and possibly low sightability of smaller groups of dolphins may have further decreased the sighting frequency.

SPUE and NPUE

Both SPUE and NPUE differed significantly between months and seasons, being higher during winter compared to summer, though high variability was observed (Fig. 3.2). The higher SPUE during winter could be caused by changes in the abundance of prey. During the wet season (summer), the whole Maputo Bay experiences a reduction in salinity and increased turbidity (Nhapulo 2000) which reduces prey abundance while the open waters may experience general increase of prey, leading to dolphin dispersion and exploitation of richer feeding areas. During winter, Maputo Bay might be one of few areas with relatively high prey abundance (Sousa 1985), attracting dolphins. Such prey abundance might be enhanced increased water salinity and better transparency, due to reduced river run-off (Chapter 2). However, the high monthly variability in SPUE and NPUE (Fig. 3.2) may be caused by depletion of prey after exploitation of the areas by large groups of dolphins or/and by high prey mobility or very patchy distribution of prey in the Bay.

Catches from hand line fishery (which captures relatively large sized pelagic and demersal fish) decreased during winter in Maputo Bay, and during this season, this fishery is practiced at only a few fishing areas in the northern part of the Bay (Chacon 1995). However, the amount of schooling fish increased in the catches between April and December (Sousa 1989), suggesting that dolphins may be targeting these fish or their predators. The area north of Maputo Bay may be the richest prey area during winter due to its location in the edge of an area of restricted offshore upwelling observed during winter (Jorge da Silva 1983, see Chapter 2). Off the east coast of South Africa, south of Maputo Bay, in winter there is an increase in dolphin abundance, following prey which moves along with sardines that spawn inshore (Peddemors 1995). There is no evidence that this phenomenon extends to Maputo Bay and apparently bottlenose dolphins from Maputo Bay do not move south during this period, despite evidence that individuals off the Kwazulu- Natal coast range over long distances (Peddemors 1995). Possibly the turbid waters of Tugela Bank may act as barrier to dolphins to move north into Mozambique waters (de la Mere 1999).

In addition, there is no evidence of large schools of pelagic fish species spawning during winter in Maputo Bay. However, catches of fish (measured as kg/day/boat) from shrimp trawlers that operate in Maputo Bay were higher from August to January, but a smaller second peak was observed during April-May (Sousa 1985). The catch composition was dominated by pelagic species during summer, maintaining levels of about 80% and decreasing to 40% in winter (Sousa 1989). On the other hand, demersal species increased during winter attaining about 60% of the total catch (Sousa 1989). The dominant pelagic species were *Leiognathus equulus*, *Gazza minuta*, *Hilsa kelee* and *Sardinella gibbosa*. Nevertheless three pelagic species increased their abundance during winter; *Secutor insidiador*, *Pellona ditchella* and *Thryssa vitrirostris* (Sousa 1989). Among the demersal species *Otholithes ruber* and *Johnius sina* were dominant during summer while *Pomadasys maculatus* dominated during winter (Sousa 1989). The feeding ecology of bottlenose dolphins of Maputo Bay is not known and the fish composition in Maputo Bay and at the Kwazulu- Natal coast is different (Sousa 1989, Peddemors 1995). Off Kwazulu- Natal coast, bottlenose dolphins feed on a wide range of species, both pelagic and demersal (Cockcroft & Ross 1990a).

The diet of bottlenose dolphins is varied in many areas but always but always with some preferred prey species (Barros & Odell 1990; Cockcroft & Ross 1990a; Corkeron 1990). However, abundance of fish species alone may not be the prime factor in prey choice, prey quality, which may include size and calorific value, may be equally important. Eight genera, recorded as the most abundant fish species in Maputo Bay, are taken by bottlenose dolphins in Kwazulu- Natal waters (Cockcroft & Ross 1990a). However, without evidence from stomach content in Maputo Bay, it will be difficult to determine which fish species are the preferred prey of bottlenose dolphins in Maputo Bay. However, in clear water with sandy sediment (Achimo 2000) and low prey diversity like the pass to the Ocean (Chuquela 1996), dolphins may not have much prey choice.

Another possible reason for the higher abundance of dolphins during winter could be the need to mate and breed. However, there was not any significant increase in the social behaviour during this season (Chapter 7) and births were spread throughout an extended period (October to July in 1996 and 1997) (Chapter 5). However, off the Kwazulu-Natal coast, bottlenose dolphins exhibited the social behaviour for reproduction, including most births, during spring (Peddemors 1995), though births occurred year round (Cockcroft & Ross 1990c). Seasonal changes in intensity of predation could possibly be another factor to which dolphins responded, but the lack of quantitative data does not allow validation of this. However, sharks would also respond to prey patchiness, by exploiting the same prey rich areas where dolphins occur.

SPUE and NPUE were negatively correlated with river run-off in Maputo Bay, but only SPUE was significantly correlated (Spearman rank correlation: r=-0.0554, p=0.049). This means that bottlenose dolphins avoid the Bay when water transparency is low, as during the wet season. Off the southern Kwazulu-Natal coast and Transkei and off Tugela Bank in northern Kwazulu-Natal, bottlenose dolphins also avoided turbid waters possibly to reduce shark attacks (Ross *et al.* 1987, Durham 1994, Peddemors 1995).

Whether this has any relation to changes in prey composition is unknown, but considering the high amount of fresh water load during summer (Chapter 2), it is highly likely that fish composition changes seasonally in Maputo Bay (Sousa 1989). Similarly, off Kwazulu- Natal coast, the abundance of some pelagic species, known as the main prey of bottlenose dolphins, altered seasonally or occurred during one season at fish aggregation devices (Peddemors 1995). In Maputo Bay the coincidence of dry season with winter further complicates the determination of main cause of changes in SPUE,several factors (salinity, temperature and turbidity) changes during this season. The results of the Maputo Bay follow the same trend as the Gulf of Guayaquil in Equador, where bottlenose dolphins were frequent during winter and avoided the estuaries during summer, when heavy rains altered the salinity of the Gulf and possibly altered prey composition (Felix 1994).

The lack of significant correlation between NPUE and river run-off was probably related to the high within-season variability in number of dolphins observed, which is suspected to be caused by local movements/distribution of prey.

SPUE and NPUE were also independent of neap/spring tides, as bottlenose dolphins were often sighted at subtidal areas. The extent of tidal amplitude is important inshore, where it determines the size of intertidal area exposed or flooded and affecting the distribution of near-shore and pelagic prey species. Furthermore, only a few small groups of bottlenose dolphins used the intertidal areas at high tide, possibly they forage efficiently on the few food resources available (Wells *et al.* 1980 and Würsig 1986). Temporal small-scale factors such as spring/neap tides are often known to affect dolphin movements, rather than their abundance (Shane *et al.* 1986).

Therefore, the increase in SPUE and NPUE in Maputo Bay during winter, is likely to result from reduction of food in many areas of their range causing the aggregation of dolphins in a few areas of high food abundance and therefore mating/social interactions could just be a result, rather than a cause of increased aggregation.

Group size

The high number of smaller groups, along with the high variability of NPUE and low sighting frequency suggest that prey abundance in the Bay is often low, and large groups may not be supported for extended periods. On the other hand, most groups consisted of or included small nursery groups, implying that these may successfully obtain the necessary prey and shelter in the Bay. Group size is determined by intra-specific competition for food, feeding efficiency and predation pressure (Würsig 1986, Wrangam & Rubestein 1986), and the distribution of prey resources (Doncaster & Krebs 1993). Smaller groups were often observed in the inner channels of Maputo Bay or close to the reef off the west coast of Inhaca both of which are shallow and have weak wave action. Likewise, bottlenose dolphins inhabiting shallow areas with either seagrass or lined by mangroves or reefs often formed smaller groups elsewhere (Shane *et al.* 1986; Ballance 1990; Grigg & Markowitz 1997), implying that prey type and abundance determine group sizes.

Larger groups were only observed at the pass between the Bay and the Ocean in eastern Maputo Bay (Fig 3.15). This area has very complex bottom topography, intense wave action and complex current systems (Kalk 1995; Chart 46659-M, INAHINA 1985, Achimo 2000). There, dolphins aggregated to feed on schooling prey. Prey schools gathered at the surface soon after dolphins dove and some dolphins were observed preying on these unidentified fish (pers. obs). Possibly large groups were formed to increase protection against predators (sharks), which may also be attracted to places of high prey abundance. However, evidence of high rate of predation is lacking in Maputo Bay, while few lactating female dolphins displayed fresh wounds or scars caused by sharks (pers. obs).

The mean group size in Maputo Bay is similar to the mean group size of dolphins off the east coast of South Africa (33.34 individuals) (Findlay *et al.* 1992). Further south, off Transkei, groups attain sizes of 199 (SD=323.1) and at Eastern Cape, 140 individuals (Saayman *et al.* 1972). Along the Kwazulu-Natal coast, Durham (1994) found a mean group size of 25.7 (SD=22.2) dolphins, which is consistent with the findings from Maputo Bay. Both in Maputo Bay and off the Kwazulu-Natal coast, the areas searched were within a depth of ≤ 20 m and counts were made from boats.

The causes for the larger group sizes off Transkei and Eastern Cape are unknown and may be related to differences in the prey abundance/distribution and searching methods used in the studies. The smaller groups reported off Kwazulu-Natal coast and Maputo Bay may also be aggravated by other factors. Dolphins are subject to incidental catches by shark nets (Cockcroft *et al.* 1989) and other fisheries (Guissamulo 1993) off Kwazulu-Natal coast and Maputo Bay, respectively. In addition, in Maputo Bay, dolphins are disturbed and their prey depleted by trawl and gillnet fisheries (Cockcroft & Krohn 1994; Massinga & Hatton 1996).

Usually, fish by-catches from shrimp trawling comprise 60% of the total catch (Sousa 1984;1989). At Transkei and Eastern Cape coast, dolphins do not suffer the prey depletion by the by-catch pressure.. However, the size of the habitats may also influence group sizes. The offshore dolphin distribution is limited to depths ≤ 30-40 m (Ross *et al.* 1987). These depths are attained close to shore off the coast of South Africa (Shannon 1989) which is steep further offshore and 90% of groups occur within a 1km strip of the shore (Ross *et al.* 1989). This may promote dolphins to gather forming larger group sizes. In Maputo Bay the area of depths ≤ 30-40 m isobaths widens up to 35 km inshore, resulting in a large area available for dolphins and, consequently, dolphins may disperse forming smaller groups than those observed off Kwazulu-Natal coast, South Africa. The intensity of predation from sharks may also contribute to dolphins aggregating into large groups.

Group sizes varied seasonally and significantly larger groups were recorded during winter in Maputo Bay, though large variability was observed between months, therefore resulting in the lack of monthly differences (Fig. 3.4). The increased group sizes during winter might be explained by the same factors influencing the increased sighting rates, which also occur in winter, viz. the intense patchiness of food supply during winter.

The variability of group sizes within the season can be caused by the temporal depletion of prey after a heavy exploitation by dolphins and fisheries, prey movements away from the study area or short term aggregation of prey. Therefore, the winter influx of dolphins in Maputo Bay may correspond to aggregation of groups to forage on patchy food. These groups may disperse during summer. Off the east coast of South Africa, winter increase in group-size has been related to the northward migration of pilchard (*Sardinops occelatus*) (Peddemors & Cockcroft 1993; Durham 1994; Peddemors 1995), which is speculated to reach Mozambican waters (Peddemors 1995). However, this phenomenon has not been documented in southern Mozambique.

Group size was not related to daylight, tidal cycles or depth. Daylight and tidal cycles are short-term variables affecting the movement of dolphins (Shane *et al.* 1986). Possibly, dolphin prey occurrence and movements in Maputo Bay may not respond to daylight and this may, therefore, not influence group size. On the other hand, the bathymetry of Maputo Bay is very complex and depth isobaths are irregular and changing abruptly. This does not allow the identification of any potential relationship between group size and depth. Bottlenose dolphins adapt flexibly to water depth ranging from shallow shoals (Wells *et al.* 1992, Shane *et al.* 1986) up to depth of 30 m (Ross *et al.* 1987; 1989; Saayman & Tayler 1979). The maximum depth of Maputo Bay is <30 m and therefore any trend between depth and group size is unlikely to occur within the Bay.

The need to feed on large fish schools force some dolphins to frequent open, deep water areas which have bottom topography of high relief, that attracts prey (Norris & Dohl 1980b and Heimlich-Boran 1988). At Aransas Pass, Texas, bottlenose dolphins frequently concentrated in such areas (Shane 1980). Therefore, in Maputo Bay, group size increased in winter in response to the increase of small pelagic schooling fish in the Bay and possibly the high patchiness of food outside the Bay. The impact of fisheries on prey patchiness during winter may be the depletion/competition for prey resources (as by catch of trawling fishery). While prey species may be abundant, the continuous long-term intense fishing activity may be reducing prey size, causing a scarcity of resources for dolphins.

Group dynamics

Mixed groups, composed of all age classes, were the most frequently sighted in Maputo Bay. Adults were dominant (54%) followed by juveniles (35%) and calves (11%). The existence of mixed composition groups, though data on sex distribution through age classes is lacking, means that a breeding population of dolphins frequents Maputo Bay to rear and protect their young. Analysis of prey consumed by bottlenose dolphins off Kwazulu- Natal waters, revealed a spatial habitat partition of dolphins based on sex and age (Cockcroft & Ross 1990a). Whether this also occurs in Maputo Bay is unknown since the study did not examine prey differences and sex of all dolphins identified. The nursery groups were more abundant than non-calf groups. Calves have precarious physical ability to travel longer distances (Connor 2000) and require large amounts of food in the first years of their development (Cockcroft & Ross 1990b). Nursing females want to occupy optimal home ranges, which warrant prey resources for their high energetic requirements for calf nourishment (McNab 1963; Cockcroft & Ross 1990a). This increased the chances of finding them in Maputo Bay. Optimal home ranges are usually enclosed areas of predictable availability of food resources. Large nursery groups arise from co-operation between mature females, including those caring for calves- the so-called allomaternal behaviour (Johnson & Norris, 1986, Shane *et al.* 1986; Connor 2000). Evidence of allomaternity was observed in Maputo Bay during events of feeding on schooling fish by large aggregations of dolphins: some known females temporarily abandoned the calves and joined the actively feeding groups while all small calves gathered together in a subgroup that remained under the supervision of other females or adults dolphins.

However, nursery groups may attract males in search of mates, because as in other delphinids, mature females maintain association with their mothers (Connors 2000). In addition, juveniles and sub-adults maintain variable levels of association with their mothers (Wells 1991, Smolker *et al.* 1992), thus contributing to the mixed group composition. In addition, if high food patchiness occurs in the study area and adjacent areas, the foraging requirements may override any group organisation and therefore dolphins of different sex and age classes may mix when preying on the same resources. Mixed group composition may arise because sub-groups of adults, females and juveniles often share overlapping home ranges, learned when reared by their mothers (Wells 1992). Connor (2000) observed that male bottlenose dolphins maintain geographic ranges which include their maternal range.

The percentage of adults and calves was similar to that of bottlenose dolphins from San Diego (Weller 1991). Felix (1994) reported an extremely high percentage of calves (23%) in the Gulf of Guayaquil. This may result from the use of that estuarine area by females from the region and adjacent areas as a calving ground, in the same sense as Kasuya & Ogi (1987) reported for Dall's porpoises, as it may provide both safety and good food resources.

The high frequency of groups with mixed composition, which masked any kind of age/sex based social organization, may have resulted from the patchy distribution of prey resources in the Bay. However, the need of improved defence against predators shall not be excluded (Shane *et al.* 1986 and Johnson & Norris 1986) and overlapping ranges of individuals can thus occur (Connor 2000).

Site fidelity

The site fidelity pattern of bottlenose dolphin individuals in Maputo Bay was variable and related only partially to age and sex. Dolphins re-sighted up to five times had a highly variable number of days between re-sightings, while those observed more than five times had a mean number of 50 days between re-sightings (Fig.3.9). Moreover, 59% of identified individuals were never re-sighted (transient) (Fig. 3.7) and consisted mostly of juveniles and adults of undetermined sex and 68% of the individuals occurred during only one season (either summer or winter). The remaining individuals occurred during all seasons, but with a variable number of days between first and last re-sightings.

The site fidelity of dolphins can also be examined by plotting the mean time between photographing occasions of a dolphin against the time between its first and last photographing occasions. Dolphins that fall in diagonal line are extreme transients, visiting the bay for a very limited period annually (Fig. 3.10). Dolphins plotted bellow the diagonal line can be divided into two groups: those at the left that are transients of several degrees and those at the right, near the x-axis that are residents (Fig 3.10). However, the discovery curve of the dolphins can influence this, when most resident individuals are progressively identified through out the study.

These results imply that a large proportion of transient dolphins visit Maputo Bay over shorter periods, possibly when prey outside the Bay is scarce, or when certain preferred prey increases in the Bay as shown by the catches in the fisheries (Sousa 1989). As some adults, including females with calves, were frequently seen, it appears that Maputo Bay is an area also used to rear calves. Pregnant females could also use the Bay for feeding and may possibly constitute the bulk of individuals of undetermined sex. Pregnant females often associate with lactating females off Kwazulu- Natal (Cockcroft & Ross 1990a). Atlantic spotted dolphins display the same pattern of association between pregnant and lactating females (Herzing & Brunnick, 1997).

However, some large bottlenose dolphins were observed during the whole year and were never seen with calves. These could either be males, females which failed to conceive or large sub-adults or juveniles misclassified as adults, based on the relative size of individuals. The low site fidelity of juvenile dolphins in Maputo Bay is disturbing, as they were expected to associate frequently with their mothers. This could be explained by the poor marking pattern of juveniles, which reduced the chances of re-sighting (Cockcroft & Ross 1990c), or possibly a high mortality rate or an earlier passage into transient life because of seasonal changes in resource availability in the Bay. The latter explanation is supported by existing lactating females which were transient and, their old calves could have begun their transient life. All three explanations are valid despite the lack of evidence.

If Maputo Bay is a marginal area for the dolphins' distribution, then the existence of many transient individuals would be expected. The occurrence of dolphin influxes during winter could be caused by the generally low pelagic prey abundance outside the Bay, but of high catches in the shrimp trawling fishery inside the Bay (Sousa 1989), suggesting an increased prey availability. However, the large groups of dolphins observed would quickly deplete the prey resources and subsequently abandon the area in search of other feeding grounds, or just follow the prey movements to the outside of the study area. The prey depletion may be caused by patchy prey distribution or exacerbated by fisheries in the Bay. In addition the shrimp fishing trawlers also degrade the substrate of benthic prey in the western Maputo Bay (Sousa 1989; Massinga & Hatton 1997) causing dolphins to rely mostly on small pelagic prey outside the fishing areas. Existing seagrass areas of eastern Maputo Bay provide shelter to most demersal prey (Kalk 1995). However, most prey is of small size (André 1995) and the large groups of dolphins observed may spend more effort to forage on those. Therefore, a large area of the south-eastern part of the Bay may be less attractive for large groups of dolphins. On the other hand, the searched area in the Bay was small and possibly most dolphins, apparently transient, may range into the shallower areas of the Bay that were less or not searched. The occurrence of larger groups during winter would further reduce the probability of re-sighting most individuals and may account for the low site fidelity observed for some individuals, with emphasis on juveniles that usually occur in large schools.

Off the Kwazulu- Natal coast, the population of bottlenose dolphins is distributed into specific areas, suggesting high site fidelity, but mixing with transient dolphins also take place (Cockcroft *et al.* 1990b, Peddemors 1995), mainly during winter following the northward migration of pilchards (Peddemors 1995). However, the existence of transient dolphins moving between communities was also documented (Peddemors 1995). If the habitat partition between age-sex categories observed in Kwazulu- Natal waters (Cockcroft & Ross 1990a), occurs between the dolphins of Maputo Bay, then the chances of identifying often lactating and pregnant females would be higher than identifying adult males and juveniles, because these would often feed offshore. Consequently, most males and juveniles would be considered transient in the Bay, because they could feed together with female groups during winter when there is prey scarcity outside the Maputo Bay.

Highly variable patterns of site fidelity have been reported for bottlenose dolphins off the coast of Argentina (Würsig & Würsig 1977 and Würsig 1978), in Galveston Bay, (Bräger *et al.* 1994), in Matagorda Bay (Balance 1992) in the Gulf of California (Lynn, 1995), off San Diego (Weller 1991), in lower Tampa Bay (Weigle 1991) and in Plettenberg Bay (Saayman & Tayler 1973) which are all open habitats. However, Wells (1991), Shane (1980), Harzen (1995), Dos Santos & Lacerda (1987), Felix (1997) and Smolker *et al.* (1992) found individuals with high levels of site fidelity, and restricted proportion of transient individuals, in Sarasota Bay and off southern Texas, the Sado Estuary, Gulf of Guayaquil and Sharks Bay respectively, which are all closed habitats. However, seasonal changes of area use and area partition between sexes affected the individual site fidelity within communities (Wells 1991 & Felix 1997). Maputo Bay is large and has a larger population (Chapter 5), than most other bays. Nevertheless, it appears that shark fishery in the past and the trawling and gillnet fisheries interacted with the dolphins in a way that they changed their distribution favouring areas with less fishing pressure. On other hand, the low accessibility for us to parts of the Bay, must contribute to the relatively small number of resident dolphins found.

In summary, in Maputo Bay, small groups of dolphins, mostly composed by females with calves, pregnant females and adults of unknown sex had high site fidelity. A large number of transient dolphins visited the Maputo Bay during winter possibly in response to increased prey availability there in relation to outside areas. Some apparently transient dolphins could have spent the summer at the less surveyed areas of the Bay while other could come form outside the Bay. Nursing females may shift from resident to transient life or increase their range in the Bay as their calves grow and become capable of swimming large distances or after weaning their calves. The fishing pressure in the western part of Maputo Bay may also have reduced feeding areas and the resources available to dolphins, promoting the adoption of transiency by most dolphins.

Social affiliations and associations

The number of affiliates increased with the number of times individual dolphins were re-sighted (Fig. 3.11) but the most re-sighted individuals were not seen with all other possible affiliates, e.g. all other identified individuals (Appendix 7) and occurred in less than half of the sightings when photographs were taken, possibly because of either their absence from the study area or from low probability of re-sighting when occurring in large groups observed during winter. Most individuals might have been missed when photographying large groups of dolphins in the Bay, despite that more time was spent with such groups. However, in many occasions, individuals were not photographed either because of inadequate weather/sea state that could damage the camera, or because dolphins disappeared after sighted, avoiding the boat. In addition, during some months (June, July and August 1997), surveys were not carried out and many non-resident individuals that transited in Maputo Bay were missed. Therefore, all these factors influenced or bias the number individuals photographed, the number of affiliates negatively. However, this biased positively the overall level of associations between individuals. Nevertheless, the general pattern of association may not have been altered.

Some of the most resighted dolphins were females and some were adults suspected to be pregnant females or cycling females. They might have moved outside the Bay, but considering the high risk to expose their calves to predation, it is more likely that females with calves and some adults moved inshore to the shallow areas which were inaccessible to surveys or outside the study area in the Bay. Nevertheless, this could, however, expose these dolphins to interactions with fisheries, which could possibly be less risky to the calves than predation from sharks. In addition, females with calves observed within large groups of dolphins, often segregated from actively feeding dolphins and often avoided the research vessel as well, reducing the possibility of being photographed. This implies that the mean number of affiliates of any dolphin is negatively biased. Similar segregation was observed on dusky dolphins (Johnson & Norris 1986). Large aggregations of dolphins are non-mutualistic and are often formed in response to prey distribution (Connor 2000), and therefore, they may artificially increase the number of affiliates of any individual if their significance is not examined.

The influence of age and sex on the number of affiliates of bottlenose dolphins of Maputo Bay was equivocal, because of the uneven sighting frequency of the different age and sex categories (Fig.3.11). Therefore, the number of affiliates did not differ significantly between individuals of different age and sex categories sighted more than four times, showing that the site fidelity was the prime factor affecting the number of affiliates of any individual dolphin. However, the role of sex on the number of affiliates is related to the different grouping strategies of males and females (Connor 2000) which may be visible in studies carried out over large areas, or with very distinct environmental gradients (depth, prey distribution, etc). The current results may only reflect the small scale of the study relative to dolphins' range.

Adult bottlenose dolphin males could not be identified in Maputo Bay. but some large dolphins of unknown sex were among the most sighted individuals. Three pairs of these dolphins (B1- B5, B4-B21 and B7-B14; see Figure 3.13) were strongly associated and could be a pair of males (Wells 1991,1992, Felix 1997, and Smolker *et al.* 1992 and Connor *et al.* 2000). These groups were loosely associated to each other. No agonistic behaviour between these three pairs of dolphins was observed, possibly, because underwater behaviour was not studied and few mating events were observed. Agonistic behaviour may be manifested during events of mating or female harassment (Connor *et al.* 2000).

The mean coefficient of association between any two individuals was 0.30 with most dolphins associated at levels between 0.01 - 0.20 (30.4% of associations) (Fig. 3.11) and associations above CA = 0.40 comprised 28.8%. The few strong associations and relatively low mean coefficient of association imply that small resident sub-populations in the Bay mixed for short periods with large number of transient dolphins. This is supported by the seasonal increase of group size in the northern Maputo Bay (Fig. 3.4) in response to changes in prey distribution and abundance in the Bay in relation to other areas outside the Bay, as inferred from Sousa (1989). The social structure of bottlenose dolphins in the region is poorly known, but off the coast of Kwazulu- Natal, some resident populations, with little interchange, mix seasonally with large numbers of transient dolphins which follow prey during the 'sardine run' (Peddemors 1995). On other hand, there are spatial and prey partition between dolphins of different sex, age and reproductive status off the Kwazulu- Natal coast (Cockcroft & Ross, 1990a). Therefore, it may be accepted that the group organization between dolphins of Maputo Bay and those from the Kwazulu- Natal coast are similar, based on the coefficient of associations and site fidelity pattern encountered in Maputo Bay.

However, since the distance that transient dolphins observed in Maputo Bay range southwards is unknown, a relationship between the dolphins from Kwazulu- Natal coast and those occurring in Maputo Bay cannot be established. Genetic isolation of bottlenose dolphins off the Kwazulu- Natal coast in relation to those off southern Mozambican waters has been observed (Goodwin 1997), possibly due caused by geologic events and kept by the turbid waters off Tugela Bank, northern Kwazulu- Natal coast (Peddemors 1995; Goodwin 1997). Therefore, any similarity in social organization may arise from similar ecological events acting on these two dolphin populations, or they may have evolved before separation of the populations.

Alternatively, the relatively low coefficient of association observed, which is typical of populations with large ranges, may be an artefact of the existence of a large population which is studied in a smaller part of its range, where most individuals spent most of their time outside the study area. This scenario is supported by the fact that most re-sighted individuals were not in the area for more than half of the photographic surveys. However, sometimes individuals might not be photographed while present in larger groups and that females with calves often avoid the boats.

The association pattern found in Maputo Bay supports the existence of a fluid group membership (Connor *et al.* 2000), given that the highly stable associations (CA>0.8) accounted only for 0.3%. From the east coast of Africa there are no published data on association patterns of bottlenose dolphins, but off Kwazulu- Natal, a large number of sightings occurred with very few frequent re-sightings suggesting the existence of fluid group membership. Open populations of bottlenose dolphins often show a low number of very strong association as Weller (1991) found only 5% of associations higher than 0.39 at San Diego. At Shark Bay (Smolker *et al.* 1992) only 16% of associations of bottlenose dolphins were above CA = 0.20 and less than 10% were above CA = 0.4. Bräger *et al.* (1994) found at Galveston Bay, that the majority of dolphins do not meet each other and that less than 5% were associated at levels above CA = 0.40. Felix (1997) found a mean association coefficient of 0.32 between bottlenose dolphins of Gulf of Guayaquil, which also shows the dominance of casual and loose associations. The findings of Harzen (1995) of CA = 0.5 in the Sado Estuary, Portugal reflect a very stable community with restricted fluidity caused by the existence of low number of available affiliates. Highly stable associations observed in Maputo Bay are mainly caused by the strong bonds between the dyads and trios of dolphins, which occurred within three clusters, to which other dolphins associated with variable strength (Fig. 3.13). Therefore, dyads and trios seem to be the meaningful units in the Maputo Bay, as found elsewhere (Connor *et al.* 2000). In Florida the dyads and trios were the most significant associations (Ballance 1990), and Würsig (1978) also noticed some long-term associations between pairs of dolphins in a stable sub-group in Argentina.

Therefore, bottlenose dolphins of Maputo Bay have dynamic and fluid associations, but with relatively high proportion of stable groups, when compared to those off the California coast (Bräger *et al.* 1994; Weller 1991).

The analysis of association by age and sex showed that CA:s between adults of undetermined sex were the highest and differed significantly from those between adult females, adult females - juveniles, adults of undetermined sex-juveniles and adults-females. Meanwhile CA:s between adults of undetermined sex and females were higher than between females themselves, who had the lowest CA (Fig. 3.12). Clearly, the group organisation plays a role on the results observed, but the lack of knowledge of sex of most individuals is the main constraint towards the determination of group organisation. About 600 km south of Maputo Bay, the analysis of stomach content of bottlenose dolphins suggested that females and calves frequent the inshore zone while juveniles, resting females and adult males occupy the offshore areas (Cockcroft & Ross 1990). The data on the degree of association obtained in Maputo Bay is consistent with this group organisation. Therefore the social structure of dolphins off the Kwazulu- Natal coast and Maputo Bay may be similar. The low coefficient of association between females is misleading, as it would be expected to be stronger, owning to the group organisation model adopted. However, this model is adopted because the low CA observed among females may be influenced by distinct parturition and nursing times across the study.

However, considering that the study was carried out during two years, and that births occurred throughout the year (Chapter 5), then the females identified would be found at different stages of lactation, with calves of varying ages requiring different levels of care. Therefore, stronger associations would occur between females which had calves of the same age, and during the study period females had parturition at different periods. The stronger associations adults of undetermined sex in Maputo Bay, suggest that these may consist of a large number of resting females, sub-adults and some mature males. Reproductively active female spotted dolphins that had parturition in the same year were strongly associated between them compared to the association with other females (Herzing & Brunnick, 1997).

High degree of variability of association between female bottlenose dolphins, characterized by less year-to-year consistency in subgroup membership, was observed at Sharks Bay (Smolker *et al.* 1992) and Gulf of Guayaquil (Felix 1997). At Sarasota, Florida, female bonds are composed of several maternal lineages (Wells *et al.* 1980) and such structure implies high association between genetically related females and low association between dolphins from distinct lineages, resulting in the overall low coefficient of association. Therefore, these two factors may play a role in the degree of association of female dolphins observed in Maputo Bay.

In summary, there were few stable associations between individuals of all age-sex classes, which had a variable site fidelity. The most re-sighted individuals interacted largely with other individuals. The population of Maputo Bay had an intermediate size (see Chapter 5), larger than those of the Sado Estuary (Harzen 1995) and Sarasota (Wells & Scott 1990) but smaller than the population off the Kwazulu-Natal coast (Peddemors 1995) and San Diego (Weller 1991) and this impacted on the number of affiliates. The mean coefficient of association between dolphins in Maputo Bay was low (CA =0.30), caused by large number of transient dolphins. These significant differences between age-sex categories of dolphins imply that there is some king of group organisation. Associations between females were weak, because parturition time in Maputo Bay occurred throughout the year.

Area use

The bottlenose dolphins at Maputo Bay, occurred throughout the daylight period following a similar pattern to that observed by Saayman & Tayler (1979) at Plettenberg Bay, implying that the pattern of feeding was not regulated by daylight. Their restricted geographic occurrence in the Bay may suggest that dolphins forage in the eastern part of Maputo Bay (see Chapter 7). This does not exclude the existence of a small resident population (judging from their site fidelity) consisting of females and calves and some adults whose sex was not determined. The daylight occurrence of bottlenose dolphins in the Bay was independent of the tide direction.

However, the main areas of occurrence of dolphins had strong tidal currents, which apparently provide feeding opportunity to dolphins. The preference of dolphins to the strong tidal currents has been widely documented (Shane *et al.* 1986; dos Santos & Lacerda 1987; Klinowska 1991; Felix 1994; Grigg & Markowitz 1997). Off the coast of Kwazulu- Natal and Plettenberg Bay, dolphins often feed at reef areas or at popular angling areas (Saayman *et al.* 1973; Peddemors 1995), reflecting distribution of prey. In Maputo Bay, the feeding areas consisted of an inshore reef and open water with bare sandy substrate. These two areas suffer strong tidal currents (Kalk 1995, Achimo 2000).

This area use of dolphins seems to be adaptative, as this species is reported to frequent estuaries over most of their range as in the Gulf of the California (Ballance 1992), in the Gulf of Guayaquil (Felix 1994) and at Sado Estuary (dos Santos & Lacerda 1997), but off the east coast of southern Africa this species is seldom seen at estuaries and at waters of high turbidity, mostly frequented by humpback dolphins. Humpback dolphin tolerance to clear waters has been proposed by Barros and Cockcroft (1999), which may result in some diet overlap, but bottlenose dolphins avoid most areas with turbid waters, to reduce predation by sharks (Ross *et al.* 1987). However, in Maputo Bay, the avoidance of estuarine and turbid areas may be associated with disturbance by boat traffic, fishing nets and prey resource depletion by artisanal and commercial fisheries. The strong reduction of salinity, which occur during the rainy season at western Maputo Bay (Nhapulo 2000) may drastically alter prey abundance and distribution.

Bottlenose dolphin schools occurred inshore, at coral reef, west of Inhaca Island, when no humpback dolphins were present, usually at high tide. At this location, most sightings of bottlenose dolphins consisted of solitary sub-adult individuals or mother-calf pairs, emphasizing the role of the area for protection of calves against predators and foraging of pregnant and lactating females. Pregnant and lactating females have high energy requirements (Cockcroft & Ross 1990a) implying that they could spend most time foraging or adopt a high feeding rate. However, to improve feeding rate and share with calf care, they have to choose a habitat of high prey density and become less selective (Cockcroft & Ross 1990a). This may explain the occurrence of solitary dolphins or groups containing lactacting females at the inshore reef.

Feeding dominated the activity of bottlenose dolphins in Maputo Bay. Despite their preference for deep waters, dolphins were always observed at areas of high relief, which permitted rapid movements. Possibly, such areas aid the process of fish capture. Consequently Maputo Bay serves as a feeding ground to many dolphins. The reduced amount of directional movement within the Bay and the restricted range suggest that most of their range is located at the open coast, outside Maputo Bay. However, some dolphins may range into shallow areas (< 2m) that were not accessible to surveys. Off the Kwazulu-Natal coast, bottlenose dolphins allocated high percentage of time to travel (Peddemors 1995), suggesting that prey patchiness is intense and feeding areas are distant from each other, or that prey distribution is unpredictable. At Algoa Bay and Plettenberg Bay, off the east coast of South Africa, bottlenose dolphins used all areas (near-shore and off-shore) of the Bay equally (Ross *et al.* 1987 & Saayman *et al.* 1972) while at the open coast off Kwazulu- Natal, they were often limited to a one km strip of coast (Ross *et al.* 1989).

Thus, bottlenose dolphins in Maputo Bay frequent two preferred areas, one at the pass to the Ocean and one at an inshore reef located at the western coast of Inhaca Island. These two areas have strong tidal currents, clear water and high relief (Kalk 1995) but different prey species. The prey species of open sea would consist of pelagic species such as squids (*Loligo* sp), and fish, namely scads (*Decapterus russelii* and *Trachurus delagoensis),*mackerel (*Rastrelliger kanagurta*) sardines (*Sardinella albela* and *Sardinella gibosa)* and spanish mackerel *(Scomberomorus commersonii*) and the demersal sole fish (*Bothus pantherinus, Pseudorhombus arsius* and *Paralichthodes algoensis*), while the inshore coral reef will be dominated by reef associated species (parrotfish, goatfish, kingfish (*Caranx* spp), carangids (*Pellona ditchela*), demersal species of serranids (*Ephinephelus* sp), lethrinids (*Lethrinus* spp.) and lutjanids (*Lutjanus* spp.), sparids (*Crenidens crenidens*) (Kalk 1995, Heemstra & Heemstra 2004) These areas may, due to differences on prey abundance, consist of different feeding grounds: the entrance of the Bay for large groups of dolphins and the inshore reef for small groups of lactating females and sub-adult dolphins.

CHAPTER 4. SEASONAL PATTERN OF OCCURRENCE, GROUP SIZE, GROUP DYNAMICS AND HABITAT USE OF HUMPBACK DOLPHINS IN MAPUTO BAY, MOZAMBIQUE

INTRODUCTION

In the Indian and Pacific Oceans, the humpback dolphin is sympatric with other species of dolphins (Guissamulo 1993, Durham 1994, Peddemors 1995, Cockcroft & Ross 1989, Pilleri & Pilleri 1979, Stensland *et al.* 2006, Parra et al.2006). However, it often occurs close inshore, and has been observed in shallow, low energy water with soft sediments and associated with rocky outcrops in areas of varying wave energy (Saayman & Tayler 1973, Karczmarski 1996, Baldwin *et al.* 2002), estuaries (Durham 1994, Jefferson 2000) coral reefs and mangroves (Pilleri & Pilleri 1979, Guissamulo 1993, Stensland *et al.* 2006). Where depth remains shallow over extended areas offshore, humpback dolphins may have an extended distribution (Corkeron 1990, Durham 1994, Atkins *et al.* 2004) Due to its inshore occurrence in Mozambican waters, it often interacts with human activities and its presence is used as an indication of fish abundance and therefore surrounded by nets, resulting in entanglement and eventual mortality in some fish gear (gill nets and beach seine nets).

In some regions in Mozambique, it is intentionally hunted in tidally exposed flats within mangrove creeks (Guissamulo 1993, Guissamulo & Cockcroft 1997). Close to large coastal cities, where industry is developed, its association with estuaries exposes it to domestic, industrial and agricultural pollution. In addition the species is caught in shark nets e.g. along the Kwazulu- Natal coast (Cockcroft & Ross 1989, Cockcroft 1991). Knowledge of its ecology is needed to examine the conservation status and delineate conservation measures and to identify priority areas for their distribution. The present chapter examines the seasonal changes of occurrence and group size, the group dynamics, site fidelity and area use in Maputo Bay.

METHODS

The methods used for studying seasonal pattern of occurrence, group size, group dynamics and habitat use of the humpback dolphins were identical to those described for bottlenose dolphins in Chapter 3.

The surveys were carried out in Maputo Bay (Fig. 2.6) between December 1995 and December 1997. The survey procedure for the determination of occurrence and group size is described in Chapter 2. Occurrence was measured using relative measures (sightings per unit effort – SPUE- and number of dolphins per unit effort - NPUE), and effort was measured as time spent searching for dolphins during the survey. In addition, between January and May 1992 ,36 surveys were carried out, that resulted in photo-identification of 6 groups of humpback dolphins. The survey procedure was similar to that described in the Chapter 2.

Patterns of occurrence in relation to month, season, tides and daylight were compared between using Kruskal- Wallis non parametric test, when a variable had more than 2 factors or with a Mann-Whitney non parametric test, when the variable varied by two factors ( )

During the dolphin follow procedure (Chapter 2), the initial and the final locations of each sighting were recorded using a GPS Magellan Trailblazer. Dolphins were followed for as much time as possible to collect the photographs of individuals and behaviour. The maximum duration to follow and observe a sighted group of dolphins was 2 hours. However, some observations were terminated if the dolphin groups disappeared from the observation field of the researcher for more than 15 minutes. The time spent observing dolphins was also recorded. It consisted of the time of approach and follow the dolphins until the group disappeared of was abandoned.

The stability and dynamics of groups of dolphins is analysed through the use of indices of associations between each pair of photographically identified dolphins. These indices of each pair are then used to produce association matrices of individuals (Cairns & Schwager 1987). In this study, the association was measured through the half weight index (HWI), (Ginsber & Young 1992; Cairns & Schwager 1987). The half weight index (referred to as Coefficient of Association - CA) was calculated using the formula:

$$CA = 2J/(A+B),$$

Where: CA = coefficient of association, J - number of times that individuals A and B were seen together, A - total number of sightings of individual A, and B - total number of sightings of individual B. This Coefficient of association varies between 0 and 1. Zero indicates that the pair was never seen forming the part of the same group, and 1 that the animals were always present in the same group.

The HWI was chosen to account for the low numbers of identified dolphins in groups, and for the avoidance of some dolphin individuals to the boat during photo-identification. These two reasons reduced the probability of photographing two individuals present in the same group and the HWI becomes a more accurate estimator of association under these conditions (Cairns & Schwager 1987).

Affiliates are defined as any identified dolphins that occurred in the same group/or sighting with any other identified dolphin. As dolphins are social animals which have a fluid association pattern (fission-fusion), individuals seen once also have affiliates, that can be either other transient individuals arriving and leaving at the same time or other individuals which meet varying time periods (Whitehead & Default 1999). The number of affiliates of any individual and the number of sightings were compared between adults of undetermined sex, adult females and for juveniles. The seasonal occurrence of all photographically identified individuals was also examined.

The number of sightings, number of affiliates and days between re-sightings were compared between age and sex categories using the Kruskal Wallis non-parametric test.

Grouping into larger social units and associations was analysed using group average cluster analysis (UPGMA) employing the software PRIMER (Clarck & Warwick 1994). Only dolphins sighted four or more times were included in the analysis. Coefficient of associations for different age and sex categories were compared using one-way ANOVA and subsequently, multiple comparison tests (least square difference - LSD at 5% significance intervals).

The distribution of sightings was plotted on a Maputo Bay chart using the Geographic Information System ArcView 3.2. version 2000 (NCC RS & IFPRI 2004).

To examine the daylight pattern of occurrence and preferred depths, sightings were partitioned into six time intervals (06:00 - 08:00, >08:00 - 10:00, >10:00 - 12:00,

>12:00 - 14:00, >14:00 - 16:00 and >16:00 - 18:00) and four water depth intervals (>0-2 m, >2-5 m, >5-10 m and >10-20 m). The depth intervals were obtained by plotting the initial location of the sightings on Hydrographical Chart No. 46659-M (National Institute of Hydrography and Navigation 1986). Comparison of frequency of sightings was carried out using Chi-square test. The distance from shore of each sighting was determined using the initial location of each sighting provided by the GPS.

The distribution of sightings along the coast between Portuguese and Inhaca Islands and the mainland at Machangulo Peninsula was examined using sightings observed within 3 km off the coast (Fig. 2.5), because their distribution was skewed towards the shoreline. This area is 14 km long, divided into 500m long sectors (after Karczmarski, 1996). The following features of each sector were also described: the type of the bottom substrate (sand, seagrass, reef, rocks), depth range, width of the channels and the type of coastline (sandy, mangrove, rocks or sand). At each sector the number of groups sighted passing the area was plotted. The number of sighted groups that passed each sector and time spent observing dolphins at each sectors varied because it depended on the speed of the dolphins followed. Therefore, a coefficient of area utilisation (AU) was calculated for each sector to compare the importance of each sector for the dolphins:

$$AU = D/T$$

Where: AU = coefficient of area utilisation
D= total time spent by dolphins in a particular sector
T= total observation time during any one day

The Activity Index (AI) was also calculated separately for feeding, travelling and social behaviours, using the formula:

$$AI = B/T$$

B= Time dolphins were engaged in a particular activity within a sector
T= Time spent by dolphins in any one sector

The mean values of the area utilisation index (AU) and activity index (AI) between sectors were compared for statistical significance using the Kruskal-Wallis ANOVA.

The types of dolphin movements and the direction of the movements were examined in relation to the semi-diurnal tides (see Chapter 2 for details). The frequencies of the types of movement and the movement direction between tidal phases (rising/ebbing) were compared for significant differences using the Chi-Square Test, based on the Contingency Tables.

RESULTS

Effort and sightings

The total number of surveys, survey time and their monthly distribution between December 1995 and December 1997 are presented in Chapter 3 (see also Fig. 3.1). There were 37 sightings in 31 surveys (21% of total number of surveys) during which 524 individuals were counted. Single sightings occurred during 28 surveys, there were two surveys of double sightings and one survey with three sightings. Joint sightings of humpback and bottlenose dolphins occurred on only three surveys (2 %). The frequency distribution of dolphins sighted is presented in Fig 4.1.

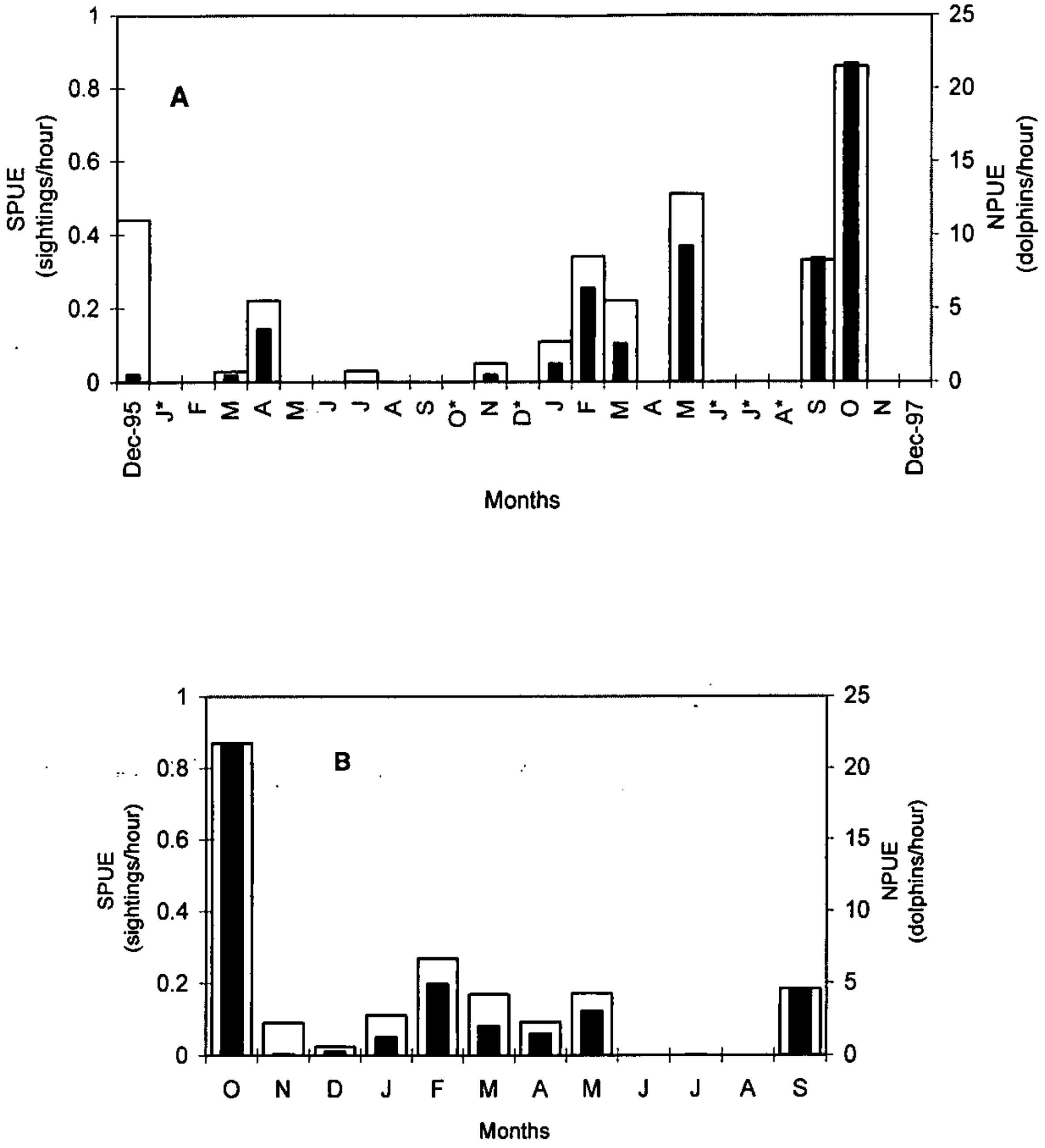


Figure 4. 1. Sighting rates of humpback dolphins: (A) total monthly number of sightings per hour searched (□) and total monthly number of dolphins sighted per hour searched (■) in Maputo Bay between December 1995 and December 1997. (B) Combined total monthly number of sightings per hour searched (□) and pooled total monthly number of dolphins sighted per hour searched (■) in Maputo Bay between December 1995 and December 1997. Stars in the figure A denotes months when surveys were not carried out.

Patterns of occurrence

The monthly distribution of mean sighting rates (SPUE) of humpback dolphins is presented in Figure 4.2.

The sightings per hour and dolphins per hour did not differ significantly between months (Kruskal-Wallis, H = 18.33, n = 144, p = 0.07 and Kruskal-Wallis, H = 15.04, n = 144, p = 0.06, respectively), season (Mann - Whitney: U = 1998, n = 95 and 49, p = 0.05 and Mann Whitney: U = 2023, n = 95 and 49, p = 0.08) or between spring and neap tides (Mann Whitney, U= 2234, n = 81 and 63, p = 0.07 and Mann Whitney, U= 2299.5, n = 81 and 63, p = 0.17 respectively).

The overall mean Secchi-depth measured was 6.30 m (S.D. = 3.47, n = 53), humpback dolphins were sighted at areas of mean water transparency equal to 2.98 (S.D. = 1.54, n = 17) with the range of 0.5 to 5.9 m. The mean daily tidal range during surveys when humpback dolphins were sighted was 2.5 m (S.D. = 0.82, n = 35) and ranged from 0.8 to 3.6 m.

Group sizes of humpback dolphins were not significantly associated with Secchi-depth (r_s = -0.0274, n = 16, p= 0.92).

Group size and composition

The mean group size was 14.91, S.D. = 7.32. The monthly mean group size and number of dolphins observed per survey is presented in Fig. 4.3. Adults formed 50% of the group (mean = 7.65, S.D. = 4.12) (Fig. 4.4).

Juveniles comprised 37 % (mean = 5.29, S.D. = 4.11) of the groups, and ranged from 0 to 13 individuals. The most frequent number was 5 juveniles. The monthly mean number of juveniles did not vary significantly (Kruskal-Wallis: H = 8.92, n = 34, p = 0.3374). There were significantly more juveniles compared to calves (Mann-Whitney: U = 880.5, n = 34 and 33, p = 0.001).

Calves comprised 13.15% of the groups (mean = 2.24, S.D. =1.37), and ranged from 0 to 4 individuals. The most frequent number was two calves. Nursing groups were significantly larger than those without calves (Mann Whitney: U = 15.5, n = 27 and 8, p < 0.001).

Group sizes did not differ significantly between months (Kruskal-Wallis, H = 13.87, p = 0.085), daylight periods (Kruskal-Wallis, H = 0.8906, n = 35 p = 0.926), depth intervals (Kruskal-Wallis, H = 4.702, n =35, p = 0.195), seasons (Mann Whitney U = 81, n = 28 and 7, p = 0.481) or between neap and spring tides (Mann Whitney U=112.5, n=24 and 11, p=0.605). Table 4.1 shows group sizes between seasons and tides.

Group dynamics of humpback dolphins

There were 34 successful photographic surveys of humpback dolphins and 723 photographs of humpback dolphins were catalogued of which 52 individuals were identified. Among these, there were 37 adult individuals of which 10 were females, and 15 juveniles. No calves were identified during the photographic surveys.

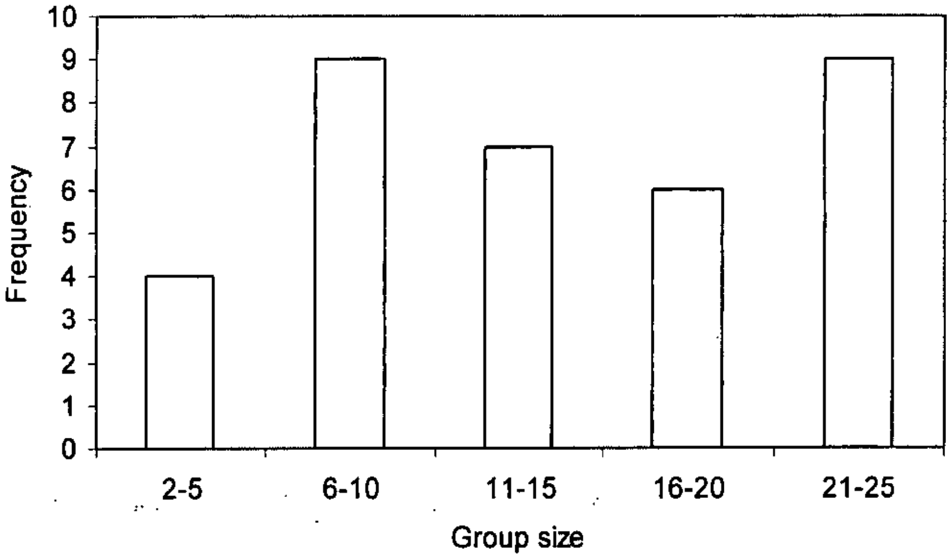


Figure 4.2. The frequency with which the various group sizes of humpback dolphins were observed in Maputo Bay between December 1995 and December 1997

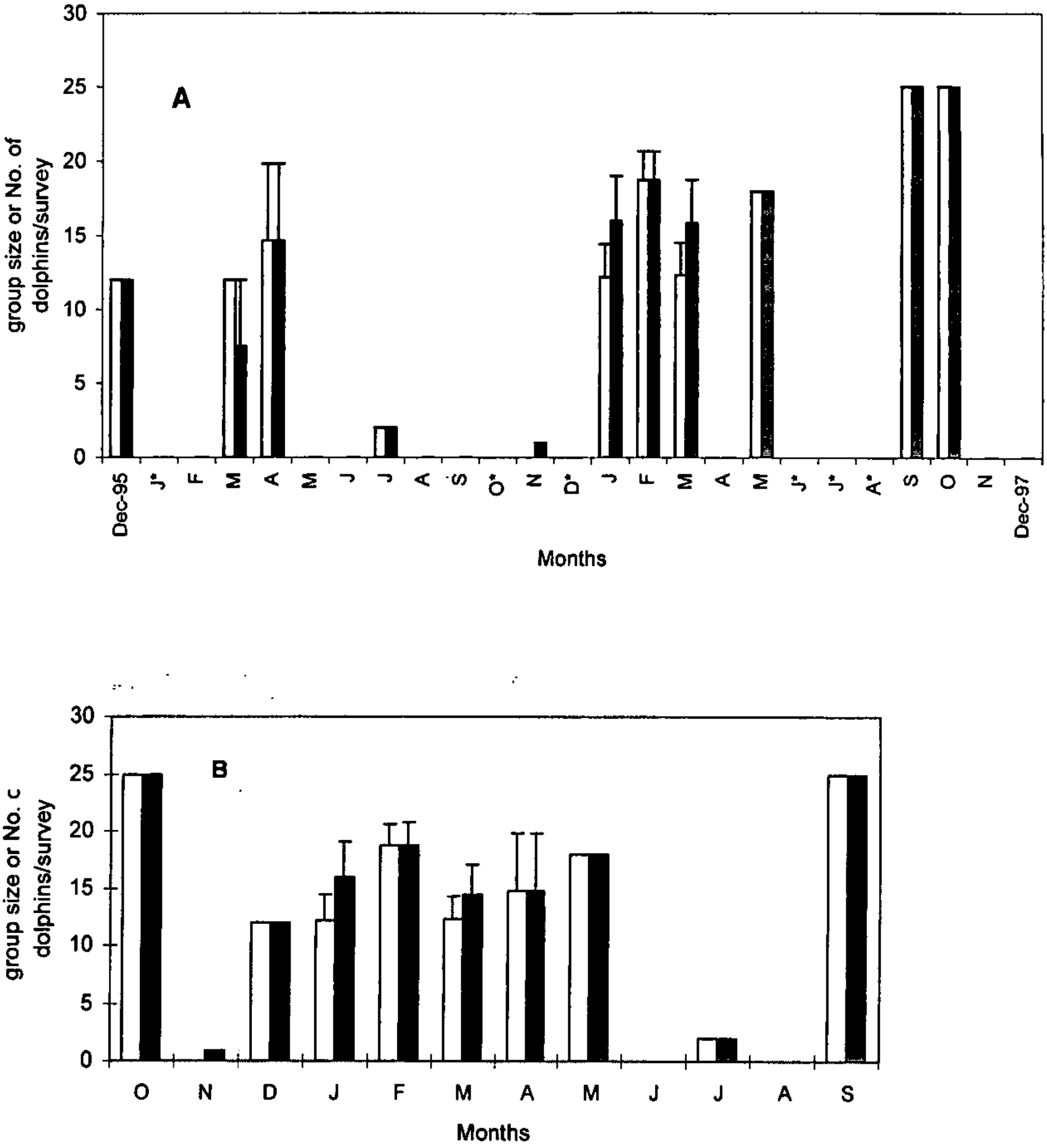


Figure 4.3. (A) Mean monthly group size (□) (and standard errors) of humpback dolphins and number of humpback dolphins observed per survey (■) in Maputo Bay between December 1995 and December 1997. (B) Pooled mean monthly group size (□) (and standard error) of humpback dolphins and pooled number of humpback dolphins observed per survey (■) in Maputo Bay between December 1995 and December 1997 (* months when surveys were not undertaken).

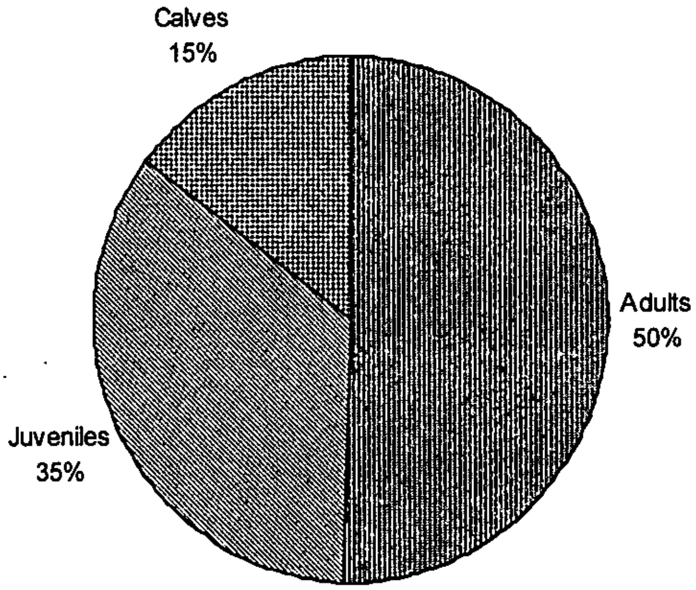


Figure 4.4. Mean proportion of adults, juveniles and calves in an average group of humpback dolphins observed in Maputo Bay between December 1995 and December 1997.

Table 4.1. Mean group sizes, sighting rates (sightings per unit effort and number of dolphins per unit effort) of humpback dolphins (± standard deviation) estimated for different seasons and semi-lunar tides (spring and neap tides) recorded in Maputo Bay between December 1995 and December 1997

	Winter	Summer	Spring tides	Neap Tides
Group size	16.3 (9.4)	14.4 (7.0)	17.2 (7.33)	15.8 (6.9)
Sightings/hour	0.04 (0.34)	0.18 (0.5)	0.26 (0.38)	0.14 (0.28)
Dolphins/hour	1.97 (7.8)	2.94 (11.6)	3.1 (13.50)	19.8 (3.7)

i) Site fidelity

There were 52 photographically identified individuals, and the number of sightings of individually identified dolphins ranged from one to 26 (Fig. 4.5). The two most re-sighted dolphins (26 and 24 sightings) are known to inhabit the area since April 1992 (Appendix 8). The next three individuals are known since December 1995 (23, 20 and 20 sightings), while the last one has been known since March 1996 (19 sightings) (Fig. 4.5).

The two most frequently sighted individuals were recorded in 70 % of the 10 months when photographic surveys were carried out. The third most re-sighted individual was recorded in 60% of the months. Eighteen individuals (35%) were seen during only one month, but with varying number of sightings: 5 in April 1996 (sighted in one survey), 5 in April 1992 (4 sighted in one survey and 1 sighted in two surveys), 4 in March 1997 (3 sighted in a sinle survey and 1 sighed in two surveys) 2 in January 1992 (sighted in one survey) and 2 in February 1997 (1 sighted in 5 surveys and 1 sighted in 2 survey). 45% of the identified dolphins were observed during one season, and adults of undetermined sex and juveniles prevailed within these groups. Most females occurred during more than one season (Appendix 9). Juveniles and females had the same pattern of seasonal occurrence. The proportion of resident adults of undetermined sex was also high, with a high proportion observed in more than three seasons.

