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Spatial Distribution of Indo-Pacific Humpback Dolphins (*Sousa chinensis*) at Richards Bay, South Africa: Environmental Influences and Behavioural Patterns

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Abstract

Humpback dolphins (*Sousa chinensis*) are caught in shark nets at Richards Bay, South Africa, at higher levels than elsewhere along the KwaZulu-Natal coast. As part of an investigation to understand the reasons for humpback dolphin capture in shark nets at Richards Bay, we studied the spatial distribution and behavioral patterns of these dolphins. The study area was divided into five offshore sectors, 13 longshore sectors, and three regions. The geographic positions of humpback dolphins were recorded during boat-based follows, as was the proportion of time focal groups spent feeding, resting, socialising, and traveling. Humpback dolphins used the area within 2 km of the shore extensively. Along the shore, "hot spots" where humpback dolphins were most likely to be found were widely spaced, but sea conditions (water depth, surface, and subsurface temperatures and water visibility) did not appear to influence this spatial distribution. This may be because most measurements were within humpback dolphins' preferred range. In general, humpback dolphins used the area south of Richards Bay Harbor most often. The inshore area was important for feeding, but humpback dolphins moved further offshore to rest. Feeding was particularly important at the entrance to the harbor, where breakwaters and an estuary mouth are found. The Harbor Mouth region may be considered a feeding area of humpback dolphins, and this is where the shark nets are placed.

Key Words: *Sousa chinensis*, Indo-Pacific humpback dolphins, behavior, spatial distribution, shark nets

Introduction

Indo-Pacific humpback dolphins (*Sousa chinensis*) occur along the eastern coastline of South Africa, in warm shallow water (Jefferson & Karczmarski, 2001; Peddemors, 1999). These humpback dolphins are dark grey over most of the body, with a pale ventral surface. The dorsal hump that gives this species its name is prominent in the South African form. Since the taxonomy of humpback dolphins is in dispute (Jefferson & Karczmarski, 2001; Jefferson & Van Waerebeek, 2004), we chose to follow the conservative approach and use the name *S. chinensis* for the humpback dolphins that occur off South Africa.

Humpback dolphins are incidentally caught in gill nets set for sharks in KwaZulu-Natal (KZN) Province, South Africa (Cockcroft, 1990, 1994; Peddemors et al., 1997). These shark nets are set to reduce the numbers of sharks and, hence, reduce the probability of shark attack (Dudley, 1997). By 1994, 40 km of shark nets were set at 45 beaches along 326 km of the KZN coastline (Davies et al., 1995), and an annual average of seven humpback dolphins were caught (Peddemors et al., 1997). The population of humpback dolphins in KZN appears to be small (Durham, 1994), with an estimated abundance of 160 (95% confidence limits 134-229), putting the annual by-catch rate at approximately 5% of the estimated population. Of the 129 humpback dolphins caught in shark nets along the KZN coast between 1980 and 1998, the majority were at Richards Bay, where the annual by-catch was 54.1 ± 5.9% (mean ± SE) of the total humpback dolphin by-catch in KZN (Natal Sharks Board [NSB], unpublished data). This high percentage of total individual catch is alarming since the mean annual fishing effort at Richards Bay was only 4.4 ± 0.2% of the total fishing effort (NSB, unpublished data). On average, 2.3 ± 0.6 km of shark nets at Richards Bay catch 3.8 ± 0.7 humpback dolphins each year.

Humpback dolphins may be prone to capture in shark nets because of their preference for shallow water (less than 20 m deep) (Corkeron, 1990; Durham, 1994; Karczmarski et al., 1998; Ross et al., 1994; Saayman & Tayler, 1979), coinciding with the placement of shark nets. Previous attempts to reduce the by-catch of humpback dolphins by the NSB met with little success, and Peddemors et al. (1990) recommended that behavioral studies be undertaken.

The objective of this study was to understand the factors underlying humpback dolphin capture in shark nets at Richards Bay. Our aim was to study space use and behavioral patterns of humpback dolphins in this area. We asked the following questions: Are humpback dolphins equally likely to be found in all parts of Richards Bay? Do environmental factors affect spatial distribution patterns? What behaviors do humpback dolphins display in various parts of Richards Bay?

