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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 km², 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).

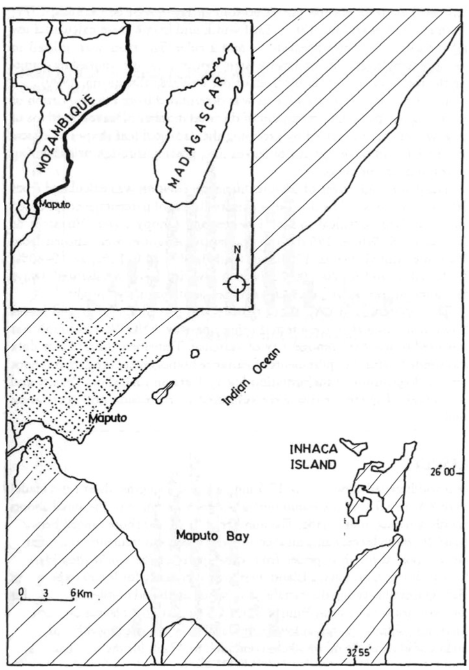

Figure 1. The location of Maputo Bay in Southern Mozambique. The study reported here concentrated around Inhaca Island.

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 km² (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,

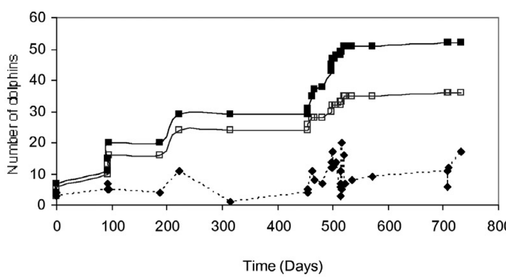

Figure 2. Cumulative number of humpback dolphins identified in Maputo Bay between January and May 1992, and between December 1995 and December 1997. ▯ = all individuals, □ = adults only; the number of dolphins identified per photo-identification survey is also shown (♦ = individuals identified in a given sighting).

[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.

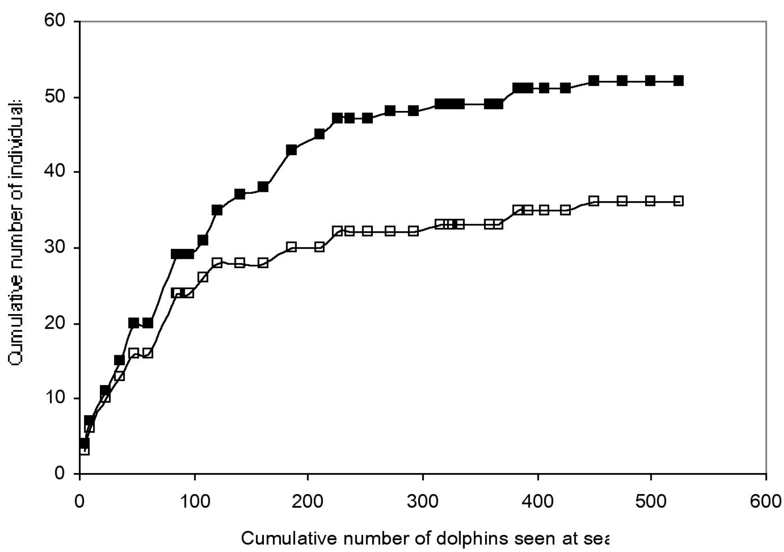

Figure 3. The relationship between the number of dolphins identified against the cumulative number of dolphins encountered during the study at Maputo Bay; ▯ = all individuals; □ = adults only

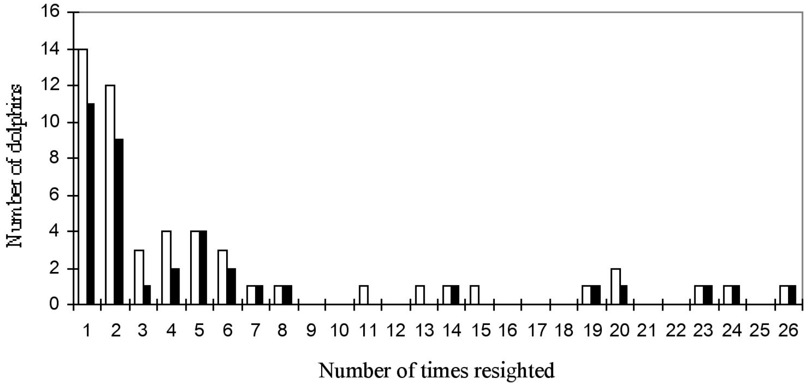

Figure 4. Frequency distribution of the number of individually identified humpback dolphins during the period between January and May 1992, and between December 1995 and December 1997. □ = all individuals; ▯ = adults only

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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