The immigration of new individuals occurred mainly in summer of each year (1992, 1996 and 1997) (Fig. 4.6). In 1995, there was an addition of new individuals, but surveys were only carried out in December 1995.

The number of days between first and last re-sightings of any individual ranged from 0 to 732 days. Eleven individuals were re-sighted after more than 400 days (Fig. 4.7).

The mean number of days between consecutive re-sightings of any dolphin varied from one to 236 days. The overall mean number of days between consecutive re-sightings of any dolphin was 59.89 (S.D. = 92.72), which was almost three times larger than the number of days between consecutive photographic surveys (mean = 21.5 days, S.D.=39.6, n = 34 surveys).

The mean number of days between re-sightings was highly variable for individuals sighted 2 to 5 times, but individuals sighted 6 or more times had the lowest number of days between re-sightings (Fig. 4.8). For 55 % of the individuals the number of days between consecutive re-sightings was higher than the mean number of days between consecutive photographic surveys. Many dolphins seen within one or two years had a mean time between photographing occasions, small than 100 days (Fig.4.9)

Analysis of the number of sightings and days between re-sightings of individuals of different sex and age- classes, shows that adult females and males (identified with erect penis during observations of mating behaviour) were the most frequently re-sighted individuals, but the number of days between re-sightings was lower for males than for females (Fig. 4.8). Adults of undetermined sex had few sightings and a low mean number of days between sightings. Juveniles were sighted less often than adult males and females and the number of days between re-sightings was smaller when compared to females. The number of sightings between individuals of distinct age and sex was significantly different (Kruskal- Wallis: $H = 8.59$, $n=52$, $p = 0.035$), but the number of days between re-sightings was not different (Kruskal-Wallis: $H = 4.04$, $n=52$, $p = 0.257$)

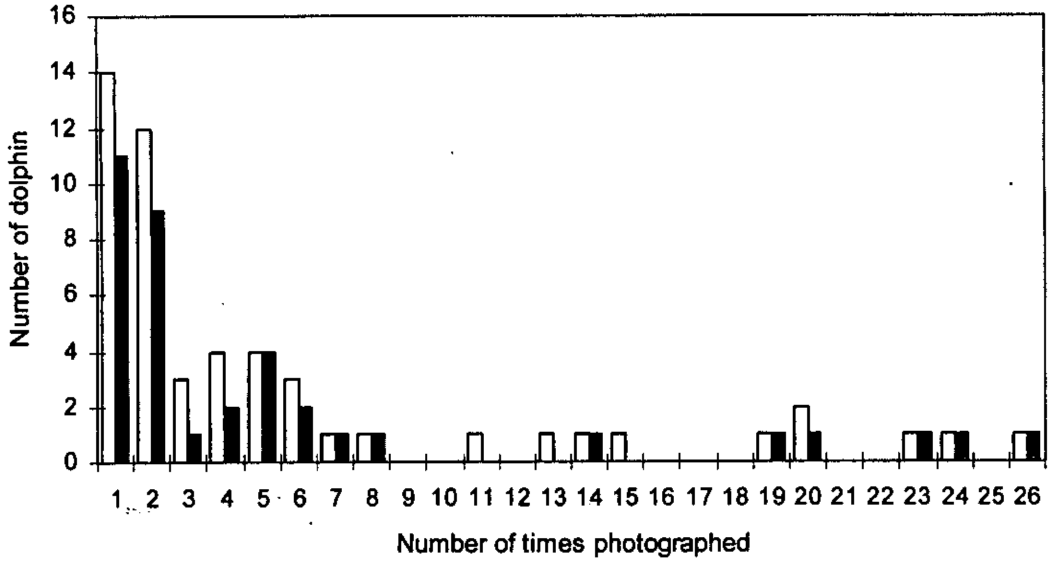


Figure 4.5. The frequency with which identifiable humpback dolphins were photographed (□ = all dolphins, ■ = adult dolphins) in Maputo Bay between January – May 1992 and between December 1995 and December 1997.

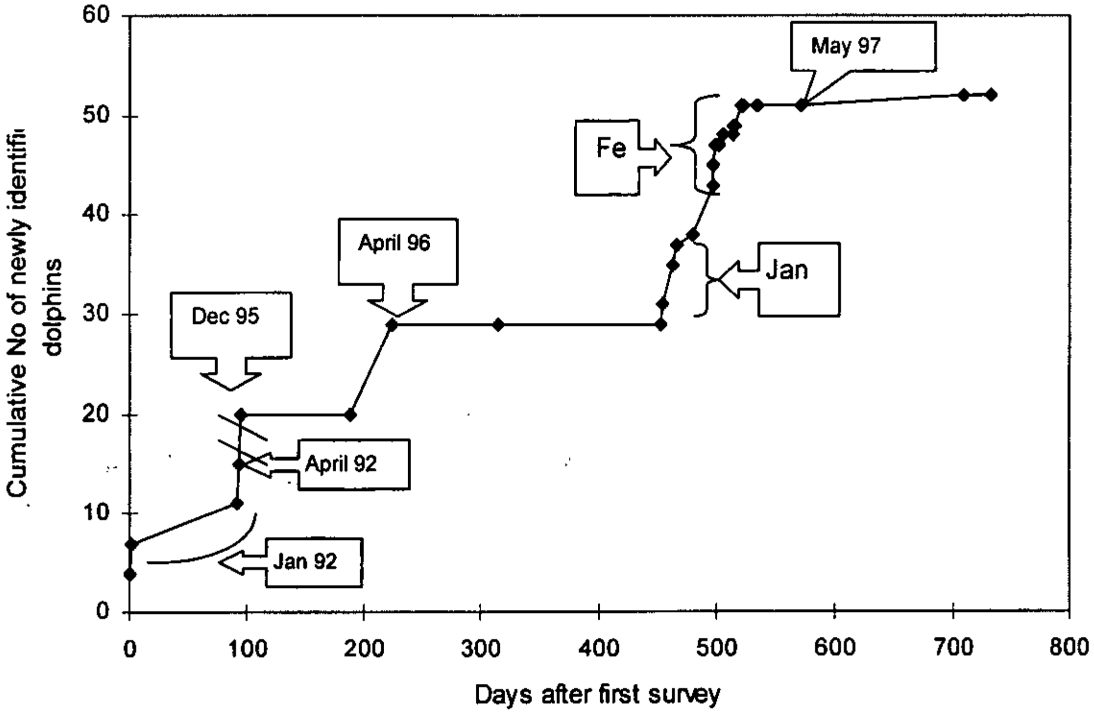


Figure 4.6 Discovery curve: the rate (dolphins/survey) at which new (never photographed and identified before) bottlenose dolphins from Maputo Bay were photographed and identified between January and May 1992 and between December 1995 and December 1997.

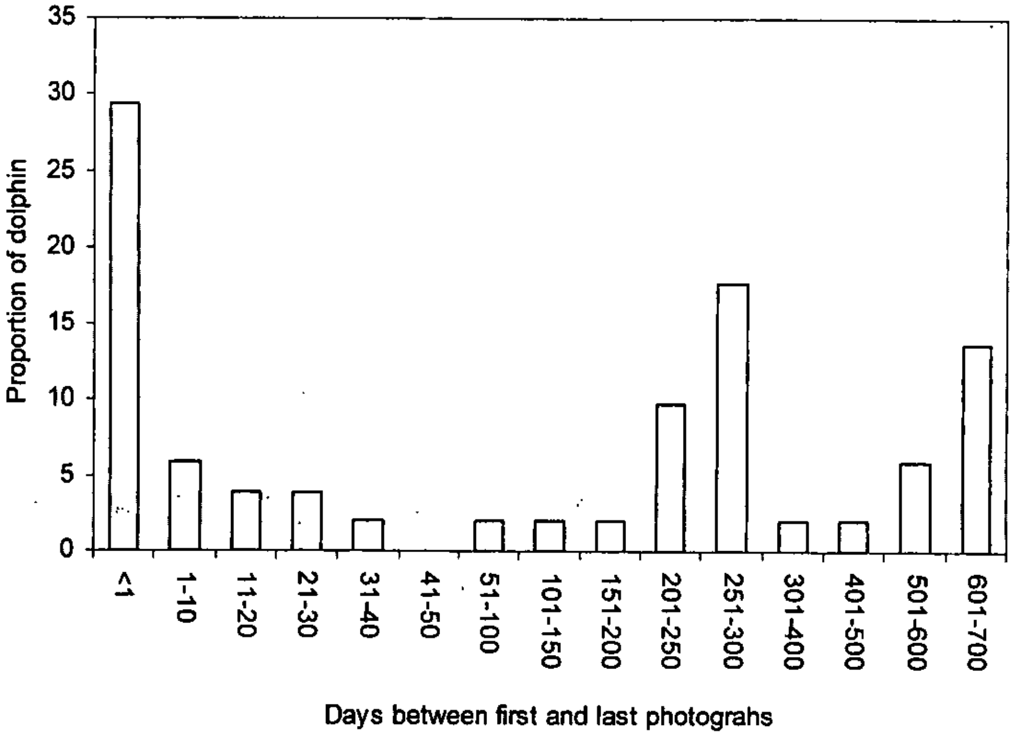


Figure 4.7. The frequency distribution of the number of days between first and last photographs of identifiable humpback dolphins from Maputo Bay between the period of January and May 1992 and between December 1995 and December 1997. The number of days between May 1992 and December 1995, when surveys were not carried out was discounted for dolphins seen first observed in 1992.

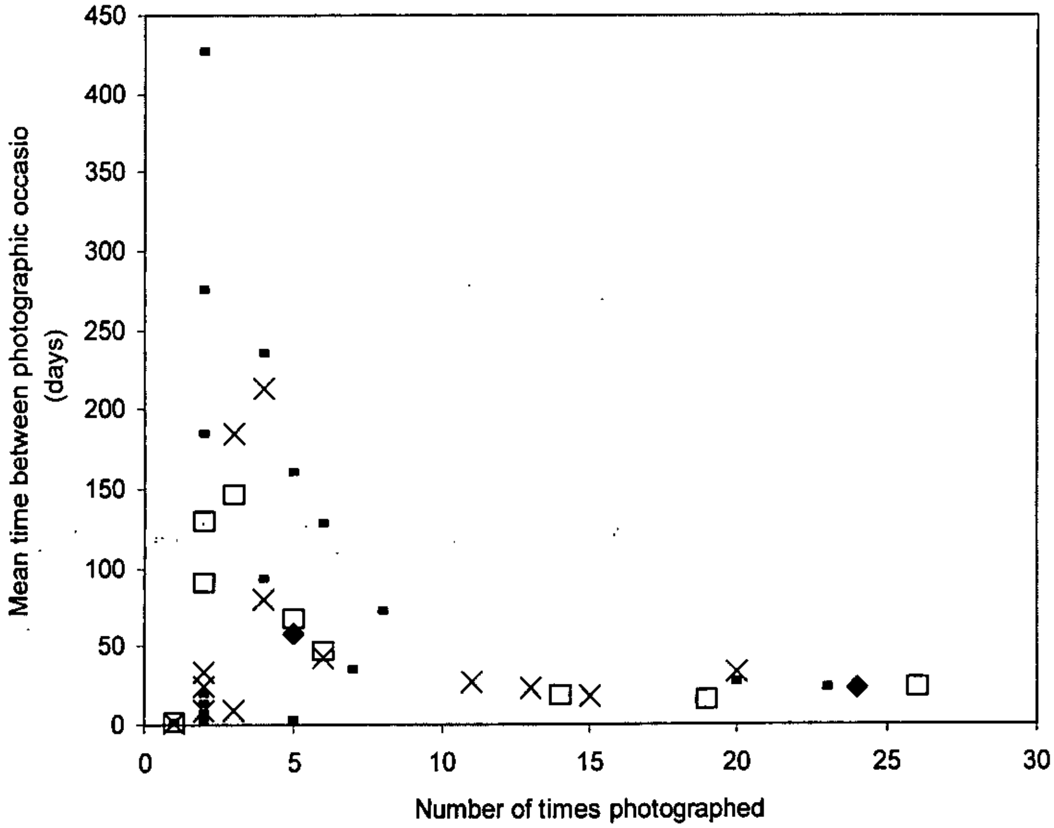


Figure 4.8. The relationship between the number of times a humpback dolphin was photographed and identified and the mean number of days between photographic occasions in Maputo Bay in Maputo Bay in the period between January and May 1992 and between December 1995 and December 1997(▪ = adults of undetermined sex, ☐ = adult females, ◆ = adult male, × = juveniles).

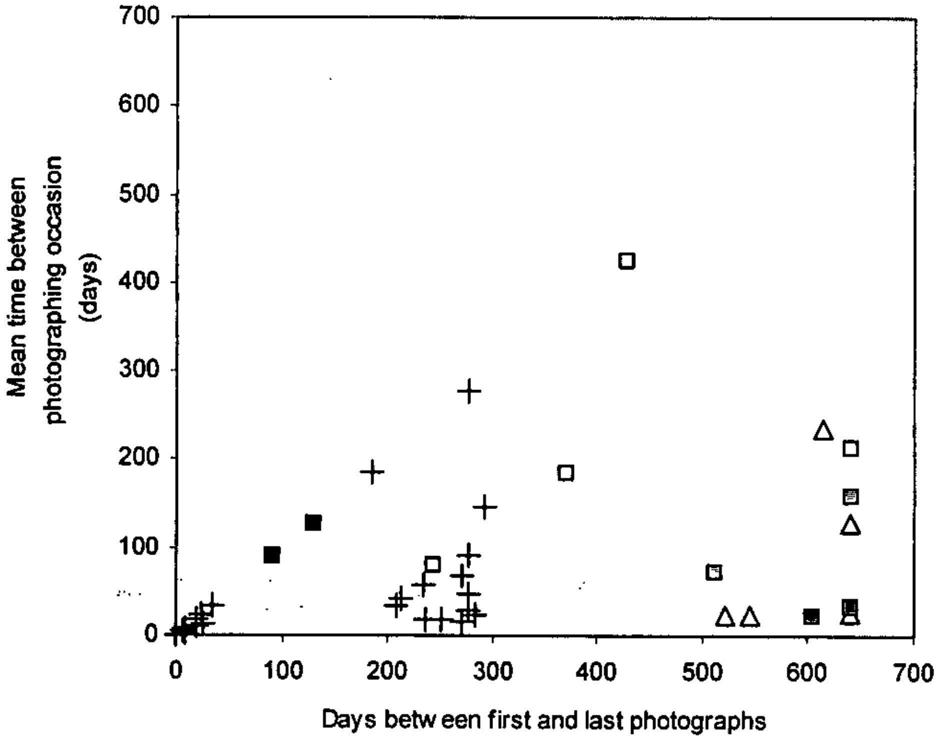


Figure 4.9. The relationship between the time (number of days) an individual was first and last photographed (identified) and the mean time (days) between all re-photographings (re-sightings) of the individual humpback dolphins in Maputo Bay between January and May 1992 and between December 1995 and December 1997 (Δ = dolphins photographed in 1992, 1995/6 and 1997, □ = dolphins photographed during 1992 and 1995/6 only, ■ = dolphins photographed during 1995/6 and 1997 only, + = dolphins photographed during 1997 only). To reduce bias by the large gap interval between May 1992 and December 1995, the number of days between May 1992 and December 1995, when surveys were not carried out was discounted for dolphins seen first identified in 1992.

ii) Social affiliations and association between individuals

Some long-term affiliations are known for some of the 52 photographically identified dolphins. Two dolphins were seen together for five years. Another four dolphins known since 1995 were seen often with these two dolphins until the end of the study period. However, 35% of the dolphins were sighted just once throughout the study period. One dolphin was first seen in 1992 was re-sighted once in 1997. Although some affiliations were of long-term duration, most were unstable (low coefficient of association).

The number of affiliates per individual increased with the number of sightings (Fig. 4.10), although it was not linear as an individual sighted 8 times had more affiliates (76.47 % of total affiliates) than those sighted on 9 to 23 occasions. In addition, the highest number of affiliates (48 individuals which is 94.12 % of all individuals) was found for an individual sighted 24 times, while the most sighted individual (26 times) had 41 affiliates (80.39 %) (Appendix 10). The overall mean number of affiliates was 21 (S.D. = 11.2) individuals. The mean number of affiliates for dolphins sighted once was 8.92 (17.49 %). The differences in the number of affiliates per sighting frequency were highly significant (Kruskal-Wallis: H = 42.15, n = 52, p = 0.004). Adult males had the highest number of affiliates, followed by females, juveniles and adults of unknown sex, respectively (Fig. 4.10). The number of affiliates was significantly different between different age-sex categories (Kruskal-Wallis: H = 8.59, n = 52, p = 0.035) when using all individuals sighted, but differences were not significant when using number of affiliates of individuals sighted more than three times (Kruskal-Wallis, H = 1.57, n = 23, p =0.666).

Two hundred and fourteen (92.64%) of the 231 possible associations were observed (Appendix 11), between individuals sighted more than 3 times (22 individuals). The overall mean CA was 0.362 (S.D. = 0.201). Most individuals were affiliated at an association index between 0.21 and 0.41 (Fig. 4.11). A comparison of CA between age classes did not show significant differences (One-way ANOVA: $F_{2,\ 223}$ = 0.320, p = 0.720).

However, comparison of the CA:s between dolphins of different sex and age categories showed significant differences (One-way ANOVA: $F_{9,216}$=2.760, p=0.044). This analysis compared four adult females (n = 4), adult males (n = 2), adults of undetermined sex (n = 9) and juveniles (n = 7). The highest CA values (mean = 0.545, S.D. = 0.181) were observed among adult females (Fig. 4.12). In addition the CA:s between the females with other classes were also high while CA:s between the remaining groups were lower and significantly different from those with females (LSD 95%). In summary, the associations of females with other groups although were the strongest. The two known males were associated at a very low CA and they were only sighted together very few times. On one mating occasion (October 1997), only one male was in the group.

Only two strong associations (CA:s > 0.80) occurred between one female and two other adult dolphins of undetermined sex and 14.95% of associations had CA:s > 0.60.

The dendrogram (Fig. 4.13), based on the matrix of CA:s, shows groups of two dolphins associated at similarity levels varying from 0.80 to 0.40. Only two groups of two dolphins (juveniles and adult females) and another of three dolphins (which include the previous two) occurred at similarity levels higher than 0.75. Another five pairs of dolphins,

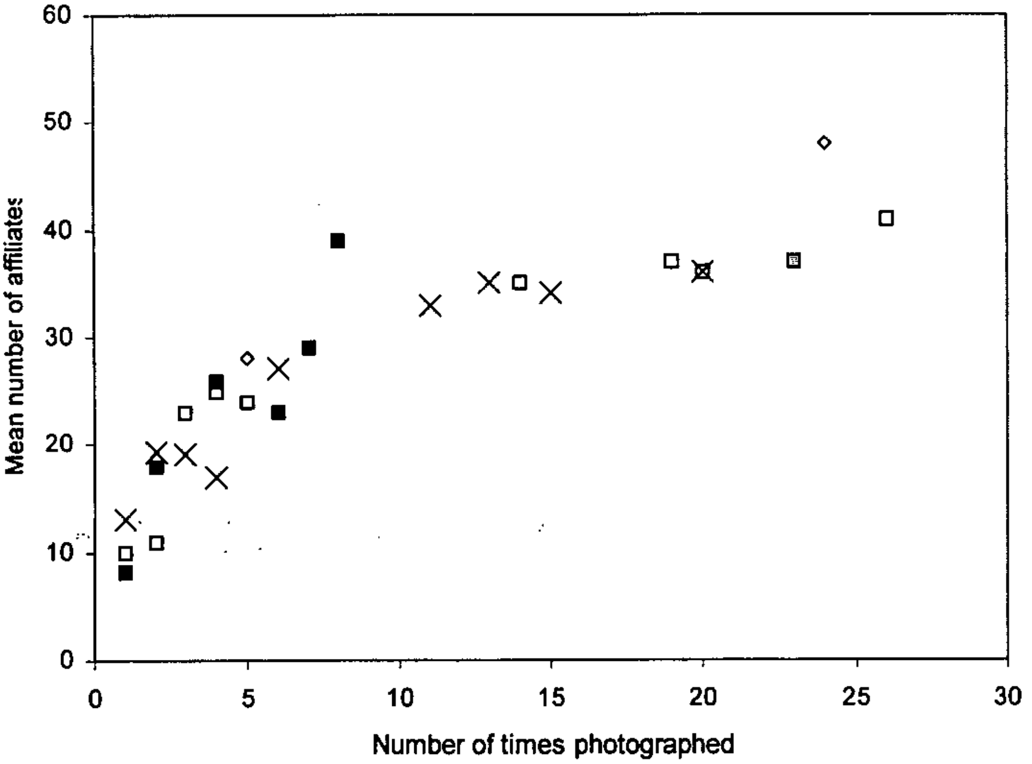


Figure 4.10. The relationship between the number of times an identified humpback dolphin was photographed and the number of affiliates (any other identified dolphin seen in the same group) seen with it in Maputo Bay between January and May 1992 and between December 1995 and December 1997 (■ = adults of undetermined sex, □ = adult females, ◇ = adult males, x = juveniles).

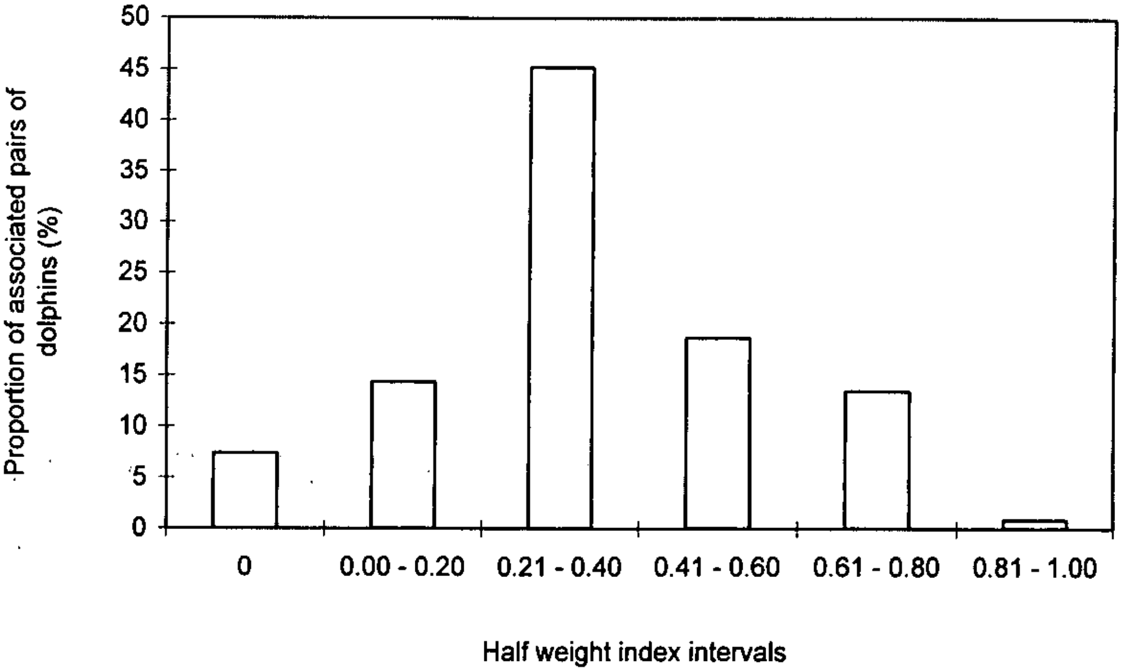


Figure 4.11. The frequency distribution of the proportion of pairs of identified humpback dolphins associated at different half weight index (coefficient of association) intervals in Maputo Bay during the periods between January and May 1992 and between December 1995 and December 1997.

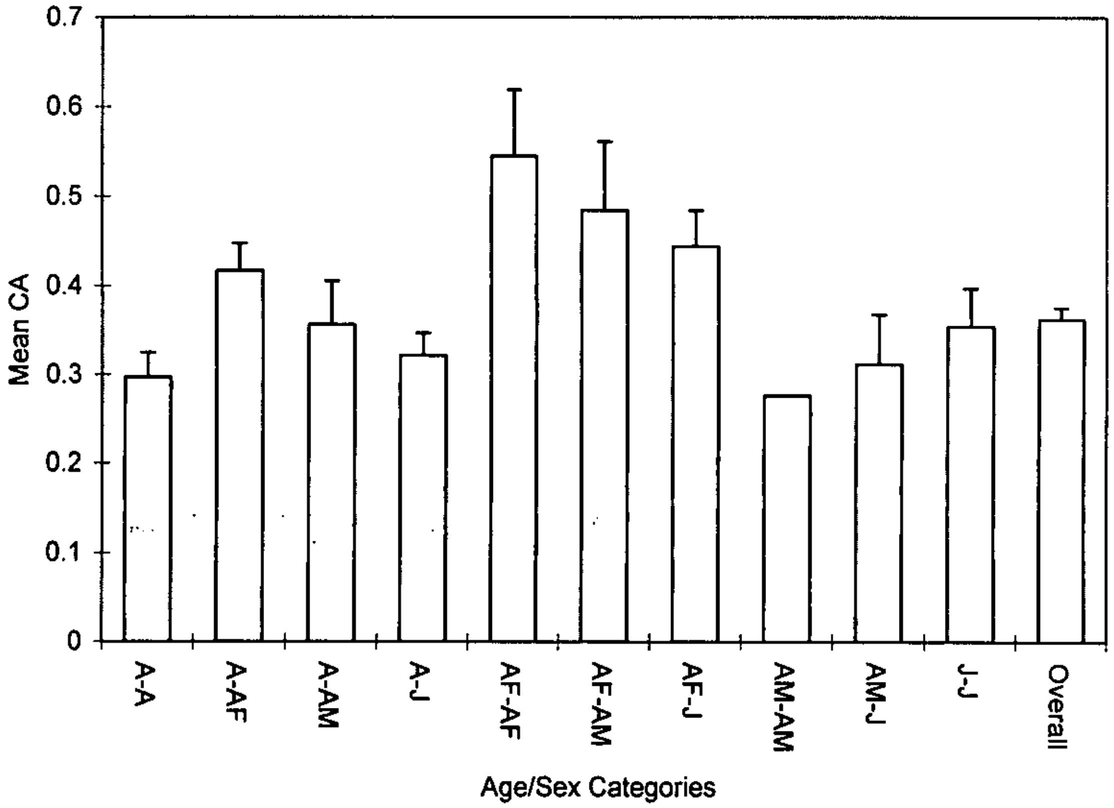


Figure 4.12. Mean values of half weight index (CA) for age and sex categories of humpback dolphins observed in Maputo Bay between January and May 1992 and between December 1995 and December 1997. (A = adults of undetermined sex, AF = adult females, AM= adult males, J = juveniles)

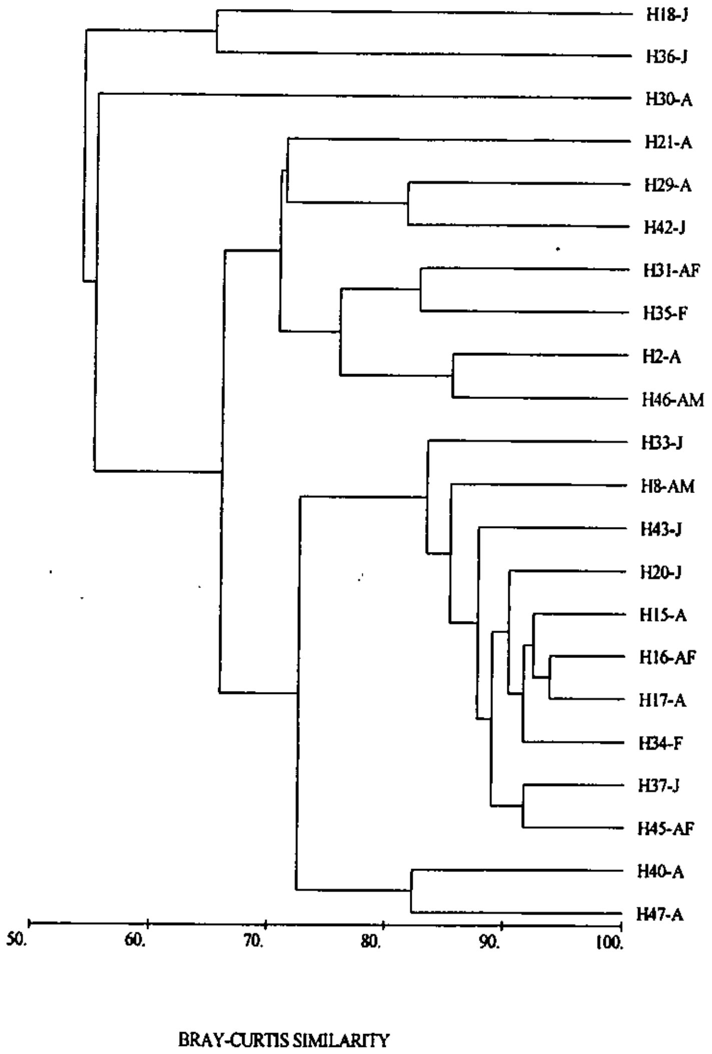


Figure 4. 13. Bray-Curtis Similarity coefficient of association of individually identified humpback dolphins photographed in Maputo Bay between January and May 1992 and between December 1995 and December 1997 (AF = adult female, A= adult of undetermined sex, AM – adult male; J= juvenile).

comprised of adult females or females-adults of undetermined sex, were associated at similarity levels between 0.75 and 0.50. Two groups of juveniles – adults of undetermined sex were associated at similarity levels between 0.50 and 0.25. In summary, dyads consisting of undetermined sex adults-juveniles dolphins were the weakest associations while dyads of adult females-juveniles were the strongest.

Each male (H46 and H8) was assigned to a different cluster. H8 is the male known since 1992 and is found within a core cluster of 9 dolphins that were associated together at a similarity level of 0.60. This group included three known females and two juveniles all sighted frequently. The second male (H46), known since January 1997, was found within a cluster of five dolphins associated at similarity level of almost 0.30. This male dolphin was closely associated to an adult known since 1992 (H2), which was less frequently re-sighted in the area. The male (H46) was loosely associated with two females (H35 and H31), which had calves.

Area use

The distribution of sightings in Maputo Bay is shown in Fig. 4.14. From the 37 sightings of humpback dolphins, 33 (89.2 %) occurred within 3 km off the west coasts of Portuguese and Inhaca islands. The features of these areas are described in the chapter 2. Among the remaining sightings, three occurred in the middle of the Bay (at Machangulo channel), along sandbanks with seagrass substrate, and a sighting of a single juvenile dolphin occurred to the west of Maputo Bay, south of Xefina Island at a depth <10 meters, turbid waters over fine sand substrate, as described by Achimo (2000). This dolphin was foraging in an area where trawlers were operating. This single dolphin exhibited an elusive behaviour and it moved towards N'Komati river when it was approached by the research vessel.

Humpback dolphin daylight sightings occurred between 08:00 to 18:00. The number of sightings was lower than expected between 08:00 to 12:00 and higher than expected between 14:00 and 18:00. (Fig 4.15) and the differences in the number of sightings between daylight intervals were significant (χ^2 = 13.74, d.f. = 5, p =0.017).

Humpback dolphins occurred at all depth intervals, but the number of sightings did not differ significantly between depth intervals (χ^2 = 1.75, d.f. = 2 and p = 0.417).

Dolphins occurred between 222 m to 6.29 km from the shore. Their mean distance from shore was 1.13 km (S.D. = 1.23, n = 37), 91% of sightings occurred within two km from shore and 67% within one km from shore, showing concentration of sightings towards nearshore areas.

Activity of humpback dolphins in eastern Maputo Bay

The mean observation time per sighting and total observation time was 0.62 hours per group (S.D. = 0.62) and 32.5 hours respectively.

Only sightings observed within three km from shore were used to evaluate the area use by dolphins along the west coasts of Inhaca and Portuguese islands, eastern Maputo Bay. Humpback dolphins were sighted along almost all sectors except for sector 27 (Fig. 4.16). Coefficients of area utilisation (AU) varied from 0.1 to 1 and the mean AU was 0.28 (S.D. = 0.23). The differences on the Coefficient of area utilisation between sectors were not significant (Kruskal-Wallis: H = 37.79, n=118, p=0.063). The number

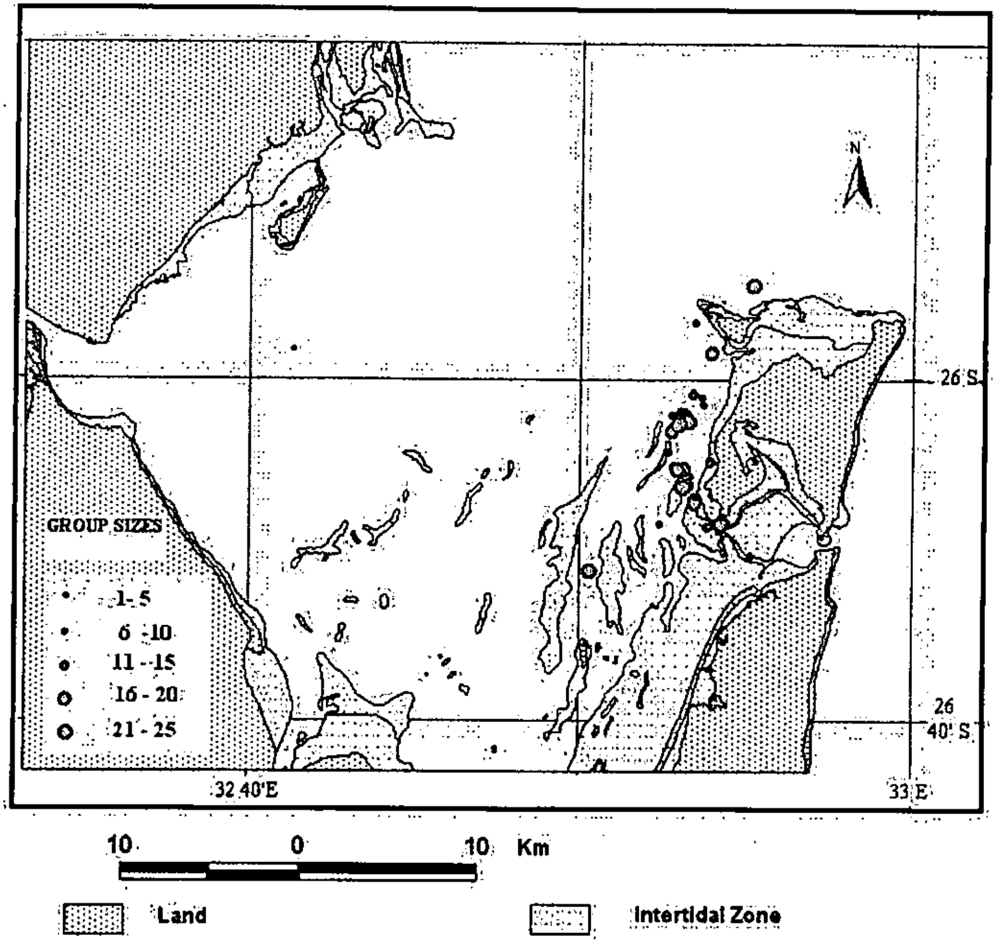


Figure 4.14. The distribution of sightings of humpback dolphins in Maputo Bay observed in the period between December 1995 and December 1997. The circles represent individual sightings and their relative sizes denote group size.

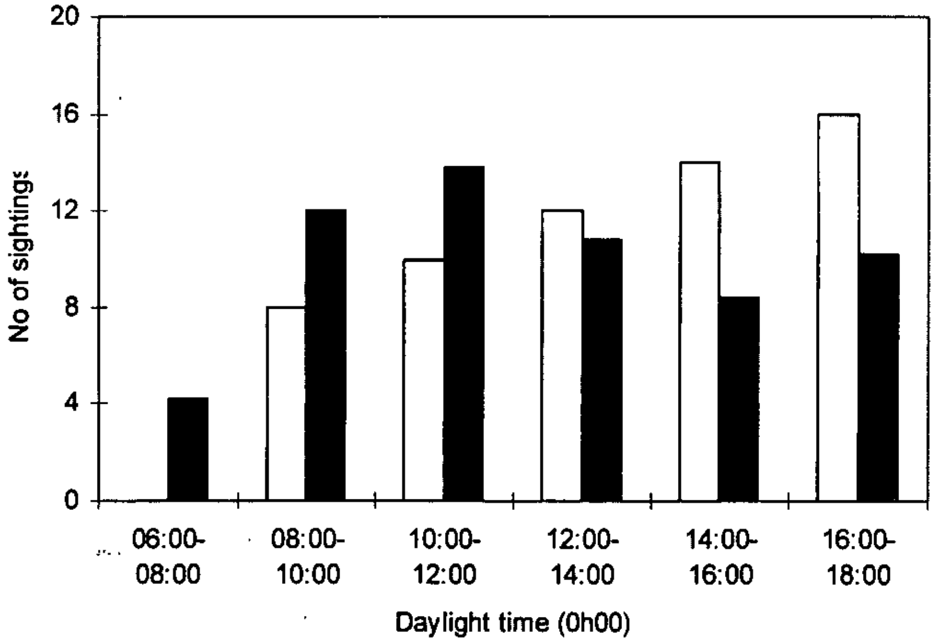


Figure 4.15. Observed (☐) and expected (■) frequency distribution of the number of daylight sightings of humpback dolphins in Maputo Bay between December 1995 and December 1997. Expected frequencies were obtained multiplying the total number of sightings by the proportion of total effort (total time spent searching for dolphins) conducted at each time interval.

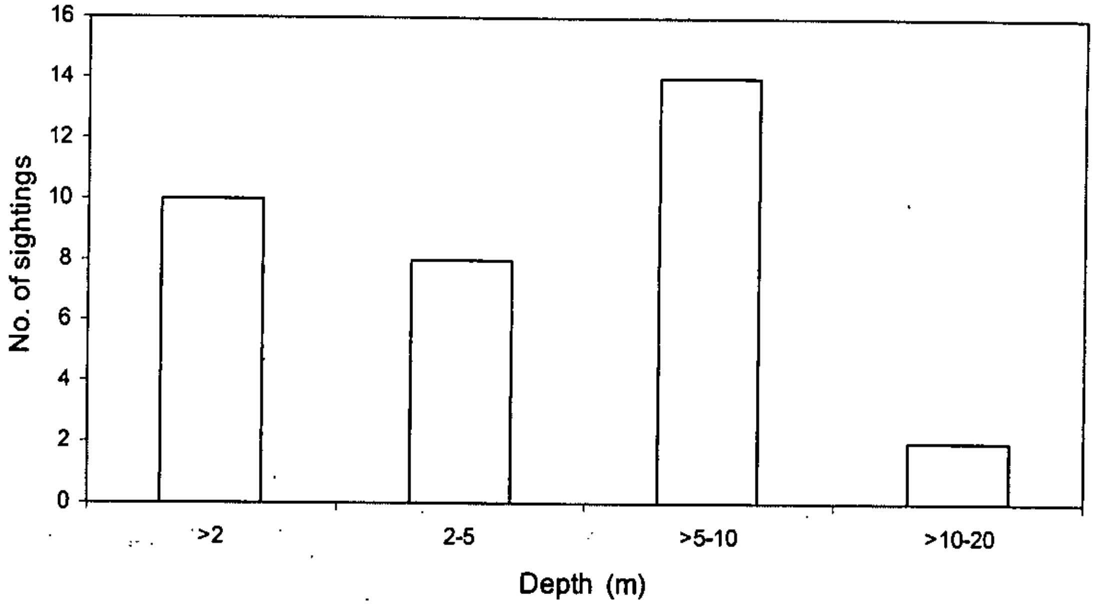


Figure 4.16. Frequency distribution of sightings of humpback dolphins in relation with depth in Maputo Bay between December 1995 and December 1997.

of sightings, however, was higher between sectors 7 and 15 (Fig 4.17), which is a relatively deep channel. This channel connects the area between the shallow sand/mud bank areas in the south of Inhaca and the coral reef at the western coast off Inhaca Island.

The mean activity index for humpback dolphins between sectors (Fig. 4.18) did not vary significantly for feeding (Kruskal-Wallis: H = 22.45, n = 89, p = 0.542), travelling (Kruskal-Wallis: H = 11.53, n=88, p = 0.977) and socialising (Kruskal-Wallis: H = 18.26, n=46, p = 0.570).

Movements of dolphins in relation to the diurnal tidal cycle.

When sighted, most humpback dolphins (57.9%) exhibited directional movements (Table 4.2), but the type of movement (directional and non-directional) was not correlated with the tidal stage (Chi-square: χ^2 = 0.707, d.f. =1, p = 0.4004). Although both northward and southward movements of dolphins were observed during each tidal stage, the direction of movement was significantly different between the tides (Chi-square: χ^2 = 7.588, D.F. =1, p =0.006).

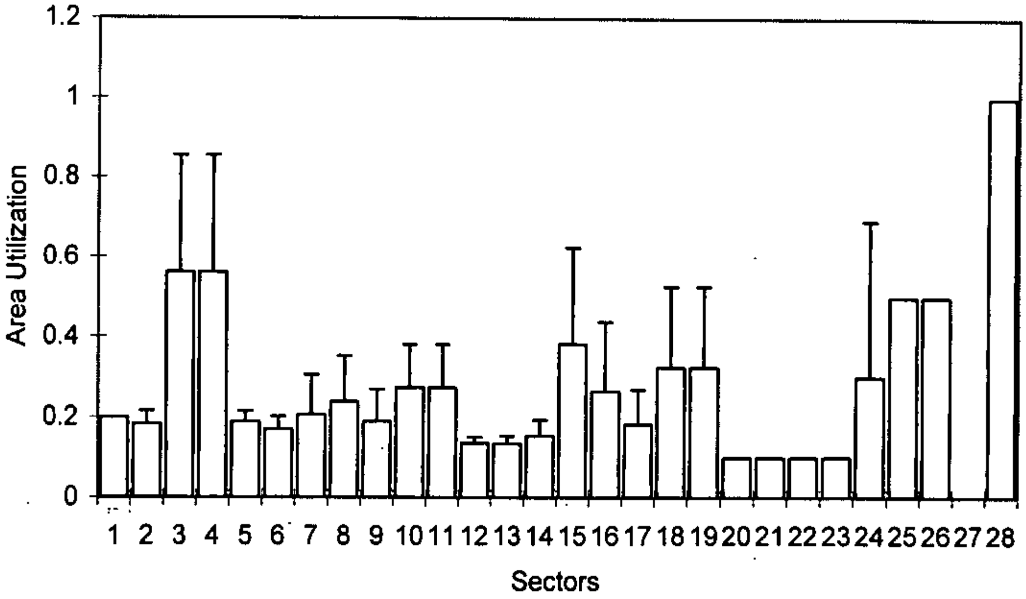


Figure 4.17. The proportion of time spent (Area use = total time spent by dolphins in a particular sector / total observation time of the dolphins during that day) by humpback dolphins in each of the 28, 500 m wide sectors of the west coast of Inhaca and Portuguese Islands , between December 1995 and December 1997. Error bars represent the standard deviation of the area use.

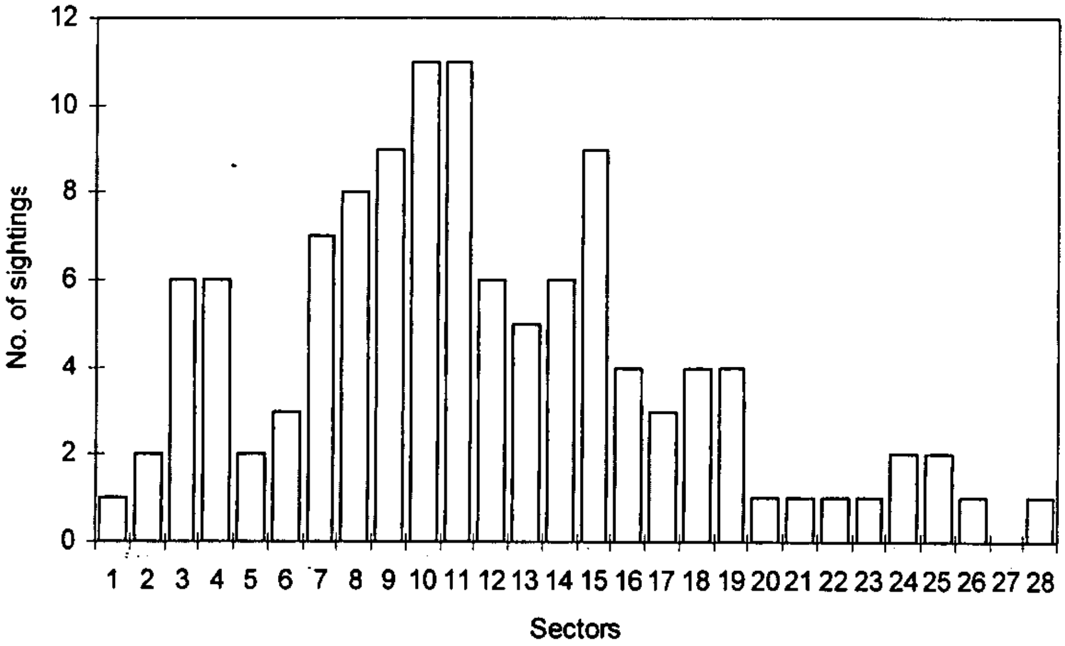


Figure 4.18. The frequency distribution of number of passes of humpback dolphin groups in each of the 28, 500 m wide sectors of the west coast of Inhaca and Portuguese Islands, between December 1995 and December 1997, during dolphin follow procedure. The sectors are described in Chapter 2.

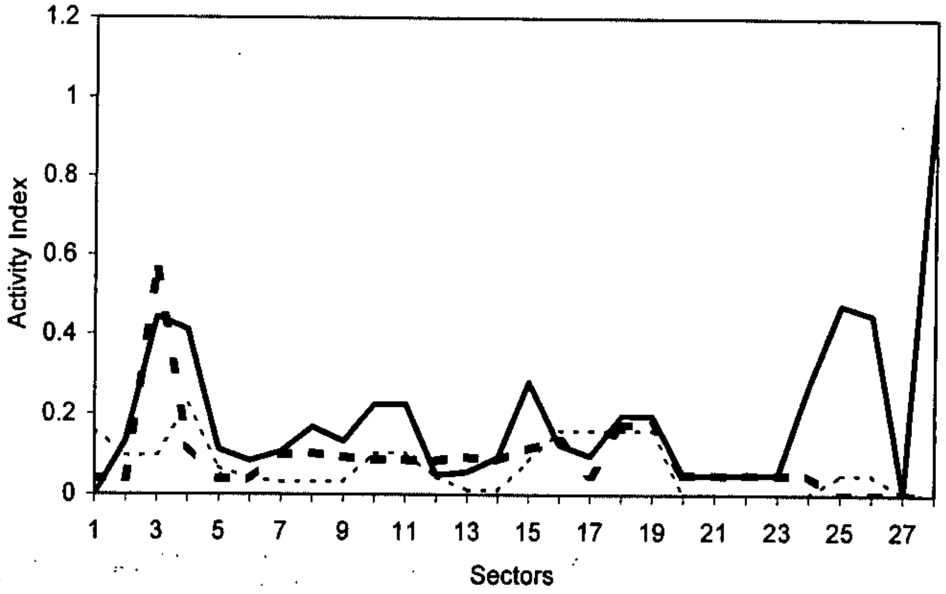


Figure 4.19. The proportion of time humpback dolphins spend feeding (——) travelling (▬▬) and socializing (----) (activity index = time dolphins spent performing a certain behaviour in a sector / the total time spent in that sector) in each of the 28, 500m wide sectors along the coast of Inhaca and Portuguese Islands between December 1995 and December 1997.

Table 4.2. The influence of tidal stage: the frequency with which humpback dolphins in Maputo Bay were observed milling (localized movements) or moving in the northerly or southerly direction between December 1995 and December 1997.

Tides	Ebb	Rising	Total
Localized movements	8	8	16
Directional movements	14	8	22
Southward	5	7	
Northward	9	1	
No. of sightings	22	16	38

DISCUSSION

Sighting frequency

The proportion of surveys when humpback dolphins were sighted in Maputo Bay was low (21%). This could be due to the following reasons: the study area is smaller than the dolphins' range, concentration of effort outside their preferred areas, smaller group sizes, weather conditions (rough sea state and high cloud cover) (Appendix 2) and low density of this species.

The study area may well have been smaller than the range of this species as most searches were restricted to relatively deep areas and dolphins might frequent shallow areas including intertidal areas that are inaccessible to surveys. Preference of dolphins to very shallow areas and tidal channels has been documented in Maputo and Bazaruto Bays (Guissamulo 1993, Peddemors & Thompson 1994), in Australia and the Indus Delta (Corkeron 1990 and Pilleri & Pilleri 1979). The distribution of humpback dolphins is limited by depth (Durham 1994). The same arguments may also indicate that the study area was a marginal part of their range and dolphins used it during low tide when most of the intertidal area emerged. In open waters off the South African coast, this species often occurs within 1 km from the shore being very restricted to the shallower water (Saayman *et al.* 1972, Findlay *et al.* 1992, Durham 1994, Karczmarski 1996)

On the other hand, dolphins occurring in small groups could be missed during surveys either due to weather conditions or to their cryptic behaviour (Peddemors & Thompson 1994), as they tend to avoid approaching boats (Findlay *et al.* 1992, Ng & Leung 2003). Smaller groups of dolphins or lone dolphins have been reported from Maputo Bay (Guissamulo 1993) and off the east coast of South Africa (Durham 1994, Karczmarski 1996, Saayman *et al.* 1972). In Hong Kong waters, groups of humpback dolphins often consisted of in pairs and trios (Porter *et al.* 1997).

The low dolphin density (Chapter 6) also supports the low sighting frequency as surveys with single groups dominated over those with multiple sightings. Along the East Coast of South Africa, humpback dolphins always occurred in small population sizes (Karczmarski 1996, Durham 1994). Aerial surveys conducted over large areas off theKwazulu- Natal coast resulted in a very small number of sightings relative to the bottlenose dolphins (Ross *et al.* 1989), supporting the low sighting density of this species, despite that small groups could also be missed (Ross *et al.* 1989).

Humpback dolphins did not undergo seasonal changes in their occurrence (both in terms of number of sightings and number of dolphins), this suggests that dolphins use the area throughout the year or that their occurrence is not related to seasonal changes in the environment, such as large changes in salinity (see Chapter 2) caused by river run-off. Seasonal changes in water temperature are small (4°C) (Chapter 2). The occurrence of this species was not significantly correlated with changes in river run-off into the Bay. River run-off affects mostly the southern and western parts of the Maputo Bay and very little the eastern part (Kalk 1995) because the currents from western Maputo Bay divert freshwater to the north outside the Bay (Achimo 2000). The eastern part of the Bay had high occurrence of dolphins. The seasonal changes of the marine environment also influenced the composition of fish caught in Maputo Bay, by commercial trawler. Catches were dominated by pelagic fish species of the families Clupeidae and Leiognathidae and demersal species of the Sciaenidae family during summer (Sousa 1989). During winter demersal fishes of the family Haemulidae and pelagic species Engraulidae and Sillaginidae dominate the by-catch of shrimp trawler

(Sousa 1989). Fish catches increased throughout winter until mid summer (in December). Humpback dolphins year round and aseasonal occurrence in the eastern Maputo Bay is caused by the restricted influence of river run-off and more stable marine conditions (Achimo, 2000), but also by their large niche width, that allows them to shift their feeding preference, when species composition change .

Humpback dolphins are reported to feed on estuarine and reef–dwelling fish off the east coast of South Africa (Cockcroft & Ross 1983, Barros & Cockcroft 1991) and evidence of feeding in both estuaries and reef areas has been reported from both South Africa (Saayman *et al.* 1972, Durham 1994, Karczmarski 1996) and Maputo Bay (Guissamulo 1993). Ross (1979) described the stomach content (5.2 kg) of a stranded specimen of humpback dolphin and it included the following species: *Pomadasys commersoni* (1 individual), *Pomadasys olivaceum*(1), *Macrura kelee* (sin. *Hilsa kelee*) (1*), Rhabdosargus thorpei* (1), *Liza richardsoni* (1), *Liza* sp.(3) and *Mugil cephalus* (6), all of sizes exceeding 30 cm. In Maputo Bay most of these fish species are very common. *Hilsa (Macrura) kelee*, is the target of the large artisanal gill net fishery carried out through most of the shallow areas of western and southern portions of Maputo Bay (Sousa 1985). The remaining species occur in the catches of seine and gill net fisheries carried out along the west and southern coast of Inhaca Island (Chuquela 1996, De Boer 2000, De Boer *et al.* 2001)

During low tide, dolphins leave the shallow waters in the north-eastern part portion of the Bay and during this time, seine net catches are dominated *by Sardinella gibbosa, Decapterus russelli, Pomadasys maculatum* and *Crenidens crenidens* which are pelagic species and by *Siganus sutor* and *Pelates quadrilineatus*, which are seagrass dwelling species (Chuquela 1996). Over-fishing in some areas of the southern part of the Bay has been observed (De Boer 2000). Low catches are also obtained at the heavily fished area at the western coast of Inhaca Island and most abundant fish species have a mean length between 11 and 14 cm. Humpback dolphins are referred to take larger sizes (Ross 1979; Barros & Cockcroft 1991). Therefore, even within their areas of occurrence, it is possible that the dolphins are experiencing local resource depletion.

At Algoa Bay, South Africa, the occurrence of dolphins was not significantly related to rainfall, but dolphins responded to seasonal changes and the numbers of sightings were significantly larger during summer and late winter (Karczmarski 1996) as result of reduction of food supply. The lack of response to rainfall could be linked to the lack of estuarine systems at Algoa Bay (Karczmarski 1996). In summary, the occurrence of humpback dolphins in Maputo Bay is independent of seasonal events and, possibly, dolphins either adapt to forage on the most abundant food species at each season or the changes in species composition are not strong enough to change the dolphin feeding habits. The winter changes in species composition are accompanied by the increase in prey abundance in the Bay (Sousa 1989) and therefore dolphins may maintain and possibly feed on the same species during winter.

Group size

The mean group size was 14.91 individuals and ranged from 2 to 25 dolphins. This group size estimate is high compared to the estimates obtained at the East Coast of South Africa (Saayman & Tayler 1973; Durham 1994 and Karczmarski 1996), who reported mean group sizes of five to seven dolphins. This group size range observed in Maputo Bay is very similar to that observed by Karczmarski (1996) and Saayman & Tayler (1973), but was smaller than the estimate from the Indus Delta where groups of up to 50 dolphins occurred (Pilleri & Pilleri, 1979).

The large mean group size observed in Maputo Bay may have been formed in response to the need of foraging on schooling prey This species often moves into intertidal areas or tidal channels in the southern Bay of Inhaca Island (Guissamulo 1993) when flooded at high tide, where the larger groups split into smaller groups to adapt the prey distribution. They may also prey on species that enter the southern bay of Inhaca Island during rising/high tides through a channel, which links this area to Ocean (personal observation). Dolphins, feeding in the entrance of the harbour where currents are apparently strong, were observed at Richards Bay area (De La Mère 1999). Such areas may possibly have relatively large size prey.

Furthermore, many small groups were possibly missed during surveys either because of their avoidance behaviour to approaching boats (Findlay *et al.* 1992, Ng & Leung 2003) or by weather conditions (Ross *et al.* 1989). The low percentage of small groups sighted was possibly further aggravated because most of the intertidal and shallow areas of the Bay (which comprise about 30% of total surface – Chapter 2) were not regularly surveyed because of their low accessibility.

As stated before, their very low occurrence (21%) in the area, suggest that this study area may be a marginal part of their home range (being only one of the few refuges used during low tide marks) where they may aggregate to increase protection, while on the other hand the pressure to forage co-operatively on schooling prey may also promote larger sizes. Bottlenose dolphins also formed larger groups in the same area (Chapter 3). The small population of humpback dolphins does not allow them to achieve larger group sizes comparable to those of bottlenose dolphins and this may limit the maximum group size. Under these circumstances, the larger group sizes of humpback dolphins seem ephemeral and casual and may disintegrate once they move back to shallow waters. However, possibly the social structure favours small groups, but probably, the study area in Maputo Bay may be a good area, which allows bigger groups than those observed in most areas off South Africa (Durham 1994; Karczmarski 1996). Such conditions must be the proximity of many productive habitats, which allow relatively rich prey availability (Kalk 1995; de Boer 2000) in relation to the east coast ofKwazulu- Natal (Durham 1994) and Algoa Bay (Karczmarski 1996). For instance, increased time is dedicated to foraging/feeding behaviour in the unsheltered areas and channels of Maputo Bay (Chapter 7). Nevertheless, larger groups could increase awareness against disturbance caused by occasional hunting by fishermen at Southern Bay of Inhaca Island (Guissamulo 1993).

The larger groups could also arise considering that the study area encloses overlapping home ranges of multiple groups. Accordingly, these large groups might result from the frequent aggregation of smaller groups at low tide, which disperse again at high tide into shallow intertidal waters. There was no data on group size by tidal cycle to support this hypothesis, but the considerable amount of time allocated to social behaviour by these dolphins in Maputo Bay when they occurred in large groups (see Chapter 7) may be an evidence of group coalescence. In Algoa Bay, larger groups were often observed engaged mainly in social behaviour (Karczmarski 1996). In Maputo Bay, two to three different sub-groups coalesce to larger groups at deeper areas and whenever multiple sightings were observed, they often consisted of smaller groups that co-occurred in larger groups.

The other cause of large groups could be the low fishing pressure in their area of occurrence (Guissamulo 1993), which prompt dolphins to confine their distribution there to escape from disturbance and resource depletion in the western part of the Bay. Though disturbance could be the possible source of changes in the area utilisation, humpback dolphins are known to coexist with fishing nets (Pilleri & Pilleri 1979; Durham 1994; Corkeron 1990). This coexistence could depend on the intensity of the disturbance, though, dolphin entanglement in shark nets in Richards Bay has been found to be independent of fishing effort (number of nets), but probably lack of attention when feeding may cause entanglement (De La Mère 1999, Atkins *et al.* 2004). Alternatively, Durham (1994) suggested that, off Tugela River,Kwazulu- Natal coast, larger groups were formed in response to high predation of dolphins by sharks, on the basis that where shark nets reduced the number of sharks, the groups of dolphins were small. Considering this, an analogy to Maputo Bay can also be made: the large groups were observed in eastern Maputo Bay, where fishing pressure (caused by both gill net and trawlers) was low (Guissamulo & Cockcroft 1997). This low fishing pressure may favour presence of sharks, and therefore the risk of predation by sharks may be high in eastern Maputo Bay. Therefore, humpback dolphins may form larger groups to increase protection against predation. However, this alone does not explain why smaller groups are found in Algoa Bay (Karczmarski 1996) and Plettenberg Bay (Saayman *et al.* 1972), where there is no shark fishery. Dolphin group size could be limited by food availability. Nevertheless, the seasonal increase of group size in Algoa Bay is associated with an influx of sharks (Karczmarski 1996). Therefore, the main reason for larger groups in Maputo Bay needs further investigation, but the hypothesis proposed is that of casual aggregation in deep waters (>5 m) during low tide to avoid stranding and reduce mortality from fishers. The relatively large size could be biased due to the concentration of effort to deep areas, where smaller groups move during low tide.

The group sizes of humpback dolphins did not differ significantly between seasons in Maputo Bay, suggesting that the groups use the area the whole year and do not respond to seasonal events. Their low sighting frequency suggests that, they might have larger ranges which help them gather enough food, despite the seasonal environmental fluctuations and changes in prey abundance (de Boer 2000). This is unlike the humpback dolphins from the Kwazulu- Natal coast and Algoa Bay whose groups changed seasonally, following changes in food resources (Saayman & Tayler 1973 and Karczmarski 1996). Maputo Bay also experiences seasonal changes of catches from fisheries (Sousa 1985), both in species composition and in abundance. Catches from the trawl fishery increase during winter to mid-summer (Sousa 1985,1989). However, because of their inshore distribution (Findlay *et al.* 1992, Ross *et al.* 1987 and Guissamulo 1993), humpback dolphins in Maputo Bay are often associated with shallow mud banks, mangrove tidal channels, seagrass meadows and coral reefs (Chapter 2), which provide predictable and evenly distributed food resources (Shane *et al.* 1986) throughout the year. Nevertheless, in the eastern Maputo Bay, catches from fisheries decreased during winter (de Boer 2000). As the population is apparently small (Chapter 6) ,they often adopt individual feeding strategies (Karczmarski *et al.* 1996), suggesting that these habitats provide enough food throughout the year. However, some individuals were not full time residents in the study area and probably moved into eastern Maputo Bay when conditions at other areas (either outside the Bay or inside), were not appropriate (see site fidelity below).