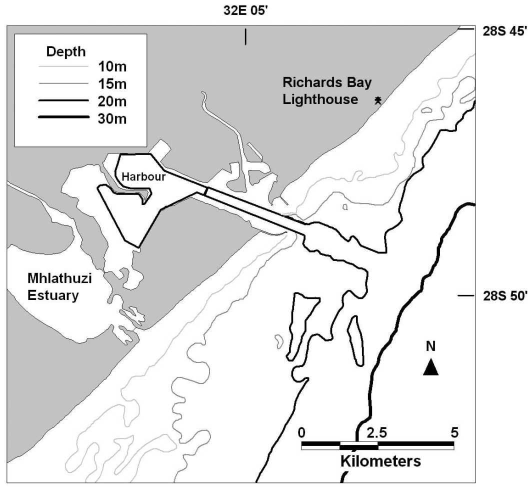

Figure 1. The Richards Bay study area (from the Mhlatuzi Estuary mouth to the lighthouse) with the bathymetry indicated; SA Navy Chart SAN1032, 1997

Materials and Methods

Study Area

Richards Bay is the northernmost beach in KwaZulu-Natal that has shark nets. It is situated on the Tugela Bank, where the continental shelf is wider than that of the rest of the KwaZulu-Natal coast. The study area was 13 km long from the Richards Bay Lighthouse to the mouth of the Mhlatuzi Estuary, and it extended 5 km offshore (Figure 1). The Richards Bay Harbor was created by modifying an existing estuary that was dredged to a depth of about 20 m. There were two river systems within the area—the Mzingazi River, which flows into the Harbor, and the Mhlatuzi River, which enters the Mhlatuzi Estuary.

The study area was divided into 1 x 1 km zones, which were designated into offshore sectors, longshore sectors, and regions (Figure 2). Offshore sectors were designated according to their distance from the shore, and longshore zones were designated according to their position along the shore (Figures 2a, b). Three regions (Figure 2c) that encompassed several offshore and longshore sectors were designated as North (zones d1 to h5; i.e., north of the Harbor Mouth); Harbor Mouth (zones i1 to k5, i.e., at the entrance to the Harbor); and South (zones l1 to p 5; i.e., south of the Harbor Mouth).

Five shark nets are permanently set in zone i1, and a sixth is permanently set in zone j1.

Data Collection

Weather permitting, a boat-based search for humpback dolphins was initiated from the Richards Bay Harbor. Most of the searches began at daybreak. Two search paths were followed for each search: one close inshore and the other further offshore (usually within 2 km from the shore). A Garmin II-Plus Global Positioning System (GPS) was used to record the position of the search path at 5-min intervals. The search area extended approximately 250 m on either side of the boat, and the search speed was 10 km/h. Searches were abandoned in sea states greater than 3 (Beaufort scale), when the occurrence of white caps and increased wave height decreased the probability of sighting dolphins (see Leatherwood & Show, 1980).

Once a humpback dolphin or group of dolphins was spotted, three variables were noted: (1) time of day, (2) geographic position (using a GPS), and (3) behavior of the majority (>50%) of the group. Thereafter, geographic position was recorded at 5-min intervals (termed "follow waypoints"). the behavior of a group of humpback dolphins (i.e., focal group) (Martin & Bateson, 1993) was recorded since solitary animals were very rarely observed. Following Karczmarski et al. (1999), a group was defined as an aggregation of dolphins in apparent association and engaged in similar activities, within visual range (i.e., within 250 m of the boat).

Focal group follows were continued for as long as possible (until the group was lost or the weather