Humpback dolphin groups did not respond to seasonal changes of food resources because their numbers could probably be below the carrying capacity of the Bay. The summer influx of new dolphins was caused by changes in area use of some individuals, but this did not significantly alter the group sizes, because some members also left the groups.

Group size did not change in response to daylight, depth, and spring/neap tides in Maputo Bay. Daylight and tides are often reported to be small-scale environmental changes, which shape the movement pattern and behaviour of dolphins (Klinowska 1986, Shane *et al.* 1986), but are unlikely to influence the group size. Humpback dolphins of Algoa Bay and Plettenberg Bay behaved accordingly (Karczmarski 1996, Saayman *et al.* 1979). Depth, on the other hand, is known to limit the offshore distribution of this species (Durham 1994, Karczmarski 1996, Saayman *et al.* 1972). Humpback dolphins off the Kwazulu- Natal coast are found at depth ≤ 15 m, and at Algoa Bay most occurred within the strip of 150-350 m from shore which corresponded to depths ≤5 m. The bathymetry of Maputo Bay is complex with several channels and sandbanks oriented north south and dolphins often moved either long shore or along the sand banks and whenever dolphins were observed at larger depth, they were often moving between shallow areas. In addition, the restricted access for surveying shallow waters (> 2 m) certainly prevented sightings of smaller groups associated with these areas. This could probably explain the lack of association between depth and group sizes. Several studies of bottlenose dolphins frequenting inshore environments and estuaries showed that group size is not affected by short-term variations such as tides and daylight (Klinowska 1986, Shane *et al.* 1986, Felix 1994, Wells 1991, 1992, Dos Santos & Lacerda 1997).

In summary, group size was not related to season, depth, daylight and string/neap tide variations. The lack of relationship between group size and depth in Maputo Bay occurred within the depth limit of distribution of this species in southern Africa (Findlay *et al.* 1992; Durham 1994; Karczmarski 1996). On the other hand, very shallow areas were not surveyed and therefore any relationship between depth and group size could not be fully established, as it seems possible that in very shallow water dolphins might disperse to increase their feeding efficiency. Groups were larger and may have been caused by need of protection against several risks (predation, strandings and entanglement) within the study area, but also by existence of sufficient resources for their survival through extensive areas of high prey availability (Kalk 1995).

Group composition

Mixed groups, composed of all age classes, were the most frequent in Maputo Bay. Adults (50%) dominated over juveniles (37%) and calves (13.2%). This group composition was consistent with those found at the east coast of South Africa (Durham 1994 and Karczmarski 1996). It appears that mixed groups may be caused by the need for protection against several sources of predation in the Bay, and by ranging within the same feeding areas. Young dolphins learn their feeding areas from their mothers and this is the may reason for grouping (Connor 2000).

However, Durham (1994) found a smaller percentage of calves (9.7%). This could result from a high predation rate of calves by sharks and mortality caused by shark nets along the Kwazulu- Natal coast (Cockcroft 1990). Catch rates of humpback dolphins in shark nets along the coast of Kwazulu- Natal does not differ between sexes (Cockcroft 1990). Reddy (1996) found that 16 female humpback dolphins caught between 1980 and 1993 in shark nets along the coast of Kwazulu- Natal, or stranded in the Eastern Cape Province were all mature (reproductively active) including one pregnant and four lactating dolphins.

Possible differences in the classification of small dolphins as calves between the two studies could also account for the differences of the percentage of calves. The current study defined the calf similarly to Karczmarski (1996).

Large groups encountered were often segregated into three sub-groups. Lactating females and their calves were usually found in one or two sub-groups: one sub-group consisting of large dolphins and some juveniles/sub-adults. Whenever mating was observed, the lactating females and their calves aggregated in a separate group, which was usually found at a varying distance from the mating subgroup, possibly to avoid harassment and calf mortality (Connor 2000). In Maputo Bay, sightings of solitary individuals were uncommon and in many cases consisted of juvenile dolphins, judging from their sizes. Karczmarski (1996) reported a relatively large proportion of solitary large dolphins that were apparently males at Algoa Bay and he suspected that they were roving throughout the area in search of mates. In Maputo Bay, this behaviour was not observed and the males seemed to be resident. Possibly, males adopt flexible mating strategies according to the location. A dominant male may be resident in the area and it possibly has to defend the female resource against other males. In Algoa Bay the humpback dolphins had low levels of site fidelity (Karczmarski 1996) and this may have made males become also transient.

Humpback dolphins often occurred at low densities throughout their range off the east coast of South Africa (Ross *et al.* 1994, Durham 1994, Karczmarski 1996). Dolphins are observed to range widely in the open ocean, taking the risk of predation, due to a scarce food supply. Maputo Bay is a large shallow area offering diverse aquatic habitats (Kalk 1995). These may support a high side fidelity of dolphins of mixed composition. Tugela bank, off the Kwazulu- Natal coast also had resident dolphins due to the existence of shallow waters (Durham 1994), and high shark predation rates (Cockcroft 1991).

In summary, mixed group composition of humpback dolphins appeared to be promoted by the availability of food in a restricted area of the Bay (eastern Maputo Bay) and by the need for improving defense from predators during low tide when shallow areas are inaccessible. The use of the area by nursing females also contributed to this mixed composition. Nursing females maintain long-term bonds with their older calves (Karczmarski 1996). Prolonged associations between old calves and their mothers were reported on several species of inshore dolphins and appear to increase calf survival (Cockcroft & Ross 1990a, Wells 1991, Smolker *et al.* 1995, Karczmarski 1996).

Site fidelity

The lack of seasonal change in the group size and occurrence of dolphins suggests a resident population in Maputo Bay. However, the humpback dolphin individuals identified in Maputo Bay showed varied site fidelity. 35% of the humpback dolphins were infrequent visitors, consisting mostly of juveniles and adults of undetermined sex. Furthermore, 45% of the humpback dolphin individuals occurred during one season only, half of the identified individuals were resident, with continuous presence throughout the study. The existence of a resident population is suggested by the sighting of individuals in the area over a five-years period, which is, at least, evidence of a long-term use of the area by dolphins. The percent of infrequent visitors was relatively high and it is unknown whether these dolphins come from outside Maputo Bay or from a seasonal shift in the area use within the Bay. In addition, it is unknown if individuals range outside the Bay or to other areas within the Bay. The habitats outside Maputo Bay are open coast sandy shores with few sparse coastal rocky reefs (Tinley 1971) and the nearest estuaries are found at ≥ 150-200 km to the north and south of Maputo Bay (Massinga & Hatton 1997). Therefore, Maputo Bay appears to be an isolated, but extensive, rich habitat, which may promote relatively high site fidelity of some individuals, compared to Algoa Bay and other areas of Kwazulu- Natal coast (excluding the Tugela Bank).

Throughout their range, humpback dolphins exhibit differences in site fidelity. The population of Algoa Bay had low levels of site fidelity (Karczmarski, 1996) while Saayman & Tayler (1979) reported high levels of site fidelity of at least three individuals at Plettenberg Bay. Durham (1994) reported high levels of re-sightings of humpback dolphin individuals in the vicinity of their first sightings, also suggesting a restricted range and some site fidelity, which was high among the female/calf pairs. In Zanzibar, identified individuals were resident for at least 2-3 years (Stensland *et al.* 2006) Year-round occurrence of humpback dolphins was also reported at the Indus Delta (Pilleri & Pilleri (1979), though they could not tell anything about site fidelity of different individuals. Such patterns could be related to the availability of food resources in those areas.

Off the Gulf of Mexico, Ballance (1990) has found bottlenose dolphins to have three different kinds of site fidelity: year round resident, seasonal visitors and infrequent visitors. The humpback dolphins off Maputo Bay showed the same pattern. However, as in the Ballance (1990) study, the study area was smaller compared to the dolphins' range. This could have influenced the conclusions, and should therefore be carefully considered. A further study of the populations of Maputo Bay and its surroundings could clarify the degree of transience and the large-scale organisation of the dolphins.

The high site fidelity pattern of some dolphins found in Maputo Bay may be related to the availability of food resources throughout the year, extensive habitats or other reasons, such as high fishing pressure in the western Maputo Bay.

Humpback dolphins inhabit the inshore, shallow areas of Maputo Bay, mostly protected from wave action from the open sea and they are lined by mangroves (Guissamulo 1993). The association of mangrove swamps, coral reef, sandbanks and seagrass meadows, together contributes to maintain enough food resources for this limited number of dolphins. Consequently, movements of resident dolphins occur between these associated habitats and their ranges are restricted. This was not the case for the humpback dolphins of Algoa Bay which fed on prey living in restricted areas with few rocky outcrops, which showed seasonal changes of prey availability (Karczmarski, 1996), promoting, therefore, low levels of individual site fidelity. Transient individuals in Maputo Bay were composed of adults of unknown sex and juveniles. Most transient individuals were observed during summer, suggesting that reproductive reasons (search for mates), associated with search of areas of rich food supply may be linked to this influx. Pregnant females could also move to Maputo Bay to fulfill their energy intake and for safe parturition. Two humpback dolphin females, not sighted before, were often re-sighted in Maputo Bay seven months prior to parturition and remained in the area with their calves afterwards. This also occurred for humpback dolphins at Algoa Bay (Karczmarski 1996). Durham (1994), at Tugela Bank,Kwazulu- Natal, suggested the existence of breeding areas at large shallow and productive habitats, where nursing females were abundant. Cockcroft & Ross (1990a) estimated that pregnant and lactating female bottlenose dolphins consume threefold more food than resting females and other dolphins. Therefore, by having small ranges within a relatively rich feeding ground, females would fulfill their energy requirements and ensure calf safety and learning (Connor 2000).

Another possible reason for the high number of transient dolphins during summer is the extreme reduction in salinity caused by the river run-off in the western and southern parts of Maputo Bay. This may promote dolphins to move to the eastern part of the Bay, which does not experience drastic changes in salinity (Kalk 1995; Achimo 2000). During early and mid summer, food supply in the western and southern Maputo Bay may be low, because of water salinity and high turbidity, which reduce the primary production (Longhurst & Pauly, 1987). Fishery catches rose at the end of the rainy season (Sousa 1989), when most suspended sediments brought by the rivers settle and the plankton production increases because of increased light penetration. The gill net fishery achieves high catches during April and fish catches in trawlers increase throughout the dry season (Sousa 1985). During winter, dolphins may possibly range widely, but probably, most stay in the eastern Maputo Bay because of the high fishing pressure, which poses risk of entanglement.

In summary, varied site fidelity was a feature of humpback dolphins of Maputo Bay, but half of the individuals were resident, of which most were lactating females (with their calves), juveniles and males. A relatively stable extensive area with heterogeneous, but productive habitats in the eastern Maputo Bay (Kalk 1995, de Boer 2000) could promote the high site fidelity of the nursing group. Large changes in group membership occur during summer, with influx of new individuals, while others leave the study area. It is likely that reduced prey abundance at the western and southern areas of the Bay and outside the Bay could be responsible for this. There was no evidence of search for mates, though this time may promote reproduction.

Social affiliations

Mother calf associations are reported to be stronger in the first two-three years, decreasing with time as the dependency of the calf to its mother reduces (Karczmarski 1996, Wells *et al.* 1980, Wells 1991, Smolker *et al.* 1992, Felix 1997, Cockcroft & Ross 1990a). In the first years calves depend on their mother because of lactation and learning. However, the present study did not examine this obvious kind of association, but examined other associations, which did not involve calves.

The number of affiliates identified (dolphins with which any individual was sighted), increased with the number of sightings, though the most re-sighted individuals did not meet all possible affiliates, suggesting a relative segregation of groups or an artefact caused by sampling distribution. However, the large changes in group membership that occur during summer might have reduced the chances of individuals being photographed with some affiliates. Among the humpback dolphins, the most re-sighted individuals were seen during 50 to 80% of the photographic surveys, which indicates a high site fidelity and therefore a higher chance of occurring in company of both resident and transient dolphins. It is not known if the most re-sighted dolphins moved outside the Bay or to areas within the Bay not surveyed, but the chances that the most sighted dolphins were overlooked when in large groups are unlikely since the largest groups (25 individuals) could easily be photographed. Nevertheless, the number of photographic surveys carried out in Maputo Bay was small and therefore the rare and brief associations could be missed. The duration of the association between dolphins of different communities in southern Africa has not been reported. Brief associations between individuals of different bottlenose dolphin communities at Gulf of Guayaquil, Equador, had varying duration ranging from a few hours to two weeks and mixing was often observed during feeding and mating behaviours (Felix 1997). The knowledge of the behaviour when unrelated dolphins meet would help determine the degree of association between individuals of different groups or communities. Tail slaps were reported as greeting or hostile interactions between bottlenose dolphins from different communities off the Kwazulu- Natal coast (Peddemors 1995). Interactions between terrestrial territorial mammals are well documented and, for instance, hostile inter-community relationships were reported in chimpanzees (Wrangam & Rubestein 1986). Whether tail-slapping also occurs in Maputo Bay when dolphins of different communities meet, it is unknown.

In Algoa Bay, the stronger associations occurred between the transient dolphins (Karczmarski 1996). In Maputo Bay, the stronger associations occurred between the most re-sighted individuals, suggesting that transient individuals might face difficulties joining stable sub-groups. However, further behavioural studies are required to establish if aggression or some kind of avoidance could occur between transient and resident individuals. Throughout the duration of the study, aggression events were not observed, but some individuals had dolphin teeth scars on their bodies, which may indicate aggressive interactions, though mating events may also cause this (Karczmarski 1996).

Lactating females showed a high degree of site fidelity and consequently the large number of affiliates that were inflated by contacts with transient dolphins. However, the number of affiliates was not different between age-sex categories, when comparing dolphins sighted more than four times. Therefore, the differences in number of affiliates between age and sex classes are due to the unequal site fidelity of individuals from different age and sex categories. This is consistent with the mixed group composition observed in Maputo Bay, which may show a high stable group membership.

Males had the highest number of affiliates, but because only two males were identified during this study, this conclusion should be considered preliminary and not necessarily applicable to other males. However, these males had a high degree of site fidelity, which increased their chances to associate with many more individuals. If males are resident, their strategy is to guard the few females within their range, and mate with them, instead of travelling longer distances to search for females of other areas. Humpback dolphins have small testis size (Cockcroft 1989) and therefore, sperm competition might not be the best mating strategy, but guarding females. In addition, parturition does not seem to be seasonal in Maputo Bay (Chapter 6) and consequently guarding females within the range rather than moving long distances to find other females could be effective. While Reddy (1996) could not examine the existence of seasonal reproduction in humpback dolphins from Eastern Cape and the Kwazulu-Natal coast, Karczmarski (1996) found evidence of seasonal reproduction in Algoa Bay and a large number of apparently transient and solitary males. These males may not need to guard females permanently, but search for females during the mating season. Accordingly, Durham (1994) found male dolphins to exhibit long-range movements (about 50 km), which support the hypothesis of males searching for females, rather than guarding a female group. In Algoa Bay, only few nursing female humpback dolphins had short ranges/high site fidelity while other females were transient and males could be following these transient females. However, the identified males were not present during all photographic surveys conducted in Maputo Bay and possibly they might have moved to other (neighbouring) areas in search of mates. Furthermore, it is likely that among adults of unknown sex some were males. Possibly males of Maputo Bay have ranges comparable to those of the bottlenose dolphin males at Sarasota Bay (Wells *et al.* 1980, Scott *et al.* 1990), ranging within the resident communities of the Bay.

In Maputo Bay humpback dolphin males might use both strategies, but more data are needed before advancing definite conclusions. The current patterns of male site fidelity and association observed in Maputo Bay, although preliminary, are consistent with those of bottlenose dolphin males in the Gulf of Guayaquil (Felix 1997), a tropical area, where reproduction occurs during the whole year and males tend to adopt the permanent female defence, rather than female search found in temperate areas (Wells *et al.* 1980). The low coefficient of association for the two adult males identified raise questions on how competition for mates occurs. Assuming that humpback dolphin groups aggregate at the channels off the western coast of Inhaca at low tide and disperse into small groups in the shallow areas of the south-eastern Maputo Bay at high tide, then, possibly, mature males may distribute themselves into those small groups, mating with the few cycling females of each group. This is consistent with findings that the two known males were associated with different clusters of dolphins. Hierarchy between the mature males may also exist and have been established for a long time and exhibited whenever the small groups coalesce. This could explain why the second male was observed mating when the apparently dominant large male was absent. Wells *et al.* (1990) suggested that roving males are the main vectors of genetic exchange in bottlenose dolphin communities at Sarasota Bay, Florida. In Maputo Bay, the study period was too short to establish how this is achieved, but the influx of new dolphins may include some males that may become resident and later may replace the dominant male.

In summary the number of affiliates increased as the number of times a dolphin was sighted also increased. In addition, differences in site fidelity between individuals of different ages and sexes resulted in differential distribution of the number of affiliates observed in Maputo Bay, nursing females and apparently resident males had the highest number of affiliates and stronger associations. Nevertheless, short-term movements of most re-sighted individuals outside the study area contributed to not being identified with all other individuals, suggesting some relatively low degree of segregation.

The degree of association between individuals among cetaceans is known to vary widely and the lack of consistency in the association and fluid membership seems to be a dominant feature in dolphin populations living at open coasts (Wursig & Wursig 1977; Weller 1991; Slooten *et al.* 1993; Peddemors 1995; Connor *et al.* 2000). However, long term bonds between dolphins which range longer distances have also been reported (Weller 1991, Würsig 1978, Wursig & Baptista 1986, Rittmaster & Thayer 1994), though these are frequent in small populations inhabiting closed habitats, which provide year round prey availability and promote high site fidelity of individuals (Wells *et al.* 1980, Harzen 1995, Dos Santos & Lacerda 1997). However, organisation of dolphins into communities also plays a role in the degree of association between resident individuals and apparently transient dolphins inhabiting large shallow habitats (Wells *et al.* 1980, Felix 1997, Ballance 1990).

In Maputo Bay, the mean coefficient of association between humpback dolphin individuals was 0.36, 45% of associations fell in the range of 0.21 - 0.40 while levels of associations above CA = 0.40 comprised 32.2%. This represents an intermediate pattern of association with both relatively stable and casual associations. The reduced amount of very strong associations reflects the differences in the individual, site fidelity, ranges and area use patterns between the most re-sighted individuals. In Algoa Bay, most associations were casual (mean CA = 0.17, S.D.=0.16) and weaker than those of Maputo Bay, because of differences in size of foraging areas and prey availability. Sightings of larger groups in Maputo Bay, despite frequent, apparently represented casual aggregations originating from the tidal cycle which emerged the extensive intertidal areas in the Southern part of the Bay, turning the habitat inaccessible. Knowledge of the areas where transient dolphins came from may explain the existence and temporal occurrence of the casual associations. Dolphins from the open coast and those from other parts of Maputo Bay could be prompted to shift their area use toward the eastern part of Maputo Bay by different factors. Dolphins from the open coast could be attracted to the Bay during winter, when reefs have low prey abundance while dolphins from western and southern Maputo Bay could be attracted during summer, when river run-off is intense. However, if reproduction is the main factor of aggregation, then it is likely that only mature dolphins would respond to reproduction needs.

Bräger *et al.* (1994) suggested that dolphins in small populations, such as those from Sarasota Bay and the Sado Estuary exhibited high levels of associations because they had a small number of available affiliates, which is the case for the humpback dolphins. Humpback dolphins in Maputo Bay have a year round low sighting frequency suggesting that they range wider than the study area or that they use the Bay infrequently or move to areas of the Bay not surveyed in this study. The existence of a relatively high number of stable associations in Maputo Bay, compared to the population in Algoa Bay (Karczmarski, 1996) indicates the dominance of stable and consistent associations in the former.

Dolphins with wide ranges are likely to maintain more contacts and therefore gain more affiliates, most of which are casual. This may have accounted for the differences in the degree of exchange of individuals between the humpback dolphins in Maputo Bay and the bottlenose dolphins from Sarasota Bay, Florida (Wells *et al.* 1980) and Port Aransas, Southern Texas (Shane 1980). Possibly, the degree of closure of the habitats functions as a barrier for the entrance of transient dolphins. Maputo Bay is a U-shaped area with an about 30-km wide entrance in the North while the Sarasota Bay and Port Aransas have very small channels connecting with the Atlantic Ocean.

Besides the existence of a small stable community in Maputo Bay (Fig.4.13), in which all age and sex groups were represented, the remaining associations consisted of dyads associated at varying similarity levels (60 to about 85% Bray Curtis Similarity Index) composed of either females-juveniles, juveniles only, male-adult of unknown sex, and adults of unknown sex only. Therefore, reasons for associations between dyads may be diverse, being either long-term bonds of female and an old calf, mostly considered persistent (Karczmarski 1996, Wells *et al.* 1980), or bonds between juveniles born in the same group (Wells *et al.* 1980) or functional associations between males (H2 and H46) which are formed to harass females and replace other males (Wells *et al.* 1980, Smolker *et al.* 1992 and Felix 1997).

Some long-term studies of the social structure of bottlenose dolphin populations living in inshore habitats found that sex, age and kinship are the main factors determining the strength of associations and therefore the social structure (Wells *et al.* 1980, Smolker *et al.* 1992 and Felix 1997). The organisation of dolphins into geographically distinct communities with overlapping ranges determines weak associations between individuals of those communities (Wells *et al.* 1980; Felix 1997; Connor *et al.*2000). The humpback dolphins in Maputo Bay showed both resident and transient groups of dolphins and this suggest that dolphins from different communities were present in the area. The clusters of individuals clearly separate the resident and stable core group from the other dolphins (Fig 4.13), which were associated to that group at variable strength.

Sex based associations between bottlenose dolphins observed in Sharks Bay, Australia, showed that most female-female, male-male and female-male associations were predominantly weak only a few associations, mostly of the same sexes, were stronger (Smolker *et al.* 1992). The humpback dolphins of Maputo Bay also showed high variability in the associations between sex and age classes, which resulted in a generally low coefficient of association. Only few associations were strong within each group. Nevertheless, females, which also had a relatively high mean number of affiliates, also had the highest coefficient of association with any other groups. Humpback dolphins of Algoa Bay, however, were mostly transient (Karczmarski 1996) and, therefore, the degree of association between individuals was different from that of this Maputo Bay.

In summary, the humpback dolphins of Maputo Bay are associated at an intermediate level (CA = 0.36) consisting of both stable and short term, but with a relatively high proportion of stable affiliations more so than that reported by Karczmarski (1996) due to the high site fidelity of most group members. Associations in dyads between individuals were not consistent with the any age-sex pattern and this may be due to many reasons, but the relatively stable mixed group composition could explain this kind of pattern. Some influx of new dolphins occurs during summer. Some calves were born between the end of August and the beginning of September (1997), almost at the end of the study period. Unfortunately, logistic constraints resulted in the lack of sampling during that period. Therefore, it could not be clarified if an influx of dolphins to the area occurred, because social interactions are known to increase at the time of reproduction (Karczmarski 1996. The existence of relatively large groups, of apparently temporary duration and high site fidelity, seems to explain the low strength of association observed.

Area use

Humpback dolphins were observed in the study area after 08:00 and occurred in the afternoon more often than in the morning. The relation between tides and daylight in Maputo Bay caused the highest frequency of sightings in the afternoon. Daylight low tides often occur at mid-day (during spring tides) and in the afternoon during neap tides (Kalk 1995). During low tides, the large shallow areas located in southern and eastern Maputo Bay are uncovered and dolphins have to move following tidal currents to the deep channels of the north-eastern Bay. Possibly, this also influences the movement/abundance of prey of humpback dolphins, mainly at those shallow areas that are not totally flushed out. At Algoa and Plettenberg Bays, dolphin occurrence had a daylight pattern, but was unrelated to the tides (Saayman *et al.* 1972 and Karczmarski 1996). Apparently tides only influenced the prey abundance, as small shallow and intertidal areas occurred at those Bays. The tidal effect was likely to influence the prey movement at Plettenberg Bay because wave action is more reduced compared to Algoa Bay.

Tidal related occurrence/movements of humpback dolphins in Maputo Bay could also be related to the increase of fishing activity in shallow waters and channels in the eastern and southern Maputo Bay at low tide (Chuquela 1996; de Boer *et al.*2001; de Boer 2000). Artisanal fishermen are often active at the ebb and low tides, when fish concentrate in the channels. At these times dolphins may move to the deep areas to avoid entanglement / intentional killings and this may cause tidal related movements. In 1992, five humpback dolphins were hunted at a tidal channel in the southern Bay of Inhaca Island, Maputo Bay (Guissamulo 1993). During high tide, dolphins move south to shallow areas. Despite reduction in prey density, dolphins may choose to forage in shallow areas because of high probability of prey capture in turbid waters. In addition, a confusion in perceiving the surroundings and navigating, which can occur in the shallow channels at low tide during foraging, may also be reduced, by frequenting the shallow areas at high tide (Connor 2000).

Daylight and tidal patterns of occurrence of *Sotalia guianensis*, a coastal dolphin species has been observed at Guanabara Bay, Brazil (Geise 1991). There, dolphins used the area for feeding, entering into the Bay in the morning and leaving in the afternoon, but this was also linked to tides as dolphins entered the Bay at high tide or beginning of the ebb tide (Geise 1991). Bottlenose dolphins inhabiting shallow areas and estuaries have variable daylight and tidal patterns of movement, which depend on the specific conditions of their habitats (Shane 1980, Shane *et al.* 1986, Felix 1994, Dos Santos & Lacerda 1987). Shane (1980) found that tidal related movements of dolphins occurred at specific parts of Port Aransas, where the tide flow was high and caused prey movement. The time of the day had high influence where the tidal currents were weak (Shane 1980). This may also be responsible for the differences observed between Algoa and Plettenberg Bays. But, in Maputo Bay, the effect of the tides is strong in the shallow southern Bay areas (de Boer 2000), then, occurrence/movements of humpback dolphins appear to be related to the tides rather than daylight.

The occurrence of humpback dolphins after 08:00 in the morning suggests that they may range long distances in shallow waters and take longer to achieve the relatively deep areas during ebb tide. On the other hand, they may stay in shallow areas during the night and dawn, initiating their movements to the deeper water when light conditions are sufficient to identify predators in deep water or they my already know the best timing to avoid predation. The time difference between high and low tide is 6 hours in Maputo Bay (INAHINA 1997). If low tides occur at mid-day or in the afternoon (Kalk 1995), the ebb-tide current begins about 5 hours before low tide. Dolphins may then leave shallow waters and enter the deeper areas accessible to surveys at 07:00 or later.

The inshore nature of the humpback dolphin is supported by their concentration (91% of sightings) within two km from shore. At the study area, the intertidal area is almost 800 m wide along the west coast of Inhaca Island, and between 4 and 8 km, south of Inhaca Island. For these reasons, many dolphins use the combined intertidal area at high tide and the neighbouring channel (which is almost one km wide) during low tide. Humpback dolphins often move at the edge of the channels close to the shallow intertidal area or at the margins of the sandbanks, which are north-south oriented. Dolphins sighted further away from shore were also associated to the margins with sandbanks, which occur in the middle of the Bay. Therefore shelter and foraging methods together explain the range of the dolphins closer to the shore. The complex bathymetry of Maputo Bay does not allow a good analysis of the effect of this tidal cycle on dolphin occurrence, because of lack of a distinct gradient of depth. Humpback dolphins stay in the deep channels during low tide, but still use the shallow area at the edge of the channels. The restricted occurrence of humpback dolphins close to the coast has been documented at Tugela Bank, Kwazulu-Natal, at Algoa Bay, Plettenberg Bay and Zanzibar (Durham 1994, Karczmarski 1996; Saayman *et al.* 1972, Stensland *et al.* 2006 respectively), where dolphins often occurred within a 150-350 m strip from shore, except for Tugela Bank where they ranged up to 4 km offshore due to extensive shallow areas (Durham 1994). However, in Maputo Bay, because of its extensive shallow areas, dolphins would therefore extend their distances further away from the shore resulting in their concentration within two km of the shores of Inhaca Island. Humpback dolphins also occurred far from shore because of the offshore distribution of shallow areas in Moreton Bay, Australia (Corckeron 1990). Therefore, water depth determines the distribution of dolphins and the distance from shore is regulated by the distribution of shallow areas.

No significant differences were observed in the area use and activity of humpback dolphins along the west coasts of Inhaca and Portuguese islands, eastern Maputo Bay, implying that this area is used for multiple purposes. Often feeding and travelling were the behaviours of longer duration (Chapter 7) and as dolphins used the shallow waters at the sandbanks and margins of the channels during their movements, they were likely to find the less abundant large prey (de Boer 2000). Therefore, they would prolong feeding and travel throughout the area distributing equally these two behaviours along the shore. As a major part of the study area consisted of deep channels where dolphins aggregate during low tide, the social behaviour is likely to occur in the area, after the dolphins had foraged. In contrast, in Algoa Bay, dolphins had specific feeding areas due to the unequal distribution of rocky outcrops and this resulted in a concentration of feeding and travelling activities and consequently a different pattern of area utilisation (Kaczmarski 1996). The same applied to Plettenberg Bay (Saayman & Tayler 1979). However, a similar pattern to that observed in Maputo Bay was found in Zanzibar (Stensland *et al.* 2006)

In summary, the tidal emergence/inundation of shallow areas is the main factor shaping the area use by humpback dolphins in the study area. The high occurrence of sightings in the afternoon is influenced by daylight pattern of tides (were daylight low tides occur In Maputo Bay around noon and later (Kalk 1995), therefore resulting in high occurrence in the afternoon. Despite prey concentration into channels at low tide, dolphins move out to avoid stranding and predation and move back to shallow areas to prey, but possibly high probabilities of prey capture in shallow, turbid waters, and of finding large prey, as well as reduced disturbance from fishing activity, account for their occurrence in shallow waters during high tide.

Dolphins occurred close inshore throughout the area possibly because of foraging efficiency, avoidance of predators and reduced drag, since these areas have less current speed than at the middle of the channels and therefore prey may be easily captured. The spread and extensive distribution of feeding areas throughout their route, have caused equal distribution of feeding, social and travel behaviours.

Movements

The proportion of directional movements displayed by the humpback dolphins in Maputo Bay did not differ significantly when compared to the amount of localised movements. This implies that dolphins utilise the whole area for multiple activities. However, the directional movement of dolphins followed the direction of the tidal currents. This movement was forced, because the shallow waters of the southern Bay of Inhaca flow out at low tide exposing the substrate and leaving only a few tidal channels. Humpback dolphins moved northward to avoid strandings, but return to the shallow areas in the following high tide. Probably prey capture in the area was more successful and dolphins may also forage on prey from the open ocean and they may experience less predation risk. Tides also influenced dolphin movements between two feeding areas at Plettenberg Bay (Saayman & Taylor 1979), primarily based on the changes of abundance of prey species. However, in Algoa Bay, movements of dolphins did not appear to be related to the tides due to the limited impact of the tidal current in relation to the wave energy (Karczmarski 1996). In Maputo Bay, the flushing of the shallow and intertidal areas supports the idea that dolphins leave the area primarily to avoid stranding/interference with intensive fishing in the few tidal channels. In Bazaruto Bay, however, dolphins took advantage of low tide to feed using beaching behaviour (Peddemors & Thompson 1994). Nevertheless, the size and depth of the channels were this feeding pattern occurred are not mentioned and apparently no human activity takes place.

The geographical location of the sightings, behaviours, tides and time spent observing dolphins could all affect the kind of movement observed. For instance, feeding and social behaviours are often associated with non-directional movement and if the time spent observing dolphins is shorter than these behaviours, it results in scoring non-directional movements.

The extent of directional movements of humpbacks dolphins, was observed to be related to the semi-lunar tidal cycles in Maputo Bay (Overvest, 1997). At low spring tides, dolphins moved to the deep and open areas of the northwest coast of Inhaca island, when almost 90% of the south-western sandbanks of Inhaca become emerged (de Boer 2000), while during neap tides the dolphins remained at the south-western coast of Inhaca because of low tidal range, which only exposes 40% of the sand banks (de Boer 2000).

In summary, humpback dolphins of Maputo Bay move from shallow waters into deep waters during ebb and low tide, because these areas emerge, becoming unavailable. In deep channels dolphins are engaged in non-directional movements during feeding/social behaviours and as the tide height increases they resume the movements back to shallow waters of southern Inhaca Island.

CHAPTER 5. POPULATION SIZE AND DYNAMICS OF BOTTLENOSE DOLPHINS IN MAPUTO BAY

INTRODUCTION

Population estimates and life parameters are important tools in the management of animal populations (Begon *et al.* 1996). For dolphins, population estimates and life parameters are available for few species, mostly those either caught during fishery operations (for example off Japan and at the Eastern Tropical Pacific), or from areas where long term studies were carried out (coast of Florida, Kwazulu- Natal coast, California coast, etc) (Klinowska 1991, Jefferson *et al.* 1993, Wells *et al.* 1990, Cockcroft & Ross 1989), but also to few locations were the status of coastal dolphins deteriorated, such as Chesapeake Bay, Virginia (Blaylock 1988). However, short and medium term studies using photo-identification are also producing abundance estimates (Williams *et al*, 1993, ,Stensland *et al.* 2006),

Life history parameters such as age at sexual maturity, calving intervals, survival rate of calves and adults, breeding season and sex ratio are necessary to assess the dynamics of dolphin population. These parameters are also available for dolphin species by-caught in the fisheries or from mass strandings (Cockcroft & Ross 1989). Long term photo-identification also provide some of these parameters, as it requires extremely long time to provide such data (Wells *et al.* 2005).

The age of sexual maturity among delphinids is known for few coastal species, usually those subjected to some sort of exploitation. Generally, females achieve the maturity in the range of 1 to 8 years earlier than males (Klinowska 1991). It is also known to range highly within different populations of the common dolphins (Klinowska 1991) suggesting that it may be genetically determined and that predation/exploitation pressures contribute to the value.

Calving interval has also been documented for few species, but varies from 2 to 6 years and high variations between and within species have also been documented (Klinowska 1991).

The reproductive season of delphinids has variable length and usually coincides with time of food abundance. Cold temperate water species have a calving peak in spring, summer and early autumn, while species inhabiting tropical, subtropical and warm temperate waters have either year round calving or an extended breeding period which starts in early or late spring and ends in summer or autumn (Jefferson *et al.* 1993).

The reproductive and mortality rates of populations are also not known for most delphinids, but they differ geographically for the common and bottlenose dolphins, and sometimes differ between sex and age of individuals (Klinowska 1991). Predation pressures/incidental catches in fisheries are undoubtedly factors influencing for the levels of reproductive and mortality rates (Tyack *et al.* 2000).

The bottlenose dolphin population estimate off the Kwazulu- Natal coast, from aerial surveys, was 700 individuals, which are clustered along 3 regions each 32 km long (Cockcroft *et al.* 1990b, Peddemors 1995). The population of the northern coast of Kwazulu- Natal is subjected to incidental catches in shark nets, which take mostly pregnant and lactating females, thus reducing the reproduction and survival of calves and this population. While an influx of dolphins have been observed during winter following the northward migration of pilchard, there is still no evidence that these dolphins may eventually replace the resident population whose reproduction is further affected by organochlorines (Cockcroft *et al.* 1989b, 1991). The population size of bottlenose dolphins of Maputo Bay is also subject to interactions with fisheries and it is not known if it mixes with the population of the Kwazulu- Natal north coast. Despite the large regional phylopatry observed in South Africa, it has very low genetic diversity and in addition, the lack of catches of this species at Tugela Bank, northern Kwazulu- Natal, suggest that it may be separated from the Mozambican population (Goodwin *et al.* 1995; Goodwin 1997). Under such circumstances, the conservation of the species in Mozambique is priority. The lack of long-term systematic studies limits the understanding the dynamics of the population in Maputo Bay.

This chapter estimates number of bottlenose dolphins of Maputo Bay and the birth rate, minimal mortality rate and survival rate of calves and discusses the population dynamics and analyses them in view of the ecological pressure, changes in habitat and resources caused by fisheries and human coastal development, providing possible scenarios for the population.

METHODS

Individual identification of dolphins was carried out from December 1995 to December 1997. The survey procedure is described in Chapter 2. Group sizes were estimated from direct counts of all individuals. Composition of groups (adults, juveniles and calves (based on relative sizes to adults)) was determined and the apparent age of calves estimated. Calf age was estimated from several features, including the first time an adult was sighted with a calf, calf size, the shape of dorsal fin, pattern of breathing and the positioning on the central side of an adult dolphin.

A newborn calf (up to two weeks old) had one third of the adult size, with the dorsal fin bent and when surfacing it was breaking the water surface with the rostrum and the head simultaneously and remained closely linked to one of the mother's flanks.

A mark recapture method was used to estimate population size and life parameters of dolphin following Hammond (1986). Photographs of dorsal fins of dolphins were taken during the boat surveys carried out in Maputo Bay, using Minolta X-700 and Canon EOS cameras equipped with lens of focal distance varying between 80-300 mm and diapositive films. These photographs were first selected initially based on clarity, focus and parallax. Only photographs of dorsal fins that had good quality were then used for photo-identification. Photographs of dorsal fins that had identifiable marks (nicks), on the profile of the dorsal fin were labeled and catalogued. Photographs of dolphin dorsal fins identified in each survey were labeled separately, If photographed in a subsequent survey, then they were considered a re-sighting (or recapture). Detailed description of the selection procedure of photographs is presented in the Chapter 2. For each dolphin identified a sighting (capture) history was produced.

The use of mark-recapture methods for population estimates is based on the argument that the proportion of marked animals recaptured in a sample of the population is equivalent to the proportion of marked animals in the total population (Hammond, 1986).

$$\frac{m_2}{n_2} = \frac{n_1}{N}$$

m_2 is the number of marked individuals present in the second sample
n_2 of the total population N and

n_1 is the number of marked animals in the population.

The multiple recapture approach, known as the Schnabel estimator (Hammond 1986) was used because naturally marked individuals were being captured and recaptured during the sampling occasions.

Estimates of size of dolphin populations were obtained using several computer programs. The program "Capture" (May 1994) was used to estimate closed populations. This computer program contains 8 models for estimation of population size . The models incorporate three sources of variation in sighting probabilities:

i) a time response which considers that sighting probability varies between sampling periods , but all animals within a sample period have the same sighting probability (M_t),
ii) behavioural responses, where animals become either 'trap shy' or 'trap happy' after their first capture (M_b),
iii) individual heterogeneity, where individuals differ in their capture probability, possibly the result of differences in their age, sex, social status, or other inherent characteristics or by inequal access to sighting surveys (M_h).

The other 5 models are combinations the above mentioned models (M_{tb}, M_{th}, M_{bh}, M_{tbh}), plus the model M_0, where capture probability remains constant.

The computer program "Capture" includes a model of selection procedure (based on goodness of fit and discriminant function analysis) to indicate the relative fit of the 8 competing models. A score of 1.00 indicates the a high probability that the model chosen is more appropriate for the data set than any of the other models. Models with value ≥ 0.75 are considered to provide good estimators and those with values <0.75 are judged to be unsuitable, and can result in a biased estimate of population size

The assumptions of the closed population models are:

i) the population is closed
ii) all animals have the same probability of being caught in the first sample
iii) marking does not affect the catchability of an animal
iv) the second sample is a simple random sample
v) animals do not loose their marks
vi) all marks are reported on recovery

Open population estimates (Jolly-Seber full model) were obtained using the program " Popan-4" (November, 1995). This model provides estimates of population size for each sampling occasion except the first and last, and estimates of survivorship and recruitment for each sample except the first and the last two. This estimator is based on two equations: an estimate of the total number of marked animals in the population at the ith sampling occasion (M_i) and a general form of the Petersen estimate for the ith Sampling occasion: $N_i = M_i n_i / m_i$, where n_i is the number marked, m_i is the number recaptured in the ith sample. The estimate M_i is obtained by assuming that two groups of animals, those marked at the time i (s_i) and those marked up to but not including time i, the ($M_i - m_i$), will be recaptured in the same proportion subsequent to time i. Thus , if z_i of the ($M_i - m_i$) and r_i of the s_i are recaptured after time I, we have the relation:

$$\frac{z_i}{M_i - m_i} = \frac{r_i}{s_i}$$

Then, substituing in the generalised Petersen estimate the population is

$$N_i = n_i\left[1 + \frac{s_i z_i}{r_i m_i}\right]$$

The assumptions of the Jolly-Seber estimate are:

i) every animal in the population, wether marked or unmarked has the same probability of being caught in the sample, given that it is alive and in the population when the sample is taken.

ii) Every marked animal has the same probability of surviving from the ith to the (i+1)th sample and of being in the population at the time of of the (i+1)th sample, given that it is alive and in the population immediately after the ith release.

iii) Every animal caught in the ith sample has the same probability of being returned to the population.

iv) Marked animals do not loose their marks and all marks are reported on recovery.

v) All samples area instantaneous

The minimum population estimate, which is the number of marked dolphins known, was computed graphically using a curve of new individuals "discovered" on each survey for the regression models from the software "Curve Expert" (Version of December 1995). This computer programme contains several built in matematical functions and it applies them to the data entered, searching for the best fit. The data entered in these computer programme consists of cummulative number of newly sighted individuals (excludes recaptures) for each survey, and the number of days after the first survey. Then, several functions are presented and the computer uses multiple regression analysis to verify the model fit.

Each model estimated the number of photo-identified adult dolphins in the population. To correct for the total population, this estimate was then divided by the mean proportion of identified adult dolphins in the group (0.54) and subsequently by the mean proportion of marked dolphins in the group (0.69). The same proportions were used to divide the the

Population parameters were calculated following the procedure of Wells & Scott (1990), Felix (1994) and Karczmarski (1996), namely: crude birth rate, recruitment rates after six-months and one year, and minimum mortality rate.

Crude birth rates (BR) were calculated using the formula:

$$BR = \frac{b}{n}$$

where: b = number of births to known females
n = number of known individuals

Recruitment rates (REC) to age six months (REC_1) and 1 year (REC_2) were calculated as:

$$REC_1 = \frac{b_1}{n-b}$$

$$REC_2 = \frac{b_2}{n-b}$$

Where:
b_1 and b_2= number of births surviving to six months and one year, respectively
n and b are as defined above.

Minimum mortality rate (MR) was defined as:

$$MR = \frac{D}{B}$$

where:

D = number of calves dead before six months after birth in a given year and,
B = number of births to known females in that given year.

The mortality rate of adults could not be calculated because no dead carcasses of dolphins were found and the duration of the study did not allow the application of the criteria used by Wells & Scott (1990).

RESULTS

Adult bottlenose dolphins comprised 54% of groups and 69% of adults seen were photo-identified. Identified dolphins were re-sighted between one (47.2% of individuals) and 14 times (4.6% individuals) during the 35 photographic surveys, between April 1996 and December 1997 (Fig. 5.1). Of adult dolphins identified, 60 (55.5%) were identified within the first four photographic surveys (from April 1996 to July 1996). A decreasing proportion of new individuals was identified throughout the end of the study period (Fig 5.2).
The number of adult dolphins photo-identified was 108 and the total number of re-sightings of identified individuals was 356.

Population estimates

Of the closed population estimates, the best estimators provided by the computer program Capture were the Jackknife and Chao – Mh. These estimators provided estimates which were similar to those obtained from the power fit curve

$$Number\_of\_marked\_dolphins = 32.8078 \times (Number\_of\_days)^{0.1928}$$

(Table 5.1). The latter predicts that the minimum estimate of marked adults is only obtained 9 years, from the beginning of the study. The open population estimate (Jolly-Seber Full model) was the lowest (Table 5.1), suggesting the existence of many

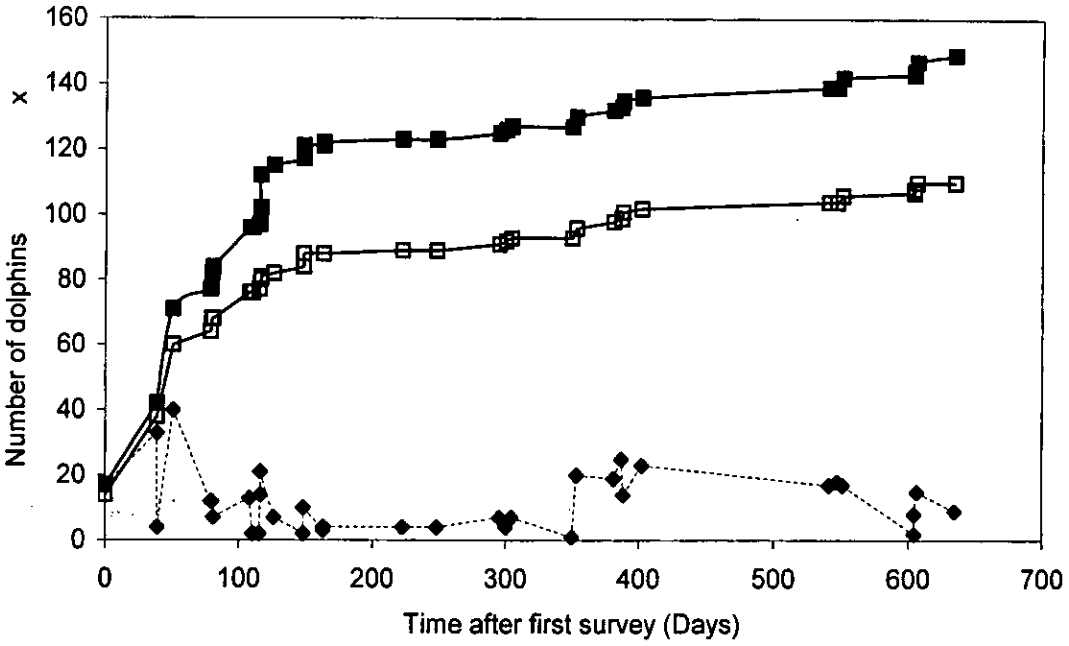


Figure 5.1 Discovery curve of bottlenose dolphins in Maputo Bay between December 1995 and December 1997; - Cumulative number of identified individuals (■ - all dolphins, □ - adults only) with time; The number of individuals newly identified and/or re-identified in each survey (◆).

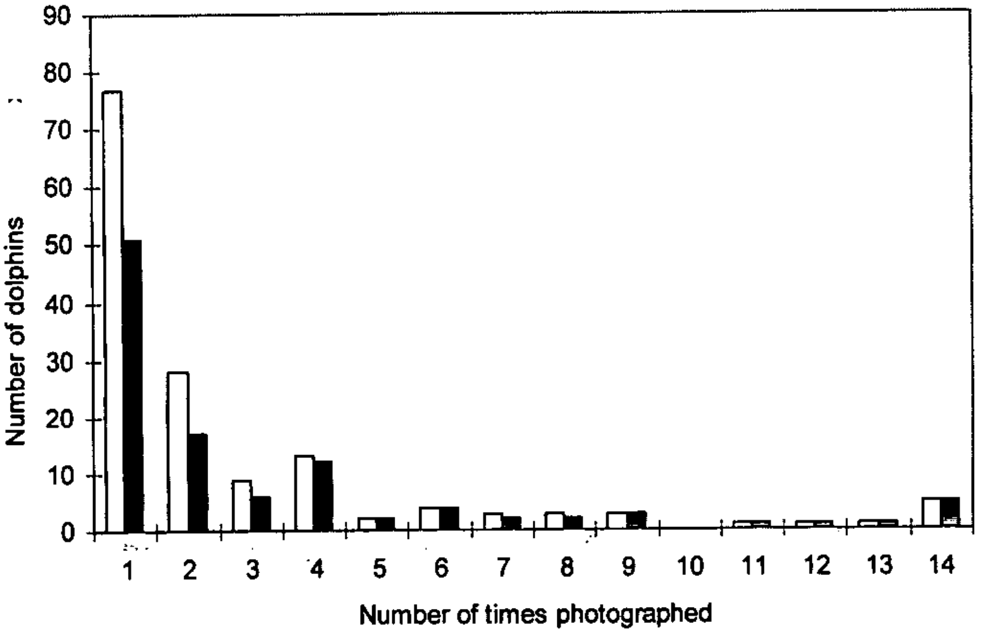


Figure 5.2. The frequency distribution of bottlenose dolphins identified and re-identified in Maputo Bay during the period between December 1995 and December 1997 (☐ - all individuals, ■ -adults only).

Table 5.1. Population estimates, both closed and open models of bottlenose dolphins in Maputo Bay, using mark-recapture data obtained between December 1995 and December 1997 (CI = Confidence Intervals).

	Estimate of photo-identified adults dolphins in the population		Mean proportion of identified dolphins in groups		Extrapolated population estimates	
Models	Estimates	Low and High 95%CI	Identified dolphins	Identified Adults	Estimates	Low and High 95% CI
CLOSED MODELS						
Jackknife	196	159 – 262	0.69	0.54	526	426.7 – 703.2
Chao-Mh	185	145 – 267			496.5	389.2 – 716.6
OPEN MODEL						
Jolly-Seber Full	63.6	16.63 – 138.57	0.69	0.54	170.8	0.0 – 371.9
Power fit	156.3	152.69 – 159.91	0.69	0.54	419.5	409.8 – 429.2

transient dolphins. The open population estimates varied between half to one third of the closed model estimates, but the confidence intervals were in some cases similar to those of the closed model estimators (Table 5.1).

The closed models estimates, after adjustment for the 69% of individuals identified, were 526 and 496 individuals for the Jackknife and Chao-Mh estimators respectively, while the Jolly Seber full model provided an estimate of 171 dolphins (Table 5.1).

Dividing the number of adults marked by the average proportion of marked individuals (0.69) a crude estimate of 157 adults was obtained for the sampling period, resulting in a population size estimate of 290 dolphins.

Reproduction and population parameters

During the study, 22 bottlenose dolphins were assumed to be females due to their consistent association with small dolphins, considered calves. Month of birth of these calves was estimated to the nearest month based on the relative size to the presumed mother and by their mode of breathing/surfacing behaviour.

Most births occurred during between January and June, that corresponds to late summer and early winter (Fig 5.3).

Seventeen births were registered during 1996 and five in 1997 (Table 5.1). Calves survived between 1 and 18 months. However, the survival of eight calves could not be followed as these calves and their mothers disappeared from the area. Of these, six mother-calf pairs disappeared before completing six months, and two disappeared later than 6 months after birth.

The number of known individuals was 88 and 56 in 1996 and 1997 respectively. This resulted in a mean crude birth rate of 0.067. Only six calves survived more than a year, resulting in a recruitment rate after one year of 0.020. There were 4 and 1 calves considered dead within a year in 1996 and 1997 respectively, resulting in a mean minimum mortality rate of 0.038 (Table 5.2).

Females showed a diverse pattern of site fidelity: seven females were among the most re-sighted dolphins (sightings varying from 7 to 14) and occurred in the area for longer periods. Another nine were re-sighted only within one or two months (less than three sightings) of their initial sighting.

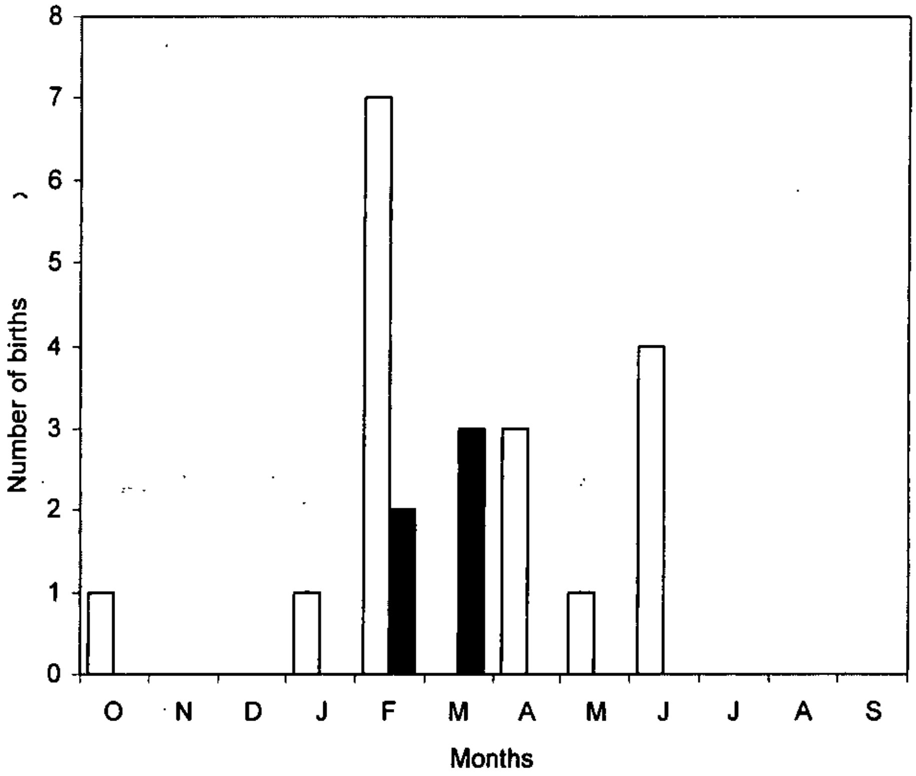


Figure 5.3. Estimated number of births and probable month of birth of bottlenose dolphins calves in Maputo Bay, based on extrapolation from calves (length & date) observed in Maputo Bay between December 1995 and December 1997 (☐ - births recorded in 1996, ■ -births recorded in 1997).

Table 5.2. Population parameters of bottlenose dolphins photographed and identified in Maputo Bay between December 1995 and December 1997 (ND = No data, SD = standard deviation).

Description of parameters		*1996*	*1997*	*Mean*	SD
Number of known individuals	N	88	56		
Number of births	B	17	5		
Number of calves surviving 6 months	B_1	9	2		
Number of calves surviving 1 year	B_2	6	-		
Number of calves surviving 18 months		2	-		
Mother-calf pairs disappearing after 6 moths		7	1		
Number of calves dead at six months	D	4	1		
Crude Birth Rate	BR*	0.193	0.107	0.067	0.042
Recruitment Rate at six months	REC_1*	0.127	0.04	0.037	0.025
Recruitment rate at 1 year	REC_2*	0.085	ND	0.020	0.013
Minimum mortality rate	MR*	0.056	0.020	0.038	0.025

- = cf text.

DISCUSSION

Population estimates were obtained from sightings of naturally marked adult dolphins which consisted of 69% of all adults and therefore only 37% of all individuals. This means that the chances of photographing naturally marked dolphins are small and will influence the actual estimates of population size. Despite their small proportion in the groups, their capture history was used to estimate the population sizes, because marks were permanent and identifiable, having low susceptibility to changes (Lockyer & Morris 1990). Even when new marks appeared on the dolphin, often old, conspicuous marks may be used to identify these dolphins. Juveniles with natural marks could have been used to increase the percentage of number of marked dolphins, but most had few and simple marks that often change, leading to miss-identification. This would bias the population size estimate (Lockyer & Morris 1990, Hammond 1990). In addition, juvenile dolphins are often associated with their mothers and therefore their sightings are not independent of their mothers (Wells 1991), and their use violate an assumption of independence of sightings (Hammond 1986).

Almost half of the individuals (47.2%) sighted in Maputo Bay were not re-sighted and few individuals (8) were resighted frequently (10-14 times). This reveals differences in site fidelity of individuals, as discussed in Chapter 3

Alternatively, the high number of apparently transient individuals could also appear from weak patterns of marking among the individuals. This would increase the number of identified individuals due to lack of recognition (Hammond 1986). Most transient individuals were sighted within a short-term period at the beginning of the surveys. Therefore it is unlikely that most dolphins could have lost their marks in such a short period of time, but, possibly some marked dolphins observed in winter 1996 were not recognized due to loss or increase of additional marks. However, a catalogue of traced fins was kept for each marked dolphin and whenever a suspected new individual was sighted for the first time, its fin was traced and compared to others present in the catalogue. This increased the recognition of previously sighted dolphins and minimized bias of the population estimates. Some dolphins that gained new marks were recognized through this method and any previously sighted dolphin would only be considered new after losing all other previous peculiar marks. The comparison of tracings of fins was found effective to reduce the possibilities of misidentification of slides (Weller 1991; Peddemors 1995).

However, the maximum number of times a dolphin was resighted was small (14 times), comprising almost half of the photographic surveys carried out for this species. This may suggest that when larger groups were observed, most dolphins could not be photographed due to the reduced probability of photographing each individual, or dolphins spent little time in the Bay, due to their high mobility and wide ranges. In fact when groups ≥ 50 dolphins occurred, possibly some dolphins were not photographed when present, either because of dilution or avoidance of the boat, as evidenced by the nursing females. However, only 19% of the groups seen consisted of ≥ 50 individuals and this cannot be the only cause for the small number of times most dolphins were re-sighted. Photo-identification of individuals occurring in groups <50 dolphins often resulted in most recognizable individuals being recorded. Alternalively, the movement of dolphins outside the Bay or in not surveyed shallow areas could also be responsible for the low number of sightings. The low number of successful sightings also supports the idea that the dolphins spend most of their time outside the study area. Nursing females, however, though they have small ranges and high site fidelity, also had low number of sightings. Possibly, the avoidance of boats by females in small groups may have also contributed to the low number of resightings. Active avoidance of boats by females, may be a strategy to escape disturbance and ensure protection of calves. Nevertheless, movements of dolphins to shallow waters increase chances of interactions with fisheries. Small groups, move into shallow areas of eastern Maputo Bay (Chapter 3). Similar movements may take place into shallow areas of the western and southern parts of Maputo Bay, where fishing activity is high (Sousa 1985;1989), There, prey resources may be low, except when immigrating pelagic schools enter during winter (Sousa 1989). However, the disturbance and entanglement may effect these dolphins (including nursing females and calves), posing risks to mortality.

In summary, high numbers of transient dolphins and low numbers of re-sightings of most dolphins may reflect movements of dolphins outside the study area, probably outside Maputo Bay, since shallow areas of inshore Maputo Bay may not support large number of dolphins. These shallow areas are subjected to intense and extensive fishing activity, which may have depleted most benthic and pelagic resources. Inshore movements may be frequent in winter when pelagic prey species abundance increases. The large number of transient dolphins may therefore reflect influx of dolphins into the study area, rather than misidentification.

Immigration rate of new individuals

The rate of discovery of bottlenose dolphins of Maputo Bay was asymptotic and attained a plateau, though few marked individuals appeared throughout the study period (Fig 5.1). The bottlenose dolphins showed an apparently high influx of new individuals during winter 1996 which coincided with the beginning of the photographic surveys, when most individuals were photographed the first time. Unfortunately, surveys were not undertaken between June and August 1997, because of unavailabily of survey vessel and if another expected winter influx occurred, it was not be detected. However, most dolphins identified during the winter of 1996 were not re-sighted during summer (October 1996 -April 1997), when groups were small (Chapter 3) and low turnover (exchange of individuals between areas) occurred. Subsequently, during March to May 1997 (beginning of winter) group size increased again. This suggests that most of those dolphins were transient, or seasonally changed their pattern of area use, frequenting Maputo Bay during winter. Nevertheless, it seems that the bottlenose dolphin population of Maputo Bay is relatively enclosed, but possibly ranges long distances due to the low prey abundance throughout the area. Some pregnant and nursing females would therefore stay in the Bay exploiting the inshore habitats to rear their calves (Chapter 3), but some also move outside the study area for unknown reasons, maybe looking at other feeding grounds. Newborn calves are not physically prepared for long distance movements, those of age < 3 months, breath with the help of their mothers and only six months after birth, they can fed on prey (Cockcroft & Ross 1990b). Only then, they can start long-range movements. Most apparently transient nursing females exhibited high site fidelity for short periods (three months with new born calves) in Maputo Bay.

Peddemors (1995) also found a small number of re-sightings among bottlenose dolphins of Kwazulu- Natal, a maximum of four re-sightings (which also represented a quarter of his surveys) over three years, despite that dolphins are known to have preferred areas along the Kwazulu- Natal coastline (Ross *et al.* 1987). Most bottlenose dolphins in Maputo Bay may either move longer distances or just spend most time outside the Bay, because the inshore habitats may not provide enough food for a large number of dolphins during long periods. These habitats may at least support a small resident group of dolphins that restrict their range/movements due to reproduction. The coast off Kwazulu- Natal lacks the combination of habitats (Peddemors 1995) such as those of Maputo Bay (Chapter 3) which may provide predictable prey availability throughout the year.

In summary, the rate of discovery of newly marked dolphins attained a plateau and showed a low turnover, suggesting the existence of an apparently enclosed population. The curve was typical of small population size. A possible influx of transient dolphins during winter 1997 may not have been detected due to lack of surveys during that period.

Population size estimates

The population estimates of bottlenose dolphins of Maputo Bay obtained from closed models and from the regression of the curve of discovery of new individuals are consistent. The discovery curve showed an apparently enclosed/limited population, but ranging outside the Bay or within unsurveyed areas of the Bay. Nevertheless large differences in site fidelity were observed between individuals (Chapter 3) and high numbers of dolphins identified in the first set of surveys were never re-sighted, suggesting an open population. It seems, therefore, that the population of bottlenose dolphins of Maputo Bay consists at least of two communities, which interact during winter. The largest community appears to live outside Maputo Bay and visits the Bay during winter, while a small community often frequents the Bay. For this reason, the open population estimate (Table 5.1) might reflect a resident population while estimates from closed models may represent the whole number of dolphins using Maputo Bay. The sampling area was very small. If extended to outside Maputo Bay and shallow areas of the Bay, possibly, the open population estimate would be different, because more individuals would be re-sighted.

Despite the consistency of the population size estimated from closed models, they were inaccurate, as 95% confidence intervals are very large (Table 5.1). The assumption of a closed population could not be met because the mark-recapture process continued over very long period and in a relarively small area (in relation to the dolphin range) increasing the chance of mortality, immigration and emigration of individuals, Another important assumption violated was that about equal capture probabilities of marked individuals. There was heterogeneity in the capture probabilities of individuals. Despite that the estimates were obtained only using adults that had consistent marking on their body, the occurrence of some individuals is not independent from others because individuals have distinct ranges (Peddemors 1995) and their social organization (Cockroft & Ross, 1990, Wells 1991). The fluid pattern of social affiliations and clustering of individuals into large groups shown in Chapter 3, supports the idea that the assumption of independence of sightings was violated (Hammond 1990), but attempts to minimise this was employed, through the use of robust estimators less sensitive to heterogeneity.

The Jackknife and the Chao-Mh estimators account for the heterogeneity in the capture probabilities of individuals (Pollock *et al.* 1990), reducing bias in the population estimates. Particularly, the Jackknife estimator is the most robust available (Pollock *et al.* 1990) and provided the largest population estimate among the closed models. Nevertheless, an over estimate of the dolphin population because it covered a long period , allowing for interchanging of individuals. This biased the population estimate upwards

The Jolly-Seber model allowed for immigration and emigration, but it is sensitive to heterogeneity (Pollock *et al.* 1990; Hammond 1990). The high level of apparently transient individuals explains partially the low population estimates of bottlenose dolphins. Nevertheless, as Hammond (1990) points out "there is no suitable estimator of population size from open population models when capture probabilities are allowed to vary from heterogeneity".

Heterogeneity in the capture probabilities are common among populations stratified by age or by sex, and this problem can only be overcame by producing separate estimates for the different categories (Eberhardt *et al.* 1979 and Pollock *et al.* 1990). However, in Maputo Bay, the age/sex categories of the majority of individuals are unknown, though this social organisation could be dependent on age/sex categories distribution (Chapter 3). Such lack of data precluded the use of such a strategy to reduce heterogeneity. The use of only identified adults to estimate population size was an attempt to reduce the heterogeneity, but most adult individuals had very low capture probabilities and, this allied to the heterogeneity, could have contributed to the imprecision (Arnason *et al.* 1995).

Hammond (1990) suggested a combination of site specificity and increasing coverage of the area to reduce heterogeneity. In the current study, the sampling effort and site specificity of the study were restricted in relation with dolphins range, and therefore they contributed to the heterogeneity and upward bias in the closed population estimates, because temporary/transient individuals were included in the computing of estimates. Logistic reasons did not allow a continuous and regular sampling effort throughout the year, but there was an intense coverage of the eastern Maputo Bay, compared to other areas of the Bay. Almost all successful photographic surveys occurred in the eastern part of Maputo Bay along the western coast of Inhaca Island. However, while some factors that could lead to heterogeneity were reduced, the precise amount of negative bias cannot be estimated. The suggestion by Hammond (1990) of computing distinct population estimates for individuals with different capture probabilities could be considered, but these samples would be diverse and very small, because of the high variability of the capture history of these dolphins. Conversely, long term photo-identification, intensive sampling effort and an increased area coverage are the best approaches because the progressive reduction of heterogeneity is obtained as more animals become available to be sampled (Hammond 1990).

Consequently, based on the aspects mentioned above, the population estimates obtained from the open and closed models are biased in distinct directions (positively biased for closed population estimates, and negatively biased for open population estimates), however, both represent the range within which this population estimate lies 170-526 dolphins. The ideal estimates should also be obtained considering the populations' spatial range/distribution. The crude population estimates of 290 dolphins fall within these estimates and seem to be more conservative. The eastern Maputo Bay covers a surface of 219.5 km^2. Consequently, the mean density estimate is 1.82 (SD=0.73) individuals/km^2. This density estimate is high given that most dolphins ranged outside the Bay and have low sighting frequency. This maximum density could be applicable for winter, rather than summer when most individuals were outside the study area or outside the Bay.

The estimated density of bottlenose dolphins in the eastern Maputo Bay was smaller than those estimated at the Kwazulu- Natal north coast and Eastern Cape, South Africa during 1985, but higher than those from the Kwazulu- Natal south coast (Ross *et al.* 1989). Mortality in the shark nets accounted for the low densities at Kwazulu- Natal south coast (Ross *et al.* 1989). However, because estimates from the Kwazulu- Natal coast were obtained through aerial surveys which may underestimate the population compared with mark-recapture techniques, because it may have missed submerged dolphins (Ross *et al.* 1989), it is highly likely that the density estimates from the

Kwazulu- Natal coast are much higher than those of Maputo Bay. The low density of dolphins in Maputo Bay in relation to the Kwazulu- Natal coast could also be caused by interaction from fisheries. Dolphins in Maputo Bay restricted their distribution to the north-eastern part (Chapter 3) possibly avoiding either the high turbidity of most shallow waters of the Bay or the interaction from fishing operations that also exploit the turbid shallow areas (Sousa 1985). Bottlenose dolphins off the Kwazulu- Natal and Transkei coasts also avoided turbid waters (Ross *et al.* 1987, Durham 1994). The precise cause of avoidance of turbid waters is unknown though it is suspected that both avoidance of predators (Cockcroft *et al.* 1989a) and the influence of suspended particles in the detection and recognition of prey are the main reasons (Peddemors 1995). The low density of dolphins could also be caused by the existence of large areas in Maputo Bay and northward outside the Bay, with depths <30 m. This would result in the dispersion of groups and therefore reduce their sighting frequency and density.

Interactions from fisheries could lead to reduction of density if dolphins are actually caught. However, bottlenose dolphins do not seem to be captured in the Bay, or the catches are very low. This means that the main effect of the fisheries could be the depletion of prey/or disturbance by sounds from engines, reducing their habitat. However, since Maputo Bay has an estuarine nature (Kalk 1995) and the dolphin preferred prey in the Bay are unknown, it is difficult to advance hypotheses about the precise influence of the fisheries in Maputo Bay. Off the Kwazulu- Natal coast, bottlenose dolphins feed on pelagic and reef fish (Cockcroft & Ross 1990). However, the bottlenose dolphin is known to be opportunistic in prey selection throughout its range (Cockcroft & Ross 1990a, Barros & Odell 1990; Barros & Wells 1990). Dolphins inhabiting areas outside Maputo Bay comprised the major portion of the population and consequently their diet would mostly consist of pelagic and reef associated prey species, because reefs, rocky outcrops and the open ocean are the only habitats available nearby outside the Bay. The high sighting frequency during winter could be associated with the changes in prey species composition, which favour non-estuarine species (Chapter 3, Sousa 1989).

In summary, though the impact of fisheries is unknown, it is also likely that the low density of dolphins in Maputo Bay may be caused by the existence of a large shallow areas (<30 m deep) inside and north of the Bay. If these areas have low prey abundance, then schools of dolphins may disperse and range over the areas to get food resources. At the open sea, north of Maputo Bay, where there is a narrow strip of depths < 30 m, dolphins may range long shore distances to exploit all small food resources available, the size of which are unknown for this area. The bottlenose dolphins of Maputo Bay appear to have most of their range outside the Bay, where they may spend most of their time, because they were observed in only 30% of the surveys (Chapter 3). However, because of lacking information on their offshore distribution and movements between the Bay and outside, a study of these topics would clarify the importance for dolphins of Maputo Bay relative to other areas and would help evaluate the density estimates from Maputo Bay.

Density estimates from other studies like Hersh *et al.* (1990) at the Indian/Banana river system in Florida were 0.27-0.54 dolphins per km^2, Felix (1994) at the Gulf of Guayaquil found 0.89 dolphins per km^2, Lynn (1995) off Central Texas 0.70 dolphins per km^2, all smaller numbers than those observed for bottlenose dolphins in Maputo Bay. A large population frequents the Maputo Bay and includes includes dolphins of the neighbouring areas. At times, such as in winter, Maputo Bay may be the most important habitat (feeding and shelter). This is possible, because Maputo Bay has both extensive shallow areas and rich habitats that appear to be favorable habitats for this species. The existence of the uppwelling outside Maputo Bay and a large estuarine system in the Bay may increase the importance of the whole region as a dolphin habitat and therefore support a large population with low site fidelity.

However, the decrease in catches from the fisheries in the Bay (Massinga & Hatton 1996) and the reduction observed in number of gill net fishing boats (Premegi 1995, Tomás 1996) suggest an extensive resource depletion in western and southern Maputo Bay. Therefore, the resident population of Maputo Bay (171 dolphins estimated from open population models) may face difficulties in fullfilling their foraging needs and extend their range outside the Bay more frequently to complement their energy requirements.

It seems that the small study area coinciding with the preferred area of the dolphins, contributed to the high density estimate figure for the eastern Maputo Bay. If the whole area of Maputo Bay is used to calculate dolphin density, then this would be smaller than densities estimated in the studies cited above. Therefore, it appears that the estimated population size and density are biased upwards. Reduction of heterogeneity and increased size of the study area would reduce these biases. Nevetheless, the current estimates of dolphin numbers are consistent with the environmental status of the Bay, in which most benthic resources in fishing areas are depleted (Massinga & Hatton 1997,Chuquela 1996, De Boer 2000). The Bay may not have the capacity to support the simultaneous requirements of the fisheries and of the high number of dolphins. In addition, the disturbance caused by motorised boats (noise) may also interfere with the foraging ability of bottlenose dolphins (Barros 1993, Lusseau 2006, Gannon *et al.* 2005).

Reproduction

22 photo-identified dolphins were identified as females, because they were often photographed with young dolphins, considered calves. But a small number of unmarked female dolphins also occurred. The latter were not included in the analysis of reproduction to avoid counting them several times. Dates of births were only estimated for the calves born to identifiable females. The data shows that 17 births were recorded for 1996 and only 5 births in 1997, possibly due to the differences in the distribution of surveys or possibly a decrease in reproduction or detection of calves. Some female-calf pairs were apparently transient and if some nursing females visited the Bay during the period June-August 1997, when surveys were not carried out, they could have been missed. At Sarasota Bay, Florida (Wells 1992) and Gulf of Guayaquil (Felix 1994), the number of births of bottlenose dolphins fluctuated sharply between years, and was caused by stochastic factors. It is possible that in Maputo Bay the difference in the number of births could be stochastic, although unlikely. In Maputo Bay, environmental factors did not seem to vary drastically between these two years. Therefore, the differences in the number of births between the years may be caused by differences in distribution of sampling effort.

Bottlenose dolphins showed a prolonged reproductive season during the study, as most new-born calves were born between February and June, suggesting a seasonal calving season. However, most calves were recorded during winter, when SPUE and group sizes were high, suggesting that Maputo Bay could possibly be either be a nursing or breeding area for dolphins. But as mentioned before, some mother-calf pairs were transient and this implies that Maputo Bay is mainly a feeding ground rather than a breeding ground. It is possible that the age of some calves could be incorrectly estimated, as they were back calculated based on their relative size and, if applicable, on the last sighting of the female before having an offspring. Therefore, this could have led to some inaccuracy in age determination, suggesting an extended breeding period into summer. However, off the Kwazulu- Natal coast, about 600 km south of Maputo Bay, bottlenose dolphins showed a peak of births during summer though mating and births were seasonally diffuse (Cockcroft & Ross 1990c). Subsequent studies of reproduction on stranded and captured dolphins in the shark nets off the east coasts of Kwazulu- Natal and Eastern Cape showed that spermatogenesis is not seasonal and therefore, males may mate throughout the year (Reddy 1996, van der Mescht 1996).

Non-seasonal reproduction has been referred as a feature common to tropical and sub-tropical areas, as it was observed in the Gulf of Guayaquil, Equador (Felix 1994). In tropical areas, water temperature and possibly food availability, do not suffer large seasonal changes, favouring reproduction at any time of the year.

On the other hand, seasonal peaks of reproduction in temperate areas like those referred to by Wells (1992) and Lynn (1995), seem to be caused by the long term adaptation of dolphins to seasonal changes in food availability. Females adjust to environmental conditions and reproduction occurs during a particular period in order to guarantee the successful rearing of calves and to satisfy their energy requirements (Wells 1992). Additionally, births are seasonal and timed in the way that the calves are weaned when prey abundance peaks (Peddemors 1995, Wells 1992, Cockcroft & Ross 1990c). This does not seem necessary in tropical areas. African antelopes behave like dolphins from temperate climates, as they exhibit peaks of breeding reflecting a synchronization to the rainfall peak, that governs food availability and the quality of vegetation, which is the source of food (Goslin 1986). Dolphins from tropical areas do not exhibit such synchronisation, because they can move between productive areas or stay in areas were the combination of heterogeneous habitats allows year round sources of food (Wells 1991, Weller 1991 and Felix 1994).

The seasonal changes in the group size and SPUE, the large number of identified dolphins re-sighted infrequently (Chapter 3) support the idea of dolphins moving between productive areas. Long-shore shifts in distribution of identified bottlenose dolphins were observed along the coast of Kwazulu-Natal where they take the advantage of seasonal increase in food during winter to wean their calves and breed, as social behaviour was reported to increase from winter to spring (Peddemors 1995). Bottlenose dolphins have one-year gestation period (Cockcroft & Ross 1990c). In Maputo Bay, the influx of individuals during winter would result in more births as well as social behaviour being recorded during this season, despite lack of significant differences with summer (Chapter 7). However, if estimated dates of births recorded in Maputo Bay are correct, then any peak observed during winter would be caused by the arrival of transient individuals that inflate groups, including some pregnant/nursing females. As breeding occurred throughout the year, then the increase of group size will imply increased mating opportunities and therefore increased chances of recording more births during that season. Despite the winter increases of group sizes off the Kwazulu-Natal coast, South Africa more births were recorded during summer (Cockcroft & Ross 1990c) because most dolphins belonged to the offshore stock, which is genetically isolated from the inshore one (Goodwin 1997). The winter increases of group size in Maputo Bay could help extending the breeding into winter months.

The small number of births recorded and the short study period may mask the real reproductive pattern, which may have been influenced by the temporal distribution of the sampling effort. In 1997 there was much effort during summer compared to the winter. Most calves were reported from May to August 1996, which coincided with the winter. However, the findings of Reddy (1996) on the lack of reproductive seasonality in bottlenose dolphins from Kwazulu-Natal and Eastern Cape (van der Mescht 1996) suggest that reproduction is aseasonal, contradicting the findings from. Cockcroft &

Ross (1990c). However, in all cases the sample sizes were not large enough to draw consistent conclusions. Possibly calves born in summer had higher survival rates than those born in winter.

In summary, bottlenose dolphins had a prolonged reproductive season and the high number of calves recorded during the transition between summer and winter is caused by an influx of large numbers of dolphins. Annual variability in the number of births recorded could be caused by unequal distribution of sampling effort. The disappearance of some female-calf pairs from the area needs to be explained. It is not known if they are transient females, which moved to other productive areas, or if the calves just died and consequently they resumed their transient life. Nothing can be predicted for the survival of these eight calves. The reasons for calf mortality are unknown, and may vary: predation, diseases or entanglement in shallow areas of the Bay.

Population parameters

Crude birth rate

The crude birth rate for bottlenose dolphins was obtained from a small sample and a short-term study period (24 months) and should be viewed with caution. Wells (1992) suggests that most new born calves died prior to recording, and in this study, these deaths were not recorded, therefore underestimating the crude birth rate.

The crude birth rate of bottlenose dolphins in Maputo Bay (0.067 (S.D. = 0.042) is consistent with ,but larger than the range of 0.043 and 0.065 estimated for bottlenose dolphins off Kwazulu- Natal by Cockcroft & Ross (1990c). This apparently high crude birth rate reported for Maputo Bay might also be influenced by the occurrence of the apparently transient female-calf pairs. Eight mother-calf pairs were only sighted within periods of one or two months of the first sighting and never re-sighted afterwards. Maputo Bay may, therefore, represent a calving ground for female bottlenose dolphins from the surrounding open coastline, because it may offer relatively more safety against predation, or relatively increased prey availability to respond to the high-energy requirements of nursing females (Cockcroft & Ross 1990a). The bottlenose dolphins often used two main areas in eastern Maputo Bay: the pass to the Ocean and the inshore reef associated with seagrass areas (Chapter 3). The latter consists of habitats that may provide a less variable food supply throughout the year, despite seasonal changes of prey composition (Kalk 1995; De Boer 2000). Therefore, nursing females might get the necessary amount of food for lactation and would then restrict their ranges, reducing the exposure of the young calves to threats/risks. Most bottlenose dolphins sighted in the inshore reef in eastern Maputo Bay consisted of pairs or trios that included a calf. In addition, a large proportion of apparently transient mother-calf pairs occurred for short periods in Maputo Bay. Consequently, this place may be used briefly during the initial months after birth to nurse young calves. Nursing females may move to the pass to the Ocean to feed along with large schools of dolphins visiting the area. This is possible because the nursing female and its calf gain extra protection and enhance feeding efficiency on schooling prey when in large schools (Würsig 1986) due to low time spent caring for calf (Connor 2000). In this way, the nursing female may take advantage of co-operative feeding to maximise feeding efficiency and obtain prey species of other quality, before the large schools of dolphins leave the area.

The crude birth rate of bottlenose dolphins from Maputo Bay is 22-24% higher than the crude birth rate (mean 0.055) reported for bottlenose dolphins from Sarasota Bay

(Wells & Scott 1990) and at the Argentinean coast (0.054), (Würsig 1978). Felix (1994) reported a lower birth rate (0.028) at Gulf of Guayaquil and attributed this to a sampling artefact, which might cause such lower birth rate over a very large area. In addition, if reproduction occurs throughout the whole year, the chances to observe new-born calves are low on large dolphin communities and consequently some offspring could die before being recorded. Low number of births and consequently of the crude birth rate reported off Gulf of Guayaquil, Equador (Felix 1994) could reflect the existence of a large population of dolphins, close to or at its carrying capacity. In equilibrium populations, the age of first parturition and the interval between births also increases and this will result in low numbers of cycling females and consequently lower the number of births (Horwood & Millward 1987). The geographic differences of the crude birth rates presented here could reflect several factors acting on the populations, such as the degree of exploitation/mortality that the population suffers, fluctuations in food availability and stages of growth of the populations. Crude birth rate fluctuated sharply between years at Sarasota Bay and actual estimates are often obtained over a period of many years, to reflect the population trends (Wells & Scott 1990).

In Sarasota Bay bottlenose dolphins had an unusual high number of births during some years, which were then followed by high mortality rates of young of the year (referred as calves in this chapter). The status of the bottlenose dolphin population of Maputo Bay is unknown, but dolphins are reported to interact with the fisheries, though there is no evidence that it resulted on dolphin mortality (Guissamulo & Cockcroft 1997). The level of predation affecting these dolphins is also unknown, but outside Maputo Bay, sharks are apparently abundant according to reports of most divers at Baixo Danae reef (about 10 km north of Inhaca Island) and at reefs located at Ponta do Ouro (about 100 km south of Maputo Bay). The relationship between the populations of Maputo Bay and those of Kwazulu- Natal are also unknown, despite that most dolphins were transient in Maputo Bay and some dolphins off the Kwazulu- Natal coast move longer distances (Peddemors 1995) implying that there is a possibility of mixing. Therefore, the high crude birth rate estimated for the population of bottlenose dolphins in Maputo Bay in relation to the bottlenose dolphin population off Kwazulu- Natal is either caused by the use of Maputo Bay as breeding/nursing ground by dolphins, or results from bias caused by the seasonal changes in the habitat use of dolphins which result in the observation of high number of calves. Some mother-calf pairs were not always present in the study area, they might have moved into the shallow fishing areas, being susceptible to mortality in fishing nets, though evidence is lacking. Increased birth rate can also be sign of an over-exploited or disturbed population, which reacts to the decreased density, or just sign of intense calf mortality, which forces females to have short intervals between births. However, this needs further verification. At the moment it is likely that the highest birth rate is linked with seasonal influx of transients into the area.

Recruitment rate and calf survival rate

The recruitment rates at six months after birth are very low (Table 5.3) because most calves born in Maputo Bay left with their mothers before completing six months. It seems therefore, that the recruitment rate was underestimated and may represent that of the resident community or, at least, those with high site fidelity. In addition, the temporal different distribution of effort may also have affected this estimate because, the absence of searches between June-August 1997 may have contributed to the lack of some of the transient mother-calf pairs seen. The recruitment rate may therefore be negatively biased.

The recruitment rates at six months and one year observed in Maputo Bay were low when compared to those found by Wells & Scott (1990) at Sarasota Bay for bottlenose dolphins. Calculated recruitment using the data from Felix (1994) at six month of age provided a value of 0.015 consistent with that for bottlenose dolphins of Maputo Bay (0.020). Mammals often have density dependent growth rates that result from regulation of births or mortality (Begon *et al.* 1996). The survival of young is very sensitive as they are vulnerable to predation, hunger and diseases. Thus, females invest more energy on their survival (Krebs & Davies 1993). While several factors could account for the differences between the studies of Sarasota and Maputo Bays, the short-term nature of the present study (24 months) compared to the 6 years at Sarasota may account strongly for the differences observed. The population of Sarasota Bay was closed and numbers were constant throughout the time, through removal of some adult dolphins (Wells & Scott 1990), predation pressure was low and the mortality of calves was natural. The population of Maputo Bay, instead, appeared to be open, with transient individuals, though turnover was low according to the discovery curve, and some female-calf pairs were never re-sighted. Transient pattern of most dolphins may reflect the low prey availability in the Bay, and here the role of the fisheries into resource depletion may be important.

All births observed were used to compute the estimated recruitment rates. Therefore, though mortality could have occurred, the loss of calves, through long-term absence from the study area accounted for the low recruitment rate found in Maputo Bay. The bottlenose dolphins of Maputo Bay consisted of at least two communities, one resident and another from outside the Bay. The ranges of the latter are unknown, but the number of births, and consequently the crude birth rate, may be a feature of both populations, but the recruitment rate seems to characterise the resident community. The extension of the study outside Maputo Bay would help identify the neighbouring communities and therefore separate estimates of recruitment could be determined. It could also help determine the fate of mother calf pairs (if they left the Bay or were killed in the fisheries).

The calf mortality rates observed for bottlenose dolphins (0.038) in Maputo Bay could be underestimated due to the following reasons: death of some new-born calves prior to the first observation (Wells 1992) and the uncertainty about the survival of the mother-calf pairs that abandoned the area. Consequently, it is likely that the maximum calf survival rates of 0.962 could be an over estimate. Wells & Scott (1990) report a maximum mortality rate of 0.038 for a seven year period in Sarasota Bay, which is an environment protected from predation, where dolphins have very restricted emigration and immigration rates. Despite the consistency between the results of Maputo Bay and those of Sarasota Bay, Florida, the dolphins of Maputo Bay inhabited also unprotected habitats outside Maputo Bay were they may be exposed to high risk of predation. Off the Kwazulu-Natal coast, 2.2 % of the estimated population of bottlenose dolphins are killed by sharks and young dolphins are more vulnerable (Cockcroft *et al.* 1989a). Shark species predating on dolphins off Kwazulu- Natal, were Zambezi (*Carcharhinus leucas*), Tiger (*Gaelocerdo cuvieri*), Great white shark (*Carcharodon carcharias*) and Dusky (*Carcharhinus obscurus*). All shark species, except the Great white also occur in Mozambique water (Fisher *et al.* 1990) and the Tiger and Zambezi sharks have been caught in a small shark fishery at Portuguese Island, Maputo Bay (pers. obs.) Only two nursing female and one juvenile/sub-adult dolphin had marks caused shark bites among the identified individuals of Maputo Bay throughout the duration of the study (24 months). Therefore, predation may be a source of calf mortality, but the amount of mortality is unknown in Maputo Bay. But if mother-calf pairs moved inshore into the shallow water fishing areas, they could also suffer mortality or disturbance from fisheries.

The present study did not allow for the estimation of non-calf survival rates because dead adults were not observed though they may have occurred. Considering that adults are not taken by fisheries and die by natural causes, the method of Reilly & Barlow (1986) for non-calf survival can be applied to these populations. There is little knowledge about reproductive parameters of bottlenose dolphins of Maputo Bay. However, off the East Coast of South Africa, the age of first parturition of female bottlenose dolphins varied between 9.5 and 11 years (Cockcroft & Ross 1990c). Despite the lack of knowledge of the genetic relationship of the populations of the Coast of Kwazulu-Natal and those of Maputo Bay, some bottlenose dolphins of Kwazulu-Natal were reported to move longer distances and have somewhat overlapping ranges (Peddemors 1995). Having this in mind, it can be assumed that age of first parturition of female bottlenose dolphins of Maputo Bay may be similar to that of Kwazulu-Natal.

The study could not determine the calving interval because the study period was short but calves were seen with their mother during 18 months in Maputo Bay. Off the Kwazulu-Natal coast, female bottlenose dolphins have one-year pregnancy duration and calves are born every three years (Cockcroft & Ross 1990c). Reilly & Barlow (1986) have found that the age and calving intervals vary regionally and appears to change according to the degree of exploitation of the wild populations.

In the absence of reliable estimates, calf survival can be assumed to equal the a square of adult survival of terrestrial mammals (Reilly & Barlow 1986). The non-calf survival can then be taken from the square root of calf survival. Therefore the value of 0.98 is obtained and it is known that it is biased since it arises from an earlier biased estimate. This value is considered unlikely, as it produces an unacceptable age structure for cetaceans (Reilly & Barlow 1986) and therefore maximum of non-calf survival rate of 0.96 proposed by Reilly & Barlow (1986) will be used. These authors produced tables of populations growth rates, based on rates of increase (ROI) of populations using the age of first parturition, the calving interval, the non-calf survival and the calf survival. Combining the data of bottlenose dolphins of Maputo Bay and parameters known for bottlenose dolphin population of the Kwazulu- Natal coast, the estimated population growth rate in Maputo Bay will vary between 4 and 5% (Reilly & Barlow, 1986). Such population growth level reflects populations that are under their carrying capacity and actively growing. In mammals, growth rates of 6-7% are considered typical of depleted populations (de la Mare 1994), and are assumed to result from hyper-compensation. The status of this population is unknown, but as an open water species, such high growth rate may have been adjusted to the occurrence of several feeding areas along the coast of southern Mozambique and to respond to relatively high levels of predation. Certainly, this growth rate is an overestimate and should be viewed with caution because it was obtained from a short term study and several parameters of this population are assumed, because they are unknown. There is no reason to believe that dolphins of Maputo Bay are growing at such high rate, despite that their density is low and considering that fisheries also take a large amount of possible prey and disturb dolphins. The restricted distribution of dolphins within the Bay suggests that fisheries are disturbing the population, but the lack of consistent data on reproductive parameters (age of first parturition and calving interval) do not provide evidence for that. Monitoring population trends, extending the study to other areas of the dolphin range could contribute to examine the impact of the habitat degradation on dolphin population. The study of dolphin diet in the Bay is also necessary to determine the level of competition with the fisheries.

CHAPTER 6. POPULATION SIZE AND DYNAMICS OF HUMPBACK DOLPHINS IN MAPUTO BAY

INTRODUCTION

Population estimates of humpback dolphins are available from the east coast of South Africa: at Algoa Bay there are 200- 400 dolphins (Karczmarski *et al.* 1999b) and approximately 160 individuals off the Kwazulu-Natal coast (Durham, 1994), 63-65 dolphins in the South coast of Zanzibar (Stensland *et al.* 2006). In the Eastern Taiwan Strait the population estimate is 99 dolphins (Wang *et al.* 2007). In Moreton Bay, the population of humpback dolphins estimated between 1984 and 1987 declined from 163 to 119 dolphins (Parra *et al.* 2004). The population of Kwazulu-Natal was experiencing mortality rate of 4% at the shark nets which is almost close to their natural growth rate (Cockcroft 1990).Similarly, in Zanzibar, the by catch rate of humpback dolphins in gill net fisheries is very high (Amir *et al.* 2002) and exceeds their natural growth rate (Stensland *et al.* 2006) In Maputo Bay, the earlier estimate was 67 dolphins (Guissamulo 1993, Guissamulo & Cockcroft 1998), that was probably biased downwards because it did was derived from a small sample size and not incorporate inter-annual variations. The population of humpback dolphins is small in the region and, in view of the mortality caused by the shark nets off the Kwazulu- Natal coast (Cockcroft 1990) and fishing operations in Maputo Bay, including the intentional catches (Guissamulo & Cockcroft 1998), and considering that the distribution is restricted to shallow areas, mangroves, estuaries or reefs, exploited by humans in various forms. The knowledge of population size and its growth rate is very important for conservation. This chapter therefore reviews the previous dolphin estimate for Maputo Bay and examines the birth rate, the mortality and survival of calves, discussing the implication of these findings on the population dynamics of humpback dolphins. It also compares the number of individuals and the relative densities and reproductive parameters in Maputo Bay with those from the region: the Kwazulu- Natal coast and Algoa Bay.

METHODS

Survey methodology, identification and calculation of population parameters were identical to those used for studies of the bottlenose dolphins (see Chapter 5). Individual identification of dolphins through photographs was carried out in two occasions January to May 1992 and from December 1995 to December 1997. The survey procedure is described in Chapter 2. Group sizes were estimated from direct counts of all individuals. Composition of groups (adults, juveniles and calves (based on relative sizes to adults)) was determined and the apparent age of calves estimated. Calf age was estimated from several features, including the first time an adult was sighted with a calf, calf size, the shape of dorsal fin, pattern of breathing and the positioning on the central side of an adult dolphin.

A newborn calf (up to two weeks old) had one third of the adult size, with the dorsal fin bent and when surfacing it was breaking the water surface with the rostrum and the head simultaneously and remained closely linked to one of the mother's flanks.

A mark recapture method was used to estimate population size and life parameters of dolphin following Hammond (1986). Photographs of dorsal fins of dolphins were taken during the boat surveys carried out in Maputo Bay, using Minolta X-700 and Canon

EOS cameras equipped with lens of focal distance varying between 80-300 mm and diapositive films. These photographs were first selected initially based on clarity, focus and parallax. Only photographs of dorsal fins that had good quality were then used for photo-identification. Photographs of dorsal fins that had identifiable marks (nicks), on the profile of the dorsal fin were labelled and catalogued. Photographs of dolphin dorsal fins identified in each survey were labelled separately. If photographed in a subsequent survey, then they were considered a re-sighting (or recapture). Detailed description of the selection procedure of photographs is presented in the Chapter 2. For each dolphin identified a sighting (capture) history was produced.

The use of mark-recapture methods for population estimates is based on the argument that the proportion of marked animals recaptured in a sample of the population is equivalent to the proportion of marked animals in the total population (Hammond, 1986).

$$\frac{m_2}{n_2} = \frac{n_1}{N}$$

m_2 is the number of marked individuals present in the second sample
n_2 of the total population N and
n_1 is the number of marked animals in the population.

The multiple recapture approach, known as the Schnabel estimator (Hammond 1986) was used because naturally marked individuals were being captured and recaptured during the sampling occasions.

Estimates of size of dolphin populations were obtained using several computer programs. The program "Capture" (May 1994) was used to estimate closed populations. This computer program contains 8 models for estimation of population size . The models incorporate three sources of variation in sighting probabilities:

iv) a time response which considers that sighting probability varies between sampling periods , but all animals within a sample period have the same sighting probability (M_t),
v) behavioural responses, where animals become either 'trap shy' or 'trap happy' after their first capture (M_b),
vi) individual heterogeneity, where individuals differ in their capture probability, possibly the result of differences in their age, sex, social status, or other inherent characteristics or by inequal access to sighting surveys (M_h).

The other 5 models are combinations the above mentioned models (M_{tb}, M_{th}, M_{bh}, M_{tbh}), plus the model M_0, where capture probability remains constant.

The computer program "Capture" includes a model of selection procedure (based on goodness of fit and discriminant function analysis) to indicate the relative fit of the 8 competing models. A score of 1.00 indicates the a high probability that the model chosen is more appropriate for the data set than any of the other models. Models with value ≥ 0.75 are considered to provide good estimators and those with values <0.75 are judged to be unsuitable, and can result in a biased estimate of population size

The assumptions of the closed population models are:

vii) the population is closed
viii) all animals have the same probability of being caught in the first sample

ix) marking does not affect the catchability of an animal
x) the second sample is a simple random sample
xi) animals do not loose their marks
xii) all marks are reported on recovery

Open population estimates (Jolly-Seber full model) were obtained using the program " Popan-4" (November, 1995). This model provides estimates of population size for each sampling occasion except the first and last, and estimates of survivorship and recruitment for each sample except the first and the last two. This estimator is based on two equations: an estimate of the total number of marked animals in the population at the ith sampling occasion (M_i) and a general form of the Petersen estimate for the ith Sampling occasion: $N_i = M_i n_i / m_i$, where n_i is the number marked, m_i is the number recaptured in the ith sample. The estimate M_i is obtained by assuming that two groups of animals, those marked at the time i (s_i) and those marked up to but not including time i, the ($M_i - m_i$), will be recaptured in the same proportion subsequent to time i. Thus , if z_i of the ($M_i - m_i$) and r_i of the s_i are recaptured after time I, we have the relation:

$$\frac{z_i}{M_i - m_i} = \frac{r_i}{s_i}$$

Then, substituing in the generalised Petersen estimate the population is

$$N_i = n_i\left[1 + \frac{s_i z_i}{r_i m_i}\right]$$

The assumptions of the Jolly-Seber estimate are:

vi) every animal in the population, wether marked or unmarked has the same probability of being caught in the sample, given that it is alive and in the population when the sample is taken.
vii) Every marked animal has the same probability of surviving from the ith to the (i+1)th sample and of being in the population at the time of of the (i+1)th sample, given that it is alive and in the population immediately after the ith release.
viii) Every animal caught in the ith sample has the same probability of being returned to the population.
ix) Marked animals do not loose their marks and all marks are reported on recovery.
x) All samples area instantaneous

The minimum population estimate, which is the number of marked dolphins known, was computed graphically using a curve of new individuals "discovered" on each survey for the regression models from the software "Curve Expert" (Version of December 1995). This computer programme contains several built in matematical functions and it applies them to the data entered, searching for the best fit. The data entered in these computer programme consists of cumulative number of newly sighted individuals (excludes recaptures) for each survey, and the number of days after the first survey. Then, several functions are presented and the computer uses multiple regression analysis to verify the model fit.

Each model estimated the number of photo-identified adult dolphins in the population. To correct for the total population, this estimate was then divided by the mean proportion of identified adult dolphins in the group (0.50) and subsequently by the mean proportion of marked dolphins in the group (0.54).

Population parameters were calculated following the procedure of Wells & Scott (1990), Felix (1994) and Karczmarski (1996), namely: crude birth rate, recruitment rates after six-months and one year, and minimum mortality rate.

Crude birth rates (BR) were calculated using the formula:

$$BR = \frac{b}{n}$$

where: b = number of births to known females
n = number of known individuals

Recruitment rates (REC) to age six months (REC_1) and 1 year (REC_2) were calculated as:

$$REC_1 = \frac{b_1}{n-b}$$

$$REC_2 = \frac{b_2}{n-b}$$

Where:
b_1 and b_2= number of births surviving to six months and one year, respectively
n and b are as defined above.

Minimum mortality rate (MR) was defined as:

$$MR = \frac{D}{B}$$

where:

D = number of calves dead before six months after birth in a given year and,
B = number of births to known females in that given year.

The mortality rate of adults could not be calculated because no dead carcasses of dolphins were found and the duration of the study did not allow the application of the criteria used by Wells & Scott (1990).

RESULTS

On average, adult humpback dolphins comprised 50% of the group and 54% of the adults were identified. There were 34 photographic surveys, and the number of repeated sightings of any individual ranged from one (14 individuals) to 26 (1 individual), (Fig 6.1). Newly marked dolphins appeared in small numbers, varying from 2 to eight dolphins per survey, but the first 24 dolphins (64.8%) were identified during

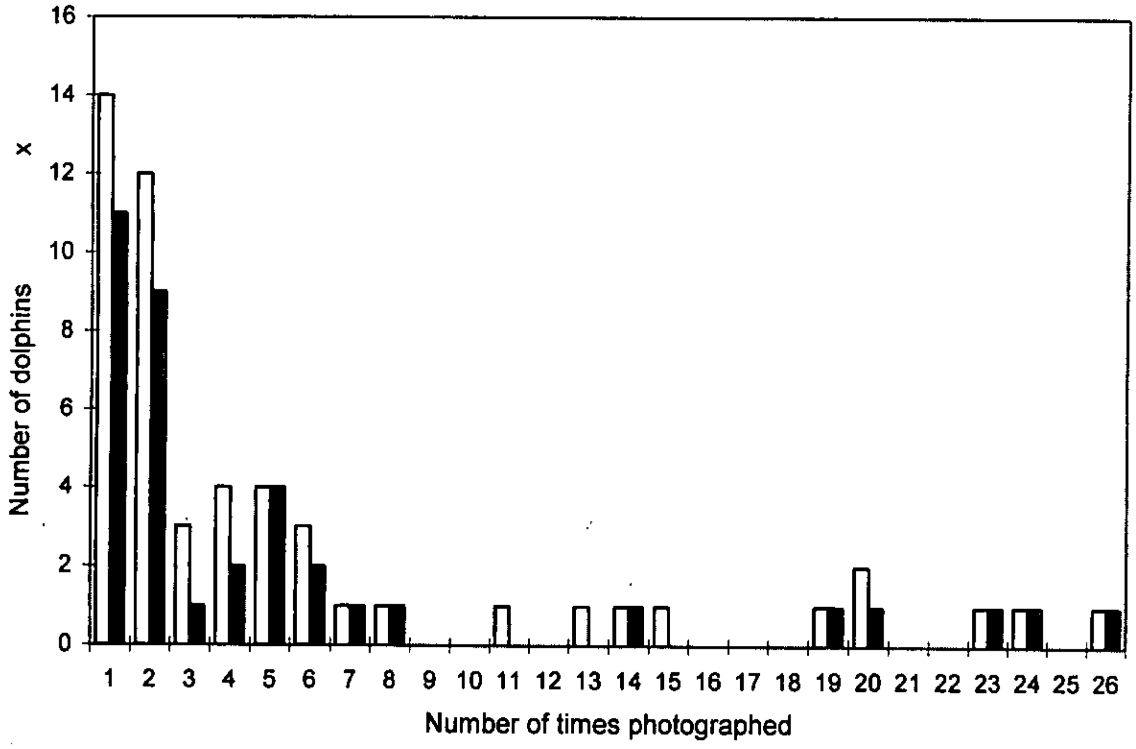


Figure 6.1. The frequency distribution of humpback dolphins identified and re-identified in Maputo Bay during the period between December 1995 and December 1997 (☐ - all individuals, ■ -adults only).

the first seven photographic occasions (13 individuals occurred during 1992, 3 during December 1995, and eight during April 1996). Although new adults were identified subsequently, they appeared in small numbers (Fig. 6.2), not exceeding two individuals until September 1997. Thirty-seven adults were sighted and the total number of re-sightings was 210.

Abundance estimates

Population estimates are presented in Table 6.1. All closed population estimates provided similar estimates. The Jolly-Seber estimator provided the lowest estimate. The minimum population estimate predicted by the power fit [number of marked dolphins = (1.7489*(number of days)$^{0.4622}$)], r=0.965, was 80 marked dolphins, which would the curve predicts would all be photographed after 11 years from the beginning of the study.

The estimate is higher than all closed and open population estimates. Based on the number of adults observed and the average proportion of marked adults it was estimated that 71 adults were observed, providing a population estimate of 142 dolphins, after adjusting for the proportion of adults in the groups.

Reproduction and population parameters

Ten births were recorded from identified humpback dolphins: one birth was assigned to 1991, one to 1995, three were assigned to 1996 and five to 1997 based on the estimated month of birth. Although sightings of mother-calf pairs began in 1992, there was an interval of almost three years (1993-1995) during which no surveys were carried out. Therefore data from 1992 were not used. In addition, a calf born in April 1995 was sighted for first time when it was one year old (April 1996), and was not included in the analysis.

Only calves born in 1996 and 1997 were used to estimate the population parameters of humpback dolphins (Table 6.2), because the number of known individuals increased and the numbers of re-sightings were relatively high compared to previous years. Most females were year round residents in the area, except for those from 1992, which were not re-sighted during the period between December 1995 and December 1997. Births occurred throughout the year and no particular breeding season was evident (Fig 6.3).

The number of calves born was 3 and 5 in 1996 and 1997 respectively. The number of known individuals was 11 and 25 in 1996 and 1997 respectively. This resulted in a mean crude birth rate of 0.048. Only one calf survived more than a year, resulting in a recruitment rate after one year of 0.09. There was only 1 calf considered dead within a year in 1996, and no dead calves were found during 1997. This resulted the mean minimum mortality rate of 0.100 (Table 6.2).

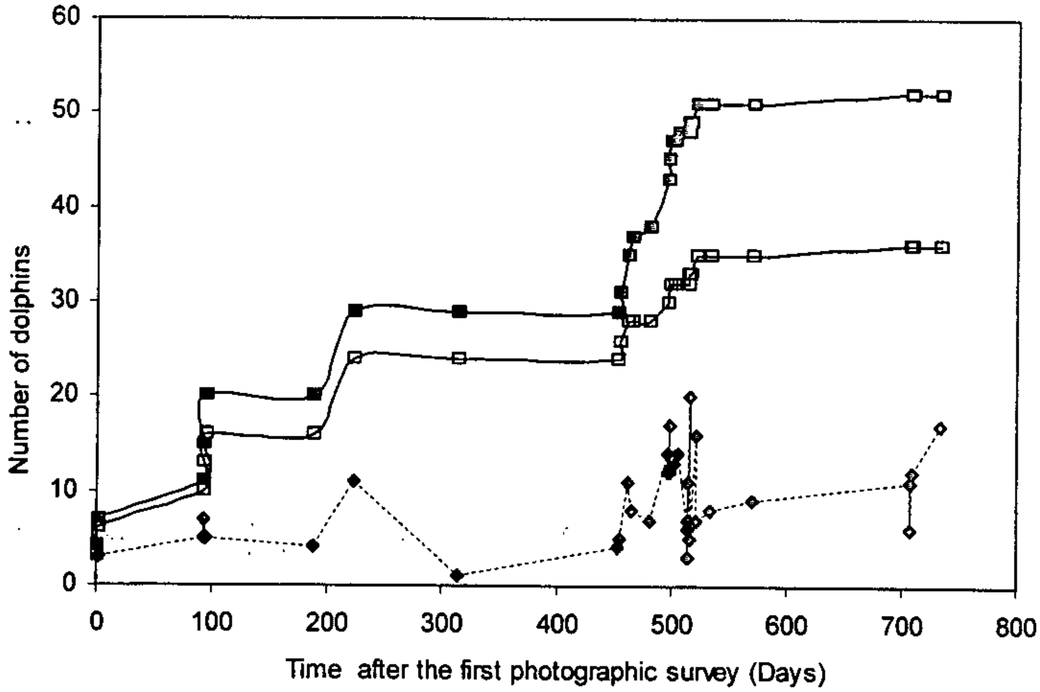


Figure 6.2 Discovery curve of humpback dolphins in Maputo Bay between January and May 1992 and between December 1995 and December 1997; - Cumulative number of identified individuals (■ - all dolphins, □ - adults only) with time; The number of individuals newly identified and/or re-identified in each survey (◆). Note:The gap interval of 910 days between May 1992 and December 1995 was removed, and thus the total effective working period was about 800 days. This gap occurred at about 100 days in the figure.

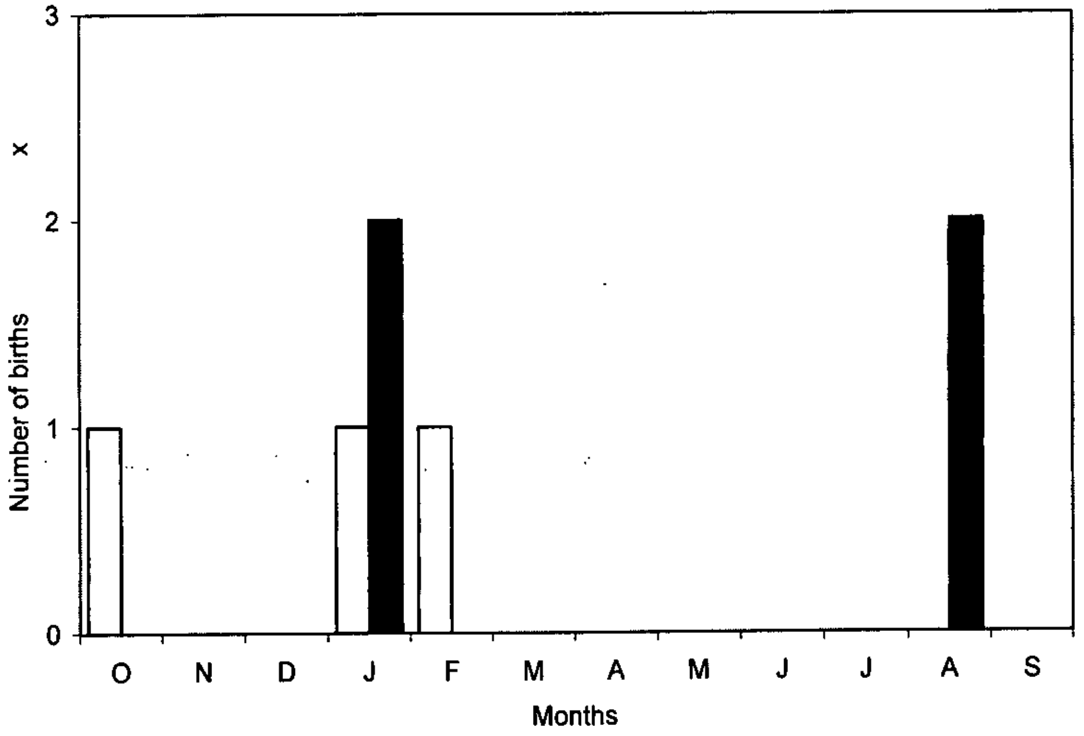


Figure 6.3. Estimated number of births and probable month of birth of humpback dolphins calves in Maputo Bay, based on extrapolation from calves (length & date) observed in Maputo Bay between December 1995 and December 1997 (☐ - births recorded in 1996 , ■ - births recorded in 1997).

Table 6.1. Population estimates , both closed and open models, of humpback dolphins in Maputo Bay, using mark-recapture data between 1995 and 1997 (CI = confidence intervals).

	Identified Dolphins		Mean proportion of identified dolphins in groups		Extrapolated Numbers	
Models	Estimates	Low and High 95% CI	Identified dolphins	Identified adults	Estimates	Low and High 95% CI
CLOSED MODELS						
Jackknife	46	41 – 62	0.52	0.5	176.9	157.7 - 238.5
Chao- Mh	45	40 – 66			173.1	153.8
OPEN MODEL						
Jolly-Seber Full	27	7.9 - 39.2	0.52	0.5	104.8	30.5 - 150.9
Power fit	80	77.3 - 82.7	0.52	0.5	307.7	297.4 - 318.1

Table 6.2. Population parameters of humpback dolphins in Maputo Bay photographed and identified between December 1995 and December 1997 (The survival of two calves born in the middle of 1997 could not be monitored for more than six months), (ND = No data, SD = standard deviation).

Description of parameters	*Parameters*	*1996*	*1997*	*Mean*	SD
Number of known adults	N	11	26		
Number of births	B	3	5		
Number of calves surviving 6 months	B_1	1	2		
Number of calves surviving 1 year	B_2	1			
Mother-calf pairs disappeared after 6 months		1	0		
Crude birth rate	BR*	0.273	0.200	0.236	0.051
Recruitment rate at six months	REC_1*	0.125	0.100	0.113	0.018
Recruitment rate at one year	REC_2*	0.125	ND	0.125	
Minimum mortality rate	MR*	0.125	0	0.063	0.088

* cf text.

DISCUSSION

Rate of discovery of new individuals

Adults with recognisable marks comprised 26% of the group members (50% of groups were adults and only 52% of the adults were recognisable through their marks). Such a relatively small proportion of marked individuals may have caused problems of resighting them. However, since the groups were often of small size (ranging between 2 and 25 individuals), almost all marked individuals were photographed. This is supported by the number of times the most frequent dolphins were re-sighted (20-26 times), which occurred in > 50% of the photographic surveys. The mean number of photographs taken per dolphin in any photographic survey was also high (about 5.68 photographs per dolphin).

About 32% of the dolphins were only sighted once. This was caused by their low site fidelity. Individuals with unreliable marks could also cause difficulties in identification, but no tag loss was observed and is unlikely because, all dolphins with unreliable marks were considered unmarked. In addition, the occurrence of small groups allowed for taking of several high quality pictures of all individuals. The negative implications of using naturally marked individuals for population estimates was discussed in Chapter 5, and they were mitigated by using adults, most of which had consistent marks and by keeping a catalogue of traced fins for comparisons.

Most individuals (65%) were recorded in the first seven photographic surveys, of which 5 were carried out during 1992 (36% individuals) and one in December 1995 and one in March 1996 (29% individuals). All these surveys were carried out during summer. Therefore, the high percentage of identified individuals may be caused by the initiation of the studies. However, in summer 1997, many individuals were identified, suggesting that an influx occurred and few new marked dolphins (immigrants) subsequently appeared in winter 1997, as it was for the winter of 1996. The preferences of this species for shallow waters along the east coast of southern Africa have been reported earlier (Guissamulo 1993, Durham 1994, Peddemors & Thompson 1994, Karczmarski 1996). Maputo Bay has extensive shallow areas that were not surveyed frequently. Therefore, it seems that the apparent seasonal influxes observed consisted of dolphins from other areas of the Bay, which visited the area.

Coalescence of distinct groups of dolphins occurs in the deeper channels of northern Maputo Bay at low tide, explaining the largest group size (Chapter 4). The same pattern occurred in Hong-Kong, where humpback dolphins showed high densities in deeper channels (Jefferson 1998, 2000). Saayman & Tayler (1979) mentioned that resident dolphins of Plettenberg Bay interacted with several dolphins when large groups were formed. At Algoa Bay, the group structure varied frequently due to the existence of high numbers of transient dolphins. The external factors leading to the stability of group composition include prey availability and intraspecific competition (Würsig 1986). In Maputo Bay, different groups of humpback dolphins interact because of fluctuating seasonal changes in prey abundance and daily tidal range (Chapter 4). The humpback dolphin sub-population of the Kwazulu-Natal coast, South Africa, has shown an extreme local phylopatry, due to year round prey availability (Goodwin 1997), while in Algoa Bay, it occurs because of nursing requirements (Karczmarski 1996). Maputo Bay humpback dolphins also have the potential for high local phylopatry and evidence from re-sightings shows that this appears to occur in eastern Maputo Bay. However, the extreme impact of the river run-off and fishing activity on pelagic and demersal fish during summer (which reduces prey availability), may probably prompt entire groups to move from western and southern Maputo Bay to the east, which at that time experiences increased fish availability (De Boer 2000). However, this study could not determine whether some individuals may come from the open coast, outside of Maputo Bay.

The rate of discovery of humpback dolphins of Maputo Bay showed alternate increases and plateaux, caused by the influxes of new individuals, mostly during summer months. All newly recognisable dolphins consisted of marked individuals with old scars, suggesting that the recruitment of unmarked dolphins to the area was not common, as fresh scars were relatively few in Maputo Bay. This implies that the population of humpback dolphins is open, it ranges beyond the study area or a relatively high proportion of seasonal migration to Maputo Bay occurs, through the changes of area utilisation by individuals from neighbouring areas. Nevertheless, it may be possible that immigration to the study area occurs through either reproductive needs or the search for feeding grounds. Interestingly, group sizes and sighting frequency did not change seasonally and therefore, the summer increases of the number of marked individuals could be compensated by the emigration of other dolphins, suggesting that large exchange of individuals occurred between communities or dolphins increase their ranges. However, a group of dolphins showed high site fidelity and was observed throughout the year in Maputo Bay. It included two dolphins observed in the Bay in 1992 (Chapter 4).

The rate of discovery pattern found in Maputo Bay was similar to that observed for the humpback dolphin population at Algoa Bay, South Africa, some 1200 km south of Maputo Bay (Karczmarski 1996). Off the Kwazulu- Natal coast, some 600 km south of Maputo Bay, Durham (1994), also found a similar pattern, though increases in the number of identifiable individuals occurred during winter. If any relationship exists between the populations of Maputo Bay and the Kwazulu- Natal coast, is unknown. The genetic distance between one individual from Maputo Bay and those from the Kwazulu-Natal coast, South Africa, suggests that the humpback dolphin population of Maputo Bay is reproductively isolated from those of the eastern coast of South Africa (Goodwin 1997). If this is true, then local phenomena are impacting the different populations. Durham (1994) resighted one dolphin about 120 km from the location where it was originally sighted, which is the distance between Maputo Bay and the northern border of the Kwazulu- Natal coast. If equal movements occur among male dolphins of Maputo Bay, then limited mixing may only occur. However, the extent of movements of humpback dolphins outside Maputo Bay is unknown. There are few humpback dolphin habitats in the area between Maputo Bay and Richards Bay, South Africa (Robertson *et al.* 1999). A small populations may occur in Sodwana Bay/Ponta do Ouro area (Berggren *et al.* 2007). However, the relationship between Maputo Bay and Sodwana Bay population is unknown. Winter increase of new marked individuals off Kwazulu- Natal may also be a response to other factors, such as avoidance of other dolphin species (bottlenose and common dolphins) which come to the shore during the "sardine run". In summary, local factors within a limited scale determine the summer influx of dolphins into eastern Maputo Bay.

Several bottlenose dolphin populations inhabiting closed areas (dos Santos & Lacerda 1987, Balance 1990, Wells 1991 and Fertl, 1994) exhibited a similar pattern, caused by the influx of dolphins from neighbouring areas. However, the short duration of the present study and the coverage of a relatively small area can also account for this pattern, because some individuals from the same population may shift their range temporarily and be considered immigrants to the area as they are captured. For example, a dolphin named H1 was first sighted in January 1992 and re-sighted again only in May 1997. If data from 1992 were not available this dolphin would be considered new to the area. This implies that humpback dolphins off Southern Mozambique have extended ranges and preferred areas, moving in response to availability of resources. Therefore, there may be a temporal/geographic dimension related to this, that a sampling regime , such as the present one, may miss.

As reproduction is not seasonal in Maputo Bay, the summer influx may result from local changes in prey availability. This in turn causes changes in the area use of the dolphins. Transient individuals would be seen briefly in the area when they occur in large groups, which form in the deeper channels during low tide (Chapter 4). The reasons for the extensive exchange between groups during summer need further studies, since they define the whole social structure and dynamics of the population of Maputo Bay. Mating does not seem to be the main cause, though some males may visit the area in search of mates. But a large male (named H8), which had high site fidelity, appeared to be dominant and apparently mated with most off the identified females, as observed during the social behaviour, though this requires verification of the paternity of calves. In addition, influxes also included small dolphins and females. There was evidence that pregnant females and nursing females had high site fidelity in eastern Maputo Bay. If, among groups from other areas of the Bay (including those frequenting the fishing areas), nursing females show high site fidelity, then possibly, these may be effected by fisheries, resulting in high calf mortality rate. However, the study could not find evidence of this.

The variety of habitats (sea-grasses, reefs and mangrove tidal channels) of eastern Maputo Bay offers stable food supply, despite the seasonal changes in prey species composition and prey abundance (De Boer 2000, De Boer *et al.* 2001), but prey may scatter over the extensive shallow waters (Chuquela 1996, De Boer 2000). At the east coast of South Africa (Barros & Cockcroft 1991; Cockcroft & Ross 1983; Saayman & Tayler 1973), the coasts of China (Jefferson 1998, 2000) and at Bazaruto Bay, Mozambique (Peddemors & Thompson 1994), humpback dolphins are known to be piscivorous and to feed mostly on demersal species. Bare sand and mud offer little shelter and less food for demersal fish than reefs, mangrove tidal channels and sea-grasses in Maputo Bay (Kalk 1995) and larger prey species are not abundant (De Boer *et al.* 2001; De Boer 2000). Large demersal fish species would only be found in large aggregations during spawning season or when their fry occur at the nursing areas (Kalk 1995). This may promote intra-specific competition between dolphins and consequently high exchange of individuals, resulting in low site fidelity of some individuals and an open population. The few observations of aggression observed during surfacing behaviour (Chapter 7), mean that the type of competition likely to occur may be the scramble competition. The trawling for prawns that occurs in the shallow south and western Maputo Bay may also aggravate prey scarcity, because demersal prey species are also taken. The exchange of group members within a stable core of individuals may occur after coalescence of subgroups of dolphins in the deep channels of the northern part of the Bay during low tides. Some dolphins may temporarily change group membership, the extent of it depending on prey availability.

Alternatively, if dolphins are organised into matrilineal communities (Saayman & Tayler 1973; Goodwin 1997), then movement of key community members may prompt the movement of closely social affiliates and this could result in influxes and/or outfluxes. Competition and other social interactions may then restructure the group membership. Saayman & Tayler (1973) and Karczmarski (1996) found a lack of cohesiveness of group membership at Plettenberg Bay and Algoa Bay respectively, despite there being a small core group of residents in both areas.

The Power fit estimates that in Maputo Bay, the plateau (with an influx of 1 individual per year) would be attained after 11 years, when the number of adults with natural marks is 80 (Table 5.1). During the study, only 38 adults (47.5%) were identified. This implies that the humpback dolphin population of Maputo Bay may be large. The open nature of the population is suggested because during the study, 47.5% of marked individuals (out of the estimated 80 individuals) were observed, and only a small portion of these (about 25%), showed a high site fidelity. Considering that the chances of missing marked individuals were small, because of the small groups, the main reason for not re-sighting new individuals may be their departure from the study area. The existence of a reasonable number of apparently transient dolphins, suggest that the population of humpback dolphins is open, or consists of several communities with overlapping ranges.

In summary, there were summer influxes of marked individuals in Maputo Bay, which created alternate increases and plateaus in the rate of discovery of individuals. These influxes consisted of new individuals visiting the study area for short periods of time and may possibly be associated with changes in food supply throughout their ranges, but also of few individuals that increased their site fidelity in the study area in 1997. The eastern Maputo Bay with its high diversity of habitats, may provide a stable food supply and be a very attractive area. The rate, at which some individuals from other communities may revisit eastern Maputo Bay, depends on the temporal and geographic changes in the distribution of food resources in their own ranges. During the study, only a relatively small fraction of marked individuals was observed, possibly resulting from low mixing rate of individuals of different communities that inhabit Maputo Bay and neighbouring areas and due to the restricted survey area. It could not be established if new individuals become resident, despite that some of them increased their site fidelity over some months after their first sighting, because of the short duration of the study. These influxes generate an increase in the re-sighting rate of individuals, underestimating the population size obtained from closed models. However, for open population models influxes and short stays are accounted for and their influence is minimum. However, it increases the fraction of marked individuals in the population and the adjusted population size is further understimated The potential for impact of the fishing activities in the southern and western parts of Maputo Bay, may promote influxes to the eastern part of the Bay.