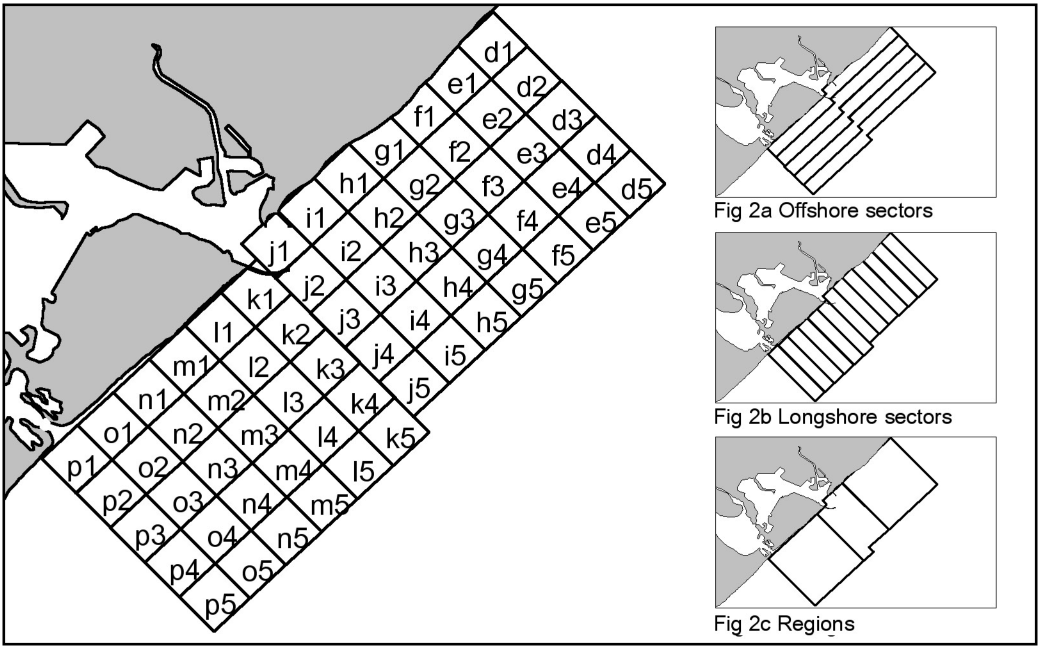

Figure 2. The Richards Bay study area divided into 1 km^2 zones. Zones were grouped into various sectors: (a) offshore, (b) longshore, and (c) regions.

or lighting conditions deteriorated). If the focal group was not seen for more than 10 min, it was considered "lost" and the time and geographic position of the last sighting were noted as the end of that follow. Only follows that were longer than 15 min were used in the behavioral analysis, and each follow, from start to finish, was considered a single replicate.

Encounter-to-Search Ratio

To determine where humpback dolphins were most likely to be found in the study area, an encounter-to-search (E/S) ratio was calculated, which was a measure of encounter frequency relative to search frequency. Therefore, the number of times humpback dolphins were first seen (encountered) in a particular sector (i.e., offshore, longshore, and regions; Figure 2) was counted and corrected for how well each sector was searched using the amount of time spent searching in that sector. The duration of the search was converted into a search frequency using the number of times the zones in that sector were searched, assuming that it took 12 min to search a zone based on three premises: (1) each zone was 1 km^2, (2) the search area was 0.250 km on either side of the boat, and (3) the search speed was 10 km/h. In other words, the search duration in a zone (S_D) was divided by 12 to yield a search frequency (S_F)—that is, $S_F=S_D/12$. The search frequencies of all the zones in a particular sector were summed (ΣS_F per sector). The number of encounters (E_F) in that sector was divided by the search frequency (ΣS_F), resulting in an E/S ratio: $E/S = E_F/\Sigma S_F$. The E/S ratio was used to estimate the probability of finding dolphins in a particular sector. To test if the probability of finding dolphins was equal in all sectors, we calculated an E/S ratio for the entire study area (i.e., Total E/S=79/915.4=0.08). Using this ratio, we calculated the expected number of encounters ($E_{F(exp)}$) per sector by multiplying the number of times the zones were searched in each sector (ΣS_F) by the overall E/S ratio: $E_{F(exp)} = S_F$* Total E_F/S_F. The observed and expected encounter frequencies were then compared using a χ^2 test.

Environmental Conditions

To establish if the spatial distribution of dolphins was related to particular environmental conditions, water depth, temperature, and visibility were measured. Water depth (in metres) was read off a bathymetric chart of the study area. Mean depth was calculated for each of the longshore sectors for the first 2 km only, since all but three dolphin encounters occurred within this distance from the shore. Water temperature (surface and 5 m below the surface) and water visibility

(Secchi Disk reading) were sampled at particular sampling sites and at regular times.