Population size estimates

As the study area did not coincide entirely with the range of this species, an appropriate model to estimate the population size could not be identified. The humpback dolphins behaved largely as an open population due to influxes during summer, though a stable core group with high site fidelity occurred (Chapter 4).

The population estimates from closed population models of the software Capture (177 and 173, Table 6.1) were consistent with the crude population estimate computed in this study (140.2 dolphins), but larger than the open population estimate (Table 6.1). The Power fit, however, provided very high population estimates (307 individuals). The consistency between the population estimates from closed models and from the crude population estimate is expected, as both suggest the existence of a closed population. The Jackknife and the Chao-Mh estimators are robust to heterogeneity in capture probability (Pollock *et al.* 1990) and therefore yielded small differences. Heterogeneity is a violation of the assumption on the equal sighting probability of individuals. This assumption is difficult to overcome in small study area, when individuals have distinct ranging pattern that goes beyond the it (Karczmarski 1999). The Jolly Seber estimator is an open population model, very susceptible to bias caused by heterogeneity in the sighting probabilities (Pollock *et al.* 1990) and for these reasons their estimation is biased downwards. Nevertheless, though biased, this population estimate is likely to represent the approximate size of the resident dolphin population, because it considers all transient individuals as emigrants and therefore excluded by the model in the estimation of population size. All estimators provide very large 95% confidence limits, showing imprecision of the estimators. Causes of the imprecision could be the violation of assumptions, mainly the one regarding equal sightability of dolphins (Pollock *et al.* 1990; Hammond *et al.* 1990)..

The causes for heterogeneity of sightings or sighting probability are diverse, being caused by differential temporal and spatial distribution of surveysl and by movements of individuals into or out of the study area. As most of the survey effort was carried out at northern and eastern parts of Maputo Bay away from the shallow areas where dolphins return at high tides, the sightability of the "resident" dolphins of northern and eastern Maputo Bay were favoured , while those dolphins frequenting western Maputo Bay and outside the Bay, were only photographed when visiting the study area, thus increasing the heterogeneity in the sighting probabilities.

The regression method, using Power fit to extend the curve of discovery of dolphins, overestimated the population size, because the equation is highly dependent on the distribution of the sampling effort and it was a short duration of the study. After two years, the influxes were still large, because the searched area was small and many new dolphins were being discovered. This inflated the discovery curve of new identified individuals. The possible reasons for the influxes were discussed in the previous section, but the level at which they occur are unknown and may depend on the annual stochastic variations of productivity of the habitats and the prey abundance. For this reason the extrapolation of data from a regression curve should be viewed with caution, since it may deviate from reality.

The implication of the seasonal influxes of dolphins on the population estimates using the regression model has been discussed. However, closed model estimates are sensitive to the influxes (Pollock *et al.* 1990), which will overestimate the population. Possibly, sampling between the periods of influxes will provide larger estimates, while sampling outside this season of influx may provide lower estimates. But influxes contribute to the different sightability of the individuals and these effects have already been discussed.

The estimated population size of humpback dolphins in Maputo Bay increased from 67 individuals in 1992 (Guissamulo 1993) to the range between 104 to 176 individuals in 1997. This increase is very high and is probably not caused by reproduction/recruitment of other dolphins, even allowing for high levels of survival and fecundity which is unlikely, because of the impact of fisheries (Massinga & Hatton 1997; Sousa 1985; 1989). Consequently, immigration, and/or differences in the survey effort between these studies may account for these increases. The seasonal influxes, evident in the rate of discovery, support the increase through immigration. During 1992, the study period was too short to allow photographing all dolphins occurring in the Bay (mostly the transients) and therefore, the estimate was lower. This again supports the idea that short study periods are unlikely to detect all marked individuals, especially if the study area is limited and dolphins exhibit low sighting frequency. Larger estimates are obtained if large areas are studied or the study is carried out over a long period of time, allowing the detection of all or most marked individuals. At Algoa Bay, which is a small study area, influxes were seasonal and were observed throughout the duration of the study (Karczmarski 1996,1999).

Eastern Maputo Bay covers a surface of 219.5 km^2 and the mean absolute density estimate of humpback dolphins is 0.87 (SD=0.39) individuals km^{-2} . The current density estimate in 1997 is almost three times higher than that obtained in 1992 (0.31 dolphins km $^{-2}$) (Guissamulo 1993). Such a large difference is unlikely to have been caused only by the population growth, but by larger sample size, the prolonged distribution of effort, a better coverage of the study area and by the increased amount of marked dolphins sighted during the photographic surveys. Possibly, increased fishing effort and reduction of prey density caused by river run-off during summer in the shallow areas may cause the influx of dolphins to the eastern Maputo Bay from the western part of the Bay. Fishermen were reported to circle dolphins with gill nets in Maputo Bay, because they use them as cues for places of fish abundance (Guissamulo 1993, Guissamulo & Cockcroft 1997). This is a source of disturbance to dolphins, interfering with their foraging activity and poses mortality risks to at least the younger dolphins through entanglement. Dolphins were less abundant in areas of low fishing intensity, suggesting the existence of historic strong interactions with fisheries (Guissamulo 1993).

The proportion of transient dolphins (sighted once) was about 45% in Maputo Bay (Chapter 4), and the Jolly-Seber population estimate is about 40% of the closed model estimates. These two figures are consistent, despite biases in the population estimate, suggesting that the latter model considered that all dolphins never re-sighted, were emigrants.

The mean relative density of humpback dolphins in Maputo Bay is about 0.09 (S.D. = 0.06) dolphins/km of survey. It was calculated using the range of speed of searching boats and the NPUE (Chapter 4, Table 4.1). Searching boat speeds ranged between 14 and 25 km per hour and these figures were multiplied with the mean NPUE (2.60 dolphins/h), (Chapter 4). This Relative density similar with that recorded in 1992 for astern part of Maputo Bay that was 0.09 dolphins/km of survey (Guissamulo & Cockcroft 1997), suggesting a constant dolphin density over time. As humpback dolphins prefer shallower water (Guissamulo 1993; Peddemors & Thompson 1994; Durham 1994; Corkeron 1990, Karczmarski 1996), this relative density might have been underestimated.

Off the east coast of Kwazulu- Natal and at Algoa Bay, densities of humpback dolphins were high (0.3 and 0.4 dolphin/km respectively) (Durham 1994 and Karczmarski 1996). The differences observed in the relative densities may be caused by the differences in the size of shallow water habitats available: Maputo Bay has a more extensive habitat. However, in both studies carried out in Maputo Bay the spatial distribution of searching effort in Maputo Bay was uneven, missing most of the potential humpback dolphin habitats (extensive intertidal habitats) and thus underestimating their densities. Along Algoa Bay and the Kwazulu- Natal coast, the tidal range is small and there is a narrow shallow (<20 m) habitat. Maputo Bay has a very large habitat (84% of its surface) and dolphins may disperse widely in search of food, but prefer areas of depths <2 m (Chapter 4: Karczmarski 1996,). Those shallow areas are also subjected to extensive trawling by fisheries which may remove most demersal prey (Sousa 1985;1989; Massinga & Hatton 1996), on which dolphins may feed (Cockcroft & Ross 1983). This disturbs dolphins and forces them to execute either extensive movements in search of food/ and/or restrict their distribution to the tidal channels of mangroves or possibly estuaries, when fishing pressure is low. The relatively low density off Kwazulu- Natal coast compared to Algoa Bay, may be caused by their mortality in the shark nets (Cockcroft 1991).

In summary, the population estimates obtained from the open and closed models represent the range of the population size, though precision is very low. The precise estimates free of bias should be sought, as the current estimates are not useful to predict population trends (Ross *et al.* 1989). These ideal estimates should also be obtained considering the populations' ranges. Thus the minimum population estimates for humpback dolphins vary between 173 and 308 individuals and represent the number of dolphins that inhabit Maputo Bay and the surrounding offshore areas.

However, the low density may reflect the historic impact of fisheries on the population but also or underestimates caused by the lack of surveys over the extensive shallow areas, inaccessible to the survey vessels, that are part of the humpback dolphin habitat

Reproduction

Eight births were recorded during 1996 and 1997, of which 3 occurred during 1996 and 5 in 1997. The increase in the number of births could be caused by immigration of pregnant dolphins which became resident in the area during 1997 (Chapter 4). This could imply that some pregnant dolphins select Maputo Bay for foraging and nursing their newly-born calves and that the contribution of this influx to the birth rate is relatively high. Karczmarski (1996) and Durham (1994) suggested that Algoa Bay and Tugela Bank, in South Africa, were nursing areas for humpback dolphins. High local phylopatry has been observed among female humpback dolphins at Tugela Bank and this was due to increased prey availability (Goodwin 1997). However, the influx of females for reproduction into eastern Maputo Bay suggests that either there are few feeding/nursing areas available within the Bay and neighbouring areas, or intense fishing within the Bay has reduced prey availability in the southern and western parts of the Bay. The features of heterogeneous, rich habitats in the eastern part of the Bay have been described in Chapter 2.

Humpback dolphins showed a long reproductive season, as newly-born calves occurred throughout the year, implying that season does not effect reproduction. A prevalence of a particular season needs further investigations, because the sample size was small. However, a-seasonal reproduction of humpback dolphins has been documented from off Kwazulu- Natal (Reddy 1996) and Eastern Cape (van der Mescht 1996). However, humpback dolphins from Algoa Bay also had a calving peak during summer (Karczmarski 1996). The gene flow in the east coast of southern Africa is low and dolphins in Maputo Bay are relatively isolated from the those (Goodwin 1997). This does not contradict the findings of other studies in the Southern Africa. However, in all cases the sample sizes were small and conclusions must be considered preliminary. Possibly, the summer breeding peak observed at Algoa Bay may be caused by seasonal differences of calf survival, or just an adaptation to changes in food availability. If this is associated with the extremely high level of transient dolphins observed at Algoa Bay, possibly the population may have distinct winter and summer breeding areas, which are consistent with the existence of seasonal migration or influxes of individuals.

Assuming that reproduction is non-seasonal, then the impact of the summer influxes to the population of humpback dolphins of Maputo Bay requires examination. The summer influxes may then be caused by the search of areas of prey abundance rather than mating. In eastern Maputo Bay, an apparently dominant humpback dolphin male existed. However, male movements would occur in search of mates and most influxes may be driven by competition for food in shallow waters, where prey may be relatively scarce, as discussed in the previous sections. In addition, nursing females had high site fidelity and some females frequented the area at least 6 months before parturition (Chapter 4). It seems, therefore, that changes in area use in search of food and safety may well be the main cause of influxes. It is likely that this male mated with these females, since it sometimes ranged outside the study area, visiting other dolphin communities.

Unstable group membership was common in Algoa and Plettenberg Bays (Karczmarski 1996; Saayman & Tayler 1973, respectively) though in Maputo Bay, some individuals maintained highly stable affiliations, despite mixing with other dolphins. However, the examination of the paternity may help explain the social structure and the possible role of the influxes in reproduction. Until this is done, the role of the influxes for genetic flow or exchange cannot be excluded.

In Algoa Bay, the peak in the number of births coincided with the summer influx (Karczmarski 1996). The humpback population of Maputo Bay is separated from the Algoa Bay population by a distance of 1200 km and the possibility of genetic exchange is low or absent (Goodwin 1997). Nevertheless, genetic exchange may occur between adjacent populations over generations, through permanent occurrence of short-term changes of area use along the east coast of Southern Africa. Among mammals, the timing of reproduction is an adaptation to sharp periodic changes of the environmental conditions, which often include food availability (Krebs & Davies 1993). Eastern Maputo Bay offers year round food resources, which may support a small population (though fluctuations in prey availability occur in different habitats (de Boer 2000)) and there are small water temperature changes (Kalk 1995), possibly allowing reproduction throughout the year. Humpback dolphins off Hong-Kong had two reproductive peaks during spring and late summer, when prey was abundant (Jefferson 1998; 2000).

The long reproductive period of humpback dolphins is similar to the findings from Felix (1994) and Fertl (1994) for bottlenose dolphin populations in Gulf of Guayaquil and Gulf of Mexico respectively. Non-seasonal reproduction is reported as a common feature for dolphins inhabiting tropical and sub-tropical areas. Seasonal peaks of reproduction in temperate areas like those referred to by Wells (1992), Lynn (1995) and Karczmarski (1996) seem to be caused by temporal food availability to guarantee the successful rearing of calves and to satisfy the females' energy requirement (Wells 1992). Coastal dolphins from tropical areas may not synchronise the reproduction with food availability because they can move between productive habitats or stay in areas were the combination of heterogeneous, highly productive habitats allows year round food availability (Wells 1991, Felix 1994).

Population parameters

The crude birth rate of 0.048 (SD=0.021) for humpback dolphins (Table 5.2) was obtained from a small sample size, which does not incorporate the range of inter-annual variations due to the short duration of the study (24 months) and should be viewed with caution. Such a low value means that the population of humpback dolphins grows slowly and a very small number of cycling females are present in the population or that the level of abortion or failure to conceive is high among females. As humpback dolphins occur in low densities throughout their range, including Maputo Bay, a small birth rate implies that the long-term growth of the population can be achieved by investing in the survival of the calves, through minimising the risks of calf loss, avoidance of predation or other sources of mortality. This may be achieved by mostly frequenting areas of high prey density, which pose low risks of mortality, and to select safe areas for nursing. In Maputo Bay, the shrimp trawling fishery exploits the extensive shallow areas preferred by the humpback dolphins. Drops in catches of shrimp from 800 to 200 tonnes/year in the last 30 years, suggest that by-caught demersal fish stocks have also suffered reduction. Fish by-catch in the shrimp trawling fishery in Maputo Bay is about 600 tonnes/year (Sousa 1985). Therefore, a deterioration of the marine benthic habitat may have occurred In addition, there was a reduction of gill net boats in the Bay (Loureiro 2001; Premegi 1995), also suggesting a reduction of stock of *Hilsa kelee* in the Bay. Between 1982 and 1984 the catches off *Hilsa kelee* were already below the sustainable level (Sousa 1985).. Despite this, the extent to which these have impacted the dolphin population , including birth rate is unknown Birth rates in free ranging marine mammals are also underestimated because of unrecorded mortality of newborn calves (Wells 1992)

The birth rate in Maputo Bay is lower than the 16% for the crude birth rate reported from off the Kwazulu- Natal coast (Durham 1994), and was high due to the contribution of humpback dolphins from Tugela river estuary, at the Kwazulu- Natal coast, where most nursing females were observed, acted as a nursery area for all females from the east coast of Kwazulu- Natal or at least northern Kwazulu- Natal, and the population sampled was composed mainly of pregnant and calving females. Low sighting rates and small numbers of identifiable dolphins occurred along the Kwazulu- Natal coast, except for Tugela River estuary (Durham 1994), probably because food was abundant in the area and the habitat was large. Maputo Bay also offer a wider shallow habitat, but has a low reproductive rate. It seems that lack of coverage in most shallow areas of the Bay or the stability of the population growth through density dependent regulation, might have reduced the number of births and consequently reduced the crude birth rate in Maputo Bay. Nevertheless, low birth rates may also be caused by lack of food resources at fishing areas, but this requires further studies.

The recruitment rate at six months after birth was 0.019 (Table 5.2) and must be considered preliminary because it arise from a short-term study and lack of information about the fate of dolphins that left the Bay. Such low recruitment rate suggests high mortality of calves and yearlings during the first six months. Several causes affected this estimate, mother–calf pairs that abandoned the study area within six months. The exact causes for losses are unknown since dead carcasses could not be found. The inaccessibility of the large inshore shallow areas to surveys might have prevented re-sightings of some mother-calf pairs. It is unknown if these mother-calf pairs are affected by fisheries, but if they occur in the fishing areas, it is likely that they will suffer from disturbance and incidental catches. Nevertheless, bias on the recruitment rate estimated for humpback dolphins may have been reduced because of the tendency for long-term site fidelity of nursing females (Chapter 4). The recruitment rates at six months and one year were lower than those of humpback dolphin populations in Algoa Bay (Karczmarski 1996). The recruitment estimated for bottlenose dolphins at six months after birth, using the data from Felix (1994), was 0.015, which is slighthly consistent with that for humpback dolphins from Maputo Bay (0.019).

This low recruitment rate raises some concern, as the survival rates of calves are low and may influence the long-term survival of the population. Any incidental mortality of calves or nursing females from fisheries will produce large decreases in the recruitment rate and the population may experience negative growth, because natural mortality of adults will not be balanced by the recruitment. Calf survival rates of less than 50% produce unsustainable growth (Reilly & Barlow 1986). The humpback dolphins in Maputo Bay are already constrained by the limited food resources in shallow areas, risks of entanglement by fisheries, disturbance and possibly predation. This may have promoted the group cohesiveness to protect calves in Maputo Bay, which results in a larger group size and consequently low sighting rates because of the need of extensive movements in search of food (Chapter 4).

The mortality rate of humpback dolphins in Maputo Bay may be underestimated, because some newly-born calves may have died prior to being first reported (Wells 1992). The distribution of effort was uneven in the Bay and the survival of calves that abandoned the study area with their mothers was uncertain. Consequently, the maximum calf survival rate was overestimated. Karczmarski (1996) reported for the open coast of Algoa Bay, a calf survival rate of 0.78 for humpback dolphins, which may be realistic, as suggested by the possible mortality caused by sharks, since circumstantial evidence shows a shark influx to Algoa Bay during summer, which coincides with the peak of natality (Karczmarski 1996). The humpback dolphins of Maputo Bay inhabit inshore areas, which are exploited by fisheries and where intentional mortality by humans also occurs (Guissamulo 1993). Therefore, to increase their survival, dolphins may have shifted to the eastern part of the Bay were disturbance is low and there are diverse habitats which provide stable food resources. Calf survival is further enhanced by dolphins forming large groups in deep channels, to which they move during low tide, they frequent very shallow waters during high tide and choose areas of low shark predation. An experimental shark fishery which operated in Maputo Bay until 1985 depleted the sharks in eastern Maputo Bay (Cockcroft & Krohn 1994) and there are no recent reports of shark attacks on humans in Maputo Bay, suggesting a reduction in number of sharks and therefore, predation on dolphins. Non of the identifiable adults showed fresh marks related to shark attacks and this suggests that either all dolphins attacked by sharks were killed or there is a low shark predation. Shark fishery is now carried out off Portuguese Island and off Xefina Island, north of the Bay, suggesting that sharks are not common in the Bay.

For a seven years period, Wells & Scott (1990) reported a maximum calf mortality rate of 0.038 at Sarasota Bay, which is a very protected environment. This is consistent with the results obtained for humpback dolphins in Maputo Bay.

The present study did not allow estimation of non-calf survival rates because dead adults were not observed. Consequently, it is difficult to predict population growth levels and only speculations can be made. Although the calving interval and age at first parturition are not known for Maputo Bay, these data are known for the adjacent dolphin populations inhabiting the eastern coast of South Africa. Female humpback dolphins are reported to attain sexual maturity at 10 years of age (Cockcroft 1989) and a calving interval of three years is proposed (Cockcroft 1989 and Karczmarski 1996). The non-calf (adults and juveniles) survival is considered a square root of the calf survival rate (Reilly & Barlow 1986). Consequently, the non-calf survival would be 0.95. Applying these values to the method suggested by Reilly & Barlow (1986) for cetaceans, a population growth rate of 2% is obtained. This low growth rate, though rough, is indicative of a stable population close to its carrying capacity. This means that the population status is vulnerable, because of the small population size. In 1992, 5 dolphins were killed (at the time about 9% of the population size), including two pregnant females. Adding to this, there is the disturbance at their feeding areas and the apparent reduction of abundance of demersal prey in the western Maputo Bay. This may have reduced dolphin habitats. Therefore, the low growth rate, and the occasional catches of females and calves are likely to affect the age structure and the reproduction of dolphins and their long-term survival. Most of the transient dolphins either leave the area for longer periods and others were never re-sighted. Whether most of these adults died, is unknown. This poses a problem regarding long-term survival of the population, as the rate of increase is very small. This population differs genetically from others of the region (Goodwin 1997). Therefore there is a chance that it could disappear and be replaced by others from transient individuals, if these come from outside the Bay. There is a need to assess this using aerial surveys and photo-identification for the distribution of the dolphins outside Maputo Bay and at the shallow areas within the Bay, in order to predict the population resilience of this species.

The effect of fisheries on the population parameters and on the population estimate cannot be predicted, due lack of data on age of first parturition, no recovery of dead animals through fisheries and lack of data on the diet. However, there is evidence that fisheries can disturb the humpback dolphin population in the Bay because of the tidal movements into the fishing areas. In addition, data on survival of calves, which apparently leave the Bay, need to be accurate.

CHAPTER 7. BEHAVIOUR OF BOTTLENOSE AND HUMPBACK DOLPHINS IN MAPUTO BAY.

INTRODUCTION

Studies of the behaviour of free-ranging dolphins have been carried out using both land and boat-based approaches (Würsig & Würsig 1979, 1980; Saayman *et al.* 1972, Norris & Dohl 1980a, Krushinskaya 1986, Shane *et al.* 1986; Lynn 1995, Peddemors 1995, Karczmarski & Cockcroft 1999, Tyack *et al.* 2000, Ng & Leung 2003, Lusseau 2006, Stensland *et al.* 2006), but are still restricted to coastal species. However, the use of electronic devices, such as radio or satellite transmitters, has permitted the continuous day and night study of dolphin behaviour, movements and habitat utilisation (Pryor & Norris, 1991, Mate *et al.* 1995, Tyack *et al.* 2000). However, these devices are limited and can only describe the behaviour of the individuals to which they are attached. In addition, the set of behavioural terms used, has not been consistent between authors, with feeding, travelling, social interactions and idling/resting the major terms used (Shane *et al.* 1986, Stensland *et al.* 2006). Feeding related behaviours and travelling occupy most of the daylight time activities of members of the family Delphinidae (Saayman *et al.* 1972; Shane *et al.*, 1986, Acevedo-Gutiérrez, 1997, Stensland et al. 2006, Peddemors 1995, Karczmarski & Cockcroft 1999). Most studies describe only the daylight behaviour due to the inherent difficulty in observing dolphin behaviour during darkness (Mann 1999). In addition, mostly surface behaviour is recorded and inferences are made of underwater behaviour occurring between surfacing occasions (Mann 1999). Nevertheless, some underwater observations have been done for dolphins during resting and feeding (Johnson & Norris 1986; Acevedo-Gutiérrez *et al.* 1999). The aggregation of dolphins complicates the recording of behaviour further, as different individuals could be performing different behaviours, though methods have been designed to deal with this problem (Altmann 1974, Mann 1999; Tyack *et al.* 2000).

The behaviour of dolphins appears to be adaptive to the features of the environment and transmitted between generations. For instance, feeding against the current is a common behaviour of inshore bottlenose dolphins along the east coast of the United States (Shane 1990, Shane *et al.* 1986) while dolphins at geographically distinct areas have learned to beach on mud and sandy substrates to catch their prey.

Bottlenose and humpback dolphins occupy partially overlapping ranges along the east coasts of South Africa and Mozambique. Fragments of the behaviour are known from the studies carried out along the east coast of South Africa. Their daylight pattern of behaviour has been described by e.g. Saayman *et al.* (1972, 1973); Karczmarski (1996) and Peddemors (1995). Bottlenose dolphins are known to have preferred areas along the coast of Kwazulu- Natal, and travelling was the main behaviour, followed by feeding (Peddemors 1995), but in Plettenberg Bay, feeding behaviour prevailed over travelling and socialising (Saayman *et al.* 1973). Humpback dolphins in Plettenberg Bay, Algoa Bay and off Kwazulu- Natal coast displayed different patterns and variable behaviours (Saayman *et al.* 1972, Karczmarski 1996 and Durham 1994). Possibly, differences in the type of habitat, distribution and abundance of prey or movement, were responsible for these differences, and there was evidence that physiological needs affected the duration of behaviours seasonally, mainly because in winter, the proportion of time allocated to feeding increased in relation to summer.

The study of bottlenose and humpback dolphin behaviour is important for management purposes, because it determines the role of the area of Maputo Bay for these two species of dolphins. This chapter presents the daylight and seasonal pattern of behaviour of bottlenose and humpback dolphins in Maputo Bay. It examines differences in behaviour of different group sizes and the effects of seasons, daylight, tides and habitats. The degree of shelter is also discussed in order to evaluate the impact of fisheries and other disturbances.

METHODS

Surveys were carried out between December 1995 and December 1997 in Maputo Bay (Chapter 2). The occurrence of the main behavioural categories and the proportion of time that dolphins spent in each behavioural category (feeding, travelling, and socialising and resting) were recorded. The behavioral categories defined here are similar to those described by Leatherwood (1975), Ballance (1992), Shane (1990) and Karczmarski (1996).

Definition of behaviours

Feeding consisted of frequent asynchronous dives in varying directions at one location. Sometimes dolphins were seen chasing and capturing prey (fish or cephalopods) and occasionally when dolphins dived, fish could be observed at the surface when dolphins chased them from beneath. Dolphins also chased prey from deep channels towards the shore or to the margins of the sandbanks, where active fish capture was observed. During this feeding geometry of the group is highly variable, changing from tight formations for a short period, to small groups scattered over a wide area.

Travelling consisted mainly of tight formations of individuals moving consistently in the same direction. In large groups, all subgroups moved in the same direction. Within a subgroup, the members dived and surfaced synchronously, sometimes with very rapid movements.

Social behaviour consisted of various vigorous activities, which could vary from those displayed by one to several members of a subgroup, involving body contact. Individual activities varied from leaping, spy-hopping, wave riding, tail slapping, while collective activities consisted of prolonged chases, body contact, aggression and occasionally mating, including dolphins leaping and jumping and displacing water. Collective movements persisted at the surface for long periods and were interrupted several times by long dives.

Resting consisted of individuals or groups displaying a prolonged surfacing pattern, almost motionless, with the head and dorsal fins breaking the water simultaneously, but some slow forward movements were often noticed. No typical dive pattern was observed and even if dolphins were underwater; the tip of the dorsal fin was often visible until the next surfacing event.

Behaviours were recorded using the scan sampling method (Altmann 1974, Mann 1999, Tyack *et al.* 2000), which consists of recording the predominant behaviour, performed by the majority of dolphins in a group, at regular time intervals of five minutes throughout the observation time. Four behavioural categories were considered: feeding, travelling, socialising and resting. Active and opportunistic feeding were not separated because of the weakness of the sampling method. Therefore, when opportunistic feeding was observed, the proportion of time on both travelling and foraging was calculated, by allocating half of the observation time to feeding and the another half to travelling, and included in each behavioural category.

The mean proportion of time spent on each behaviour throughout the study period was calculated for each species.

Seasonal differences in the proportion of time spent by dolphins in any behaviour were tested for significance by the non-parametric Mann-Whitney U test. The Kruskal Wallis ANOVA was also used to test for significant statistical differences in the mean proportion of time spent on each behaviour; between diurnal tidal stages, daylight intervals and features of habitat. When not applicable, the Mann-Whitney U test was used.

Differences between groups of ≤ 6 and those > 6 individuals in the proportion of time spent on each behaviour, were also compared using the Mann-Whitney U test.

Three habitats were defined; unsheltered open sea area (deep areas with a direct influence of the open ocean with strong wave action), channels (deep areas of variable width up to 1000 m) usually bordered by shoals and/or shores which emerge at low tide) and shallow shoals (large shallow areas of depth < 2 m at high tide, which emerge at low tide).

RESULTS

Database

Dolphins were followed for 81 hours of which 48.4 hours were for bottlenose dolphins and 32.5 for humpback dolphins. The mean maximum time spent with dolphins was 1.20 (S.D. = 1.02) hours in May 1996 and the minimum mean time 0.17 (S.D. = 0.37) hours in December 1996. The observation time per sighting ranged from 10 to 163 minutes. Mean observation time was 0.83 (S.D.=0.65) hours per group for 52 sightings of bottlenose dolphins and 0.62 (S.D. = 0.62) hours per group for the 36 sightings of humpback dolphins.

For bottlenose dolphins, the observation time of sightings comprising ≤ 6 dolphins was 12.8 hours (n=17), and for > 6 dolphins, 35.6 hours (n= 35). The mean time spent observing the larger groups was significantly greater (Mann-Whitney, U = 197, p=0.001).

For humpback dolphins, the observation time of groups comprising ≤ 6 dolphins was 3.4 hours (n=6), while that for groups > 6 dolphins was 31.8 (n= 30). The mean time spent observing the larger groups was not significantly different (Mann-Whitney, U = 45, p=0.069).

Behaviour of bottlenose and humpback dolphins in Maputo Bay

The frequency of behaviours of bottlenose and humpback dolphins is presented in Figure 7.1. Bottlenose dolphins were observed feeding during 60 % of encounters and travelling during 20% of encounters, while humpback dolphins were observed feeding on 43% of encounters and travelling on 36 % of encounters. Social and resting behaviours had almost similar frequency on humpback and bottlenose dolphins (Fig. 7.1). However, in terms of duration of behaviours, the results are slightly different (Fig. 7.2). Feeding was the activity to which both bottlenose and humpback dolphins in Maputo Bay committed most of their time (Fig. 7.2). However, bottlenose

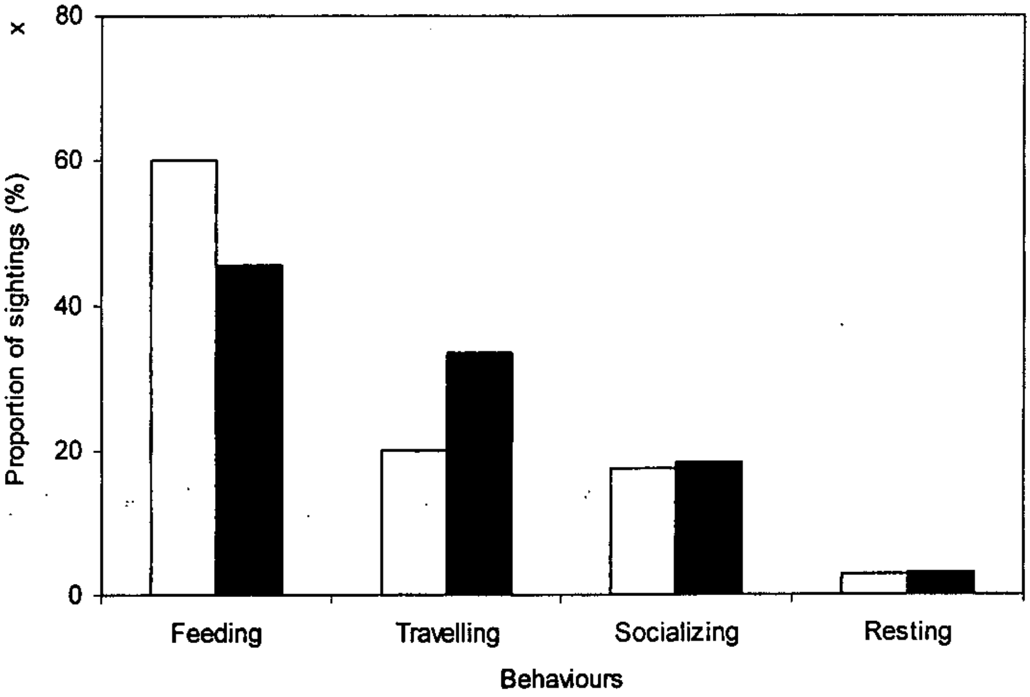


Figure 7.1. Frequency distribution of behaviours of bottlenose dolphins (□) and humpback dolphins (■) in Maputo Bay between December 1995 and December 1997.

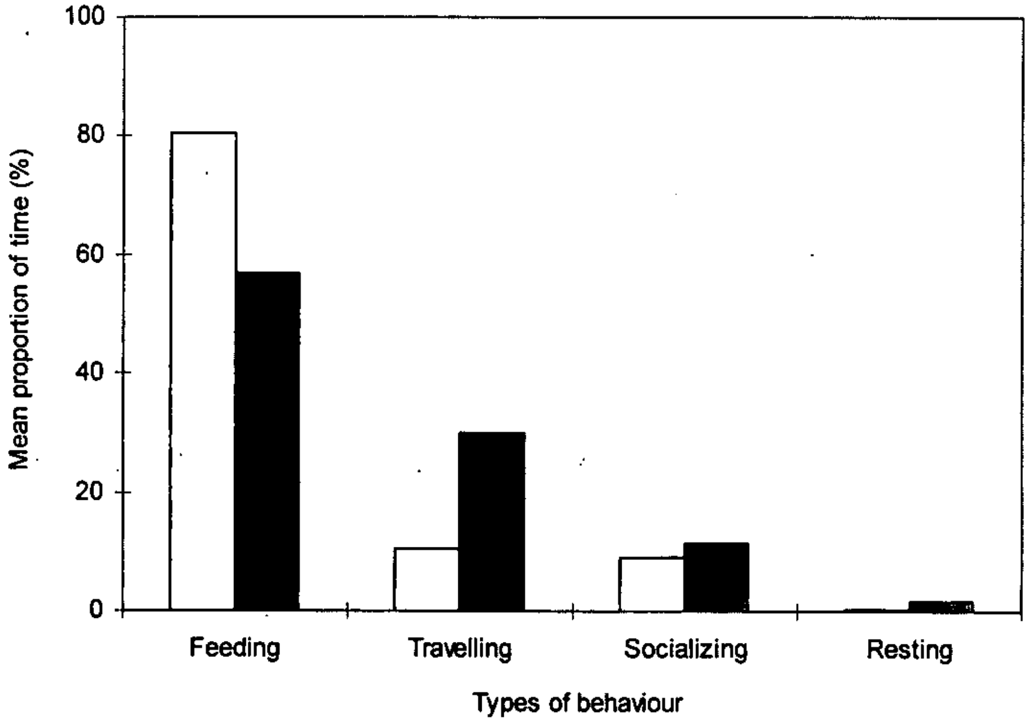


Figure 7.2. Mean proportion of time (%) allocated to feeding, travelling, socializing and resting by bottlenose dolphins (☐) and humpback dolphins (■) in Maputo Bay between December 1995 and December 1997.

dolphins spent most of their time feeding (81%) compared with the humpback dolphins (57%). Travelling was the second major activity of humpback dolphins (30% of the time), while for bottlenose dolphins it accounted for the same proportion of time as social behaviour (10% and 9% respectively). Humpback dolphins had the same proportion of time socialising as had bottlenose dolphins (11%). For both species, resting accounted for a very small proportion of time (2%).

Season

Figures 7.3 and 7.4 show the influence of season on the proportion of time (%) bottlenose dolphins and humpback dolphins spent feeding, travelling, socializing and resting in Maputo Bay, respectively.

For bottlenose dolphins, the proportion of time allocated to feeding did not change seasonally. For travelling and socialising, very small changes occurred between winter and summer, but these differences were not significant (feeding: Mann-Whitney U = 300, n =

19 and 33, p = 0.789; travelling: Mann-Whitney U = 309, n = 19 and 33, p = 0.905; social: Mann-Whitney U = 286, n = 19 and 33, p = 0.503; resting: Mann-Whitney U = 290, n = 19 and 33, p =0.682).

For humpback dolphins, the proportion of time allocated to feeding increased slightly during summer, while travelling decreased and social behaviour was only recorded during summer. However, there were no significant differences in the mean seasonal proportion of time spent on any of the behavioural categories (feeding: Mann-Whitney U = 98, n = 29 and 7, p = 0.887; travelling: Mann-Whitney U = 75, n = 29 and 7, p = 0.270; social behaviour: Mann-Whitney U = 63, n = 29 and 7, p = 0.059; and resting: Mann-Whitney U = 90, n =29 and 7, p = 0.247).

Daylight and Tides

Figures 7.5, 7.6, 7.7 and 7.8 show the mean proportion of the behavioural categories of bottlenose and humpback dolphins observed in Maputo Bay throughout the daylight and tidal range. The differences in the mean proportion of time spent on each behaviour did not differ significantly between tidal stages, for bottlenose dolphins (feeding: Kruskal-Wallis: H = 0.4580, n = 52, p = 0.9280; travelling: Kruskal-Wallis: H = 2.865, n = 52, p = 0.4128; social behaviours: Kruskal-Wallis: H = 4.5601, n = 52, p = 0.2070; resting: Kruskal-Wallis: H = 1.7333, n = 52, p = 0.6295) and for humpback dolphins (feeding: Kruskal-Wallis: H = 6.0405, n = 36, p = 0.1097, travelling: Kruskal-Wallis: H = 3.2462, n = 36, p = 0.355, social behaviours: Kruskal-Wallis: H = 1.3047, n = 36, p = 0.7280; resting: Kruskal-Wallis: H = 1.3326, n = 36, p = 0.7238).

Also for daylight time intervals, the mean proportion of time spent on feeding, travelling, social and resting behaviours did not differ significantly between bottlenose and humpback dolphins; for bottlenose dolphins (feeding: Kruskal-Wallis: H = 3.770, n = 52, p = 0.5830, travelling: Kruskal-Wallis: H = 7.5254, n = 52, p = 0.1844, social: Kruskal-Wallis: H = 1.5840, n = 52, p = 0.9032, resting: Kruskal-Wallis: H = 1.2404, n = 52, p = 0.0521) and for humpback dolphins (feeding: Kruskal-Wallis: H = 2.6118, n = 36, p = 0.6247, travelling: Kruskal-Wallis: H = 4.3927, n = 36, p = 0.3555, social: Kruskal-Wallis: H = 6.2328, n = 36, p = 0.1824, resting: Kruskal-Wallis: H = 4.1143, n = 36, p = 0.3908 respectively).

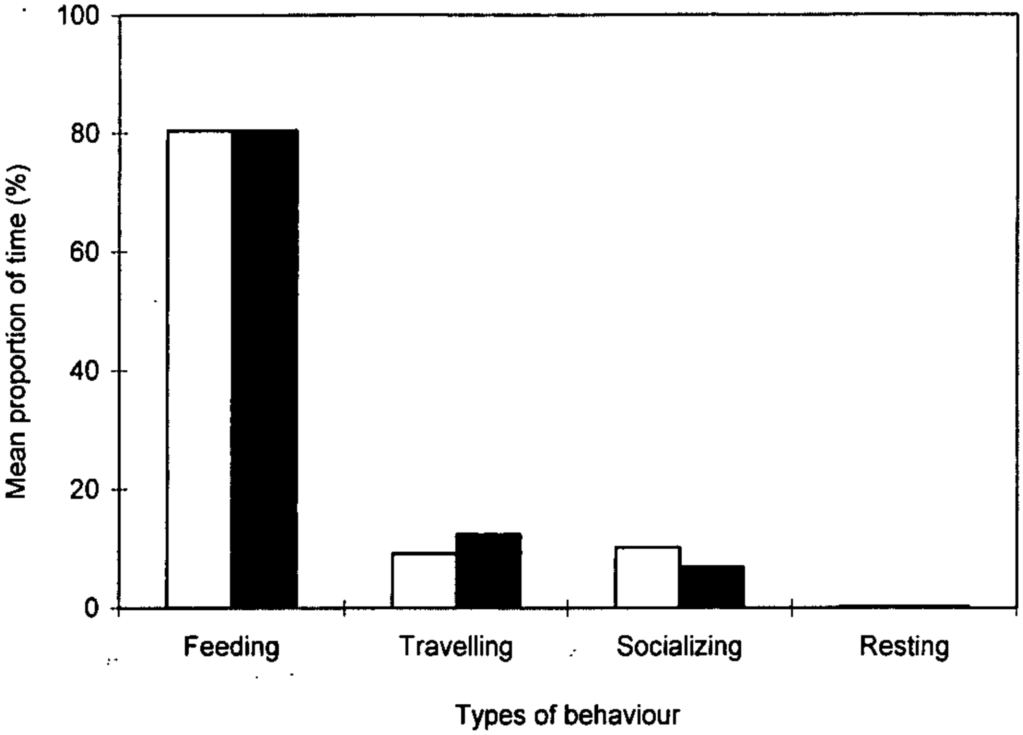


Figure 7.3. The influence of season on the proportion of time (%) bottlenose dolphins spent feeding, travelling, socializing and resting in Maputo Bay between December 1995 and December 1997 (□ - winter, ■ - summer).

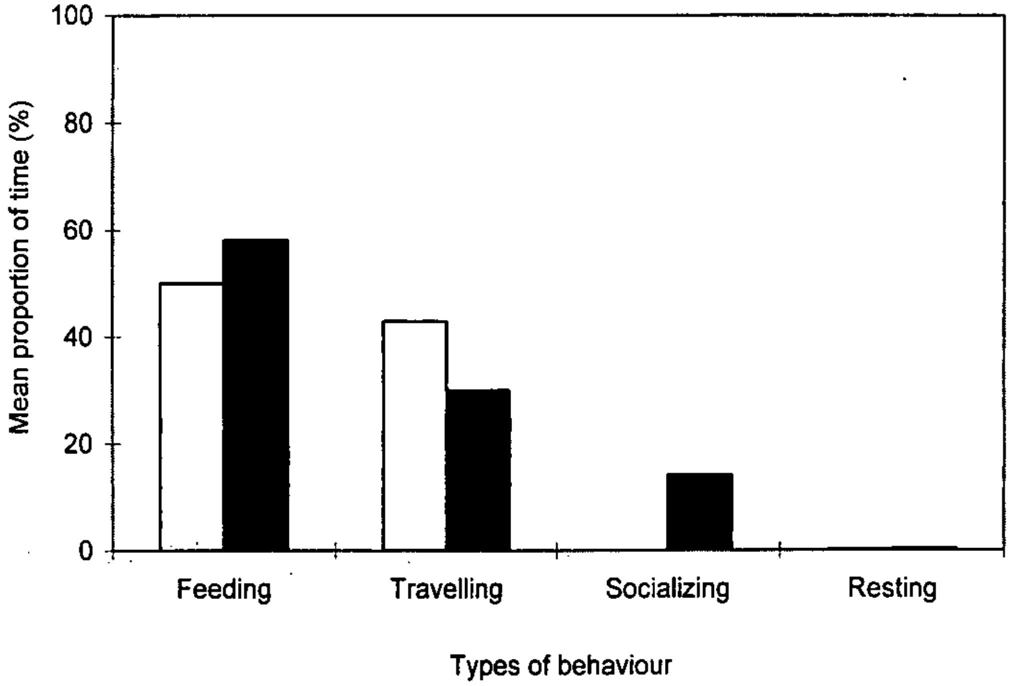


Figure 7.4. The influence of season on the proportion of time (%) humpback dolphins spent feeding, travelling, socializing and resting in Maputo Bay between December 1995 and December 1997 (□-winter, ■-summer).

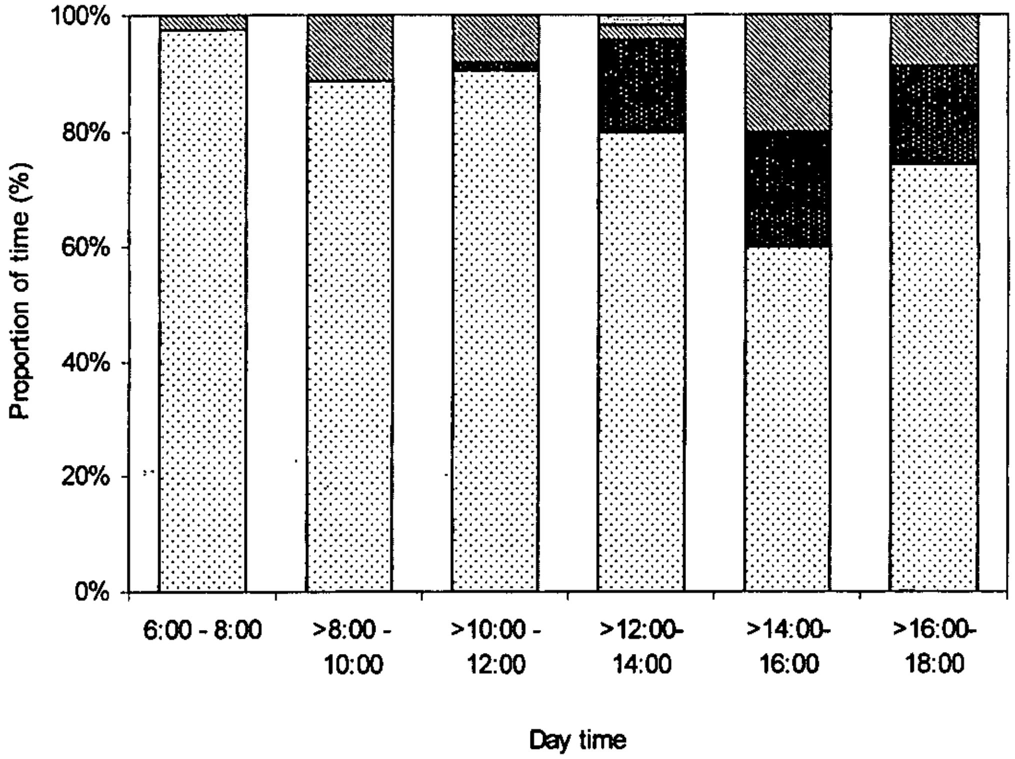


Figure 7.5. Proportion of time allocated to different daylight behaviours by bottlenose dolphins in Maputo Bay between December 1995 and December 1997 (□ -feeding ▦-travelling, ▨-socializing, ⊡ -resting).

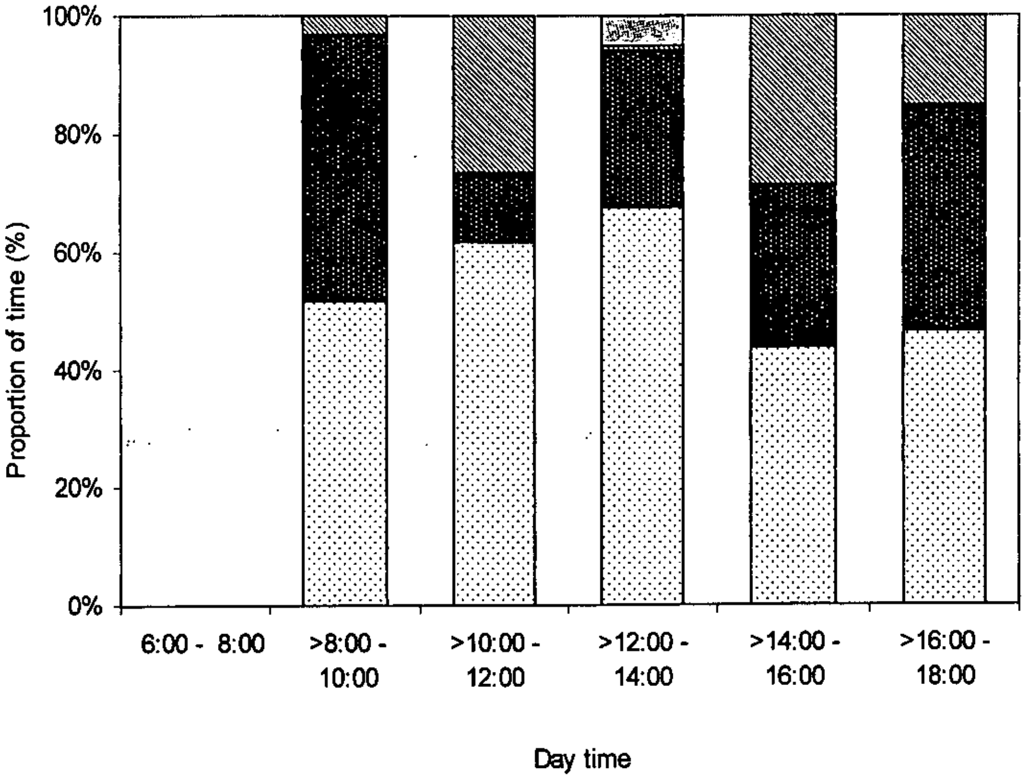


Figure 7.6. Proportion of time allocated to different daylight behaviours by humpback dolphins in Maputo Bay between December 1995 and December 1997 (☐ -feeding ▩-travelling, ▨-socializing, ▣ -resting).

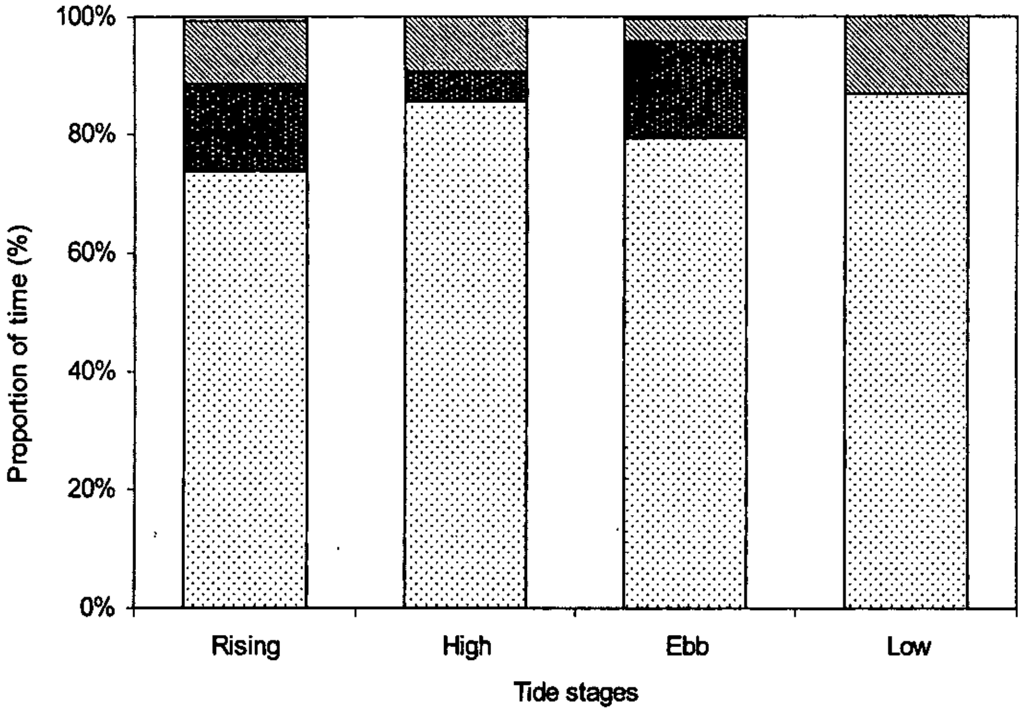


Figure 7.7. Proportion of time allocated to different daylight behaviours by bottlenose dolphins in Maputo Bay between December 1995 and December 1997 (☐ -feeding ■-travelling, ▨-socializing, ⬚ -resting).

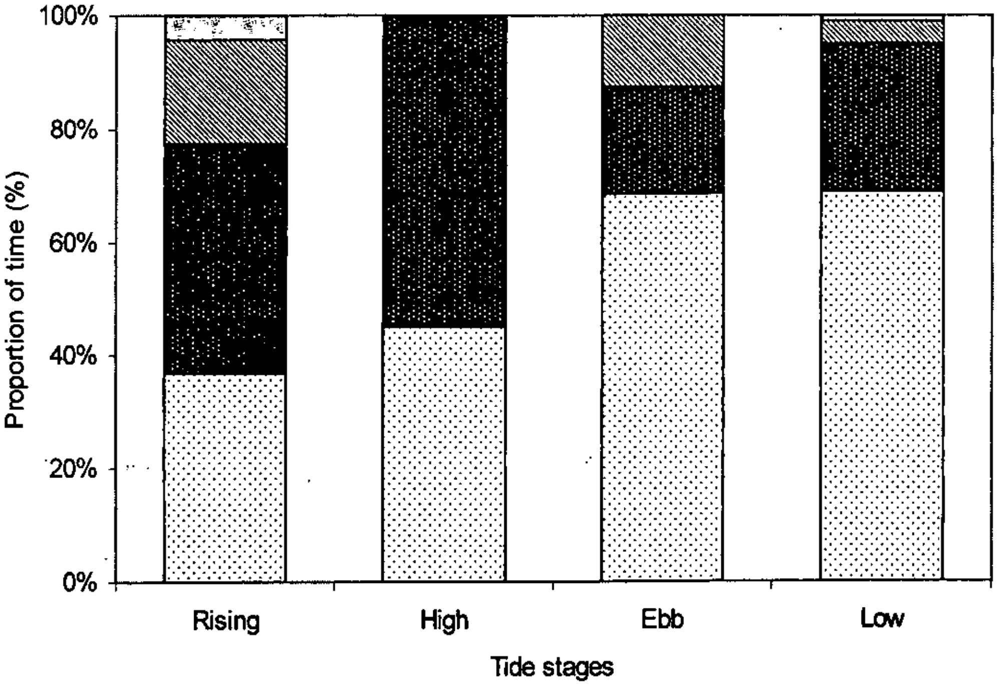


Figure 7.8. The influence of semi-diurnal tidal phases on the proportion of time humpback dolphins spent feeding (☐) travelling (■) socializing (▨) and resting (▫) in Maputo Bay between December 1995 and December 1997.

Degree of shelter of the habitat

Tables 7.1 and 7.2 show the mean percentage of time spent by bottlenose and humpback dolphins, respectively, in each habitat type. Bottlenose dolphins were only observed in two habitats, unsheltered open areas and channels. In both areas feeding prevailed over all other behaviours (Table 7.1), while social behaviour and resting seemed to be greater in the channels. However, feeding, travelling, social behaviour and resting did not differ significantly between habitats (Mann Whitney U = 229.5, n = 39 and 13, p = 0.584, Mann-Whitney U = 238, n = 39 and 13, p = 0.646, Mann-Whitney U = 237, n = 39 and 13, p = 0.655 and Mann-Whitney U = 234, n = 39 and 13, p = 0.403 respectively)

Humpback dolphins also spent a high proportion of time feeding (95%) in the unsheltered open areas rather than in the channels and sheltered shallow areas. A large amount of time was spent travelling in the channels and in shallow water social behaviour increased (Table 7.2).

However, in all cases the differences were not significant (feeding: Kruskal Wallis, H = 4.8, n = 36, p = 0.089; travelling: Kruskal Wallis, H = 2.85, n = 36, p = 0.242; social behaviour: Kruskal Wallis, H = 3.97, n = 36, p = 0.137 and resting: Kruskal Wallis, H = 2.05, n = 36, p = 0.357).

Group sizes

23 groups of bottlenose dolphins consisting of up to 6 individuals and 35 groups larger than 6 dolphins were seen. All types of behaviour were observed in these two group categories (Table 7.3), and the differences in the proportion of time performing feeding, travelling, social behaviour and resting, did not differ significantly (Mann- Whitney U = 352.0, n = 17 and 35, p = 0.292; Mann Whitney U =290.0, n = 17 and 35, p =0.891; Mann-Whitney U = 225.5, n = 17 and 35, p = 0.163; Mann- Whitney U = 298.0, n = 17 and 35, p =0.865 respectively).

For humpback dolphins, only 6 groups had up to 6 members and 30 groups were larger than 6 members. Groups larger than 6 dolphins exhibited all types of behaviours, but groups ≤ 6 dolphins did not perform social behaviour (Table 7.4). The differences in the proportion of time spent feeding, travelling and resting were not significant between these two group categories (Mann- Whitney U = 60.0, n = 6 and 30, p = 0.210; Mann Whitney U =136.5, n = 6 and 36, p =0.051; Mann-Whitney U = 84.00, n = 6 and 30, p = 0.815 respectively).

Table 7.1. The proportion of time (%) bottlenose dolphins spent feeding, travelling, socialising and resting in three distinct habitats types (unsheltered, channels and shallow shoals) between December 1995 and December 1997 (standard deviation in brackets).

Habitat	Feeding	Travel	Social	Resting	Sightings
Unsheltered	82.1 (28.1)	10.4 (25)	7.3 (15.2)	0.13 (0.81)	39
Channels	75.3 (36.2)	10.0 (28)	13.8 (29.0)	0.76 (2.77)	13
Shallow shoals	-	-	-	-	0
Mean	80.5 (30.1)	10.3 (26.2)	8.94 (19.4)	0.29 (1.60)	-

Table 7.2. The proportion of time (%) humpback dolphins spent feeding, travelling, socialising and resting in three distinct habitats types (unsheltered, channels and shallow shoals) between December 1995 and December 1997 (standard deviation in brackets).

Habitat	Feeding	Travel	Social	Resting	Sightings
Unsheltered	95.0 (5.8)	2.5 (5.0)	2.5 (5.0)	0	4
Channels	53.3 (36.5)	35.3 (39.6)	8.05 (22.8)	3.33 (11.9)	18
Shallow shoals	49.6 (36.6)	31.1 (34.9)	18.2 (26.9)	0	14
Mean	56.5 (36.6)	30.0 (36.3)	11.4 (23.6)	1.7 (8.5)	-

Table 7.3 The proportion of time (%) bottlenose dolphins spent feeding, travelling, socialising and resting, when occurring in groups of ≤ 6 dolphins or > 6 dolphins between December 1995 and December 1997 (standard deviation in brackets).

Group size	Feeding	Travel	Social	Resting	Sightings
≤ 6 dolphins	83.5 (33.0)	13.5 (33.3)	2.4 (7.5)	0.6 (2.4)	17
> 6 dolphins	79.0 (28.9)	23.7 (8.7)	12.1 (22.5)	0.1 (0.8)	35
Mean	80.5 (30.1)	10.3 (26.2)	8.94 (19.4)	0.29 (1.60)	52

Table 7.4 The proportion of time (%) humpback dolphins spent feeding, travelling, socialising and resting, when occurring in groups of ≤ 6 dolphins or > 6 dolphins between December 1995 and December 1997 (standard deviation in brackets).

Group size	Feeding	Travel	Social	Resting	Sightings
≤ 6 dolphins	38.3 (46.6)	61.7 (46.6)	0.0 (0.0)	0.0 (0.0)	6
> 6 dolphins	60.2 (34.1)	23.7 (31.1)	13.7 (25.3)	2.0 (9.3)	30
Mean	56.5 (36.6)	30.0 (36.3)	11.4 (23.6)	1.7 (8.5)	36

DISCUSSION

Circadian and seasonal rhythms are more intense in coastal areas and are therefore likely to effect the prey occurrence/ abundance and therefore the occurrence, distribution and behaviour of coastal dolphins (Klinowska 1991).

Bottlenose dolphins

In Maputo Bay, feeding was the behaviour in which dolphins spent the highest proportion of time, implying either low prey abundance or small size prey at feeding areas. Dolphins spent less proportion of time travelling, socialising and resting. The relative duration of behaviours did not change significantly between seasons, daylight periods, tides, water depth or group size, but some trends occurred. Possibly, the relatively short mean observation time and the coincidence of the study area with feeding area resulted in the dominance of feeding over all other behaviours.

The same pattern was also observed in Plettenberg Bay (Saayman & Tayler 1973) and Kvarneric', northern Adriatic Sea (Bearzi *et al.*1999), but it contrasts with the findings off the Kwazulu-Natal coast, South Africa, where bottlenose dolphins spend a large proportion of time travelling (Peddemors 1995). Dominance of travelling over feeding was observed at the open coast areas along the Central Texas coast (Lynn 1995), in the Gulf of California (Ballance 1992) and along the San Diego coast, California (Hanson & Defran 1993). Probably, habitats in Maputo Bay prey distribution reduces travelling needs. However, along large open coastlines, prey may be generally scarce and concentrated at few locations, such as reef and angling areas (Peddemors 1995) or estuaries (Ballance 1992), and therefore dolphins may move more often, between feeding areas.

Despite that the north-eastern part of Maputo Bay is a feeding area, dolphins also showed, in small proportion, other behaviours (travelling, social and resting), implying that the habitats of Maputo Bay are multi-purpose for dolphins. This was also observed in Kwazulu-Natal (Peddemors 1995), Sanibel Island, Florida (Shane 1990), Central Texas coast (Lynn 1995) and Gulf of California (Ballance 1992) and Zanzibar, Tanzania (Stensland et al. 2006). In Plettenberg Bay, peaks of social and resting behaviours occurred after feeding peak (Saayman & Tayler 1973) or feeding, feeding/travel behaviour in the Kvarneric,, northern Adriatic Sea (Bearzi *et al.*1999).

Dolphins spent a small proportion of time resting in Maputo Bay. Resting behaviour has been rare during daylight, at Sarasota Bay (Barros 1993). But a tracked dolphin of Tampa Bay rested more during night and early morning (Mate *et al.*1995). This suggests that this behaviour may possibly dominate at other daily periods in Maputo Bay.

The lack of seasonal differences on the duration of behaviours in Maputo Bay contrasts with findings of the Kwazulu- Natal coast and Plettenberg Bay, South Africa, where bottlenose dolphins increased feeding during winter time (Peddemors 1995, Saayman et al. 1972), as in Texas coast (Bräger 1993, Lynn 1995). It was suggested that increased feeding in winter compensate the heat-loss by dolphins caused by the decrease in sea water temperature (Cockcroft & Ross 1990a). Nevertheless, there was no consistent seasonal pattern in Kvarneric, Adriatic Sea, but there was a trend towards reduction of travel from spring to fall (Bearzi *et al.* 1999). The seasonal changes in water temperature in Maputo Bay are very small (Chapter 2) and may therefore not affect the energy demands of dolphins significantly (Cockcroft & Ross 1990a). However, these patterns may not also be visible at areas where prey density is low, as in Kvarneric (Bearzi *et al.*1999).

The frequency and percent of time allocated for surface social behaviour was small, but increased slightly in winter. The duration of social behaviour was expected to increase substantially (Peddemors 1995) when large groups occurred during winter in Maputo Bay (Chapter 3). These findings suggest that social behaviours (including mating) occur throughout the year. However, off the Kwazulu- Natal coast, the percent of duration of social behaviour was small and varied seasonally, increasing during cold season (autumn to spring) (Peddemors 1995). but at Sanibel Island, Florida, the percent of occurrence of social behaviour did not change seasonally (Shane 1990). At Kvarneric, Adriatic Sea social behaviours peaked at different seasons between years (Bearzi *et al.* 1999). These patterns suggests that habitat features influence occurrence and duration of social behaviour of dolphins.

In Maputo Bay, the social behaviour displayed by few dolphins in large groups was ignored, because of the type of sampling method used, which was scan-sampling (Altmann 1974). Usually, mating and other social behaviours are displayed by some dolphins in large groups, where other individuals display diverse behaviours (Saayman *et al.* 1973). Therefore, the constraint of the method used to record the behaviour resulted in negative bias for social behaviour. This could be overcame by analysing the social behaviours in small groups and avoid large feeding aggregations.

There are strong relationships between daylight and tides, and between tides, dolphin group size and the degree of shelter of habitats in Maputo Bay (Kalk 1995). Their influences on dolphin behaviour pattern are associated.

Despite the lack of significant influence of daylight on duration of the behaviours, there was a pattern of high percent of feeding in early morning, a decrease as the day progresses and a an increase again in the evening. Travelling and social behaviour increased in the afternoon, after the feeding bouts. These are consistent with the activity pattern observed in Plettenberg Bay (Saayman *et al.* 1973), in Sanibel Island, Florida (Shane 1990), Texas (Bräger 1993, Lynn 1995) and partially in theKwazulu-Natal coast (Peddemors 1995). However, bottlenose dolphins did not show any distinct diurnal behaviour cycle at Sarasota Bay, Florida (Irvine *et al.* 1981) and Kvarneric, Adriatic Sea (Bearzi *et al.*1999). This indicate that dolphin behaviour shows plasticity according to the habitat.

The habitat features of Maputo Bay, namely the topography and tides may cause a less cyclic prey availability throughout the day. Prey availability influence diurnal dolphin activity on other species: hawaiian spinner dolphins that rest and socialise during the day in shallow waters and feeding during the night in the deep waters on the scattered layer organisms (Norris & Dohl 1980a). Dusky dolphins at the Gulf of San José, Argentina, feed during the day and rest during early morning and during the night (Würsig & Würsig 1980),

In Maputo Bay, behaviours peaked at distinct tyde marks, with feeding peaking at high and low tides, travel decreased at high tides and did not occur at low tide, when social behaviour peaked, decreasing subsequently from rising to ebb tides. This indicates that despite the lack of significant differences, tides have some influence on behaviour. Bottlenose dolphins in Maputo Bay occurred away from intertidal areas, but their feeding behaviour appears to follow a tidal cycle, that possibly influence prey species availability. Tides influence some particular behaviours at other locations and other species. Bottlenose dolphins at Gulf of San Jose, Argentina followed fish movements, which were associated with tides (Würsig & Würsig 1979).In contrast, at Plettenberg Bay, bottlenose dolphins behaviour was not influenced by tides (Saayman *et al.* 1973; Klinowska 1986). Dusky dolphins, however, travelled under influence of tides nearshore, but their activity offshore was not related with tides (Wursig 1982). Hector's dolphins at deep areas (≥ 20m) of Arakoa Bay, New Zealand did not have strong associations with tides, despite that they seemed to move against the tidal current (Stone *et al.* 1995).

Bottlenose dolphins were only observed in two types of habitats in Maputo Bay; the channels (including that adjacent to a coral reef) and the unsheltered open sea (the pass to the Ocean). In both areas, feeding prevailed over all other behaviours, while social behaviour and resting prevailed in the channels. However the duration of the behaviours did not differ significantly between habitats, indicating that they have similar importance for this species in Maputo bay is similar.

In most studies, the behaviour pattern of bottlenose dolphins varied significantly between habitat types. In open waters, bottlenose dolphins spend a high proportion of time travelling: Off the Kwazulu- Natal coast, travelling prevailed in sandy bottom areas, feeding at reefs and angling areas and social behaviours occurred at locations of onshore-offshore movements (Peddemors 1995). Off San Diego, California, the bottlenose dolphins spent most of their time travelling (Hanson & Defran 1993) while feeding predominated in Gulf of Mexico waters near shore (estuaries) and was replaced by travelling away from estuaries (Ballance 1992). In Central Texas coast, travel dominated over feeding in all habitats, but the proportion of feeding activity was higher in deep areas (the channels and jetties) than in shallow waters (Lynn 1995). These patterns are responses to different prey distribution among habitats.

However, in Kvarneric, Adriatic Sea, bottlenose dolphins had no distinct areas for specific behaviours, but foraged at deeper areas near rocky reefs borders, slopes and areas of strong marine currents (Bearzi *et al.* 1999).

Groups of bottlenose dolphins were significantly larger in the unsheltered open sea than in channels (Chapter 3). However, percent of duration of the different behaviours did not differ significantly between group categories. Changes did not occur on the duration of feeding behaviour, but larger groups socialized more, while smaller groups increased their proportion of time allocated to travel.

Large groups are usually temporary coaslescence of different social units (Saayman *et al.* 1973) that provide chances for more active surface social interactions between dolphins including establishment of hierarchy, courtship and mating. In small groups, less social activity could be a consequence of existing established social relationships between individuals, but the high travelling activity could either be caused by boat disturbance or less prey at the shallow habitats. .

In Galveston Bay, Texas, small groups were seen milling, and large groups were feeding, travelling and socialising (Fertl 1994). Similarly, in Central Texas coast (Lynn 1995) and Kvarneric , Adriatic Sea (Bearzi *et al.*1999) social behaviour occurred in larger groups.

Humpback dolphins

Throughout the Indo-Pacific Oceans, the humpback dolphin prefers shallow waters, often associated with inshore habitats (Ross 1979, Pilleri & Pilleri 1979, Corkeron 1990, Saayman *et al.* 1972, 1979; Guissamulo 1993; Durham 1994; Porter 1995; Karczmarski 1996, 2000, Jefferson 1998, 2000, Jefferson & Karczmarski 2001).

The prevailing behaviours of humpback dolphins in Maputo Bay were feeding and travelling, while social and resting behaviours were observed less. The percent of time this species spent travelling was higher than that for bottlenose dolphins, because it has tide-related movements between extensive intertidal shallow waters and deep channels/open sea habitats (Chapter 4). In Maputo Bay, the proportion of time allocated to feeding was higher (57%) than that in Algoa Bay (46%), (Karczmarski 1996) while travelling had a similar proportion of time in both bays. Large feeding areas occur in Maputo Bay while in Algoa Bay feeding took place at restricted rocky outcrops where feeding took place were only found in a restricted area, whose access was not restricted by tides (Karczmarski 2000, Karczmarski & Cockcroft 1999).

In South Africa, the proportion of time spent feeding was high in Algoa Bay (Karczmarski 1996, Karczmarski & Cockcroft 1999), while travelling prevailed in Plettenberg Bay (Saayman & Tayler 1973) and these differences were related to differences in habitat structure and distribution of feeding areas (Karczmarski 1996, Karczmarski . 2000).

In Maputo Bay, groups of humpback dolphins were large (Chapter 4), but most social and feeding behaviours were performed by few (3-5) individuals. The focal method of studying behaviour (Altmann 1974), does not allow the quantification of these behaviours because it emphasizes the behaviour carried out by more than half of the individuals. Dos Santos & Lacerda (1987) reported difficulties in distinguishing different behaviours of schools of bottlenose dolphins at the Sado Estuary, because dolphins often combined two behaviours. This study did not resolve this issue, but this could be overcame by adopting a procedure that also records the occurrence of secondary behaviours in groups (Tyack *et al.* 2000).

In Maputo Bay, humpback dolphins travelled slowly in narrow channels and over seagrass meadows and interrupted their movements for foraging/feeding behaviour (Chapter 4), implying patchy prey distribution along their route. This opportunistic feeding may be a strategy to cope with the unexpected low prey abundance in other habitats. Off the coast of South Africa, humpback dolphins feed on a diversity of species, despite a preference for estuarine and reef dwelling prey (Barros & Cockcroft 1991, 1999). Humpback dolphins off Hong-Kong foraged on low-trophic levels and small prey-size in response to prey depletion caused by fisheries (Porter *et al.* 1997). It is possible that in Maputo Bay, the same causes (disturbance and large-size prey depletion) both in the western and southern parts of the Bay (Massinga & Hatton 1997), at the west coast off Inhaca (Chuquela 1996) and in the southern Bay of Inhaca Island (de Boer *et al.* 2001), may increase the proportion of time allocated to opportunistic feeding (combined travelling and foraging) in the humpback dolphins.

Travelling behaviour of humpback dolphins from shallow waters to channels was obligatory because the intertidal areas, which they frequented, were inaccessible during low tides (Kalk 1995, De Boer 2000) and dolphins could only return in the rising tides. Staying in the nearest tidal pools and mangrove creeks could expose them to danger of capture by humans, a limited amount of prey available or cause stranding.

However, at open coast, travel is mainly carried out as a foraging strategy (Saayman *et al.* 1979; Karczmarski 1996).

Social behaviours such as leaping and chasing were often performed by young dolphins, when groups travelled slowly from shallow areas into channels and the open sea. In the Indus Delta Region, young dolphins leaped more frequently than adults (Zbinden *et al.* 1977). The reasons for leaping are unknown. Social behaviour occur for several reasons, such as establishing dominance or mating (Saayman *et al.* 1973; Peddemors 1995), when new immigrants joined the stable groups and for play and reinforcement of social bonds between group members. In the deep channels of the north-eastern part of the Maputo Bay, distinct sub-groups engaged in different types of behaviours, including social behaviours .

The relative duration of behaviour did not change significantly between seasons, despite the increase in social behaviour during summer coinciding with the influx of immigrants (Chapter 6), which however did not alter group size and occurrence (Chapter 4). This suggests that, in general, prey availability is maintained throughout the dolphins range, despite existing evidences of varying prey abundance inferred by the seasonal changes of catches of artisanal fishery between seasons (De Boer *et al.* 2001). In Algoa Bay, South Africa, humpback dolphins increased time for feeding during winter in a small reef patch (Karczmarski & Cockcroft 1999).

The diurnal behaviour pattern of humpback dolphins in Maputo Bay consisted of a feeding behaviour increasing between the morning and noon (12:00) decreasing after 14:00 hours. Travelling was high in the morning and moderate between noon towards late afternoon. Dolphins socialised more during late morning and late afternoon, when the percent of the time spent feeding or travelling decreased, and resting occurred at noon (12:00 – 14:00h). Nevertheless, this pattern was not significantly associated with the daylight, possibly because prey availability in Maputo Bay may not change significantly the daylight in the dolphin habitats. Dolphins move between two ecological zones (shallow areas and deep channels) caused by the tidal range. The semi-diurnal tidal cycle vary through the daylight in Maputo Bay (Kalk 1995). Most sightings were recorded when low tides occurred at with midday. This increased the time allocated to travel behaviour throughout the morning and late afternoon, when dolphins moved between shallow water areas and deep channels. The peak of resting behaviour during mid-day occurred probably because dolphins reached safe deeper water driven by tides after they have completed feeding sessions. Bottlenose dolphins of the shallow Sarasota Bay, Florida, did not show any diurnal pattern of movement (Irvine *et al.* 1981), but a daylight influenced activity pattern of humpback dolphins occurred in Algoa Bay (Karczmarski 1999) and in Plettenberg Bay (Saayman & Tayler 1979). Apparently a more daylight pattern occurs at small feeding areas, while areas of continuous habitat where prey is equally available may mask this pattern.

The percent of time allocated to feeding behaviour by humpback dolphins in Maputo Bay increased from rising tide, through high, ebb and low tides, but the proportion of time spent travelling showed a reverse trend, peaking at high tide. The percent of time dolphins socialized peaked at rising and ebb tides, and dolphins rested at low and rising tides. However, tides did not affect significantly the percent of duration of different behaviours. In Sarasota Bay, large groups of bottlenose dolphins also moved with tides (Irvine *et al.* 1981).

In Maputo Bay, circadian tides vary throughout the daylight, and the tide range exposes the extensive intertidal areas in the south of the Bay (Chapter 2; Kalk 1995). Dolphins have to move between two different ecological areas, one at the shallow areas that they exploit during high tide and another at deep channels, or when dolphins have achieved a safe place during low tides. The availability of shallow water habitats only at high tide, determines the increased percent of time allocated for travelling during rising and ebb tides, when dolphins have to move to or from the deep channels. The social behaviour peaks during low tide, when coalescence of different groups at deep channels, increasing interactions or because members reinforce their social bonds, while they wait for the tides to return to the shallow areas. Possibly, the movement caused by tides also created opportunities for exchange of group membership in Maputo Bay. Changes of types of social behaviours, from play at ebb tides to sexual behaviour at low and rising tides were observed and need to be examined.

Near the Robberg Peninsula, in Plettenberg Bay, the behaviour activity of humpback dolphins was influenced by tides, which also conditioned the use of two different ecological zones (Saayman & Tayler 1972). However, in Algoa Bay, feeding was the only behaviour that increased at high tide (Karczmarski 1996, Karczmarski & Cockcroft 1999).

During low tides, in areas of shallow water of Maputo Bay, humpback dolphins face risks of human disturbance and of stranding because fishing activity intensifies in the channels of the southern Bay of Inhaca Island (de Boer 2000, de Boer *et al.* 2001). In May 1992, 5 humpback dolphins were hunted and killed in a mangrove creek south of Inhaca Island, Maputo Bay, during low tide (Guissamulo 1993). However, ,in Bazaruto Bay, central Mozambique, humpback dolphins beached to feed in shallow channels during low tide (Peddemors & Thompson 1994), but this happened away from the prime fishing areas, where human disturbance was low. Bottlenose dolphins in St. Augustine, Florida frequented rivers and creeks at high tide and returned to the Bay during low tide (Schevill & Bakus 1960). On the contrary, Hector's dolphins at Arakoa Harbour moved into the Bay without any tidal influence at depth ≥ 20m, but moved inshore at falling tides and offshore of the Bay at rising tides (Stone *et al.* 1995).

Humpback dolphins seen in the unsheltered open water areas, spent a large proportion of time feeding, while an increasing proportion of time was dedicated to travelling and social behaviours in the channels and shallow waters (Table 7.2). This suggests that either feeding or prey capture is more difficult in deep channels. In Plettenberg Bay, humpback dolphins spent a high percent of time feeding and travelling in unsheltered areas (open sea), while in sheltered areas, were they also foraged, they performed social interactions and rested more time (Saayman & Tayler 1972). Off Kwazulu- Natal coast, at Tugela Bank, where preys density is high, the proportion of sightings when dolphins foraged was similar to that of in Maputo Bay. However, a high proportion of the sightings made outside Tugela Bank consisted of travelling behaviour (Durham 1994), possibly, because of relatively poor prey abundance or uneven prey distribution. A subsequent study, demonstrated that humpback dolphins feed more inshore, near the harbour entrance and rested more offshore (Atkins *et al.* 2004).

Courtship and mating events, that are social behaviours were only observed in the channels west of Inhaca Island, when groups coalesced. This may possibly help males find females in estrous and stay with them when groups move dispersing into shallow waters at rising tides in Maputo Bay. This is supported by the increasing social behaviour in shallow habitats (Table 7.2). Karczmarski (1996) described the mating behaviour as very active and intermittent, with dolphins performing courtship and aggressive behaviours for longer periods.

Behaviour was not different between different group sizes, but social behaviour was not observed in groups ≤ 6 dolphins. However, because only six groups of ≤ 6 dolphins were observed, these results must be considered preliminary. Possibly, disturbance caused by boats prevented the absence of social behaviour in small groups, or small groups do not engage often in surface social behaviours and may use more sub-surface social signs. However, small groups of bottlenose dolphins in the Gulf of Guayaquil, Equador, performed social interactions 1-2 hours after collective feeding of large groups (Felix 1994).

Feeding also occurred in the deep channels (up to 10 m deep) off the western coast of Inhaca island, north-eastern Maputo Bay. Here dolphins formed large groups and often herded prey co-operatively, by forming a barrier and synchronizing the swimming to avoid prey escape between the channel and the shallow shoals. However, the final prey capture was not coordinated, since all dolphins dispersed to pursue and catch fish, behaving differently to bottlenose dolphins, which showed co-operation when feeding on schooling prey (pers. obs.). In the Indus Delta Region, Zbinden *et al.* (1977) observed humpback dolphins feeding individually in areas where Scianidae fish (which produce sound) were abundant, but in aggregations in deep waters outside the areas were Scianidae species occurred.

Possibly, the formation of tight schools by humpback dolphins in deep areas of north-eastern Maputo Bay reduces predation risks from sharks. The shark fishing carried out in north-eastern Maputo Bay, suggests that sharks may be more frequent there. Off the Kwazulu- Natal coast, South Africa, humpback dolphins are subject to attacks by sharks and most scars were observed at the paler ventral portions of the body (Cockcroft 1991).However these scars were not observed in humpback dolphins in Maputo Bay, suggesting either low level of shark attacks or lack of record on photographs of individuals, because most occur in ventral areas (Cockcroft 1991) and the lack of dead dolphin specimens.

Interactions between species

Distribution of humpback and bottlenose dolphins overlapped in eastern Maputo Bay. Humpback dolphins often moved northward during low tide (Chapter 4) to areas frequented by bottlenose dolphins (Chapter 3). Small schools of bottlenose dolphins frequented the channels in the Bay mostly at high tide and during late afternoon (Chapter 3) in areas (reef in the south of the Bay) frequented by humpback dolphins at low tide (Chapter 4). However, large distance movements were shown by humpback dolphins. There was a low percentage of joint sightings of the two species (sightings of schools of mixed species). However, in the open sea (in north-eastern Maputo Bay), bottlenose dolphin occurrence was independent of tides (Chapter 3). The only two sightings of mixed schools of bottlenose and humpback dolphins occurred at ebb and low tide, when humpback dolphins moved northward (Chapter 4), when the shallow intertidal areas were flushed (drained), because of the largest tide range (Overvest 1997). In these events, both species were seen feeding, but no inter-specific co-operation was observed. It is not known if the two species fed on the same prey during the joint occurrences. However, Barros & Cockcroft (1999) observed an overlap in the diet of bottlenose and humpback dolphins off the Kwazulu- Natal coast.

Humpback dolphins tolerate a wide range of water transparency; frequenting excessively turbid waters associated with river mouths (Ross *et al.* 1989; Chapter 4) and frequented shallower waters than bottlenose dolphins (Ross *et al.* 1989; Durham 1994). Barros & Cockcroft (1999) suggested that bottlenose dolphins tolerated humpback dolphins by behavioural displacement. However, in Moreton Bay, Australia, bottlenose dolphins dominated over humpback dolphins when feeding behind trawlers, because they were numerous, but no aggressive behaviour between the species was reported (Corkeron 1990). In Plettenberg Bay, mixed schools of these species were only observed when engaged in travelling and play behaviours (Saayman & Tayler 1979). Possibly, small schools of humpback dolphins may travel in the open sea, gaining extra protection or awareness against predation. In the Indus Delta region, humpback dolphins seldom moved into the open sea where bottlenose dolphins occurred, suggesting that they have mutually exclusive territories (Zbinden *et al.* 1977). However, in Maputo Bay, mixed schools of the two species were observed feeding in the same area without any apparent conflicts, despite that bottlenose dolphins occurred in larger numbers. The sample size was however very small for drawing consistent conclusions about these interactions.

Assuming that bottlenose dolphins were dominant over humpback dolphins, this dominance may only be displayed when the prey resource is scarce. When feeding on large schools of fish, bottlenose dolphins may probably tolerate other species of dolphins, in the same way that they tolerated terns and gannets feeding in the same assemblages of prey in Maputo Bay (personal observations).

Interactions between species may be very advantageous, as the case of associations between spinner dolphins and spotted dolphins in the eastern tropical Pacific Ocean and in Hawaiian waters (Johnson & Norris 1986). Bottlenose dolphins in the eastern tropical Pacific formed mixed schools with other species of small cetaceans (Anganuzzi 1991), which helped to improve foraging and reduced predation risks. Possibly, bottlenose dolphins tolerated mixing with the small groups of humpback dolphins, because they may not compete strongly for prey, but the low frequency of sightings of schools of mixed species composition, indicate that these interactions are uncommon.

However, interaction between species may commence long before the species mix physically, because they may be aware of the presence of other species by listening their sounds produced by another species at a distance. These inshore species may have similar sound repertoire to describe prey abundance, or know each other repertoire, so that they may mix when a large school of prey has been located by another species.

In summary, overlap in habitat use occurred in the channels and unsheltered areas, but mixed schools were only observed in the unsheltered open sea, where feeding behaviour prevailed at low tide. Humpback dolphins moved to shallow areas at high tide to feed on other resources. It is unknown if the humpback dolphin movements to shallow areas alleviates competition with bottlenose dolphins.

CHAPTER 8. CONCLUSIONS & CONSERVATION RECOMMENDATIONS

GENERAL CONCLUSIONS

Bottlenose dolphin

Bottlenose dolphins occurred at low frequency throughout the year in Maputo Bay (36% of surveys): some individuals appeared to be frequent visitors, suggesting they range outside the Bay area. The number of sightings per hour of survey (SPUE), the number of dolphins observed per hour of survey (NPUE) and mean group size were significantly higher during winter. This correlates with the increase in fish catches and changes of fish species composition of the shrimp-trawling fishery in the Bay (Sousa 1989), and on which dolphins may forage (Ross 1979, Cockcroft & Ross 1983, 1990a, Peddemors 1995). Most sightings occurred in clear water, with a sandy bottom. Group sizes ranged between 2 and 150 individuals and the mean group size was 27.5 (S.D.= 32.2) dolphins, which is smaller than the group size estimates from the east coast of South Africa (Findlay *et al.*, 1992). This suggests that within the Bay, bottlenose dolphins may have relatively low food resources, and consequently individuals disperse, proliferating in small groups. Group sizes did not differ significantly between daylight intervals, spring and neap tides and depth, implying that these do not effect group size (Chapter 3).

Most identified individuals (59%), were adults of undetermined sex and juveniles, and all had low site fidelity (occurring in <10 % of months). In addition, 68% occurred only in a single season, implying that a large number of individuals are transient. A small number of resident dolphins in Maputo Bay consisted of nursing females and few other adults of undetermined sex, suggesting that the Bay is a breeding and nursing area. Dolphins sighted < 5 times showed the highest variability in the number of days between re-sightings, and nursing females that were the most frequently re-sighted dolphins, had a large, but less variable mean number of days between re-sightings (Chapter 3). There was a temporary winter influx of individuals into the Bay, and these dolphins mixed with the frequently seen dolphins. It could not be established whether these influxes influenced reproduction.

On average, each bottlenose dolphin individual interacted with 33.3 (S.D.=24.5) affiliates and this increased significantly as the number of re-sightings increased, implying that dolphins with high site fidelity interacted with many dolphins. Consequently, nursing females, that have high site fidelity, had the highest number of affiliates, while juveniles had the lowest number of affiliates. The number of affiliates did not differ significantly among individuals sighted > 3 times.

Eighty five percent of associations between pairs of identified individuals were observed, suggesting that the exchange of group membership is high.

The mean coefficient of association between identified individuals was 0.30 showing the prevalence of weak and fluid associations (Bräger *et al.* 1994 and Smolker *et al.* 1992). Only two pairs, consisting of adults of undetermined sex, (0.39%) were more strongly associated (CA = 0.8) (Chapter 3). These were suspected to be adult males, because of their strong coefficient of assotiation that represents strong functional associations (Wells *et al.* 1986, Felix 1997). Coefficients of association between individuals of different age and sex categories were significantly different, suggesting that these influence group organization, as found by Cockcroft & Ross (1990a) on the Kwazulu-Natal coast, South Africa. On the other hand, identified dolphins of undetermined sex had the highest levels of association, implying that their groups are stable groups or that some members form highly stable functional associations (Wells 1991). Low coefficients of association were found between nursing females, possibly because they had different reproductive and parturition times and therefore, they increased their site fidelity in the Bay at different times.

The assignment of associations of dolphins into clusters, showed that dyads (pairs) are the main form of associations between individuals (CA > 70%), despite their diverse sex and age composition (Chapter 3). Larger groups associated at lower Bray-Curtis similarity levels (60 and 30%). It is interesting that all dolphins re-sighted most often were assigned to a single cluster, suggesting that they may form a separate dolphin community.

Bottlenose dolphins had a restricted distribution in the Bay: many sightings occurred at the pass between the Ocean and the Bay and a few sightings of small groups of dolphins occurred inside the Bay, near the coral reef off the western coast of Inhaca Island. They occurred throughout the daylight period, but the number of sightings differed significantly between depth intervals: low number of sightings at depth < 2 m, implying that their habitat excluded intertidal areas. Eighty three per cent of sightings occurred within 3 km from shore, 64% within 2 km and 35% occurred within 1 km (Chapter 3), showing that they use a wide and varied habitat. Few sightings occurred in the deep channels of the middle and in the western coast of the Bay during winter, suggesting that bottlenose dolphins seasonally adjust their habitat size in the Bay. This feature has been observed in other areas of the world (Cockcroft & Ross 1990a; Cockcroft *et al.* 1990b; Peddermors & Cockcroft 1993; Felix 1994; Kenney 1990; Wilson *et al.* 1997).

Bottlenose dolphins used the area near Portuguese Island (near the pass between the Ocean and the Bay) significantly more than the area near a coral reef on the west coast of Inhaca, possibly because of different abundance of prey and disturbance by humans. The reef may not support large feeding groups for extended periods and in addition it is subjected to disturbance by powerboats and fishing takes place nearby, decreasing prey abundance. However the activity index for behaviours did not differ significantly between these sectors (Chapter 3), implying that both areas are suitable for any type of behaviour. Feeding was the prime activity of bottlenose dolphins in Maputo Bay (80%). Neither season, nor semi-diurnal tide nor daylight time influenced the pattern of behaviour. There was a slight increase in the time allocated to social and resting behaviours in the unsheltered areas in relation to the channels (Chapter 7), possibly because dolphins are less harassed there by boats and fishing activity.

Non-directional movements of dolphins were more frequent than directional ones, because feeding and other behaviours predominated over travel behaviour. The direction of dolphin movements was not influenced by tides (Chapter 3).

The appearance of many new individuals in winter suggests bottlenose dolphins enter and leave the Bay during winter (Chapter 5), implying that the population is seasonally open. Most dolphins had low site fidelity and occurred during winter (Chapter 5), suggesting seasonal movements of dolphins from other areas into the Bay, perhaps in search of food and mates (Cockcroft & Ross 1990c, Peddemors & Cockcroft 1993, Wells 1992).

Using various models, population estimates for bottlenose dolphins in Maputo Bay varied between 170-526 individuals, but no model was satisfactory due to the large confidence intervals, because the assumptions of independence of sightings and heterogeneity of capture probabilities were violated. However, the small extent of the study area, allowed for individuals to range outside it increasing the heterogeneity of capture probabilities and therefore this low precision. Numbers estimated from closed population models were consistent with those obtained from the regression method (Chapter 5), because are both based on the discovery curve and do not consider emigration/immigration and mortality of individuals throughout the duration of the study

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The mean density estimate of 1.82 (S.D.=0.73) dolphins/km^2, was high for Maputo Bay, but was lower than the density off the east coast of South Africa (Ross *et al.* 1989). Lower density in Maputo Bay may be caused by its extensive habitat, which allows dispersal of groups. The density of dolphins was higher in the eastern part of Maputo Bay than in other parts of the Bay, possibly because dolphins avoided areas of intense fishing activity (Guissamulo 1993, Guissamulo & Cockcroft 1997).

No seasonal peak in births was observed, possibly because the sample size was small. However, this may imply that the Bay has favourable conditions for calf survival and nursing throughout the year. This contrasts with the winter influx of bottlenose dolphins off Kwazulu-Natal coast, that increased the parturition during winter (Cockcroft & Ross 1990c, Peddemors & Cockcroft 1993). There were large inter-annual differences in the number of births, possibly caused either by differences in the search and study effort distribution between years (Chapter 3), or by differences in births detected or availability of estrous females.

The recruitment rate was 0.02, mortality rate was 0.04 and the crude birth rate was 0.067. The birth rate was inflated by the presence of transient female-calf pairs in the Bay. This highlights the role of Maputo Bay as breeding and nursing area for this species. The recruitment rate was low because a high number of transient female-calf pairs left the Bay or, possibly, of calf mortality, though evidence for this is lacking.

The population growth rate of this species is estimated to be above 4-5% (Chapter 5). This value is high and should be considered preliminary because it derives from a small sample size and from minimum estimates of life parameters. Nevertheless this growth rate is either an over-estimated or that the population is hyper-compensating its growth after instability (Reilly & Barlow 1986). However, no instability is known to this population before or during this study,

Humpback dolphins

Humpback dolphins occurred throughout the year in Maputo Bay, but were only observed on 21% of surveys. This low sighting rate was probably a result of; a concentration of effort outside the shallower areas; navigability limitation; low density of the species, and possibly low sightability of small groups or individual dolphins. The low species density has been recorded along the coast of South Africa (Ross 1979, Cockcroft 1991, Findlay *el al.* 1992, Karczmarski 1996) and elsewhere in their range in the Indo-Pacific Region (Baldwin *et al.* 2002, Parra *et al.* 2004, Stensland *et al.* 2006, Wang *et al.* 2007) The sightings per hour of survey (SPUE) and the number of dolphins observed per hour of survey (NPUE) did not differ significantly between months, seasons and neap and spring tides. Season may not influence occurrence because these dolphins have a wide prey preference (Cockcroft & Ross 1983; Barros & Cockcroft 1991, 1999; Jefferson & Karczmarski 2001). Dolphins moved into and out of intertidal areas, following the tides in the study area. They frequented nearshore, shallow turbid waters (mean water clarity = 2.98, ± 1.54 m) (Chapter 4). Along the east coast of South Africa, humpback dolphins prefer near-shore shallow water, described by Saayman *et al.* (1972), Ross (1979), Cockcroft (1991), Peddemors & Thompson (1994), Karczmarski (1996, 2000), Karczmarski *et al.* (1998), and Durham (1994), while their relation with turbid water was described by Durham (1994) and Cockcroft (1991). This habitat choice is also typical of other populations such as the Hong Kong (Jefferson 2000), Eastern Taiwan Strait (Wang *et al.* 2007), Moreton Bay (Parra et *al.* 2004) and Arabian Region (Baldwin *et al.* 2002)

Group sizes ranged between two and 25 individuals and the mean group size was 14.91 (S.D.= 7.32) dolphins. This mean group size was high, compared with those off South Africa (Findlay *et al.* 1992, Karczmarski *et al.* 1999a). Possibly, in Maputo Bay, small groups share partially overlapping ranges and coalesce at the channels during low tide, when shallow intertidal waters, are not accessible. However, the relatively large group size found in Maputo Bay may mean that groups gather in the Bay for social reasons. Group sizes did not differ significantly between months, daylight time, depth, season and neap and spring tides (Chapter 4). Most sightings occurred outside the intertidal areas. Groups may not change their size significantly in relation to depth because the depth range of large areas of Maputo Bay lies within the reported range of this species (<15 m) (Ross 1979, Corkeron 1990, Karczmarski 1996, Karczmarski *et al.* 2000, Jefferson & Karczmarski 2001). River run-off had little influence in eastern Maputo Bay (Kalk 1995). However, its influence on the group size could not be established.

Many groups consisted of individuals of mixed age and sex composition (Chapter 4) possibly promoted by coalescence of small groups in the deep channels during low tide. This may also be because of the existence of nursing females, that attract other individuals and maintain long term association with older calves (Karczmarski 1996, Karczmarski *et al.* 1999b, Jefferson & Karczmarski 2001).

Fifty-two dolphins were identified by their natural markings (notches and scars on their fins). Some identified individuals exhibited long term site fidelity (>5 years), but 45 % of dolphins (mostly adults of undetermined sex and juveniles) occurred only in one season. This diverse site fidelity pattern may be caused by temporal and spatial changes of resources (prey, mates and nursing areas). Dolphins photographed and identified < 5 times showed the highest variability in the number of days between re-sightings. However, adults of undetermined sex were less re-sighted and had greater number of days between re-sightings and were similar to those of adult females. Adult females were more frequently re-sighted and had the least variable mean number of days between re-sightings (Chapter 3). There was a temporary summer influx of individuals into the Bay, and these dolphins mixed with the frequently seen dolphins. It could not be established whether these influxes influenced reproduction.

Influxes of new individuals occurred during summer, but did not influence group size (Chapter 4), possibly because the competition for food encouraged other individuals to leave the Bay. However, it is unknown whether this influenced reproduction. A number of males and most nursing females were resighted frequently and over multiple years, suggesting that they form a resident community in the Bay, and that eastern Maputo Bay is a nursing area.

Some long-term affiliations between individuals were observed and a few lasted for at least five years, while 35% of dolphins were sighted only once (Chapter 4). The number of affiliates per identified individual increased significantly as the number of times it was resighted increased. Adult males had the highest number of affiliates, followed by adult females and juveniles, but the number of affiliates did not differ significantly between individuals sighted >3 times (Chapter 4), highlighting the effect of transient dolphins. Differences in the observed number of affiliates of individuals of different age and sex groups were caused by unequal site fidelity of the individuals. About 93 % of possible associations between pairs was observed. Most had

Coefficients of Association (CA) in the range of 0.21 to 0.40, while 32.5% had CA > 0.40 (Chapter 4). This reflects the mixing of resident and transient individuals in the Bay. Coefficients of Association did not differ significantly between dolphins of different age classes, but were sex and age linked: adult females had the highest level of association; adult males the lowest coefficient of association (Chapter 4). As among bottlenose dolphins, group organization of humpback dolphins may be based on sex and age classes. However, the high level of association between females indicates that most females spent a substantial amount of time in the Bay and formed a common grouping, independent of their reproductive stage.

Dyads and a trio, which included a dyad of nursing females, were associated at Bray-Curtis similarity levels varying between 60% and 80%. Pairs consisting of adult females and juveniles were strongly associated (Bray-Curtis similarity <75%) (Chapter 4), suggesting that juveniles were probably weaned calves that maintained strong bonds with their mothers (Krushinskaya 1986, Karczmarski 1996, Jefferson & Karczmarski 2001), that remain associated with their mothers or occupy the same range (Krushinskaya 1986, Wells 1992, Cockcroft & Ross 1990a). However, juveniles associated weakly with adults of undetermined sex. The two known mature males were associated with different clusters of females and other dolphins, suggesting that they belong to different dolphin communities in Maputo Bay.

Most sightings occurred along the west coast of Inhaca Island, eastern Maputo Bay. There were few sightings, in the middle of the Bay and only one sighting was made in an intensively fished area of Maputo Bay. However, this distribution also reflects a decreasing survey effort across the Bay, as previous studies showed that dolphins were abundant at eastern Maputo Bay (Guissamulo & Cockcroft 1997).

Ninety-one percent of sightings occurred within 2 km of the shoreline, of which 67% were within 1 km from shore (Chapter 4), implying that the dolphin habitat is narrow, as they frequented inshore areas: seagrass meadows, tidal channels, reefs and mangrove creeks. This is consistent with findings of Ross (1979), Findlay *et al.* (1992), Karczmarski (1996) and Karczmarski *et al.* (1998), Jefferson & Karczmarski (2001), along the east coast of South Africa, Stensland *et al.* (2006) in the south coast of Zanzibar, Wang *et al.* (2007) in the Eastern Taiwan Strait.

Sightings occurred after 08:00, and were more frequent in the afternoon. Probably this was caused by the relationship between tides and daylight in Maputo Bay: low tides occurring around mid-day, forcing dolphins to abandon intertidal areas and moved into the deeper areas of the Bay, after 08:00. The high frequency of afternoon sightings occurred because dolphins spent most of the daylight time in the study area, when low tide occurred around mid-day (11:00 to 13:00). Depth did not significantly influence the distribution of sightings in the Bay (Chapter 4), possibly because the Bay depth range is within that reported for the species in the region (Ross *et al.* 1987; Findlay *et al.* 1992; Durham 1994; Karczmarski 1996, Karczmarski *et al.* 1998, Stensland *et al.* 2006).

Humpback dolphins used all of the western coast of Inhaca and Portuguese Islands, exploiting the diverse habitats (seagrasses, channels, reef, shallow inshore open sea) and, the coefficient of area use of the area along the coast of Portuguese and Inhaca Islands did not change significantly. However, the largest number of sightings occurred in a channel along the west coast of Inhaca, which was primarily used for traveling.

The mean activity index for feeding, traveling and socializing did not differ significantly between sectors along the west coasts of Portuguese and Inhaca Islands (Chapter 4). However, feeding was the main activity (57% of time) carried out by humpback dolphins in Maputo Bay, followed by travel behaviour (30% of time), implying that daily tidal cycles and spatial differences of prey density determine dolphin movements within the study area. Social behaviour was the third important activity (11% of time). Nevertheless the daylight duration of behaviours did not differ significantly between seasons, semi-diurnal tides, daylight time or group sizes (Chapter 7). The duration of feeding behaviour decreased from the unsheltered open sea towards the channels and shallow shoals of the south of the Bay (Chapter 7). Social behaviour, in turn, increased as the degree of shelter of the habitat increased, but the duration of travel behaviour was higher in the channels (Chapter 7), implying that these habitats have different importance to the daylight behaviour of humpback dolphins.

The proportion of directional and non-directional movements was not significantly different, though directional movements occurred on 57% of occasions (Chapter 4). The direction of movement was significantly associated with semi-diurnal tide stages (Chapter 4), because tides determine habitat availability and safety of dolphins: in the channels, dolphins exhibited either directional movements, when arriving to or departing shallow waters, while non-directional movements occurred during social, resting or feeding behaviours. Therefore, tides affect the movements of dolphins differently in different habitats of the Bay.

Most individuals (65%) were first identified during the first seven surveys, though these occurred over two periods: January-April 1992 and March-April 1996. However, an influx of individuals observed in January-February 1997 suggests that the first two survey periods also occurred during the time of seasonal influx of individuals into the Bay. The seasonal influxes created a stair-shaped curve, typical of other populations in the region (Durham 1994, Karczmarski 1996, Karczmarski *et al.* 1999b, Atkins *et al.* 2004, Keith *et al.* 2002). In contrast this pattern was not observed in the south coast of Zanzibar (Stensland *et al.* 2006) and Eastern Taiwan Strait (Wang *et al.* 2007), where the level of re-sightings was high.

Using various models, the population estimates of humpback dolphins in Maputo Bay ranged between 104.8 and 308 individuals. These estimates varied widely and had low precision, possibly because of violations of model assumptions (equal sightability) and distribution of effort, and should be considered preliminary. Closed population estimates (173-178 dolphins) appear to better represent the numbers of humpback dolphins inhabiting Maputo Bay and neighbouring areas. The density is 0.87 (S.D.= 0.39) dolphins/km^2 and the mean relative density is 0.09 (S.D. = 0.06) dolphins/km of survey. These are lower than the estimates from east coast of South Africa, possibly, because dolphins disperse in the extensive shallow areas of Maputo Bay. The long-term site fidelity and large number of re-sightings, suggests that there is a resident community of humpback dolphins that interacts seasonally with transient dolphins.

Few births were recorded and there was no evidence of seasonality. The crude birth rate was 0.09, mortality rate 0.100 and the recruitment rate (at six months) 0.048. The crude birth rate and recruitment rate (at six months) were low. The estimated growth rate is expected to be in the region of 2% (Chapter 6) and represents a population approaching its carrying capacity (Reilly & Barlow 1986). Lower population growth rates are typical of populations that are deacelerating their growth (Begon *et al.* 1996), due as a result of resource scarcity, given the restricted habitat requirement of humpback dolphins. The population appears vulnerable because occasional killing of female-calf pairs occurs and the species interactions with fisheries (Guissamulo & Cockcroft 1997, de Boer 2001).

SUMMARY WITH DISCUSSION OF RESEARCH QUESTIONS

This study had five main aims:

- What (tidal cycles, turbidity, depth, daylight and season (changes in water temperature)) influences the occurrence, group size, area use and behaviour of dolphins in Maputo Bay?
- What is the site fidelity and group dynamics of dolphins in Maputo Bay?
- What are the population estimates and reproductive parameters of dolphins species inhabiting Maputo Bay?
- How is the fishing activity and habitat degradation interfering with the ecological requirements of the dolphins species inhabiting Maputo Bay?
- What strategies must be considered for coastal development to ensure sustainable conservation of the inshore marine habitats? What practices must be adopted to ensure the co-existence of the inshore dolphins and development?

Bottlenose dolphins

Occurrence of bottlenose dolphins was not influenced by tides and daylight, but was limited to depth > 2m, avoiding intertidal areas, and increased significantly during winter and were common in clearer water. Dolphins extended their distribution towards the west of Maputo Bay when river run-off was low. However, no relationship between river run off and occurrence could be established, because bottlenose dolphins occurred at eastern Maputo Bay, which is less affected by river run off, while rivers are located at the western coast of the Maputo Bay and water mass circulation drives the river run-off outside the Bay. The relationship between river run-off and occurrence of bottlenose dolphins can be investigated by comparing data obtained from seasonal aerial and boat surveys in relation to the extent of changes of water salinity, caused by river run off across the Bay. Seasonal fish surveys stratified across the salinity gradient caused by river run-off may also investigate the influence of river run off on occurrence and distribution of dolphin prey species.

Group sizes of bottlenose dolphins were not influenced by depth, tides and daylight in the Bay. However, season significantly influenced the group size of bottlenose dolphins, through immigration and increase of group members during winter. This is supported by the winter influx of newly identified individuals. Investigating the extent of the dolphin habitat inside and outside Maputo Bay and the seasonal variations on abundance of prey and/or identifying the potential predators and their distribution may explain this.

The area use by bottlenose dolphins was not influenced by daylight and depth. The influence of season, run off and turbidity on the area used by bottlenose dolphins was not investigated, because of large differences in occurrence and restricted study area. This can be best examined through a long-term longitudinal study. Likewise, river run-off was not examined, because its influence on salinity and turbidity was small in the eastern Maputo Bay, where the species was more abundant. Nevertheless, the apparent extension of distribution of bottlenose dolphins towards the western Maputo Bay during winter suggests some influence of season that needs further verification. Therefore, it is recommended that a more stratified boat, or aerial, survey across the

Bay be undertaken to resolve this relationship. Additional insight would be provided by the deployment of satellite tags on some of the most re-sighted individuals, as it may derive useful data to measure the extent and timing of area use.

Bottlenose dolphins spent a greater proportion of time feeding, and the proportion of time spent by bottlenose dolphins performing each type of behaviour was not influenced by tides, daylight or season. However, depth, measured in the form of degree of shelter of habitats (unsheltered open sea, channels, and shallow intertidal areas) appeared to inversely influence the proportion of time that this species spent feeding and performing social behaviours.

The influence of turbidity was not examined, because this required both temporal and spatial measurements of turbidity and behaviours, during each observation period, and this could not be measured consistently during the study.

Site fidelity of photographed and identified bottlenose dolphin individuals was age and sex linked. A large proportion of adults and juveniles of unknown sex were transient, they were common during winter in Maputo Bay. The fact that they consisted of all different ages, suggests that complete social units (groups of mixed composition) visit Maputo Bay seasonally. Genetic profiles would clarify this.

Many nursing females were seen frequently in the Bay and they became resident long before parturition, but some abandoned the Bay when their calves were at least six months old, implying that Maputo Bay is a nursing area for bottlenose dolphins.

The assessment of the relationship between the degree of site fidelity, age and sex and the verification of the suggestion that entire social units seasonally visit the Bay can be investigated by combining photo-identification technique with the collection of biopsies of known resident and transient dolphins. Genetic analysis should, amongst other information, reveal the sex and degree of relatedness between individuals.

Identified bottlenose dolphin individuals had a variable number of affiliates (identified dolphins that occurred together it in the same groups), that increased as the number of times individuals were photographed. The social structures of bottlenose of Maputo Bay were fluid. Nursing females had strong associations between themselves, with some adult dolphins of unknown sex and with juveniles. This suggests that sex and age had an important role in the social organization. The role of sex and age on social organization can be improved by comparing data from photo-identification with data collected from genetic analysis of biopsies obtained from the dolphins in Maputo Bay. Genetic analysis can also provide insight of the degree of relationship between the communities of transient and resident dolphins, through analysis of transfer of genes, relatedness between individuals of distinct sexes and their degree of association.

The proportion of bottlenose dolphin individuals with natural markings in groups was satisfactory (0.69) for the use of mark recapture techniques, but the population estimates varied had poor precision, because some assumptions (independence of sightings and equal sightability of individuals) of the population models were violated and of a large number of transient individuals. Nevertheless, the use of mark recapture is useful because it also permitted the collection of data for the study of the social organisation of the dolphins.

Accurate estimates must be pursued, primarily by increasing sampling effort and effort distribution through out the time in the Bay and by extending mark-recapture methods to areas outside the Bay to cover the most of the geographic range of the species and by reduction of other potential sources of bias. In addition, where dolphins are common, other methods such as boat line transect methods can be used, instead of mark-recapture.

Likewise the estimated reproductive parameters (number of births, survival rates of calves and seasonality of births) require improvement. The current estimates of reproductive parameters of bottlenose dolphins are derived from small and short-term data sets and may not represent the actual average population parameters. In addition, the influence of long-term cyclic factors, such as el Ninõ, and catastrophic events cannot be accounted for, with small data sets. Bottlenose dolphins had large inter-annual variations on number of births, that might have been influenced by the monthly distribution of effort, and the disappearance of mother-calf pairs from the study area. This can be resolved by extending research to other areas outside Maputo Bay to cover most of the dolphins range. Survival parameters (calf and adult mortality) can be obtained through a long-term monitoring of individuals in the population.

Mortality of adult dolphins in fishing gear could not be obtained, because of the difficulty in monitoring all fishing landing areas in Maputo Bay. In addition, the study was carried out in eastern Maputo Bay and fish catches could be monitored mainly at western part of Maputo Bay, where most of the fishing fleet occurs. A dedicated extensive and long term study is required to obtain these types of data. In addition, the current dolphin protection measures and law enforcement procedures penalises fishermen for incidentally catching dolphins, and therefore, prevents them reporting any dolphin by-catch. However, there is a need to develop trust between researchers and fishermen, and the fisheries management authorities must stimulate the fishermen to report and deliver of by-caught dolphins to the authorities.

Humpback dolphins

Occurrence of humpback dolphins was not influenced by semi-lunar tide cycles, tide amplitudes, turbidity, depth and season. However, the humpback dolphins occurrence was significantly influenced by daylight, as they were only observed in the area only after 08:00 and seen more often during afternoons. Their occurrence before 08:00 cannot be investigated through the extension of boat surveys to shallow waters, because of navigability. Therefore, the deployment of satellite or radio tracking on a few resident individuals may provide these types of data and other behaviours (such as the precise movement pattern and their surface behaviours).

The influence of river run off could not be established, because this had little influence on the study area. Considering that estuaries and mangroves are some of the critical habitats of humpback dolphins, they would be more exposed to the effect of run-off. The intense fishing at western Maputo Bay prevents an examination of the influence of river run off. An alternative can be to examine this at estuaries exposed to less fishing effort or in Maputo Bay, investigate the occurrence of dolphins through comparisons of seasonal surveys (aerial or boat surveys) carried out both inside and outside the Bay, and compared with measurements of salinity across the water column at selected sampling areas. Tracking individuals with satellite transmitters can also provide useful indications.

Group sizes of humpback dolphins were not influenced by depth, tides, daylight and season in the Bay. Despite the summer influx of humpback dolphins, it appears that some individuals also emigrate during this season, or at least redistribute in the Bay. Investigating the extent of the dolphin habitat inside and outside Maputo Bay and the seasonal variations on abundance of prey and/or potential predators and their distribution may help explain these different responses to season.

The area use was not influenced by depth, but was influenced significantly by daylight, because dolphins frequented the area more often during the afternoon and tides. The small size of the study area and the large differences of data samples between seasons prevented an examination of seasonal influence on area use. This can be best examined through a long-term longitudinal study and extension of the study area. Therefore, it is recommended that a more stratified boat, or aerial, survey across the Bay be undertaken to resolve this relationship.

The proportion of time spent by humpback dolphins performing each type of behaviour was not influenced by tides, daylight and season. Humpback dolphins spent a large proportion of time feeding and traveling, moving extensively inside Maputo Bay between shallow intertidal flats and deep channels. The impact of extensive traveling on the condition and reproductive success of humpback dolphins is unknown, since they spent less daylight time feeding than bottlenose dolphins. Possibly, this can be assessed studying their day and night behaviours and area use using satellite transmitters deployed on photographically identified individuals, of distinct sex and age. In addition, the decrease of depth (and degree of shelter of habitats: unsheltered open sea, channels, and shallow intertidal areas) appeared to decrease the proportion of time that humpback dolphins spent feeding and increase the social behaviours.

The influence of turbidity was not examined, because this required both temporal and spatial measurements of turbidity and behaviours. This could not be measured consistently during the study. Humpback dolphins occur quite commonly in turbid waters. However, turbidity may not influence behaviour because dolphins use more acoustics for communication and orientation.

Site fidelity of photographed and identified humpback dolphin individuals was age and sex linked. A large proportion of adults of unknown sex and juveniles were transient, and were frequent during summer in Maputo Bay. Most nursing females were sighted frequently in the Bay, and their occurrence in Maputo Bay increased long before parturition. Some abandoned the Bay when their calves were at least six months old. Maputo Bay appears therefore to be a good nursing area for female humpback dolphins.

The relationships between the degree of site fidelity, age and sex and the verification of the suggestion that entire social units seasonally visit the Bay can be investigated by combining photo-identification technique with the collection of biopsies of known resident and transient dolphins for genetic analysis of the sex and degree of relatedness between individuals.

The number of affiliates of identified humpback dolphin individuals increased with the number of times individuals were photographed. In general the social structure of humpback dolphins of Maputo Bay was fluid, with a large proportion of weak associations between pairs of identified individuals. Females had strong associations between themselves, with some adult dolphins of unknown sex and with juveniles, suggesting that sex and age had an important role in the social organization. Nevertheless, the understanding of factors regulating social organization can be improved by comparing data from photo-identification with data collected from genetic analysis of biopsies obtained from the dolphins in Maputo Bay.

The humpback dolphin population estimated from mark-recapture had poor precision, possibly, because of the violation of some assumptions (independence of sightings and equal sightability of individuals) of the population models. The proportion of individuals with natural markings (0.52) was satisfactory. Accurate population estimates must be pursued, by increasing sampling effort, and by extending mark-recapture methods to areas outside the Bay to cover the major part of the geographic range of the species and through reduction of other potential sources of bias.

Humpback dolphins had large inter-annual variations in the number of births. This might have been influenced by the monthly distribution of effort. The survival of some calves could not be certified, because they disappeared from the area with their mothers. Likewise the estimated reproductive parameters (number of births, survival rates of calves and seasonality of births) require improvement. The current estimates of reproductive parameters for both species were derived from small and short-term data sets and may not represent the actual average population parameters, or incorporate the influence of long-term cyclic factors and catastrophic events. Extending research to other areas and a long term monitoring of survival of individuals and their reproduction may increase the precision.

Mortality of adult dolphins in fishing gear could not be obtained, because of the difficulty in monitoring all fishing landing areas in Maputo Bay. In addition, the study was carried out in eastern Maputo Bay whereas fish catches were landed and most of the fishing fleet operates in western Maputo Bay. A dedicated extensive and long term study is required to obtain these types of data.

Some of the ecological requirements of dolphin populations in Maputo Bay were identified during this study: Bottlenose dolphins use open, clear water and reef areas of eastern Maputo Bay, but do not frequent intertidal areas. During winter their distribution extends towards the western part of the Bay.

Humpback dolphins are more restricted to inshore areas, including the extensive shallow intertidal areas of the Bay consisting of seagrass areas, rocky shores, reefs, and shallow channels near mangroves, and they therefore move extensively with tides. A large proportion of the dolphin populations are transient, and use the Bay seasonally, though most females spend a large portion of their time in the eastern Bay to nurse their calves.

CONSERVATION STRATEGIES

The western part of Maputo Bay has been intensively fished for shrimp (for export and tourist market) and for small pelagic and benthic fish species and there are signs of decline of fish catches and a reduction of fishing fleet (Tomás 2001, Loureiro 2001, Premegi 1995). This may increase exploration of other fishing areas of the Bay, including the eastern part of Maputo Bay, where dolphins are more common. This is exacerbated because a formal system to manage the distribution of fishing effort does not exist in the Bay.

At Inhaca Island, eastern Maputo Bay, the subsistence fisheries are expanding because it is the main source of subsistence and income of the people and there are areas of localized depletion of fishing resources and invertebrates in the fragile shallow areas (Kalk 1995, De Boer *et al.* 2001). Therefore, the susceptibility of dolphin populations to be by- caught or disturbed because of increased fishing activity is high. Therefore the expansion of human presence will also reduce quality of the environment and interfere with the dolphin ecological requirements, affecting their survival. The existence of a large proportion of transient dolphins shows that the carrying capacity of habitats of eastern Maputo Bay for dolphins is limited and varies seasonally, implying that any increase of unsustainable fishing activity can be harmful to the dolphin populations.

Quantitative evaluation of the biomass and productivity of the fishing resources, and assessment of the sustainable fishing yield are necessary to mitigate the impact of the fisheries on dolphins. In addition, research must evaluate the relative importance of Maputo Bay in relation to areas outside the Bay, and identify the prey of the two dolphin species. Knowing dolphin prey species will allow the measurement of the degree of competition between dolphins and fisheries, particularly if fishing practices that do not kill or cause harm to dolphins are allowed to expand. This knowledge will also provide information for the establishment of management quotas and conservation measures. Prey species can be studied by analyzing stomach contents of recovered dead dolphin carcasses by-caught in fisheries or by analysis of fatty acids obtained from biopsies.

Degradation of habitats on the western coast of Maputo Bay is presently caused by unplanned coastal development and the lack of integrated coastal zone management system and lack of capacity to enforce dolphin protection. The western area of Maputo Bay is experiencing a localized, but severe microbial water pollution (Fernandes 1996), and a devastation of mangroves forests and seagrass through increased exploitation of wood and benthic invertebrates by thousands of poor people (Massinga & Hatton 1997).

The relatively isolated eastern part of Maputo Bay, however, is now experiencing an increasing impact because coastal resources are limited and comprise the only source of subsistence for poor people (Premegy 1995, Chuquela 1996, De Boer *et al.* 2001). The development is slower, however, because of logistic difficulties and existing proclaimed coastal and marine protected areas around Inhaca Island (Kalk 1995). Nevertheless, the impact of people on marine resources is already high and expanding (De Boer 2000, De Boer *et al.* 2001).

However, coastal zone development in Maputo Bay and the rest of Mozambique is inevitable, because of its economic importance for Mozambique and as a source of subsistence for people, that, live near the coast and have, for centuries, exploited marine and coastal resources (Newitt 1997). Therefore, many habitats will be transformed and consumptive and non-consumptive exploitation of resources will take place. Concerns for coastal degradation of habitats in Maputo Bay are increasing as the research on the knowledge of the status of the marine environment increases (Massinga & Hatton 1997, MICOA & UICN 1988,Kemp *et al.* 2000).

Some practical solutions for conservation of cetaceans have been developed, and there are efforts to find alternative innovative solutions for other threats (Reeves *et al.* 2003). Nevertheless, the economies of the developing countries, like Mozambique, are unable, without external support, to implement some of these solutions (UNEP 1997), mostly because they divert limited resources from development (Mulvaney 1996, Kemp *et al.* 2000).

Any strategy to protect marine mammals must address the needs of the human population that inhabits the coastal areas, namely, ensuring the sustainable use of marine resources as a way to increase or maintain the quality of life. This approach will also protect the marine mammals, that are also dependent on the quality of the habitats. Consumptive exploitation of marine resources needs to be sustainable to allow its continued exploitation and warrants subsistence to human populations.

Therefore, the strategy to protect marine mammals and sustainably manage the coastal habitats needs to consider both immediate (short-term) and long term actions.

Immediate (short term) actions must be based on the application of a precautionary conservation measure (Mayer & Simmonds 1996, Parra *et al.* 2004, Wang *et al.* 2007), to allow research to improve our knowledge about dolphins, and subsequently, refine their management. In the case of Maputo Bay this means: to increase the protection and management of coastal waters of eastern Maputo Bay, by limiting the current fishing effort, prohibiting the introduction of new fishing techniques that can cause incidental mortality of dolphins, proclaiming temporal and spatial closed fishing seasons when applicable, as well as improve management of any current and recreational and development activity at sensitive habitats. Any new proposed development must include in their environmental impact studies marine mammals and produce measures of impact, mitigation and an environmental management plan that addresses issues relating to dolphins and other marine mammals. Another short-term action should be an awareness program targeting fishermen, recreational operators and other users of marine and coastal resources of the Bay.

A long-term action must include the continuation, of applied research for management of marine mammals and their environment, fundamental research and the development of a management action plan to deal with sustainable management of coastal resources, including dolphins and their habitats.

This management action plan must aim at increased enforcement of fishing law, improve the management of fisheries, based on scientific knowledge of the capacity of the environment, partition of the fishing effort in the Bay spatially and temporally, disseminate the property rights of the sea to subsistence fishers, and address other threats to dolphins such as habitat degradation, noise and dolphin harassment.

In addition the management plan of Maputo Bay must promote responsible dolphin eco-tourism and recreational fisheries as a way to shift from the increasing consumptive use of resources towards non-consumptive use at eastern Maputo Bay.

DETAILED ACTION PLAN FOR DOLPHIN CONSERVATION IN MAPUTO BAY

The conservation of dolphins in Maputo Bay requires a strategy that addresses present and potential threats, source of disturbance and the knowledge of their ecology.

Goal: To ensure the long term ecological viability of the dolphin populations inhabiting Maputo Bay.

Objectives:

- Improve the status of the dolphin populations in Maputo Bay
- Prevent habitat degradation by current and future man made sources
- Allow maintenance or expansion of the dolphin populations habitats

This plan addresses anthropogenic (human induced) threats or sources of disturbance for dolphins. The following sections present briefly the list of threats and sources of disturbance.

Coastal development

Development is taking place along the coast of Bay and include the increasing human settlement and presence in the coastal dunes and beaches, construction of coastal protection infrastructures (such a piers, concrete barriers to reduce erosion) , marinas, bridges and tourist resorts. These bring several impacts to the marine environment which include modification of the nearshore waters flow, illumination of nearshore sea waters, increase sound emission into the water either by construction or recreational activities, increased pollution by disposal of solid (plastic, can, glass containers) and sewage effluents. These nearshore activities impact animals that frequent the inshore marine environment.

Recommended actions for coastal development include:

(i) the establishment of mandatory impact environment assessment prior to any coastal development and assess its impact on marine mammals.

(ii) the implementation and promotion of awareness and good practices such as proper disposal of discarded debris (plastic, cans and bottles) and sewage effluents to decrease or cease urban pollution,

(iii) awareness to the beach users and bathers on their impact on dolphins and the marine environment.

(iv) establishment of standards measures to minimize acoustic disturbance on dolphins by maritime activities

Recreational boat traffic

Two marinas and yatch clubs exists in Maputo Bay that promotes several recreational activities, which includes include moto-boats races and fishing competitions. Boats use powerful outboard engines, that produce high frequency sounds and the boat traffic extends to the areas of high dolphin abundance. Tourist resorts of Maputo City and Inhaca Island offers fishing tours as part of their guests recreational activities. The current level of traffic is not intense and constant throughout the year (it is high at weekends and throughout summer). Boats have been shown to disturb humpback dolphins (Ng & Leung 2003, Parra *et al.* 2004) and bottlenose dolphins (Lusseau 2006) and the exposure to long term disturbance may recline their relative abundance (Bedjer et al. 2006). The prospect for the development of marine based tourist recreational activity is increasing, following the planned developments in the north of Maputo City. Therefore, acoustic pollution and direct disturbance by boats will increase. In many locations, skippers tend to approach and follow dolphins by curiosity (personal observation) or sometimes, the waves generated by boats at high speed attract dolphins that bow riding them. These can harm, stress or displace them from their key habitats, depending on their intensity (Ng & Leung 2003; Lusseau 2006; Bejder 2006, Wang *et al.* 2007). Dolphins breed and nurse their calves in Maputo Bay and therefore, harassments can cause calf mortality and influence population growth (Mann & Watson-Capps 2005).

Acoustic disturbance by boats may also interfere with dolphin communication and ultimately disrupt their reproductive success, as dolphins may abandon the optimal areas and use less productive/unsafe areas, thus decreasing their survival.

The recommended actions include:

(i) to educate recreational skippers about the status of dolphins and ways to avoid disturbing dolphins,

(ii) to establish a code of conduct for boat skipper on how to interact with dolphins, that include the use to minimum speed at areas where dolphins are present and approaching protocols,

(iii) to establish the minimum distance and direction of boats when approaching dolphins.

(iv) at known areas of dolphin occurrence (such as the west coast of Inhaca Island), define the maximum boat speed and routes for boats

(v) To promote the use of noiseless boats (sail boats, wind surf, etc) for recreation

(vi) Regulate the use of jet-ski and other powerful engine boats in the Bay

Commercial vessels (ship traffic to the harbour)

Large commercial vessels pass across the Bay to access the Maputo City harbour, through a dredged access channel to the harbour which depth varies between 9 and 12 m at low speed and generate sound frequencies of large spectrum. Their potential for direct harassment of dolphins is low because of apparently low dolphin occurrence. However, their chances of vessels avoiding dolphins is also negligible, because they are constrained by the small width of the channel and limited maneuverability . This traffic will persist and has the tendency for growing as the trade and shipping of goods increases.

The importance of the dredged channel to dolphins is unknown, but appear to be relatively less frequented by dolphins, because of the general low density in western part of the Bay. Additional research is recommended along the dredged channel to establish its level of utilization by dolphins.

Urban pollution

There is an increasing development along the beach, especially through construction of resorts, mansions, petrol stations and restaurants. Their location near the sea level height, and their isolation from the main city sewage treatment plant result in the construction of several small independent sewage plants, leading to increased drainage of effluents to the existing water treatment plants in Maputo Bay. The level of microbial contamination of sea water along some sections of the beach of Maputo Bay was declared to have exceeded the minimum safety levels for humans to bath and the presence of *Vibrio cholerae* (the most deadly water contaminant bacteria) was found in the water. These sections of the beach have been closed to utilization by humans. Fernandes (1996) showed that the microbial pollution in the Bay have expanded towards the east.

Recommended actions include:

(i) Establishing another water treatment system to serve the resorts and residences located along the waterfront
(ii) Oblige the resorts and residences to have individual sewage disposal systems that can accumulate/retain their sewage effluent and prevent it from disposal in the sea
(iii) Promotes the use of water cleaning systems that will reduce the level of microbial and chemical contamination

Chemical pollution

The construction of car service stations nearshore is increasing. Chemical pollutants (mainly oil and lubricants that come from car wash are also discharged into sea without treatment), discharged without treatment and in addition spills take place at the harbours and these stations when oil. When large spills occur in seawater dispersants are used. However, they are more toxic to the environment.

It is therefore recommended that:

(i) service stations nearshore retain their effluents resulting from car wash.
(ii) Introduction of a system of recycling oil and lubricants to reduce pollution of waters of the Bay.

The Municipal authorities must:

(i) set the minimum standards for the quality of effluent and a implement mandatory procedure to deal with these types of pollution.
(ii) establish a monitoring system of these types of pollution in the marine environment

Agriculture pollution (pesticides, herbicides and ferlilizers)

Upstream of the rivers basins (Maputo, Umbeluzi and Nkomati rivers) discharging in Maputo Bay, there are several commercial farming activities, including mainly the sugar cane plantations. Large quantities of pesticides, herbicides and fertilizers are used and ultimately, through run off they are discharged in Maputo Bay, mainly in the wet season when river flow increases. Organochlorines are some of the pesticides employed in the sugar cane plantations and are known to accumulate through the food chain in the bottlenose and common dolphins along the coast of Kwazulu-Natal (Cockcroft *et al.* 1989b, Cockcroft *et al.* 1990a). There are no measures of the amount of pollutants loaded.

It is recommended to:

(i) describe and quantify the level and types of pesticides discharged in the rivers

(ii) promote the installation of water treatment plants at large scale farming operations and any large factories (such as sugar mills) to reduce the load of pesticides, herbicides and fertilizers and other chemicals.

(iii) Water management authorities must set the minimum level of pollutants allowed in the water effluents at the farms and establish a monitoring system.

(iv) Evaluate and monitor the level of chemical pollutants on dolphins in Maputo Bay, through analysis of biopsy samples

Entanglement and mortality of dolphins in fisheries operation

Several types of fisheries are practiced in the shallow waters (depth<10 m) of the south and western part of the Bay and include the artisanal gill net fishery, the shrimp trawl fishery and the beach seine for fish and shrimps. The largest and more extensive fishery is the artisanal gill net fishery, that takes pelagic species (mainly the kelee shad). The semi-industrial shrimp trawl industry has also a significant impact on the benthic environment of the shallow waters. Marine mammals interaction with fisheries have been documented worldwide (Fertl & Leatherwood 1997), including Maputo Bay (Guissamulo 1993; Guissamulo & Cockcroft 1998). Humpback and bottlenose dolphins are referred to interact with shrimp trawlers in Hong Kong (Jefferson 1998, 2000) and Australian waters (Corckeron 1990) and suffer mortality in the gillnet fisheries in Zanzibar (Amir *et al.* 2002). These interactions with fisheries may also influence their social structure of the species (Chilvers & Corkeron 2001). However, the most important impacts of fisheries are (i) entanglement and mortality of dolphins, (ii) resource depletion and (iii) acoustic disturbance by noise produced by the engines. It is important to document the level of disturbance of dolphins and the degree of mortality.

Recommendations for these may include :

(i) education and awareness for among fishers and public about the threats and status of dolphins
(ii) monitoring the level of entanglement and mortality of dolphins in the fisheries
(iii) to restrict the use of certain fishing gear (gill nets) in areas of high dolphin density
(iv) evaluation of the feasibility of introducing closed seasons at areas of high dolphin density
(v) evaluate of the feasibility of use of pingers or other repellent devices to reduce dolphin entanglement in nets in areas where fisheries may not be banned, but that may have high potential of entanglement.
(vi) To create a dolphin by-catch recovery and stranding network

Dredging

Dredging operations takes place every year at the ship access channel and in the harbour in Maputo Bay. The size of the sediment grain removed during dredging varies from coarse sand at deep areas to mud in the harbour. Sediments are removed from the access channel and deposited in the shallow waters of the south-western area of the Bay. In addition, dredging for the purpose of land reclamation around an island (Xefina Island) is planned in the near future, due to tourism development. The selection criteria of the site of sediment disposal are unknown as well as the impacts of the disposal on the bottom and water column. During dredging sediments are removed, displaced and re-suspended and any pollutants and the nutrients enter the water column, increasing the water turbidity. The duration, extent and effect of turbidity depends on the current and wind strength. This may impact bottlenose dolphins, that are negatively sensitive to decreased water transparency in eastern coast of southern Africa (Cockcroft *et al.* 1990b; Peddemors 1995, Guissamulo & Cockcroft 1998). In addition, the re-suspension of sediments increases locally the level of pollutants and therefore contaminates the food chain and ultimately impact on dolphins.

Recommendations

(i) To implement mandatory Impact Environment Studies for selection of the location of disposal of sediments and analyze their impact on dolphins and mitigation measures.

(ii) To conduct/promote research on dolphins occurrence and ecology at locations selected for sediment disposal, research is recommended.

(iii) To measure and monitor the level of pollutants in the sediments removed and their impact at the disposal site in the Bay.

Dolphin watch tourism

Tourism based on dolphins is a growing industry that has a very strong educational and awareness potential for marine conservation and may be an alternative job or income generation for fishers (Berggren *et al.* 2006). However, it has the strongest potential to disturb directly the dolphins and affect their behaviour pattern (Stensland *et al.* 2006; Bejder *et al* 2006; Lusseau 2006; Ng& Leung 2003). It may displace the dolphins from their optimal habitats and influence their survival.

Recommendations for these activity includes,

(i) licensing of operators, training of skipper and tour operator on dolphin behaviours,

(ii) the adoption of a strict code of conduct that establish the interaction time, the procedure of approach dolphins, the need to avoid feeding dolphins, number of boats simultaneously following/interaction with dolphins, interpreting the dolphin behaviour including alarm signs, the need to avoid disturbing the cow-calf pairs or schools, among other actions.

Creation of dolphin interest group/forum for Maputo Bay.

An action plan for dolphin conservation in the Bay needs a coordinating institution to address the issues raised and this may be a dolphin interest/working group. Its function will be to liase with several management authorities (water, fisheries, marine operations, tourism, municipality), research institutions, environmental organizations and community groups on dolphin conservation, identify and promote research needs.

Appendix 1. Geographic coordinates of main waypoints for boat surveys carried out in Maputo Bay between December 1995 and December 1997.

Waypoint codes	Names	Latitude (degrees South)	Longitude (degrees East)
EBMI	EBM	26.041667	32.898333
XE	Xefina Island	25.603333	32.683333
PE	Ponta dos Elefantes	25.960000	32.886667
MC	Machangulo	26.161667	32.798333
CT	Catembe	25.981667	32.548333
CD	Canal Direito	26.088333	32.841667
MA	Maritimo	25.951667	32.618333
PP	Ponta Ponduine	26.071667	32.903333
PR	Ponta Rasa	26.053333	32.895000
CB	Cockburn	25.945000	32.871667
RB	Baixo Ribeiro	25.913333	32.801667
RM	Maputo River	26.168333	32.685000
BC	Baixo Capitania	25.986667	32.755000
HI	Hotel Inhaca	26.000000	32.906667
BG	Baixo Gibao	25.976667	32.870000
BS	Banco do Saco	26.081667	32.925000
PM	Ponta Maone	26.025000	32.600000
P2	WPO2	26.008333	32.791667
PT	Santa Maria Peninsula	26.081667	32.951667
IP	Ilha dos Portugueses	25.973333	32.900000
GR	Banco Grande	26.033333	32.843333

Appendix 2. Time of beginning and end of each survey, and geographic coordinates of each leg during the boat surveys carried out in Maputo Bay between December 1995 and December 1997.

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
1	960217	1	MA-P2	15:00	25.951667	32.618333		26.008333	32.791667
		2	P2-IP		26.008333	32.791667		25.973333	32.900000
		3	IP_EBMI		25.973333	32.900000	17:00	26.041667	32.898333
2	960218	1	EBMI-MA	11:50	26.041667	32.898333	12:50	25.951667	32.618333
3	960218	1	MA-RB	12:50	25.951667	32.618333		25.913333	32.801667
		2	RB-MA		25.913333	32.801667	14:50	25.951667	32.618333
4	960224	1	MA-P2	11:00	25.951667	32.618333		26.008333	32.791667
		2	P2-EBMI		26.008333	32.791667	13:50	26.041667	32.898333
5	960302	1	MA-RM	11:00	25.951667	32.618333		26.168333	32.685000
		2	RM-BC		26.168333	32.685000		25.986667	32.755000
		3	BC-MC		25.986667	32.755000		26.161667	32.798333
		4	MC-PP		26.161667	32.798333	15:00	26.071667	32.903333
6	960303	1	EBMI-IP	11:00	26.041667	32.898333		25.973333	32.900000
		2	IP-MC		25.973333	32.900000		26.161667	32.798333
		3	MC-MA		26.161667	32.798333	14:00	25.951667	32.618333
7	960303	1	EBMI-IP	11:00	26.041667	32.898333		25.973333	32.900000
		2	IP-MC		25.973333	32.900000		26.161667	32.798333
		3	MC-MA		26.161667	32.798333	14:00	25.951667	32.618333
8	960304	1	EBMI-IP	12:00	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-EBMI		25.976667	32.870000		26.041667	32.898333
9	960316	1	MA-CT	10:00	25.951667	32.618333		25.981667	32.548333
		2	CT-XE		25.981667	32.548333		25.603333	32.683333
		3	XE-RM		25.603333	32.683333		26.168333	32.685000
		4	RM- CB		26.168333	32.685000		25.945000	32.871667
		5	CB-EBMI		25.945000	32.871667	15:00	26.041667	32.898333
10	960317	1	EBMI-IP	11:00	26.041667	32.898333		25.973333	32.900000
		2	IP-MA		25.973333	32.900000		25.951667	32.618333
11	960327	1	MA-CT	11:15	25.951667	32.618333		25.981667	32.548333
		2	CT-RM		25.981667	32.548333		26.168333	32.685000
		3	RM-IP		26.168333	32.685000		25.973333	32.900000
		4	IP-CD		25.973333	32.900000		26.088333	32.841667
		5	CD-PR		26.088333	32.841667		26.053333	32.895000
		6	PR-EBMI		26.053333	32.895000	14:30	26.041667	32.898333
12	960327	1	EBMI-CD	15:00	26.041667	32.898333		26.088333	32.841667
		2	CD-IP		26.088333	32.841667		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	17:00	26.041667	32.898333
13	960407	1	EBMI-HI	8:56	26.041667	32.898333		26.000000	32.906667
		2	HI-IP		26.000000	32.906667		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	15:08	26.041667	32.898333

Appendix 2 (continuation 1)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
14	960407	1	EBMI-HI	8:56	26.041667	32.898333		26.000000	32.906667
		2	HI-IP		26.000000	32.906667		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	15:08	26.041667	32.898333
15	960407	1	EBMI-HI	8:56	26.041667	32.898333		26.000000	32.906667
		2	HI-IP		26.000000	32.906667		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	15:08	26.041667	32.898333
16	960408	1	EBMI-BS	8:17	26.041667	32.898333		26.081667	32.925000
		2	BS-EBMI		26.081667	32.925000	10:34	26.041667	32.898333
17	960409	1	EBMI-PT	9:17	26.041667	32.898333		26.081667	32.951667
		2	PT-EBMI		26.081667	32.951667	10:24	26.041667	32.898333
18	960425	1	EBMI-MC	9:00	26.041667	32.898333		26.161667	32.798333
		2	MC-BC		26.161667	32.798333		25.986667	32.755000
		3	BC-C		25.986667	32.755000		25.981667	32.548333
		4	C-RM		25.981667	32.548333	11:50	26.168333	32.685000
19	960505	1	EBMI-PP	8:00	26.041667	32.898333		26.071667	32.903333
		2	PP-CD		26.071667	32.903333		26.088333	32.841667
		3	CD-EBMI		26.088333	32.841667	13:00	26.041667	32.898333
20	960505	1	EBMI-PT	8:00	26.041667	32.898333		26.081667	32.951667
		2	PT-CD		26.081667	32.951667		26.088333	32.841667
		3	CD-IP		26.088333	32.841667		25.973333	32.900000
		4	IP-EBMI		25.973333	32.900000	12:00	26.041667	32.898333
21	960505	1	EBMI-IP	15:00	26.041667	32.898333		25.973333	32.900000
		2	IP-EBMI		25.973333	32.900000	17:00	26.041667	32.898333
22	960512	1	EBMI-CD	15:00	26.041667	32.898333		26.088333	32.841667
		2	CD-BG		26.088333	32.841667		25.976667	32.870000
		3	BG-EBMI		25.976667	32.870000	17:15	26.041667	32.898333
23	960516	1	EBMI-PT	7:40	26.041667	32.898333		26.081667	32.951667
		2	PT-PR		26.081667	32.951667		26.053333	32.895000
		3	PR-IP		26.053333	32.895000		25.973333	32.900000
		4	IP-EBMI		25.973333	32.900000	12:00	26.041667	32.898333
24	960516	1	EBMI-PT	15:00	26.041667	32.898333		26.081667	32.951667
		2	PT-EBMI		26.081667	32.951667	16:00	26.041667	32.898333
25	960517	1	EBMI-PE	7:00	26.041667	32.898333		25.960000	32.886667
		2	PE-EBMI		25.960000	32.886667	11:40	26.041667	32.898333
26	960614	1	EBMI-BG	16:00	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	17:30	26.041667	32.898333
27	960615	1	EBMI-BG	11:00	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	13:10	26.041667	32.898333
28	960615	1	EBMI-BG	16:10	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	17:50	26.041667	32.898333

Appendix 2 (continuation 2)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
29	960616	1	EBMI-BG	15:30	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	17:50	26.041667	32.898333
30	960707	1	EBMI-BG	9:20	26.041667	32.898333		25.976667	32.870000
		2	BG-IP		25.976667	32.870000		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	12:40	26.041667	32.898333
32	960707	1	EBMI-PR	15:30	26.041667	32.898333		26.053333	32.895000
		2	PR-PP		26.053333	32.895000		26.071667	32.903333
		1	PP-PT		26.071667	32.903333	17:30	26.081667	32.951667
33	960713	2	EBMI-BG	13:00	26.041667	32.898333		25.976667	32.870000
		3	BG-MC		25.976667	32.870000		26.161667	32.798333
		4	MC-IP		26.161667	32.798333	15:30	25.973333	32.900000
34	960715	1	EBMI-IP	15:30	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-EBMI		25.976667	32.870000	17:00	26.041667	32.898333
35	960720	1	EBMI-IP	16:00	26.041667	32.898333		25.973333	32.900000
		2	IP-EBMI		25.973333	32.900000	17:30	26.041667	32.898333
36	960721	3	EBMI-BG	8:20	26.041667	32.898333		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	12:00	26.041667	32.898333
37	960721	1	EBMI-BG	16:20	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	17:20	26.041667	32.898333
38	960722	1	EBMI-GR	9:00	26.041667	32.898333		26.033333	32.843333
		2	GR-MA		26.033333	32.843333	11:00	25.951667	32.618333
39	960801	1	EBMI-BG	8:00	26.041667	32.898333		25.976667	32.870000
		2	BG-CD		25.976667	32.870000		26.071667	32.903333
		3	CD-BV		26.071667	32.903333		26.015000	32.900000
		4	BV-EBMI		26.015000	32.900000	13:00	26.041667	32.898333
40	960801	1	EBMI-BG	15:15	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	17:50	26.041667	32.898333
41	960803	1	EBMI-RM	7:30	26.041667	32.898333	10:30	26.168333	32.685000
42	960808	1	HI-MA	15:00	26.000000	32.906667	18:00	25.951667	32.618333
43	960823	1	MA-HI	10:30	25.951667	32.618333	14:00	26.000000	32.906667
45	961105	1	EBMI-BG	8:00	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	9:30	26.041667	32.898333
46	961105	1	EBMI-MA	11:00	26.041667	32.898333	12:00	25.951667	32.618333
47	970106	1	EBMI-BG	6:47	25.976667	32.870000		26.041667	32.898333
		2	BG-IP		26.041667	32.898333		25.973333	32.900000
		3	IP-PR		25.973333	32.900000		26.053333	32.895000
		4	PR-EBMI		26.053333	32.895000	8:35	25.976667	32.870000
48	970106	1	EBMI-BS	13:30	25.976667	32.870000		26.081667	32.925000
		2	BS-PR		26.081667	32.925000		26.053333	32.895000
		3	PR-EBMI		26.053333	32.895000	16:00	25.976667	32.870000
49	970106	4	EBMI-BG	16:20	26.041667	32.898333		25.976667	32.870000
		5	BG-EBMI		25.976667	32.870000	18:20	26.041667	32.898333

Appendix 2 (continuation 3)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
50	970107	1	EBMI-BG	5:35	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	7:30	26.041667	32.898333
51	970107	1	EBMI-BS	14:15	26.041667	32.898333		26.081667	32.925000
		2	BS-PT		26.081667	32.925000	15:50	26.081667	32.951667
52	970107	1	PT-EBMI	16:20	26.081667	32.951667	17:15	26.041667	32.898333
53	970108	1	EBMI-IP	7:30	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-EBMI		25.976667	32.870000	11:30	26.041667	32.898333
54	970108	1	EBMI-IP	7:30	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		1	BG-EBMI		25.976667	32.870000	11:30	26.041667	32.898333
55	970109	2	EBMI-IP	6:30	26.041667	32.898333		25.973333	32.900000
		1	IP-BG		25.973333	32.900000		25.976667	32.870000
		2	BG-IP		25.976667	32.870000		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	8:00	26.041667	32.898333
56	970116	1	EBM-BS	16:30	26.041667	32.898333		26.081667	32.925000
		2	BS-PT		26.081667	32.925000		26.081667	32.951667
		3	PT-EBMI		26.081667	32.951667	19:07	26.041667	32.898333
57	970117	1	EBMI-BG	9:25	26.041667	32.898333		25.976667	32.870000
		2	BG-IP		25.976667	32.870000		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	11:30	26.041667	32.898333
58	970118	1	EBMI-IP	12:30	26.041667	32.898333		25.973333	32.900000
		2	IP-EBMI		25.973333	32.900000	13:40	26.041667	32.898333
59	970119	1	EBMI-IP	7:50	26.041667	32.898333		25.973333	32.900000
		2	IP-PP		25.973333	32.900000		26.071667	32.903333
		3	PP-EBMI		26.071667	32.903333	11:45	26.041667	32.898333
60	980120	1	EBMI-PT	13:20	26.041667	32.898333		26.081667	32.951667
		2	PT-BS		26.081667	32.951667		26.081667	32.925000
		3	BS-EBMI		26.081667	32.925000	15:30	26.041667	32.898333
61	970121	1	EBMI-PT	11:45	26.041667	32.898333		26.081667	32.951667
		2	PT-BS		26.081667	32.951667		26.081667	32.925000
		3	BS-EBMI		26.081667	32.925000	14:00	26.041667	32.898333
62	970122	1	EBMI-MA	8:44	26.041667	32.898333	11:38	25.951667	32.618333
63	970122	1	MA-HI	15:50	25.951667	32.618333	18:00	26.000000	32.906667
64	970124	1	EBMI-PT	7:45	26.041667	32.898333	9:30	26.081667	32.951667
65	970124	1	EBMI-BS	16:15	26.041667	32.898333		26.081667	32.925000
		2	BS-PT		26.081667	32.925000	18:30	26.081667	32.951667
66	970125	1	EBMI-BS	9:48	26.041667	32.898333		26.081667	32.925000
		2	BS-PT		26.081667	32.925000	12:00	26.081667	32.951667
67	970126	1	EBMI-BG	8:38	26.041667	32.898333		25.976667	32.870000
		2	BG-IP		25.976667	32.870000		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	11:00	26.041667	32.898333

Appendix 2 (continuation 4)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
68	970208	1	EBMI-IP	8:30	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-EBMI		25.976667	32.870000	15:30	26.041667	32.898333
69	970210	1	EBMI-MA	6:30	26.041667	32.898333	9:38	25.951667	32.618333
70	970211	1	EBMI-IP	9:30	26.041667	32.898333		25.973333	32.900000
		2	IP-PE		25.973333	32.900000		25.960000	32.886667
		3	PE-EBMI		25.960000	32.886667	12:00	26.041667	32.898333
72	970212	1	EBMI-IP	16:00	26.041667	32.898333		25.973333	32.900000
		2	IP-PR		25.973333	32.900000	17:50	26.053333	32.895000
73	970221	1	EBM-PP	7:11	26.041667	32.898333		26.071667	32.903333
		2	PP-BV		26.015000	32.900000	8:13	26.088333	32.841667
74		1	EBM-PP	13:48	26.041667	32.898333		26.071667	32.903333
		2	PP-BV		26.071667	32.903333	15:08	26.088333	32.841667
75	970224	1	EBMI-BV	14:47	26.041667	32.898333		26.015000	32.900000
		2	BV-PP		26.015000	32.900000		26.071667	32.903333
		3	PP-EBMI		26.071667	32.903333	15:52	26.041667	32.898333
76	970225	1	EBMI-BV	7:10	26.041667	32.898333		26.015000	32.900000
		2	BV-PP		26.015000	32.900000		26.071667	32.903333
		3	PP-EBMI		26.071667	32.903333	9:02	26.041667	32.898333
77	970225	1	EBMI-BV	13:25	26.041667	32.898333		26.015000	32.900000
		2	BV-PP		26.015000	32.900000		26.071667	32.903333
		3	PP-EBMI		26.071667	32.903333	14:25	26.041667	32.898333
78	970225	1	EBMI-BV	15:12	26.041667	32.898333		26.015000	32.900000
		2	BV-PP		26.015000	32.900000		26.071667	32.903333
		3	PP-EBMI		26.071667	32.903333	17:25	26.041667	32.898333
79	970228	1	EBMI-BV	11:54	26.041667	32.898333		26.015000	32.900000
		2	BV-PP		26.015000	32.900000		26.071667	32.903333
		3	PP-BS		26.071667	32.903333		26.081667	32.925000
		4	BS-PT		26.081667	32.925000		26.081667	32.951667
		5	PT-EBMI		26.081667	32.951667	14:40	26.041667	32.898333
80	970228	1	EBMI-BG	17:25	26.041667	32.898333		25.976667	32.870000
		2	BG-IP		25.976667	32.870000		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	18:40	26.041667	32.898333
81	970307	1	EBMI-IP	16:07	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-PP		25.976667	32.870000		26.071667	32.903333
		4	PP-EBMI		26.071667	32.903333	18:00	26.041667	32.898333
82	970308	1	EBMI-PP	7:26	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	9:46	26.041667	32.898333

Appendix 2 (continuation 5)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
83	970308	1	EBMI-BV	11:00	26.041667	32.898333		26.015000	32.900000
		2	BV-IP		26.015000	32.900000		25.973333	32.900000
		3	IP-PP		25.973333	32.900000		26.168333	32.685000
		4	PP-EBMI		26.071667	32.903333	14:30	26.041667	32.898333
84	970308	1	EBMI-PP	16:09	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	18:28	26.041667	32.898333
85	970309	1	EBMI-PP	7:32	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	10:30	26.041667	32.898333
86	970309	1	EBMI-BV	12:05	26.088333	32.841667		26.015000	32.900000
		2	BV-PP		26.015000	32.900000		26.071667	32.903333
		3	PP-IP		26.071667	32.903333		25.973333	32.900000
		4	IP-PR		25.973333	32.900000		26.053333	32.895000
		5	PR-EBMI		26.053333	32.895000	15:30	25.976667	32.870000
87	970309	1	EBMI-PP	12:05	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-IP		25.976667	32.870000		25.973333	32.900000
		5	IP-EBMI		25.973333	32.900000	15:30	26.041667	32.898333
89	970309	1	EBMI-PP	16:40	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-EBMI		25.976667	32.870000	18:00	26.041667	32.898333
90	970310	1	EBMI-PP	7:49	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-BG		25.973333	32.900000		25.976667	32.870000
		4	BG-IP		25.976667	32.870000	10:04	25.973333	32.900000
91	970310	1	IP-BG	11:30	25.973333	32.900000		25.976667	32.870000
		2	BG-BV		25.976667	32.870000		26.015000	32.900000
		3	BV-PP		26.015000	32.900000		26.071667	32.903333
		4	PP-EBMI		26.071667	32.903333	14:30	26.041667	32.898333
93	970310	1	EBMI-PP	16:00	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	17:30	26.041667	32.898333
94	970313	1	EBMI-PP	16:29	26.041667	32.898333		26.071667	32.903333
		2	PP-IP		26.071667	32.903333		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	18:38	26.041667	32.898333
95	970314	1	EBMI-PP	12:14	26.041667	32.898333		26.071667	32.903333
		2	PP-BV		26.071667	32.903333		26.015000	32.900000
		3	BV-IP		26.015000	32.900000		25.973333	32.900000
		4	IP-EBMI		25.973333	32.900000	14:13	26.041667	32.898333

Appendix 2 (continuation 6)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
96	970315	1	EBMI-IP	8:00	26.041667	32.898333		25.973333	32.900000
		2	IP-HI		25.973333	32.900000		26.000000	32.906667
		3	HI-EBMI		26.000000	32.906667	9:00	26.041667	32.898333
97	970315	1	EBMI-PP	14:22	26.041667	32.898333		26.071667	32.903333
		2	PP-BV		26.071667	32.903333		26.015000	32.900000
		3	BV-EBMI		26.015000	32.900000	17:27	26.041667	32.898333
98	970316	1	EBMI-IP	8:46	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-PP		25.976667	32.870000		26.071667	32.903333
		4	PP-EBMI		26.071667	32.903333	13:30	26.041667	32.898333
99	970316	1	EBMI-IP	8:46	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-PP		25.976667	32.870000		26.071667	32.903333
		4	PP-EBMI		26.071667	32.903333	13:30	26.041667	32.898333
100	970326	1	EBMI-BS	13:25	26.041667	32.898333	14:00	26.081667	32.925000
101	970329	1	EBMI-PP	8:00	26.041667	32.898333		26.071667	32.903333
		2	PP-EBMI		26.071667	32.903333	11:00	26.041667	32.898333
102	970330	1	EBMI-BS	10:00	26.041667	32.898333		26.081667	32.925000
		2	BS-EBMI		26.081667	32.925000	11:00	26.168333	32.685000
103	970405	1	MA-EBMI	14:40	25.951667	32.618333	16:00	26.168333	32.685000
104	970413	1	EBMI-IP	7:17	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-PT		25.976667	32.870000	8:54	26.081667	32.951667
105	970413	1	PT-BG	9:54	26.081667	32.951667		25.976667	32.870000
		2	BG-IP		25.976667	32.870000		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	11:06	26.041667	32.898333
106	970419	1	EBMI-IP	13:55	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-PR		25.976667	32.870000		26.081667	32.925000
		4	PR-BS		26.053333	32.895000	15:15	26.081667	32.925000
107	970419	1	BS-IP	13:55	26.081667	32.925000		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-BV		25.976667	32.870000		26.015000	32.900000
		4	BV-EBMI		26.015000	32.900000	15:15	26.041667	32.898333
108	970420	1	EBMI-BG	6:30	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	7:30	26.041667	32.898333
109	970420	1	EBMI-BG	13:50	26.041667	32.898333		25.976667	32.870000
		2	BG-HI		25.976667	32.870000	14:55	26.000000	32.906667
110	970504	1	EBMI-BG	6:50	26.041667	32.898333		25.976667	32.870000
		2	BG-IP		25.976667	32.870000		25.973333	32.900000
		3	IP-PR		25.973333	32.900000		26.053333	32.895000
		4	PR-EBMI		26.053333	32.895000	8:50	26.041667	32.898333

Appendix 2 (continuation 7)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
111	970504	1	EBMI-PR	10:40	26.041667	32.898333		26.053333	32.895000
		2	PR-BG		26.053333	32.895000		25.976667	32.870000
		3	BG-IP		25.976667	32.870000		25.973333	32.900000
		4	IP-EBMI		25.973333	32.900000	11:54	26.041667	32.898333
112	970504	1	EBMI-HI	13:21	26.041667	32.898333	14:00	26.000000	32.906667
113	970421	1	EBMI-MA	12:30	26.041667	32.898333	14:30	25.951667	32.618333
114	970219	1	EBMI-PP	8:00	26.041667	32.898333		26.071667	32.903333
		2	PP-BV		26.071667	32.903333		26.015000	32.900000
		3	BV-EBMI		26.015000	32.900000	10:00	26.041667	32.898333
115	970219	1	EBMI-PP	16:00	26.041667	32.898333		26.071667	32.903333
		2	PP-BV		26.071667	32.903333		26.015000	32.900000
		3	BV-EBMI		26.015000	32.900000	17:45	26.041667	32.898333
116	951214	1	MA-HI	13:00	26.041667	32.898333	15:30	26.000000	32.906667
117	951213	1	EBMI-PP	16:00	26.041667	32.898333		26.071667	32.903333
		2	PP-EBMI		26.071667	32.903333	17:00	26.041667	32.898333
118	951214	1	EBMI-RB	7:00	26.041667	32.898333		25.951667	32.618333
		2	RB-MA		25.951667	32.618333	8:30	25.951667	32.618333
119	951214	1	MA-EBMI	10:00	25.951667	32.618333	11:30	25.951667	32.618333
120	951215	1	EBMI-MC	11:00	26.041667	32.898333		26.161667	32.798333
		2	MC-IP		26.161667	32.798333		25.973333	32.900000
		3	IP-EBMI		25.973333	32.900000	14:00	26.041667	32.898333
121	951216	1	EBMI-PM	5:30	26.041667	32.898333		26.025000	32.600000
		2	PM-MA		26.025000	32.600000	7:30	26.041667	32.898333
122	951221	1	MA-EBMI	11:00	26.041667	32.898333	13:00	26.041667	32.898333
123	971222	1	EBMI-MA	14:00	26.041667	32.898333		26.041667	32.898333
		2	MA-EBMI		26.041667	32.898333	16:30	26.041667	32.898333
124	971223	1	EBMI-MA	6:00	26.041667	32.898333	8:00	26.041667	32.898333
125	960907	1	EBMI-BG	9:20	26.041667	32.898333		25.976667	32.870000
		2	BG-MC		25.976667	32.870000		26.161667	32.798333
		3	MC-EBMI		26.161667	32.798333	12:40	26.041667	32.898333
126	960907	1	EBMI-BG	9:20	26.041667	32.898333		25.976667	32.870000
		2	BG-CD		25.976667	32.870000		26.088333	32.841667
		3	CD-EBMI		26.088333	32.841667	12:40	26.041667	32.898333
127	960907	1	EBMI-IP	9:20	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-GR		25.976667	32.870000		26.033333	32.843333
		4	GR-EBMI		26.033333	32.843333	12:40	26.041667	32.898333
128	960907	1	EBMI-PP	15:30	26.041667	32.898333		26.071667	32.903333
		2	PP-PT		26.071667	32.903333		26.081667	32.951667
		3	PT-IP		26.081667	32.951667		25.973333	32.900000
		4	IP-BG		25.973333	32.900000		25.976667	32.870000
		5	BG-EBMI		25.976667	32.870000	17:00	26.041667	32.898333

Appendix 2 (continuation 8)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
129	960908	1	EBMI-MC	9:30	26.041667	32.898333		26.161667	32.798333
		2	MC-BG		26.161667	32.798333		25.976667	32.870000
		3	BG-GR		25.976667	32.870000		26.033333	32.843333
		4	GR-EBMI		26.033333	32.843333	11:00	26.041667	32.898333
130	960908	1	EBMI-PP	15:30	26.041667	32.898333		26.071667	32.903333
		2	PP-BG		26.071667	32.903333		25.976667	32.870000
		3	BG -HI		25.976667	32.870000	16:30	26.000000	32.906667
131	960909	1	HI-MA	7:00	26.000000	32.906667	9:30	26.041667	32.898333
134	970919	1	EBMI-BV	8:00	26.041667	32.898333		26.015000	32.900000
		2	BV-EBMI		26.015000	32.900000	10:00	26.041667	32.898333
135	970919	1	EBMI-BG	15:15	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	16:10	26.041667	32.898333
136	970920	1	EBMI-BV	10:00	26.041667	32.898333		26.015000	32.900000
		2	BV-IP		26.015000	32.900000	12:30	25.973333	32.900000
137	970920	1	EBMI-BG	10:00	26.041667	32.898333		25.976667	32.870000
		2	BG-HI		25.976667	32.870000	12:30	26.000000	32.906667
138	970926	1	EBMI-IP	10:00	26.041667	32.898333		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-EBMI		25.976667	32.870000	13:15	26.041667	32.898333
139	970929	1	EBMI-IP	10:45	26.041667	32.898333		25.973333	32.900000
		2	IP-EBMI		25.973333	32.900000	11:30	26.041667	32.898333
140	970930	1	EBMI-PR	14:30	26.041667	32.898333		26.053333	32.895000
		2	PR-PE		26.053333	32.895000		25.960000	32.886667
		3	PE-EBMI		25.960000	32.886667	17:30	26.041667	32.898333
141	971014	1	EBMI-BG	7:45	26.041667	32.898333		25.976667	32.870000
		2	BG-HI		25.976667	32.870000	8:30	26.000000	32.906667
142	971014	1	HI-EBMI	9:55	26.000000	32.906667	11:55	26.041667	32.898333
143	971014	1	EBMI-BG	15:45	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	16:56	26.041667	32.898333
144	971015	1	EBMI-IP	9:15	25.973333	32.900000		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-HI		25.976667	32.870000	10:15	26.000000	32.906667
145	971017	1	EBMI-IP	15:50	25.976667	32.870000		25.973333	32.900000
		2	IP-BG		25.973333	32.900000		25.976667	32.870000
		3	BG-PR		25.976667	32.870000		26.053333	32.895000
		4	PR-EBMI		26.053333	32.895000	16:50	25.976667	32.870000
146	971120	1	MA-HI	9:40	26.041667	32.898333	10:40	26.000000	32.906667
147	971120	1	EBMI-BV	15:56	25.976667	32.870000		26.015000	32.900000
		2	BV-BS		26.015000	32.900000	16:30	26.081667	32.925000
148	971121	1	EBMI-PE	15:50	26.041667	32.898333		25.960000	32.886667
		2	PE-HI		25.960000	32.886667		26.000000	32.906667
		3	HI-PP		26.000000	32.906667		25.960000	32.886667
		4	PP-EBMI		25.960000	32.886667	18:20	26.041667	32.898333

Appendix 2 (continuation 9)

Data sheet	Date	Leg Number		Beginning of the survey			End of the survey		
	yymmdd	Leg Number	Leg description	Time	Latitude (degrees South)	Longitude (degrees East)	Time	Latitude (degrees South)	Longitude (degrees East)
149	971122	1	EBM-PT	9:14	26.041667	32.898333		26.081667	32.951667
		2	PT-BS		26.081667	32.951667		26.081667	32.925000
		3	BS-CD		26.081667	32.925000		26.088333	32.841667
		4	CD-PE		26.088333	32.841667		25.960000	32.886667
		5	PE-IP		25.960000	32.886667		25.973333	32.900000
		6	IP-EBMI		25.973333	32.900000	14:00	26.041667	32.898333
150	971122	1	EBMI-IP	16:20	26.041667	32.898333		25.973333	32.900000
		2	IP-PE		25.973333	32.900000		25.960000	32.886667
		3	PE-PP		25.960000	32.886667		25.960000	32.886667
		4	PP-EBMI		25.960000	32.886667	18:10	26.041667	32.898333
151	971123	1	EBMI-PE	8:50	26.041667	32.898333		25.960000	32.886667
		2	PE-PP		25.960000	32.886667		25.960000	32.886667
		3	PP-EBMI		25.960000	32.886667	10:45	26.041667	32.898333
152	971124	1	EBM-PE	7:50	26.041667	32.898333		25.960000	32.886667
		2	PE-EBMI		25.960000	32.886667	10:15	26.041667	32.898333
153	971124	1	EBMI-PT	11:20	26.041667	32.898333		26.081667	32.951667
		2	PT-EBMI		26.081667	32.951667	12:25	26.041667	32.898333
154	971124	1	EBMI-BG	16:20	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	18:20	26.041667	32.898333
155	971221	1	EBMI-IP	7:30	26.041667	32.898333		25.973333	32.900000
		2	IP-PE		25.973333	32.900000		25.960000	32.886667
		3	PE-PP		25.960000	32.886667		26.071667	32.903333
		4	PP-EBMI		26.071667	32.903333	9:00	26.041667	32.898333
156	971221	1	EBMI-IP	16:20	26.041667	32.898333		25.973333	32.900000
		2	IP-PE		25.973333	32.900000		25.960000	32.886667
		3	PE-PP		25.960000	32.886667		26.071667	32.903333
		4	PP-EBMI		26.071667	32.903333	17:40	26.041667	32.898333
157	971222	1	EBMI-IP	11:00	26.041667	32.898333		25.973333	32.900000
		2	IP-PE		25.973333	32.900000		25.960000	32.886667
		3	PE-EBMI		25.960000	32.886667	13:40	26.041667	32.898333
158	971223	1	EBMI-IP	8:00	26.041667	32.898333		25.973333	32.900000
		2	IP-PE		25.973333	32.900000		25.960000	32.886667
		3	PE-PR		25.960000	32.886667		26.053333	32.895000
		4	PR-EBMI		26.053333	32.895000	12:30	26.041667	32.898333
159	971223	1	HI-RM	14:30	26.000000	32.906667	17:00	26.168333	32.685000
160	971228	1	EBMI-BG	14:20	26.041667	32.898333		25.976667	32.870000
		2	BG-EBMI		25.976667	32.870000	16:00	26.041667	32.898333
161	971224	1	EBMI-BG	8:50	26.041667	32.898333		25.976667	32.870000
		2	BG-PP		25.976667	32.870000		26.071667	32.903333
		3	PP-EBMI		26.071667	32.903333	11:00	26.041667	32.898333

Appendix 3. Sea state, cloud cover and tides during each survey carried out in Maputo Bay between December 1995 and December 1997.

Date (yymmdd)	data sheet (survey number)	Sea state (Beaufort)	Cloud cover	Wind direction	Semi-lunar type of tides	Semi diurnal tidal phases	Tidal range (m)
960217	1	0	0	east	spring	high	2.8
960218	2	0	0	east	spring	rising	3.1
960218	3	0	0	east	spring	rising	3.1
960224	4	3	0	north	neap	low	2.2
960302	5	3	0	north	spring	rising	2.7
960303	6	2	4	south	spring	rising	2.5
960304	8	0			spring	rising	2.9
960316	9	1	0	east	neap	rising	2
960317	10	1	1		spring	rising	2.6
960327	11	0	0	east	neap	receeding-low-rising	0.8
960327	12	0	0		neap	rising	0.7
960407	13	2	1	north	spring	receeding-low-rising	3
960408	16	2	1	east	spring	receeding	2.6
960409	17	3	1	south	spring	receeding	2.1
960425	18	2	0	north	neap	receeding	1.1
960505	19	0	0	east	spring	low	3.1
960505	20	0	0	east	spring	high	3.1
960512	22	1	0	east	neap	rising	1.2
960516	23	1	6	south	spring	low	2.8
960516	24	1	1	south	spring	high	2.8
960517	25	2	0	south	spring	rising	2.9
960614	26	2	0	south	spring	low	2.4
960615	27	1	0	south east	spring	rising	2.6
960615	28	1	2	east	spring	high	2.6
960616	29	2	0	south east	spring	rising-high	2.7
960707	30	1	0	east	neap	rising	1.8
960707	32	1	0	east	neap	receeding	1.8
960713	33	2	0	east	spring	rising	2.1
960715	34	1	0	east	spring	high	2.6
960720	35	1	0	south	spring	rising	2.5
960721	36	1	0	south	spring	receeding	2.3
960721	37	1	0	south	spring	rising	2.3
960722	38	0	0	east	neap	receeding	1.9
960801	39	1	0	east	spring	receeding-low-rising	3.2
960801	40	2	0	east	spring	high	3.2
960803	41	1	1	east	spring	receeding	3
960808	42	2	1	south	neap	receeding	0.8
960823	43	0	0	east	neap	receeding	1
961105	45	2	0	east	neap	rising	0.8
961106	46	1	0	north	neap	high	0.8

Appendix 3 (continuation 2)

Date (yymmdd)	data sheet (survey number)	Sea state (Beaufort)	Cloud cover	Wind direction	Semi-lunar type of tides	Semi diurnal tidal phases	Tidal range (m)
970106	48	2	0	east	neap	high	2
970106	49	2	0	east	neap	receeding	2
970107	50	1	2	south	spring	receeding	2.5
970107	51	2	0	south east	spring	high	2.5
970107	52	3	0	south east	spring	receeding	2.5
970801	53	0	3	east	spring	receeding-low	2.6
970109	55	3	1	north	spring	receeding	2.9
970116	56	2	0	east	neap	low-receeding	1.1
970117	57	3	4	east	neap	high	1.2
970118	58	3	8	south	neap	high	1.1
970119	59	1	4	south	neap	receeding	1.4
970122	62	1	0	east	spring	low	2.3
970120	60	3	0	south east	neap	high	1.8
970121	61	2	5	east	neap	rising	2.2
970124	64	2	4	south	spring	receeding	2.7
970122	63	3	0	east	spring	high	2.6
970124	65	1	3	east	spring	high	2.8
970125	66	1	1	south	spring	low	2.8
970210	69	3	7	south	spring	high-receeding	3.3
970126	67	1	0	east	spring	receeding	2.7
970208	68	2	3	east	spring	low-receeding	3.3
970211	70	1	5	east	neap	receeding	0.8
970211	71	0	6	east	neap	rising	0.6
970212	72	1	6	east	neap	rising	0.5
970221	73	2	1	east	spring	receeding	2.6
970221	74	1	1	east	spring	rising	2.7
970224	75	3	6	east	spring	rising	3
970225	76	0	1	east	spring	receeding	2.9
970225	77	2	1	east	spring	rising	2.9
970225	78	2	1	east	spring	rising	2.9
970228	79	2	8	east	neap	low	2.2
970228	80	1	3	east	neap	high	2.1
970307	81	2	3	south	spring	high	2.8
970308	82	3	7	south	spring	receeding	3.1
970308	83	2	1	south	spring	receeding	3.1
970308	84	3	0	south	spring	high	3.3
970309	85	0	8	east	spring	receeding	3.4
970309	86	2	8	east	spring	rising	3.4
970309	89	2	7	east	spring	high	3.5
970310	90	1	8	east	spring	receeding	3.6
970310	91	2	4	east	spring	low	3.6
970310	93	3	0	east	spring	high	3.6
970313	94	1	1	east	spring	rising	2.6
970314	95	3	4	south	neap	high	2.4

Appendix 3 (continuation 3)

Date (yymmdd)	data sheet (survey number)	Sea state (Beaufort)	Cloud cover	Wind direction	Semi-lunar type of tides	Semi diurnal tidal phases	Tidal range (m)
970315	97	3	4	south	neap	high-receeding	1.5
970316	98	2	1	south	neap	high	1
970316	99	2	1	south	neap	receeding-low	1
970326	100	2	1	north	spring	rising	3
970329	101	3	5	north	spring	receeding	2.4
970330	102	3	5	south	neap	high-receeding	1.9
970405	103	2	0	east	spring	rising	2.6
970413	104	2	8	east	neap	high	1.7
970413	105	0	7	north	neap	receeding	1.7
970419	106	0	4	north	neap	rising+high	2.1
970420	108	3	5	south	spring	receeding	2.5
970420	109	1	5	north east	spring	rising	2.5
970504	110	1	1	south west	spring	low	2.4
970504	111	0	3	south west	spring	rising	2.5
970504	112	0	0	east	spring	high	2.5
960421	113	1	2	east	spring	low	2.6
970297	114	3	0	north	spring	low	1.9
970219	115	0	7	north	spring	receeding	1.9
951214	116	1	0	north	neap	rising	1.7
951213	117	1	0	north	neap	rising	1.7
951214	118	2	1	north	neap	high	1.7
951214	119	3	0	north	neap	receeding	1.4
951215	120	3	3	north	neap	receeding	1.1
951216	121	3	8	south	neap	rising	1.2
951221	122	3	0	north	spring	rising	2.7
971222	123	3	0	north	spring	high-rising	3
971223	124	3	4	north	spring	receeding	3.1
960907	125	1	0	east	neap	rising	0.7
960907	128	0	0	east	neap	receeding	0.7
960908	129	1	7	north	neap	rising	1.2
960809	130	3	0	north	neap	receeding	1.3
960909	131	0	0	east	neap	low	1.5
970919	134	1	0	north	spring	receeding	3.5
970919	135	1	0	north	spring	high	3.5
970920	136	1	0	north	spring	low	3.1
970926	138	0	0	east	neap	high	0.9
970929	139	0	0	east	spring	receeding	2.6
970930	140	0	0	east	spring	rising	2.8
971014	141	1	8	south	spring	receeding	2.6
971014	142	1	8	south	spring	rising	2.7
971014	143	2	7	south	spring	high	2.7
971015	144	2	8	south	spring	rising	3.3
971017	145	2	6	east	spring	rising	3.5
971120	146	1	5	south	neap	rising	1.7
971120	147	3	0	south	neap	receeding	1.6

Appendix 3 (continuation 4)

Date (yymmdd)	data sheet (survey number)	Sea state (Beaufort)	Cloud cover	Wind direction	Semi-lunar type of tides	Semi diurnal tidal phases	Tidal range (m)
971122	149	1	2	north	neap	receeding	0.8
971122	150	3	0	north	neap	rising	0.8
971123	151	3	1	north	neap	rising	0.9
971124	152	1	7	north	neap	rising	1.1
971124	153	2	0	north	neap	rising	1.1
971124	154	3	0	north	neap	high	1.1
971221	155	1	4	east	neap	receeding	1.5
971221	156	3	0	east	neap	rising	1.2
971222	157	2	3	north	neap	low	1
971223	158	2	4	north	neap	high-receeding	1
971223	159	3	0	north	neap	rising	1.2
971228	160	1	2	north	spring	rising	2.5
971229	161	3	3	north	spring	receeding	3.4

Appendix 4. Sighting history (re-photographs and identifications) of all individual bottlenose dolphins identified in Maputo Bay between December 1995 and December 1997 (stage/sex = sex and age category when first sighted, A = adult, AF = adult female, J = juveniles, the date is presented format is year, month, day –yymmdd, ID. No. – Identification Number).

Names	ID No.	Sex/Stage	960427	960505	960517	960614	960615	960616	960713	960715	960720	960721	960801	960823	960907	961105	970106	970117	970122	970126	970313	970316	970413	970419	970420	970504	970920	970926	970930	971122A	971122B	971124	971222
CELIA	1	A	X	X	X	X	X	X														X	X	X	X	X		X	X				X
ANGELINA	2	A	X		X		X													X		X	X	X	X	X							
B.D.-31	3	A		X	X																		X				X	X	X	X	X		
B.D.-2	4	A	X		X																	X	X			X							
GOVE	5	A	X	X	X		X					X		X									X	X	X	X		X				X	
ALMEIDA	6	A	X	X	X	X	X	X							X							X		X	X	X		X					X
NARROW TIP	7	A	X	X	X	X										X	X					X	X	X		X			X		X	X	X
SERGIO	8	AF	X	X	X				X							X	X					X	X	X		X	X		X		X	X	
UKE	9	A	X	X				X				X																					
LINA	10	AF					X					X	X									X	X	X	X	X	X	X					
B.D.-38	11	A			X							X								X	X												
B.D.-33	12	A			X							X												X							X		
B.D.-52	13	A			X														X	X		X	X	X		X							
ZACARIAS	14	A		X	X		X	X									X					X	X	X		X			X		X	X	
LU	15	AF			X							X			X							X		X		X		X	X			X	
B.D.-67	16	A							X				X						X														
B.D.-39	17	A			X															X		X	X									X	X
B.D.-45	18	A			X							X											X	X									
VINCENT	19	A																				X	X	X		X							
RACHEL	20	A					X																X	X	X	X	X	X				X	
ALZIRA	21	A			X	X		X			X	X												X									
SHARKIE	22	A																					X	X		X							

Appendix 4 (Continuation 1)

Names	ID No.	Sex/Stage	960427	960505	960517	960614	960615	960616	960713	960715	960720	960721	960801	960823	960907	961105	970106	970117	970122	970126	970313	970316	970413	970419	970420	970504	970920	970926	970930	971122A	971122B	971124	971222
SANDRA	24	A			X	X																X		X	X	X		X	X				
B.D.-76	25	A										X			X							X	X	X		X							
B.D.-16	26	A		X	X												X					X	X	X	X	X	X	X	X		X	X	X
B.D.-22	26	A		X																		X											
ROSA	27	A					X			X			X		X	X											X		X			X	
B.D.-51	28	A			X							X							X				X										
B.D.-55	29	J			X	X																		X									
SANTOS	30	A		X	X							X			X										X								
B.D.-79	32	A										X	X					X															
B.D.-10	33	A	X	X	X																												
B.D.-17	34	A		X								X																					
B.D.-9	35	A	X	X																													
B.D.-29	37	A		X														X															
B.D.-44	37	A			X													X														X	
B.D.-37	38	A			X							X																					
B.D.-53	40	A			X																				X		X	X					
LUCILIA	41	A			X															X												X	X
B.D.-66	42	A							X					X																			
B.D.-69	43	A							X					X													X						
B.D.-70	44	A							X					X													X	X					
B.D.-72	45	A							X											X													
TITA	46	A							X																	X							
B.D.-75	47	A									X	X																					
B.D.-94	48	A												X	X																		
ODETE	49	A																X						X				X					

Appendix 4 (continuation 3)

Names	ID No.	Sex/Stage	960427	960505	960517	960614	960615	960616	960713	960715	960720	960721	960801	960823	960907	961105	970106	970117	970122	970126	970313	970316	970413	970419	970420	970504	970920	970926	970930	971122A	971122B	971124	971222
B.D.-105	50	A																				X		X									
FELIZ	23	A			X							X						X				X	X			X							
SPOTY	51	A																				X		X									
B.D.-106	52	A																						X	X								
B.D.-108	53	A																							X	X							
B.D.-109	54	A																							X	X	X	X					
B.D.-57	55	J				X								X																			
B.D.-60	56	J				X						X																					
B.D.-71	57	J							X					X																			
BELA	58	J							X	X																							
B.D.-85	59	J										X							X										X				
B.D.-15	60	A		X																													
B.D.-1	61	J	X																														
B.D.-21	61	A		X			X																										
B.D.-5	62	J	X																														
B.D.-3	62	A	X																														
B.D.-6	63	J	X																														
B.D.-4	64	A	X																														
B.D.-18	65	J		X																													
B.D.-7	66	A	X																														
B.D.-34	67	J			X																												
B.D.-8	68	A	X																														
B.D.-42	69	J			X																						X	X					
B.D.-11	70	A		X																													
B.D.-46	71	J			X																							X					

Appendix 4 (continuation 4)

Names	ID No.	Sex/Stage	960427	960505	960517	960614	960615	960616	960713	960715	960720	960721	960801	960823	960907	961105	970106	970117	970122	970126	970313	970316	970413	970419	970420	970504	970920	970926	970930	971122A	971122B	971124	971222
B.D.-12	72	A		X																													
B.D.-50	73	J			X																												
B.D.-54	75	J			X																												
B.D.-14	76	A		X																													
B.D.-61	77	J					X																										
B.D.-19	78	A		X																													
B.D.-63	79	J						X																									
B.D.-20	80	A		X																													
B.D.-64	81	J						X																									
B.D.-23	82	A		X																													
B.D.-68	83	J							X																								
B.D.-24	84	A		X																													
B.D.-74	85	J							X																								
B.D.-25	86	A		X																													
B.D.-80	87	J										X																X					
B.D.-26	88	A		X																													
B.D.-81	89	J										X																					
B.D.-27	90	A		X																													
B.D.-82	91	J										X																					
B.D.-28	92	A		X																													
B.D.-77	77	J										X												X		X	X						
B.D.-83	78	J										X															X						
B.D.-30	79	A		X																													
B.D.-86	80	J										X																					
B.D.-32	81	A		X																													
B.D.-87	82	J										X																	X				
ISABEL	83	A		X																													

Appendix 4 (continuation 5)

Names	ID No.	Sex/Stage	960427	960505	960517	960614	960615	960616	960713	960715	960720	960721	960801	960823	960907	961105	970106	970117	970122	970126	970313	970316	970413	970419	970420	970504	970920	970926	970930	971122A	971122B	971124	971222
B.D.-88	84	J										X															X	X					
B.D.35	85	A			X																												
B.D.-89	86	J										X																					
B.D.-36	87	A			X																							X					
B.D.-90	88	J										X																					
B.D.-40	89	A			X																												
B.D.-92	90	J											X																				
B.D.-41	91	A			X																												
B.D.-93	92	J											X																				
B.D.-43	93	A			X																												
B.D.-101	94	J													X																		
B.D.-47	95	A			X																												
B.D.-107	96	J																							X								
B.D.-48	97	A			X																												
B.D.-49	98	A			X																												
B.D.-56	99	A				X																											
B.D.-58	100	A				X																											
B.D.-59	101	A				X																											
LUCINDA	102	A				X																											
B.D.-62	103	A					X																										
B.D.-65	104	A							X																								
B.D.-73	105	A							X																								
B.D.-78	106	A										X																					
B.D.-84	107	A										X																					
B.D.-91	108	A											X																				

Appendix 4. (continuation 6)

Names	ID No.	Sex/Stage	960427	960505	960517	960614	960615	960616	960713	960715	960720	960721	960801	960823	960907	961105	970106	970117	970122	970126	970313	970316	970413	970419	970420	970504	970920	970926	970930	971122A	971122B	971124	971222
B.D.-95	109	A												X																			
B.D.-96	110	A												X																			
B.D.-97	111	A												X																			
B.D.-99	112	A												X																			
B.D.-100	113	A												X																			
B.D.-102	114	A														X																	
BENIGNA	115	A																X															
B.D.-103	116	A																	X														
B.D.-104	117	A																		X													
BENT FIN	118	A																					X										
B.D.-110	119	A																								X	X		X				
JOELMA	110	A																									X	X	X				
B.D.-111	111	J																									X						
B.D.-112	112	A																									X						
B.D.-113	113	J																											X				
B.D.-114	114	J																											X				
B.D.-115	115	A																											X				
ELLEN	116	A																												X	X		
SARITA	117	A																													X	X	
LENA	118	A																														X	
B.D.-116	119	J																														X	
GINHA	120	A																														X	
NINA	121	AF																														X	
HALF FIN	122	J																															X
B.D.-117	123	J																															X

Appendix 5. Number of sightings (re-photographs and identifications) for winter and summer of 1996 and 1997 of all bottlenose dolphins identified in Maputo Bay (Stage: A = adults of undetermined sex, AF = adult females, J = juveniles)

		Year	1996		1997		Times
Name	ID Number	Stage	Winter	Summer	Winter	Summer	Seen
No. of photographic surveys			**17**	**7**	**4**	**7**	35
GOVE	6	A	8		4	2	14
CELIA	5	A	6	1	4	3	14
NARROW TIP	7	A	4	3	3	4	14
B.D.-16	26	A	2	2	4	6	14
ALMEIDA	1	A	7	1	3	2	13
ZACARIAS	14	A	4	2	3	3	12
B.D.-31	12	A	2		1	5	8
B.D.-52	21	A	1	3	3		7
FELIZ	24	A	2	2	2		6
B.D.-76	30	A	2	1	3		6
B.D.-39	18	A	1	2	1	2	6
B.D.-2	4	A	2	1	2		5
B.D.-51	20	A	3	1	1		5
B.D.-17	11	A	4				4
B.D.-45	19	A	2		2		4
VINCENT	33	A		1	3		4
B.D.-33	16	A	2		1	1	4
B.D.-53	41	A	1		1	2	4
LUCILIA	42	A	1	1		2	4
B.D.-109	60	A			2	2	4
B.D.-10	3	A	3				3
B.D.-67	29	A	2	1			3
B.D.-44	40	A	1	1		1	3
B.D.-69	46	A	2			1	3
ODETE	55	A		1	1	1	3
B.D.-110	56	A			1	2	3
B.D.-9	35	A	2				2
B.D.-15	61	A	2				2
B.D.-21	26	A	2				2
B.D.-22	37	A	1	1			2
B.D.-29	38	A	1	1			2
B.D.-66	45	A	2				2
B.D.-72	49	A	1	1			2
TITA	50	A	1		1		2
B.D.-105	56	A		1	1		2
SPOTY	57	A		1	1		2
B.D.-106	58	A			2		2
B.D.-36	59	A	1			1	2

Appendix 5 (continuation 2)

		Year	1996		1997		Times
Name	ID Number	Stage	Winter	Summer	Winter	Summer	Seen
No. of photographic surveys			17	7	4	7	35
JOELMA	139	A				2	2
ELLEN	143	A				2	2
SARITA	144	A				2	2
B.D.-3	145	A	1				1
B.D.-4	146	A	1				1
B.D.-7	147	A	1				1
B.D.-8	148	A	1				1
B.D.-11	149	A	1				1
B.D.-12	150	A	1				1
B.D.-13	151	A	1				1
B.D.-14	152	A	1				1
B.D.-19	153	A	1				1
B.D.-20	154	A	1				1
B.D.-23	155	A	1				1
B.D.-24	156	A	1				1
B.D.-25	157	A	1				1
B.D.-26	158	A	1				1
B.D.-27	159	A	1				1
B.D.-28	160	A	1				1
B.D.-30	161	A	1				1
B.D.-32	162	A	1				1
ISABEL	163	A	1				1
B.D.-35	164	A	1				1
B.D.-40	165	A	1				1
B.D.-41	166	A	1				1
B.D.-43	167	A	1				1
B.D.-47	168	A	1				1
B.D.-48	169	A	1				1
B.D.-49	170	A	1				1
B.D.-56	171	A	1				1
B.D.-58	172	A	1				1
B.D.-59	173	A	1				1
LUCINDA	174	A	1				1
B.D.-62	175	A	1				1
B.D.-65	176	A	1				1
B.D.-73	177	A	1				1
B.D.-78	178	A	1				1
B.D.-91	179	A	1				1
B.D.-96	180	A	1				1
B.D.-97	181	A	1				1
B.D.-99	182	A	1				1
B.D.-100	183	A	1				1

Appendix 5 (continuation 3)

		Year	1996		1997		Times
Name	ID Number	Stage	Winter	Summer	Winter	Summer	Seen
No. of photographic surveys			17	7	4	7	35
B.D.-102	184	A		1			1
BENIGNA	185	A		1			1
B.D.-103	186	A		1			1
B.D.-104	187	A		1			1
BENT FIN	188	A			1		1
B.D.-112	138	A				1	1
B.D.-115	142	A				1	1
NINA	145	A				1	1
GINHA	146	A				1	1
LENA	147	A				1	1
SERGIO	8	AF	4	3	3	4	14
LINA	10	AF	3	1	4	3	11
ANGELINA	2	AF	3	2	4		9
LU	23	AF	3	1	2	3	9
RACHEL	27	AF	1		4	4	9
SANDRA	25	AF	2	1	3	2	8
SANTOS	13	AF	6		1		7
ROSA	28	AF	4	1		2	7
ALZIRA	15	AF	5		1		6
UKE	9	AF	4				4
B.D.-38	17	AF	2	2			4
B.D.-79	32	AF	3	1			4
B.D.-70	47	AF	2			2	4
SHARKIE	34	AF			3		3
B.D.-37	37	AF	2				2
B.D.-75	52	AF	2				2
B.D.-94	54	AF	2				2
B.D.-108	59	AF			2		2
B.D.-84	60	AF	1				1
B.D.-95	61	AF	1				1
B.D.-77	77	J	1		2	1	4
B.D.-42	78	J	1			3	4
B.D.-55	22	J	2		1		3
B.D.-85	53	J	1	1		1	3
B.D.-57	43	J	2				2
B.D.-60	44	J	2				2
B.D.-71	48	J	2				2
BELA	51	J	2				2
B.D.-46	52	J	1			1	2
B.D.-1	62	J	1				1
B.D.-5	63	J	1				1
B.D.-6	64	J	1				1

Appendix 5 (continuation 4)

		Year	1996		1997		Times Seen
Name	ID Number	Stage	Winter	Summer	Winter	Summer	
No. of photographic surveys			17	7	4	7	35
B.D.-18	65	J	1				1
B.D.-34	66	J	1				1
B.D.-50	67	J	1				1
B.D.-54	68	J	1				1
B.D.-61	69	J	1				1
B.D.-63	70	J	1				1
B.D.-64	71	J	1				1
B.D.-68	72	J	1				1
B.D.-74	73	J	1				1
B.D.-80	74	J	1				1
B.D.-81	75	J	1				1
B.D.-82	76	J	1				1
B.D.-83	77	J	1				1
B.D.-86	78	J	1				1
B.D.-87	79	J	1				1
B.D.-88	80	J	1				1
B.D.-89	81	J	1				1
B.D.-90	82	J	1				1
B.D.-92	83	J	1				1
B.D.-93	84	J	1				1
B.D.-101	85	J	1				1
B.D.-107	86	J			1		1
B.D.-111	137	J				1	1
B.D.-113	140	J				1	1
B.D.-114	141	J				1	1
HALF FIN	148	J				1	1
B.D.-117	149	J				1	1

Appendix 6.Number of days between first and last photographs and re-identification, number of times photographed, mean number of days between photographs and number of affiliates of each photographically identified bottlenose dolphin in Maputo Bay between December 1995 and December 1997 (ID. No. – identification number, stage = age and sex categories, , A = adult, AF = adult female, J = juveniles).

Name	ID. No	Stage	Days from first to last photographs	No. of times photographed	Days between photographs	No. of affiliates
GOVE	6	A	606	14	46.62	116
CELIA	5	A	634	14	48.77	112
B.D.-16	26	A	595	14	45.77	99
NARROW TIP	7	AF	553	14	46.08	104
SERGIO	8	AF	606	14	46.62	113
ALMEIDA	1	A	635	13	52.92	100
ZACARIAS	14	A	567	12	51.55	94
LINA	10	AF	554	11	55.40	74
LU	23	AF	555	9	69.38	79
ANGELINA	2	AF	403	9	50.38	70
RACHEL	27	AF	526	9	65.75	64
B.D.-31	12	A	559	8	79.86	82
SANDRA	25	AF	500	8	71.43	55
B.D.-52	21	A	351	7	58.50	60
SANTOS	13	AF	349	7	58.17	83
ROSA	28	AF	526	7	87.67	40
FELIZ	24	A	530	6	106.00	60
B.D.-76	30	A	286	6	47.67	38
B.D.-39	18	A	577	6	115.40	54
ALZIRA	15	AF	336	6	67.20	70
B.D.-2	4	A	402	5	100.50	62
B.D.-51	20	A	330	5	82.50	68
B.D.-17	11	A	77	4	25.67	58
B.D.-45	19	A	336	4	112.00	54
VINCENT	33	A	49	4	12.25	37
B.D.-33	16	A	553	4	184.33	55
LUCILIA	42	A	583	4	194.33	50
B.D.-109	60	A	159	4	53.00	36
UKE	9	AF	116	4	38.67	51
B.D.-38	17	AF	299	4	99.67	47
B.D.-79	32	AF	179	4	59.67	39
B.D.-53	41	AF	496	4	165.33	55
B.D.-70	47	AF	439	4	146.33	34
B.D.-77	77	J	425	4	141.67	48
B.D.-42	78	J	500	4	166.67	61

Appendix 6 (continuation 2)

Name	ID. No	Stage	Days from first to last photographs	No. of times photographed	Days between photographs	No. of affiliates
B.D.-10	3	A	51	3	25.50	69
B.D.-67	29	A	192	3	96.00	17
B.D.-44	40	A	555	3	277.50	43
ODETE	55	A	252	3	126.00	31
B.D.-69	46	A	433	3	216.50	32
B.D.-110	47	A	149	3	74.50	37
SHARKIE	34	AF	21	3	7.00	33
B.D.-55	22	J	336	3	168.00	56
B.D.-85	53	J	435	3	217.50	35
B.D.-9	35	A	39	2	39.00	42
B.D.-15	61	A	0	2	0.00	32
B.D.-21	26	A	41	2	41.00	34
B.D.-22	37	A	314	2	314.00	43
B.D.-29	38	A	256	2	256.00	46
B.D.-66	45	A	40	2	40.00	18
B.D.-72	49	A	196	2	196.00	14
TITA	50	A	294	2	294.00	38
B.D.-105	56	A	34	2	34.00	27
SPOTY	57	A	34	2	34.00	27
B.D.-106	58	A	1	2	1.00	29
B.D.-36	59	A	496	2	496.00	46
JOELMA	139	A	10	2	10.00	23
ELLEN	143	A	0	2	0.00	7
SARITA	144	A	2	2	2.00	17
B.D.-37	37	AF	65	2	65.00	44
B.D.-75	52	AF	1	2	1.00	20
B.D.-94	54	AF	15	2	15.00	4
B.D.-108	59	AF	14	2	14.00	25
B.D.-57	43	J	69	2	69.00	19
B.D.-60	44	J	37	2	37.00	18
B.D.-71	48	J	40	2	40.00	18
BELA	51	J	2	2	2.00	13
B.D.-46	52	J	496	2	496.00	46
B.D.-80	53	J	1	2	1.00	29
B.D.-83	54	J	1	2	1.00	35
B.D.-87	55	J	1	2	1.00	34
B.D.-88	56	J	1	2	1.00	34
B.D.-3	57	A	1	1	0	15
B.D.-4	58	A	1	1	0	15
B.D.-7	59	A	1	1	0	15
B.D.-8	60	A	1	1	0	15

Appendix 6 (continuation 3)

Name	ID. No	Stage	Days from first to last photographs	No. of times photographed	Days between photographs	No. of affiliates
B.D.-11	61	A	1	1	0	32
B.D.-12	62	A	1	1	0	32
B.D.-13	63	A	1	1	0	32
B.D.-14	64	A	1	1	0	32
B.D.-19	65	A	1	1	0	32
B.D.-20	66	A	1	1	0	32
B.D.-23	67	A	1	1	0	32
B.D.-24	68	A	1	1	0	32
B.D.-25	69	A	1	1	0	32
B.D.-26	70	A	1	1	0	32
B.D.-27	71	A	1	1	0	32
B.D.-28	72	A	1	1	0	32
B.D.-30	73	A	1	1	0	32
B.D.-32	74	A	1	1	0	32
ISABEL	75	A	1	1	0	32
B.D.-35	76	A	1	1	0	39
B.D.-40	77	A	1	1	0	39
B.D.-41	78	A	1	1	0	39
B.D.-43	79	A	1	1	0	39
B.D.-47	80	A	1	1	0	39
B.D.-49	81	A	1	1	0	39
B.D.-56	82	A	1	1	0	11
B.D.-58	83	A	1	1	0	11
B.D.-59	84	A	1	1	0	11
LUCINDA	85	A	1	1	0	11
B.D.-62	86	A	1	1	0	10
B.D.-65	87	A	1	1	0	12
B.D.-73	88	A	1	1	0	12
B.D.-84	89	A	1	1	0	20
B.D.-91	90	A	1	1	0	20
B.D.-96	91	A	1	1	0	8
B.D.-97	92	A	1	1	0	8
B.D.-99	93	A	1	1	0	8
B.D.-100	94	A	1	1	0	8
B.D.-102	95	A	1	1	0	3
BENIGNA	96	A	1	1	0	5
B.D.-103	97	A	1	1	0	4
B.D.-104	98	A	1	1	0	6
BENT FIN	99	A	1	1	0	19
B.D.-112	138	A	1	1	0	16

Appendix 6 (continuation 4)

Name	ID. No	Stage	Days from first to last photographs	No. of times photographed	Days between photographs	No. of affiliates
B.D.-115	142	A	1	1	0	15
NINA	145	A	1	1	0	14
GINHA	146	A	1	1	0	14
LENA	147	A	1	1	0	14
B.D.-48	148	AF	1	1	0	39
B.D.-78	149	AF	1	1	0	12
B.D.-95	150	AF	1	1	0	1
B.D.-1	62	J	1	1	0	15
B.D.-5	63	J	1	1	0	15
B.D.-6	64	J	1	1	0	15
B.D.-18	65	J	1	1	0	32
B.D.-34	66	J	1	1	0	39
B.D.-50	67	J	1	1	0	39
B.D.-54	68	J	1	1	0	39
B.D.-61	69	J	1	1	0	16
B.D.-63	70	J	1	1	0	6
B.D.-64	71	J	1	1	0	6
B.D.-68	72	J	1	1	0	12
B.D.-74	73	J	1	1	0	12
B.D.-81	74	J	1	1	0	20
B.D.-82	75	J	1	1	0	20
B.D.-86	76	J	1	1	0	20
B.D.-89	77	J	1	1	0	20
B.D.-90	78	J	1	1	0	20
B.D.-92	79	J	1	1	0	6
B.D.-93	80	J	1	1	0	6
B.D.-101	81	J	1	1	0	3
B.D.-107	82	J	1	1	0	13
B.D.-111	137	J	1	1	0	16
B.D.-113	140	J	1	1	0	16
B.D.-114	141	J	1	1	0	16
HALF FIN	148	J	1	1	0	8
B.D.-117	149	J	1	1	0	8

Appendix 7. Half weight index of association for all identified bottlenose dolphin individuals photographed > 3 times in Maputo Bay between December 1995 and December 1997.

Individ.	B6-A	B5-A	B7-A	B8-AF	B26-A	B1-A	B14-A	B10-AF	B2-AF	B23-AF	B27-AF	B25-AF	B12-A	B13-AF	B28-AF	B15-AF	B24-A	B30-A	B18-A	B4-A	B20-A
B6-A																					
B5-A	0.643																				
B7-A	0.500	0.714																			
B8-AF	0.500	0.417	0.857																		
B26-A	0.571	0.667	0.786	0.786																	
B1-A	0.593	0.870	0.593	0.444	0.593																
B14-A	0.519	0.750	0.769	0.769	0.769	0.560															
B10-AF	0.560	0.667	0.400	0.400	0.640	0.583	0.435														
B2-AF	0.609	0.696	0.522	0.522	0.522	0.636	0.571	0.600													
B23-AF	0.522	0.522	0.414	0.522	0.522	0.455	0.571	0.500	0.556												
B27-AF	0.609	0.609	0.435	0.522	0.696	0.455	0.571	0.700	0.556	0.556											
B25-AF	0.455	0.727	0.545	0.455	0.636	0.667	0.500	0.526	0.588	0.706	0.588										
B12-A	0.364	0.455	0.455	0.545	0.636	0.286	0.500	0.316	0.235	0.353	0.471	0.375									
B13-AF	0.571	0.286	0.190	0.190	0.286	0.300	0.211	0.222	0.250	0.375	0.125	0.267	0.267								
B28-AF	0.190	0.095	0.190	0.286	0.190	0.100	0.211	0.333	0.125	0.250	0.375	0.000	0.133	0.143							
B15-AF	0.300	0.400	0.300	0.200	0.200	0.421	0.333	0.235	0.267	0.400	0.133	0.429	0.143	0.308	0.267						
B24-A	0.400	0.400	0.400	0.400	0.400	0.316	0.444	0.353	0.533	0.400	0.267	0.429	0.286	0.308	0.267	0.133					
B30-A	0.400	0.400	0.400	0.400	0.400	0.421	0.444	0.471	0.533	0.400	0.400	0.429	0.143	0.154	1.000	0.143	0.308				
B18-A	0.300	0.400	0.500	0.400	0.500	0.316	0.444	0.353	0.400	0.400	0.267	0.286	0.286	0.154	0.000	0.167	0.500	0.333			
B4-A	0.421	0.526	0.526	0.526	0.421	0.444	0.471	0.375	0.600	0.429	0.286	0.462	0.154	0.167	0.000	0.182	0.727	0.545	0.545		
B20-A	0.421	0.211	0.211	0.211	0.211	0.111	0.235	0.250	0.286	0.286	0.143	0.154	0.308	0.500	0.000	0.364	0.545	0.364	0.364	0.400	
B9-AF	0.333	0.333	0.222	0.222	0.111	0.353	0.250	0.000	0.154	0.000	0.000	0.000	0.167	0.364	0.000	0.200	0.200	0.200	0.000	0.222	0.222
B11-A	0.444	0.111	0.111	0.111	0.111	0.353	0.125	0.133	0.000	0.154	0.000	0.000	0.167	0.727	0.000	0.200	0.200	0.200	0.000	0.000	0.444
B17-AF	0.222	0.111	0.111	0.111	0.111	0.118	0.125	0.000	0.154	0.154	0.000	0.167	0.167	0.364	0.000	0.200	0.400	0.200	0.400	0.222	0.444
B19-A	0.444	0.333	0.333	0.333	0.222	0.118	0.375	0.000	0.462	0.267	0.308	0.308	0.333	0.364	0.182	0.400	0.600	0.600	0.400	0.444	0.667
B32-A	0.222	0.000	0.000	0.000	0.000	0.235	0.000	0.267	0.000	0.154	0.000	0.000	0.000	0.364	0.000	0.200	0.400	0.200	0.000	0.000	0.444
B33-A	0.333	0.444	0.000	0.444	0.444	0.000	0.500	0.364	0.615	0.462	0.615	0.500	0.167	0.000	0.000	0.200	0.600	0.800	0.400	0.667	0.222
B16-A	0.333	0.222	0.333	0.333	0.333	0.353	0.375	0.381	0.308	0.308	0.154	0.333	0.167	0.364	0.182	0.400	0.400	0.400	0.200	0.222	0.444
B77-J	0.333	0.222	0.222	0.333	0.333	0.235	0.250	0.182	0.308	0.308	0.462	0.333	0.167	0.182	0.182	0.200	0.400	0.600	0.000	0.222	0.222
B41-A	0.333	0.333	0.111	0.222	0.444	0.235	0.125	0.400	0.308	0.154	0.462	0.500	0.500	0.364	0.182	0.200	0.200	0.000	0.200	0.222	0.222
B42-A	0.222	0.222	0.333	0.222	0.333	0.235	0.250	0.316	0.154	0.308	0.154	0.167	0.167	0.182	0.182	0.200	0.200	0.000	0.800	0.222	0.222
B47-AF	0.222	0.111	0.000	0.222	0.222	0.118	0.000	0.154	0.000	0.154	0.308	0.167	0.333	0.000	0.182	0.000	0.000	0.000	0.000	0.000	0.000
B60-A	0.333	0.333	0.125	0.222	0.444	0.235	0.125	0.533	0.308	0.154	0.615	0.500	0.333	0.182	0.182	0.000	0.200	0.200	0.000	0.222	0.000
B78-J	0.222	0.333	0.222	0.333	0.444	0.235	0.250	0.267	0.154	0.462	0.462	0.500	0.667	0.182	0.182	0.200	0.200	0.000	0.200	0.222	0.222
B21-A	0.381	0.476	0.500	0.476	0.476	0.400	0.421	0.421	0.625	0.500	0.375	0.533	0.267	0.143	0.000	0.308	0.615	0.615	0.615	0.667	0.500

Appendix 7(Continuation)

Individ.	B9-AF	B11-A	B17-AF	B19-A	B32-A	B33-A	B16-A	B77-J	B41-A	B42-A	B47-AF	B60-A	B78-J
B6-A													
B5-A													
B7-A													
B8-AF													
B26-A													
B1-A													
B14-A													
B10-AF													
B2-AF													
B23-AF													
B27-AF													
B25-AF													
B12-A													
B13-AF													
B28-AF													
B15-AF													
B24-A													
B30-A													
B18-A													
B4-A													
B20-A													
B9-AF													
B11-A	0.500												
B17-AF	0.250	0.250											
B19-A	0.250	0.250	0.500										
B32-A	0.250	0.500	0.250	0.250									
B33-A	0.000	0.000	0.000	0.500	0.000								
B16-A	0.250	0.250	0.500	0.750	0.250	0.250							
B77-J	0.250	0.250	0.250	0.500	0.250	0.500	0.500						
B41-A	0.000	0.000	0.250	0.000	0.000	0.000	0.250	0.250					
B42-A	0.000	0.000	0.500	0.250	0.000	0.000	0.250	0.000	0.250				
B47-AF	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.250	0.500	0.000			
B60-A	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.500	0.750	0.000	0.500		
B78-J	0.000	0.000	0.250	0.250	0.000	0.000	0.250	0.250	0.500	0.250	0.500	0.500	
B21-A	0.000	0.000	0.364	0.545	0.000	0.727	0.364	0.364	0.182	0.364	0.000	0.182	0.182

Appendix 8. Sighting history (re-photographs and identifications) of all individual humpback dolphins photographed and identified in Maputo Bay in 1992 and between December 1995 and December 1997 (sex/stage = sex and age categories when first sighted, A = adult of undetermined sex, AF = adult females, AM = adult male, J = juvenile; the date is presented format is year, month, day –yymmdd; ID. No. – Identification Number).

Names	ID No	Sex/Stage	920118	920119	920419	920420	951214	960316	960421	960721	970107	970108	970116	970119	970203	970219A	970219B	970221	970225A	970225B	970228	970308	970309A	970309B	970309C	970309D	970310A	970310B	970315	970316	970329	970504	970919A	970919B	970920	971014
H-1	1	J	X								X		X																							
H-2	2	A	X															X									X		X	X						X
H-3	3	A	X																										X							
LUCAS	4	A	X																																	
SONIA	5	AF		X	X																															
CARLOS	6	A		X																																
H-4	7	A		X		X																					X								X	
BIG HUMP	8	AM			X	X		X	X		X	X	X	X	X		X	X	X	X	X	X	X	X			X	X	X	X		X		X	X	
H-5	9	A			X																															
H-6	10	A			X																															
LESZEK	11	A			X	X																														
AIDA	12	AF				X			X																											
H-8	13	A				X																														
H-9	14	A				X																														
LESZEK2	15	A					X	X						X		X	X	X	X	X	X	X	X	X		X	X		X		X	X	X		X	X
POINTED FIN	16	AF				X		X		X		X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X		X	X
FRED	17	A					X	X			X	X	X	X	X	X		X	X	X	X	X	X		X	X	X		X		X		X	X	X	X
H-10	18	J					X														X										X					X
KIKI	20	J					X				X		X	X		X	X	X		X	X		X		X	X		X	X		X	X	X	X	X	X
H-13	21	A					X										X			X															X	X
CARMEN	21	AF							X																											
H-14	22	A							X										X																	
H-15	23	J							X																											
H-16	24	A							X																											

Appendix 8 (continuation)

Names	ID No	Sex/Stage	920118	920119	920419	920420	951214	960316	960421	960721	970107	970108	970116	970119	970203	970219A	970219B	970221	970225A	970225B	970228	970308	970309A	970309B	970309C	970309D	970310A	970310B	970315	970316	970329	970504	970919A	970919B	970920	971014
H-17	25	A							X									X																		
H-18	26	A												X	X						X												X			
H-20	26	J							X																											
H-19	27	A							X																											
LIZ	28	AF							X									X					X													
NARROW FIN	29	A							X							X							X			X	X		X						X	X
WHITE FIN	30	A										X	X				X					X		X						X						
WHITE TIP	31	AF										X	X														X									X
FRONTNOTCH	32	J											X			X																				
HUMPNOTCH	33	J											X			X		X	X	X	X	X	X	X			X									X
LONGNOTCH	34	AF											X	X	X	X	X	X	X	X			X		X		X		X	X	X	X	X	X	X	X
SERRA	35	AF											X				X										X						X			X
H-21	37	J													X		X	X	X	X			X			X	X	X	X		X	X		X	X	X
H-22	38	A														X											X									
H-23	39	J														X													X							
H-24	40	AF														X	X		X	X	X															
H-25	41	J														X					X															
STELIO	42	J														X		X									X	X				X			X	
DESIRE	43	J												X	X	X		X	X	X	X						X		X		X	X	X			X
H-26	44	J															X	X									X									
TINO	45	AF															X	X	X	X	X					X	X		X	X		X	X	X	X	X
ALENY	46	AM																X						X			X			X						X
IVA	47	A																X	X	X	X			X			X						X			
H-27	48	A																											X							
H-28	49	A																					X						X							
H-29	50	J																											X							
H-30	51	A																											X							
H-30	51	J																															X			X
H-31	52	A																															X			X

Appendix 9. Number of sightings (re-photographs and identifications) for winter and summer of 1992, 1996 and 1997/8 of all humpback dolphins identified in Maputo Bay (stage: A = adults of undetermined sex, AF = adult females, AM = adult males, J = juveniles)

		Year	1992		1995/6		1997		Total
		Season	Summer	Winter	Summer	Winter	Summer	Winter	
Photographic surveys			2	2	2	2	20	6	34
Name	ID No.	Stage							
FRED	17	A			2		17	4	23
LESZEK2	15	A			2		14	4	20
NARROW FIN	29	A				1	6	1	8
IVA	47	A					6	1	7
WHITE FIN	30	A					5	1	6
H-2	2	A	1				4	1	6
H-24	40	A					5		5
H-13	21	A			1		3	1	5
H-4	7	A	1	1			1	1	4
H-3	3	A	1				1		2
LESZEK	11	A		2					2
H-14	22	A				1	1		2
H-17	25	A				1	1		2
H-22	38	A					2		2
H-28	49	A					2		2
H-31	52	A					1	1	2
LUCAS	4	A	1						1
CARLOS	6	A	1						1
H-5	9	A		1					1
H-6	10	A		1					1
H-8	13	A		1					1
H-9	14	A		1					1
H-16	24	A				1			1
H-18	26	A				1			1
H-19	27	A				1			1
H-27	48	A					1		1
H-30	51	A					1		1
POINTED FIN	16	AF		1	1	1	18	5	26
LONGNOTCH	34	AF					13	6	19
TINO	45	AF					9	5	14
SERRA	35	AF					4	1	5
WHITE TIP	31	AF					4		4
SONIA	5	AF	1	1					2
AIDA	12	AF		1		1			2
CARMEN	21	AF				1			1
BIG HUMP	8	AM		2	1	1	16	4	24
ALENY	46	AM					4	1	5
LIZ	28	F				1	2		3

Appendix 9 (continuation)

Year			1992		1995/6		1997		Total
Season			Summer	Winter	Summer	Winter	Summer	Winter	
Photographic surveys			2	2	2	2	20	6	34
Name	ID No.	Age Stage							
KIKI	20	J			1		14	5	20
H-21	37	J					11	4	15
DESIRE	43	J					9	3	13
HUMPNOTCH	33	J					11		11
STELIO	42	J					4	2	6
H-10	18	J			1		2	1	4
H-20	26	J					3	1	4
H-1	1	J	1				2		3
H-26	44	J					3		3
FRONTNOTCH	32	J					2		2
H-23	39	J					2		2
H-25	41	J					2		2
H-15	23	J				1			1
H-29	50	J					1		1

Appendix 10. Number of days between first and last photographs and re-identification, number of times photographed, mean number of days between photographs and number of affiliates of each photographically identified bottlenose dolphin in Maputo Bay between January and March 1992 and between December 1995 and December 1997 (ID. No. – identification number, stage = age and sex categories, A = adult, AF = adult female, AM = adult male, J = juveniles).

Name	ID. No	Stage	Days from first to last photographs	No. of times photographed	Days between photographs	No. of affiliates
POINTED FIN	16	AF	546	26	22.75	41
BIG HUMP	8	AM	522	24	22.74	48
FRED	17	A	603	23	22.88	37
LESZEK2	15	A	639	20	27.41	36
KIKI	20	J	639	20	33.63	36
LONGNOTCH	34	AF	270	19	15.00	37
H-21	37	J	252	15	18.00	34
TINO	45	AF	236	14	18.15	35
DESIRE	43	J	283	13	23.58	35
HUMPNOTCH	33	J	278	11	27.80	33
NARROW FIN	29	A	510	8	72.86	39
IVA	47	A	209	7	34.83	29
H-2	2	A	639	6	127.80	29
WHITE FIN	30	AF	278	6	46.33	19
STELIO	42	J	212	6	42.40	27
H-24	40	A	9	5	2.25	23
H-13	21	A	639	5	159.75	23
SERRA	35	AF	270	5	67.50	25
ALENY	46	AM	234	5	58.50	28
H-4	7	A	614	4	235.66	26
WHITE TIP	31	A	278	4	92.67	25
H-10	18	J	639	4	213.00	20
H-20	26	J	242	4	80.67	14
LIZ	28	AF	292	3	146.00	23
H-1	1	J	369	3	184.50	13
H-26	44	J	19	3	9.50	25
H-3	3	A	427	2	427.00	6
LESZEK	11	A	1	2	1.00	7
H-14	22	A	276	2	276.00	21
H-17	25	A	185	2	185.00	24
H-22	38	A	19	2	19.00	23
H-28	49	A	6	2	6.00	15
H-31	52	A	25	2	12.50	18

Appendix 10. (continuation)

Names	ID. No.	Stage	Days from first to last photographs	No. of times photographed	Days between photographs	No. of affiliates
SONIA	5	AF	91	2	91.00	6
AIDA	12	AF	129	2	129.00	16
FRONTNOTCH	32	J	34	2	34.00	19
H-23	39	J	24	2	24.00	21
H-25	41	J	9	2	9.00	18
LUCAS	4	A	1	1	0	3
CARLOS	6	A	1	1	0	2
H-5	9	A	1	1	0	4
H-6	10	A	1	1	0	4
H-8	13	A	1	1	0	7
H-9	14	A	1	1	0	7
H-16	24	A	1	1	0	10
H-18	26	A	1	1	0	10
H-19	27	A	1	1	0	10
H-27	48	A	1	1	0	16
H-30	51	A	1	1	0	16
CARMEN	21	AF	1	1	0	10
H-15	23	J	1	1	0	10
H-29	50	J	1	1	0	16

Appendix 11. Association index (half weight index) for all identified humpback dolphin individuals photographed in Maputo Bay > 3 times between January and May 1992 and December 1995 and December 1997.

Individ.	H2-A	H8-AM	H15-A	H16-AF	H17-A	H18-J	H21-A	H20-J	H29-A	H30-A	H31-AF	H33-J	H34-F	H35-F	H36-J	H37-J	H40-A	H42-J	H43-J	H45-AF	H46-AM
H2-A																					
H8-AM	0.267																				
H15-A	0.308	0.636																			
H16-AF	0.278	0.800	0.826																		
H17-A	0.276	0.711	0.791	0.809																	
H18-J	0.200	0.071	0.333	0.200	0.296																
H21-A	0.200	0.207	0.400	0.258	0.286	0.444															
H20-J	0.091	0.591	0.750	0.696	0.607	0.333	0.400														
H29-A	0.429	0.313	0.500	0.400	0.452	0.000	0.308	0.444													
H30-A	0.167	0.400	0.231	0.375	0.207	0.000	0.182	0.154	0.000												
H31-AF	0.400	0.214	0.167	0.267	0.296	0.250	0.222	0.167	0.333	0.444											
H33-J	0.353	0.514	0.645	0.595	0.588	0.267	0.250	0.452	0.421	0.375	0.400										
H34-F	0.118	0.651	0.718	0.773	0.762	0.174	0.308	0.769	0.444	0.286	0.261	0.533									
H35-F	0.364	0.207	0.320	0.323	0.296	0.222	0.400	0.320	0.308	0.444	0.667	0.375	0.417								
H36-J	0.000	0.214	0.250	0.267	0.296	0.250	0.000	0.250	0.000	0.000	0.000	0.133	0.261	0.222							
H37-J	0.381	0.615	0.686	0.683	0.632	0.211	0.400	0.686	0.522	0.111	0.211	0.462	0.765	0.300	0.105						
H40-A	0.000	0.276	0.400	0.323	0.286	0.222	0.400	0.320	0.154	0.182	0.000	0.500	0.333	0.200	0.222	0.300					
H42-J	0.333	0.207	0.385	0.375	0.276	0.000	0.182	0.385	0.429	0.000	0.200	0.353	0.333	0.182	0.000	0.476	0.222				
H43-J	0.444	0.486	0.727	0.667	0.667	0.353	0.222	0.606	0.381	0.000	0.235	0.583	0.750	0.333	0.471	0.643	0.500	0.421			
H45-AF	0.500	0.579	0.706	0.650	0.595	0.222	0.421	0.647	0.455	0.250	0.222	0.480	0.686	0.421	0.235	0.759	0.533	0.400	0.667		
H46-AM	0.727	0.276	0.320	0.323	0.214	0.000	0.200	0.160	0.308	0.400	0.444	0.500	0.333	0.400	0.000	0.300	0.000	0.364	0.333	0.421	
H47-A	0.333	0.387	0.519	0.424	0.400	0.182	0.167	0.296	0.133	0.167	0.182	0.667	0.385	0.200	0.364	0.364	0.545	0.308	0.600	0.571	0.500

Appendix 12

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Ecology and Population Estimates of Indo-Pacific Humpback Dolphins (*Sousa chinensis*) in Maputo Bay, Mozambique

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Abstract

The ecology and abundance of humpback dolphins inhabiting Maputo Bay were studied between December 1995 and December 1997 through boat-based surveys and photo-identification mark-recapture analysis. The sighting rate was low, corresponding to 21% of 146 surveys conducted. Estimated group size (mean=14.9 SD 7.32 individuals) was the largest reported for the eastern Africa region and did not change significantly with month, season, daylight, or tidal state. The proportion of individually marked adults was high among adults (0.52) and in a dolphin group (0.26). There is evidence for summer influxes of humpback dolphins into eastern Maputo Bay, and there are considerable numbers of apparently transient individuals. Nevertheless, a substantial proportion of humpback dolphins (13.5%) display high site fidelity to eastern Maputo Bay and could be long-term residents. Mark-recapture analysis (Jolly-Seber model) suggests a population size of approximately 105 dolphins, but the precision of the estimate is low (30.5-150.9). Births seem to occur throughout the year, and the birth rate is relatively high (0.11); however, the recruitment rate to six months in eastern Maputo Bay is low (0.05) and the calf mortality (or mortality and emigration) rate is high (0.47). Current conservation issues include primarily fishery interactions and habitat alteration, but the levels of impact on the dolphin population require further assessments.

Key Words: humpback dolphins, *Sousa chinensis*, site fidelity, population estimates, birth, recruitment, calf mortality, conservation, Maputo Bay, Mozambique, southeast Africa

Introduction

Indo-Pacific humpback dolphins (*Sousa chinensis*) are known to occur in coastal waters of the East African region (Jefferson & Karczmarski, 2001; Ross et al., 1994). Their piscivorous diet (Barros & Cockcroft, 1991, 1999) and preference for inshore habitats (Guissamulo & Cockcroft, 1997; Karczmarski et al., 2000) places them in direct interaction with coastal fisheries, both artisanal (subsistence) and commercial (Cockcroft & Krohn, 1994; Guissamulo & Cockcroft, 1997). Throughout the region, fishing effort is high, and competition between dolphins and humans for the same resources are likely (Cockcroft & Krohn, 1994). Furthermore, both intentional and non-intentional catches are known to take place in various areas throughout the western Indian Ocean (Cockcroft & Krohn, 1994; Karczmarski, 2000). Many other human activities along the African east coast have led to a large-scale habitat degradation (Anonymous, 1982). Destruction of coral reefs, mangroves, and large estuaries represent especially important issues, as these are the types of coastal habitats upon which humpback dolphins depend for feeding (Durham, 1994; Karczmarski, 2000; Klinowska, 1991).

Understanding of the population ecology of humpback dolphins remains limited, and so is knowledge of the conservation issues related to particular populations (Jefferson & Karczmarski, 2001). In Africa, apart from the KwaZulu-Natal coast of South Africa, there are no reliable reports on mortality rates and their possible impacts on local humpback dolphin populations. Only a few studies so far have provided population estimates (e.g., some 470 dolphins in the Algoa Bay region, South Africa [Karczmarski et al., 1999a]; *ca* 200 dolphins along the Natal coast [Durham, 1994]; and 74 dolphins at Richards Bay [Keith et al., 2003]). Early estimates for Maputo Bay were of some 70 dolphins (Guissamulo & Cockcroft, 1997), although this figure was very likely an underestimate and did not account for interannual variations. The present paper summarizes the current state of knowledge on the humpback dolphin population that inhabits Maputo Bay, presents estimated population figures, examines some of the population parameters, and discusses implications of these findings on the population dynamics and conservation of humpback dolphins in the region.

Study Area

Maputo Bay is located in southern Mozambique between latitudes 25°35' S and 26°15' S and longitudes 32°35' E and 33°00' E (Figure 1). Its surface area covers 1,100 km^2, excluding estuaries. The Bay lies in the transition between temperate and tropical climates with hot, but not very wet, summers and dry winters (Kalk, 1995). The depth ranges from 1 to 20 m, decreasing in the north-south direction; the 10-m isobath indents strongly, forming channels surrounded by long sandbanks which run north-south. The intertidal area comprises 29.3% of the total surface, and the subtidal area about 60.4% (Hydrographic chart no. 46659, 1995, INAHINA).

Five rivers discharge into the Bay. The N'komati River is in the north and the Maputo River is in the south. The remaining three rivers—Umbeluzi, Matola, and Tembe—form the Espírito Santo Estuary at western Maputo Bay (Kalk, 1995).

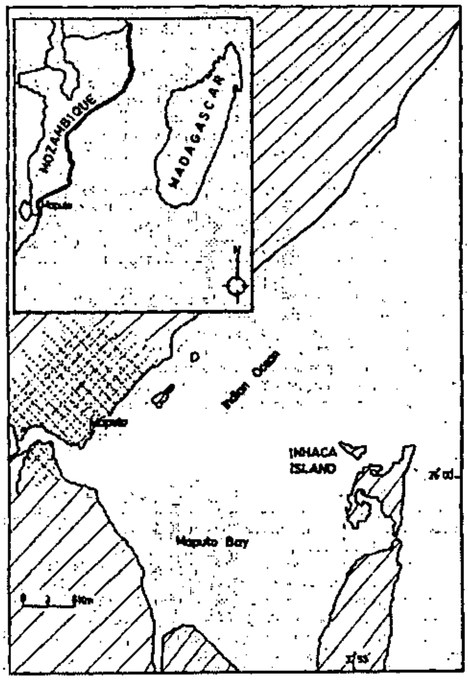

Figure 1. The location of Maputo Bay in Southern Mozambique. The study reported here concentrated around Inhaca Island.

Rivers affect the marine environment off the western coast of Maputo Bay, influencing the salinity, which drops significantly during summer; therefore, truly marine water only occurs at the northeastern part of the Bay (Nhapulo, 2000).

Daily tide changes are semi-diurnal, and the mean tidal range is 2 m. Waves are low at <0.5 m high (Kalk, 1995). Benthic sediments vary from clay-silt (phi=3.67) at the southern and western part of the Bay to medium-size sand (phi=1.73) at the north and east part of the Bay (Achimo, 2000). Mangroves border the coastal areas of the Bay, but they are suffering deforestation (De Boer, 2000), while the most extensive seagrass meadows occur at the eastern part of the Bay (Kalk, 1995).

An extensive gill-net fishery (449 boats) and an intensive commercial prawn trawling fishery (23 boats) operate throughout the year at the shallow areas of the southern and western part of the Bay in a total fishing area of 680 km^2 (Cockcroft & Krohn, 1994), but more than 50% of this fishing area is only accessible at high tide. Other subsistence fisheries also take place in the Bay, such as beach seining and line-fishing. The artisanal gill-net fishing fleet declined from 438 to 157 boats between 1985 and 1997, but it is unknown whether this influenced fishing effort.

Materials and Methods

Boat-based surveys took place between December 1995 and December 1997, using two types of boats: a 10-m boat with a 40-hp inboard engine, and a 5.5-m inflatable Zodiac with two 30-hp outboard engines. Surveys were conducted between 0600 h and 1800 h, in sea conditions not exceeding Beaufort 3. Most of the survey effort (about 80%) concentrated in the region of Inhaca Island (north of latitude 26°07' S), where surveys could easily be carried out regardless of the tides.

For each sighting, group size was estimated from direct counts of all individuals, and group composition (adults, juveniles, and calves; based on the relative size) was determined. The age of calves of known females was estimated using several features: (1) the time the particular adult was first sighted with a calf, (2) calf size relative to adult size, (3) the shape of the dorsal fin, (4) the pattern of breathing, and (5) the positioning of calf along the side of an adult dolphin when surfacing (Connor et al., 2000). A newborn calf was one-third of the adult size, had visible fetal folds, remained close to the mother's flank, and, when surfacing, lifted the whole head above the water.

Group size was compared between months and daylight periods using a Kruskal-Wallis test and between seasons and tides using a Mann-Whitney U test. Seasons were defined as follows: winter was the period between May and October, and summer between November and April (Kalk, 1995).

During boat surveys, individual dolphins were photographed using a Minolta X-700 camera, equipped with a zoom (80-250 mm) lens and 100 ASA slide film. Subsequently, the laboratory individual identification procedure followed the approach described by Karczmarski and Cockcroft (1998). Photographic data collected during reconnaissance surveys conducted between January and May 1992 also were included in the analysis.

The rate of discovery of new individuals was plotted as the cumulative number of newly identified dolphins against time (in days) from the start of the project (December 1995) until its termination (December 1997), and includes the period January to May 1992. The discovery curve also was plotted as the relationship between the number of newly identified dolphins and the cumulative number of dolphins seen at sea (total cumulative number of individuals identified per photo-identification survey, as by Wilson et al., 1999). An estimate of population size (N) was obtained using three methods: (1) an open population estimate (Jolly-Seber full model), using the software program *Popan-4* (November 1995)[1]; (2) a crude estimate, using the number of identified adults relative to the number of identifiable adults; and (3) the power fit (Number of marked dolphins = [1.7489 (number of days)$_{0.4622}$]), which was computed using the curve of new individuals discovered" on each survey for constructing regression models with the software *Curve Expert* (December 1995). Only data on photo-identified adults were used in these analyses, and, consequently, the calculated numbers represent the estimates of the total number of naturally marked adults. The final population size estimate (N) was obtained through the equation (sensu Karczmarski et al., 1999a):

$N = X / (Y . Z)$

where: X = estimated number of adults, Y = ratio of identified adults (0.52), and Z = mean proportion of adults in a group (0.50). The same formula was used to calculate the confidence intervals.

Population parameters were calculated following the procedure of Wells & Scott (1990) and Karczmarski (1996), namely crude birth rate, recruitment rates after six months and one year, and minimum mortality rate.

Crude birth rates (BR) were calculated using the following formula:

$BR = B/N$

where, B = number of births to known females, and N = number of known individuals.

Recruitment rates (REC) to age six months (REC_1) and one year (REC_2) were calculated as

$REC_1 = B_1/(N - B)$

$REC_2 = B_2/(N - B)$

where, B_1 and B_2 = number of births surviving to six months and one year, respectively.

N and B are as defined above.

Minimum calf mortality rate (MR) was defined as

$MR = D/B$

where, D = number of calves dead before six months after birth in a given year and B = number of births to known females in that given year.

The mortality rate of adults could not be calculated because no carcasses of dolphins were found, and the duration of the study did not allow the application of the criteria used by Wells & Scott (1990).

Results

Between December 1995 and December 1997, 146 at-sea surveys were conducted. Humpback dolphins were only seen on 31 surveys (37 sightings, 21% of total number of surveys). The 1995-1997 surveys were preceded by three successful photo-identification reconnaissance" surveys in 1992, which brings the total number of successful surveys to 34 (Figure 2).

Groups ranged between two and 25 individuals, and the mean group size was 14.9 (SD=7.32, n=37) individuals. The mean group size did not differ significantly among months (Kruskal-Wallis H=13.9; p=0.085), daylight periods (Kruskal-Wallis H=0.8906, n=35, p=0.9259), seasons (Mann-Whitney U=81, n=28 and 7, p=0.481), or neap and spring tides (Mann-Whitney U=112.5,

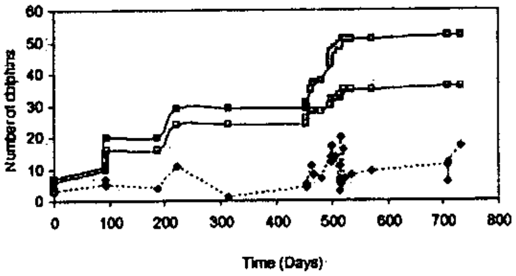

Figure 2. Cumulative number of humpback dolphins identified in Maputo Bay between January and May 1992, and between December 1995 and December 1997. = all individuals, = adults only; the number of dolphins identified per photo-identification survey is also shown (= individuals identified in a given sighting).

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[1] A justification of the choice of Jolly-Seber model for mark-recapture analyses is presented in the Results section.

n=23 and 12, *p*=0.605). On average, adult humpback dolphins comprised 50% of the group members, while juveniles and calves comprised 37% and 13%, respectively. Fifty-eight percent of adults and 43% of juveniles were photographically identifiable, but no calves were photographically identified.

After the completion of the 34 successful photographic surveys, with over 2,000 identification-photographs examined, 723 photographs of humpback dolphins were catalogued. This represents 52 identifiable individuals. Among these, there were 37 adults (10 females) and 15 juveniles. Twenty-four adults (64.86%) were identified during the first seven photographic sessions (between 0 and 450 days) (Figure 2), with 13 adults (25%) identified during the three surveys in 1992. The discovery curve shows an alternating pattern of increases and plateaus (Figure 2). The greatest increase occurred over the period 450 days to 525 days, which coincided with summer. This period had a marked increase in number of successful photographic surveys. Furthermore, the relationship between the cumulative number of discovered individuals and the cumulative number of dolphins seen at sea (Figure 3) shows a steep increase at the corresponding range of 100 to 200 dolphins seen at sea, suggesting an influx of humpback dolphin into the study area. Over this period, the rate of discovery of all individuals rose more steeply than that of adults only (Figures 2 & 3), implying that many of the newly discovered individuals were juveniles.

The frequency of sightings per individual (Figure 4) ranged from one (n=14; 26.9% of all identified individuals) to 26 times (n=1; 1.9%). The majority of adults (n=20; 59.4%) were sighted infrequently (not more than twice), but five adults (13.5%) were seen on more than half of the successful surveys. Of the juveniles, 40.0% (n=6) were sighted once or twice only, but one (6.7%) was sighted on more than half the successful surveys.

As the pattern of discovery curve and sighting frequencies suggested influx, and potentially outflux, of humpback dolphins, an open population Jolly-Seber model was used for further mark-recapture analyses. All analyses presented here are based on 210 sighting records of the 37 identifiable adults, all of which were photo-identified before the end of 1997. The Jolly-Seber estimator provided an estimate of 105 individuals, although there was a broad confidence interval (see Table 1). The crude population estimate was similar at 142 dolphins; however, the estimate obtained with the power fit (number of marked dolphins = [1.7489 (number of days)$_{0.4622}$]), r_2=0.931, was considerably higher (308 dolphins). The numbers in the equation are the coefficient (1.7489) and exponent (0.4622) generated by the power fit regression model.

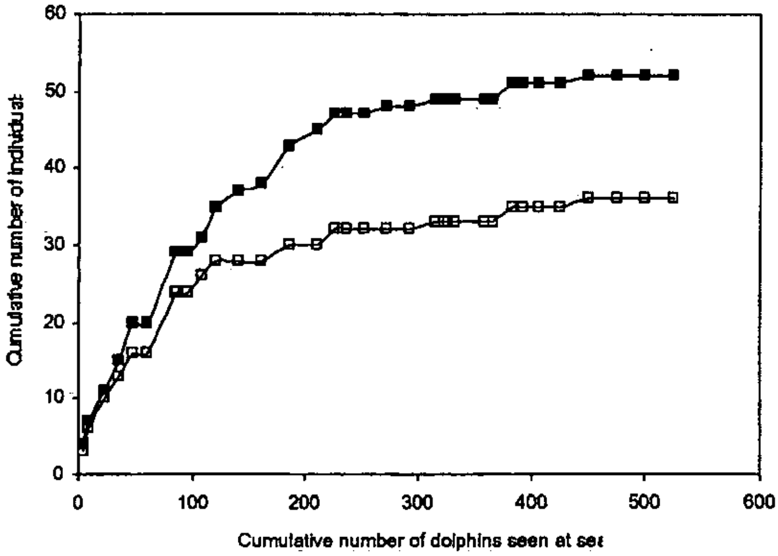

Figure 3. The relationship between the number of dolphins identified against the cumulative number of dolphins encountered during the study at Maputo Bay; = all individuals; = adults only

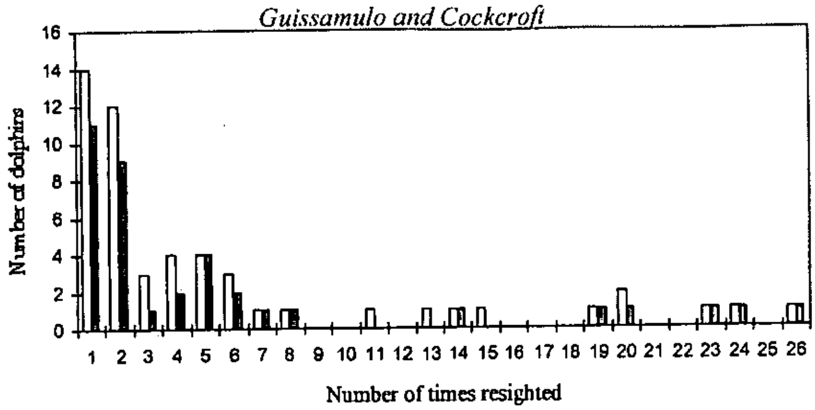

Figure 4. Frequency distribution of the number of individually identified humpback dolphins during the period between January and May 1992, and between December 1995 and December 1997. = all individuals; = adults only

Only the photo-identification data collected in 1996 and 1997 enabled the calculation of population parameters. Births occurred throughout the year, January 1996 (one birth), February 1996 (one birth), October 1996 (one birth), January 1997 (two births), and August 1997 (two births), with no defined season. The mean crude birth rate was estimated at 0.11, while the recruitment past one year was 0.05 and the mean minimum calf mortality rate was 0.47 (Table 2). These parameters are based on a small dataset, however, and should, therefore, be considered preliminary.

Discussion

The mean group size observed in Maputo Bay is the largest reported for humpback dolphins in the East African region. Several other authors described mean group sizes of about seven individuals (Durham, 1994; Findlay et al., 1992; Karczmarski et al., 1999b; Ross et al., 1989; Saymaan & Tayler, 1979). These large groups can be explained by coalescence of small groups of dolphins at the deeper waters of northern Maputo Bay during low tide. Most shallow waters in the Bay are not accessible to dolphins at low tide, and they may remain in the nearby channels. Although reasons for coalescence of groups are unknown, it has also been observed in waters around Hong Kong (Jefferson, 2000) and in Plettenberg Bay, South Africa (Saymaan & Tayler, 1979). In Maputo Bay, fishing activity intensifies during low tide (De Boer, 2000), posing risks of direct catches or incidental entanglements in fishing gear (Guissamulo & Cockcroft, 1997).

Adults with recognizable marks represented a moderate proportion of all adults (52%) and 26% of groups. This was unlikely to influence the probabilities of being photographed, however, groups were small (2-25 individuals) and every individual present could be identified during sightings. This is further supported by the high number of re-sightings of some dolphins that were seen on > 50% of the successful photographic surveys (irrespective of the distinctiveness of their natural marks), and by the high mean number of

Table 1. Abundance estimates for humpback dolphins in Maputo Bay observed between January and May 1992, and between December 1995 and December 1997; CI = confidence interval, Prop ID = proportion identified, Prop Adults = proportion adults.

	Marked dolphins				Total population	
Models	Estimates	95% CI	Prop ID	Prop Adults	Estimates	95% CI
Open Model						
Jolly-Seber Full	27	7.9-39.2	0.52	0.5	104.8	30.5-150.9
Crude Estimate	71			0.5	142	
Power Fit	80	77.3-82.7	0.52	0.5	307.7	297.4-318.1

Table 2. Population parameters for humpback dolphins in Maputo Bay observed between December 1995 and December 1997; two calves were born in the middle of 1997, and their survival could not be monitored for more than six months.

Description of Parameters		1996	1997	Mean	SD
Number of known adults	N	37	37		
Number of births recorded	B	3	5		
Number of calves surviving six months	B_1	1	2		
Number of calves surviving one year	B_2	1			
Number of calves dead before six months after birth	D	1	3		
Mother-calf pairs that disappeared after six months		1	0		
Crude birth rate	BR	0.08	0.14	0.11	0.04
Recruitment rate at six months	REC_1	0.03	0.06	0.05	0.02
Recruitment rate at one year	REC_2	0.03	-		
Minimum calf mortality rate	MR	0.33	0.60	0.47	0.19

photographs taken for each identifiable dolphin per survey (mean=5.68 photographs per dolphin). The exclusion from the analysis of individuals with unreliable identification marks contributed to the smaller proportion of marked individuals, but increased the accuracy of the estimate, as demonstrated by Forcada & Aguilar (2000).

The mean proportion of identified individuals in groups (about 50% of individuals) was lower than that of Richards Bay (Keith et al., 2002) and Algoa Bay (Karczmarski et al., 1999a), off the South African coast. The reason for that is hard to explain. It could be that dolphins in Maputo Bay are less exposed to factors that increase marks on the body (scars from predators, social interactions, entanglement in fishing gear, or interactions with their habitat). In the Algoa Bay region, for instance, humpback dolphins feed primarily in rocky reef areas (Karczmarski & Cockcroft, 1999), and the numerous scratches on their bodies (Karczmarski & Cockcroft, 1998) could be caused by incidental contacts with the reefs. Alternatively, although the individual photo-identification procedure applied in all these studies was similar (following Karczmarski & Cockcroft, 1998), individual differences in the assessment of photo-identification data cannot be excluded as a potential cause of the differences in the ratio of individually identified animals.

Some individuals frequently were seen in Maputo Bay (including several that frequented the Bay for at least five years), suggesting strong site fidelity of at least some (possibly resident) individuals. Their numbers are larger than that found in Algoa Bay (Karczmarski, 1999; Karczmarski et al., 1999a), possibly because eastern Maputo Bay is a large area with diverse habitats (extensive shallow areas with large seagrass meadows, reefs, and several mangrove creeks), suggesting a large resource availability; however, there was also a substantial number of transient dolphins in Maputo Bay (32%), mostly adults, implying that this population interacts with other humpback dolphin communities. In Algoa Bay, South Africa, the low site fidelity of individuals is seemingly caused by restricted availability of food and feeding areas (Karczmarski, 1999), which force the animals to range over large distances in search of food.

The two initial increases of the discovery curve (occurring in summer around the period of about 90 days, and around 190-225 days) coincided with the onset of the study (Figure 2); the first in 1992 (initial reconnaissance" surveys), and the second in December 1995/early 1996. Consequently, only the last increase (period between 450 and 525 days) supports the summer influx of dolphins (Figure 2). During summer, water salinity drops at the southern and western parts of Maputo Bay as a result of river discharges (Nhapulo, 2000). This changes fish diversity and causes strong reductions of fishing catches at these parts of the Bay (Sousa, 1989), suggesting a decrease in the abundance of fish preyed upon by humpback dolphins (Cockcroft & Ross, 1983), namely of the families Mugilidae, Scianidae, and Haemulidae. The eastern part of Maputo Bay, however, with water of marine salinity (Kalk, 1995; Nhapulo, 2000), experiences an increase in fish catches and fish abundance (De Boer, 2000). Similar seasonal influxes of humpback dolphins, probably related to food abundance, were reported at Algoa Bay (Karczmarski et al., 1999a, 1999b) and off the Natal coast, South Africa (Durham, 1994). Interestingly, group sizes did not increase significantly during summer in Maputo Bay, implying that influxes may be compensated by changes in group membership and possibly extended area use by some dolphins. This differs from findings along the southeast coast of South Africa (Karczmarski et al., 1999a, 1999b), where the total number of animals seen in summer was greater than in winter.

Influxes and the considerable number of apparently transient dolphins indicate an open" character of the humpback dolphin population of eastern Maputo Bay, supporting the choice of the Jolly-Seber model for mark-recapture population estimates. This model accounts for the type of sampling restrictions that occurred in this study (e.g., unequal sampling intervals, considerable disproportions between samples in the number of identified individuals, etc.), suggesting that this estimator produced probably the best population estimate; however, the large confidence intervals imply that some violation of the model assumptions might have taken place (Hammond, 1990). Unequal catchability could be one of them, which would bias downward the estimated population numbers. The crude population estimate was consistent with the Jolly-Seber estimator (Table 1), but the power-fit model was inconsistent with the previous two, and produced the highest estimate (probably an overestimate) of the population. This was likely because this estimator is dependent on the shape of the cumulative curve of newly marked dolphins. In the current study, the population estimate was calculated after a series of influxes and plateaus, and any large influx inflates the population estimate.

The current population estimate of 105 humpback dolphins in Maputo Bay in 1997 is considerably higher than the previous estimate of 67 dolphins in 1992, most likely a reflection of the considerably higher intensity of photo-identification surveys across different seasons. The eastern Maputo Bay area has a surface area of 219.5 km$_2$. Consequently, the mean absolute density estimate of humpback dolphins is 0.47 individuals per km$_2$. This density is consistent with the one from Algoa Bay (Karczmarski et al., 1998) and the Kwazulu-Natal coast (Durham, 1994), South Africa. In other areas of Maputo Bay, which are heavily affected by fisheries, the density may be lower as disturbing fishing practices (fishermen using dolphins as fishing cues) take place (Guissamulo & Cockcroft, 1997).

A total of eight births were recorded during 1996 and 1997, with an increase of 40% between these two years. Evidence from photo-identification shows that some pregnant females immigrated to the area in 1997, implying that eastern Maputo Bay may provide a foraging and nursery ground, and possibly a shelter for pregnant and nursing females and their offspring. Similar nursery functions of some coastal areas were suggested for Algoa Bay (Karczmarski, 1999) and Tugela Bank (Durham, 1994) in South Africa. Whether most of the dolphins in eastern Maputo Bay come from southern and western areas, where fishing intensity is high, is unknown, but it is likely because these areas also have suitable habitats for dolphins.

Newborn calves occurred throughout the year, and because the number of births recorded was small, no peak was identified and any prevalence of a particular season needs further investigation. Similarly, nonseasonal reproduction of humpback dolphins has been suggested for the KwaZulu-Natal coast, South Africa, by Cockcroft (1989), although this was based on limited evidence. In contrast, in the Algoa Bay region, South Africa, births have been reported to occur predominantly in summer (Karczmarski, 1999). It is possible that the breeding pattern may differ relative to the variation in climate and resource availability (for discussion, see Karczmarski, 1999). In Algoa Bay, the seasonal difference in water temperature, and possibly prey availability, is considerable (Karczmarski et al., 1999b). This is not so in Maputo Bay (Kalk, 1995) and, thus, is likely to affect the dolphin reproductive pattern.

The current dataset for humpback dolphins in Maputo Bay is relatively small and, therefore, the population parameters presented in this study should be viewed with caution. The crude birth rate was relatively high, larger than that observed at Algoa Bay, South Africa (Karczmarski et al., 1999a), possibly because pregnant and nursing females frequent eastern Maputo Bay, overestimating the real proportion. The recruitment rates at six months after birth and one year are low (Table 2), suggesting a smaller contribution of calves to the population growth and implying a high rate of calf mortality, the causes of which remain unknown. Alternatively, emigration should also be considered, and, in fact, abandonment of the area by some mother-calf pairs has been seen and it heavily affected the recruitment rate estimate. More long-term data are necessary for a more thorough analysis. Nevertheless, despite possible biases, the recruitment rates at six months and one year in Maputo Bay were generally low, lower than those of the humpback dolphin population in Algoa Bay (Karczmarski et al., 1999a), and may indicate low calf survival in the Bay. Potential causes of mortality are unknown, but may include intense fishing effort and associated risks of entanglement (Cockcroft & Krohn, 1994). Predator pressure is likely to be low, as the shark population in the Bay has already been substantially reduced (Sousa, 1989).

The effect of fisheries on the population parameters and population estimate cannot yet be predicted because of a lack of data on dolphin mortality by fisheries and the lack of data on their diet; however, fishing practices utilized in the Bay can cause severe disturbance to humpback dolphins (Guissamulo & Cockcroft, 1997) and may influence the extent of their use of shallow-water fishing areas. A good and accurate long-term dataset on births and survival histories, including those of dolphins that apparently range outside the eastern Maputo Bay, is needed.

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