Five sampling sites were chosen that were in recognisable places so that they could be found again with ease. One site was located in the northern part of the study area (zone e1), two sites were at the extremes of the shark net installation (zone i1), a fourth site was on the south side of the Harbor Mouth (zone k1), and a fifth was found at the southern extreme of the study area (zone p2; note that breaking waves inhibited sampling in p1; Figure 2). Midway through the study, we had followed humpback dolphins close to these sampling points infrequently and consequently had few measurements that were taken when dolphins were present. This prompted an additional sampling strategy—measuring water temperature and visibility every hour on the hour during searches and follows (i.e., whether the dolphins were present or absent). Differences in the surface water temperature and water visibility were compared when dolphins were present or absent using a *t*-test.

To characterise environmental factors in the longshore sectors, water temperature and visibility data collected from the set sampling sites and the regular sampling times were combined and averaged per day for each longshore sector (again for the first 2 km only, which was where 97% of the encounters occurred). These data and those for water depth were tested for a linear relationship with the E/S ratio in the longshore sectors using a linear regression model. Similar analyses were not done for offshore sectors and regions because there were too few categories for offshore sectors (5) and regions (3) to allow for statistical analyses.

Activity Indices

The frequency of the following behaviors was scored continuously when humpback dolphins were observed: feeding, resting, socialising, and traveling (see Karczmarski et al., 2000, for definitions of these behaviors); behaviors that could not be classified in any of these four categories were scored as "undetermined." These categories represented behavioral states (i.e., behavior patterns of relatively long duration) (Martin & Bateson, 1993).

Behavior in the various sectors was quantified using Activity Indices (Karczmarski et al., 2000). This index, which ranged between 0 and 1, was used as a measure of the duration of time that the animals were engaged in each of the five behaviors in a particular sector as a proportion of the total time dolphins were observed in that sector during that follow. This can be expressed as IA=B/S, where IA is the Index of Activity, B is the duration of a particular activity in a sector, and S is the total duration of the follow in that sector. The geographic positions recorded at 5-min. intervals (follow waypoints) were used to calculate S. The predominant behavior associated with each follow waypoint was used to calculate B for each activity (predominant behavior was defined as behavior of the longest duration within the five-minute sample interval). The Activity Indices were arcsine transformed and analysed using MANOVA, with sector as the independent variable and behaviors as the dependent variables. The Tukey's post-hoc test was used to reveal differences between factors. Due to paucity of observations, data for offshore sector 5 and longshore sector d (Figure 2) were excluded from these analyses.

Results

Between 25 April and 12 November 1998, 84 searches were conducted and 54 (64.2%) searches were successful, resulting in 108 encounters with humpback dolphins. Of the 108 encounters, 83 resulted in follows that exceeded 15 minutes. Field effort consisted of 319.7 hours, of which 113.7 hours (35.6%) were spent following humpback dolphins.

Encounter-to-Search Ratio

The E/S ratio was not uniform in the offshore sectors ($\chi^2_4 = 12.2$; $p<0.05$); it was greatest in offshore sectors 1 and 2, low in offshore sector 3, and zero in sectors 4 and 5 (Figure 3a). The E/S ratio was not evenly distributed in the longshore sectors ($\chi^2_{12} = 29.0$; $p<0.01$). Figure 3b shows that sector n was particularly high, and that sectors e, j, l, m, and o had higher than the average E/S ratios. The E/S ratio in the three regions was not uniform ($\chi^2_2 = 9.4$; $p<0.01$); it was high in the South, intermediate in the Harbor Mouth, and low in the North (Figure 3c).

Environmental Conditions

Mean water depth in the first 2 km of the longshore sectors ranged from 6.0 m (sector f) to 17.4 m (sector j). In general, the longshore sectors north of the Harbor (d-h) were relatively shallow (7.7 $\pm$ 0.7 m), the sectors around the Harbor Mouth (i – k) were relatively deep (14.5 $\pm$ 1.5 m), and the sectors south of the Harbor (l-p) were intermediate between the other two (11.2 $\pm$ 0.4 m). A linear regression analysis showed no relationship between mean depth and the E/S ratio in the longshore sectors ($r^2_{12} = 0.24$; $p>0.05$).

There was little variation in mean water temperature in the longshore sectors. The mean surface temperature ranged from 20.8 °C (sector d) to 21.8° C (sector h); and the subsurface

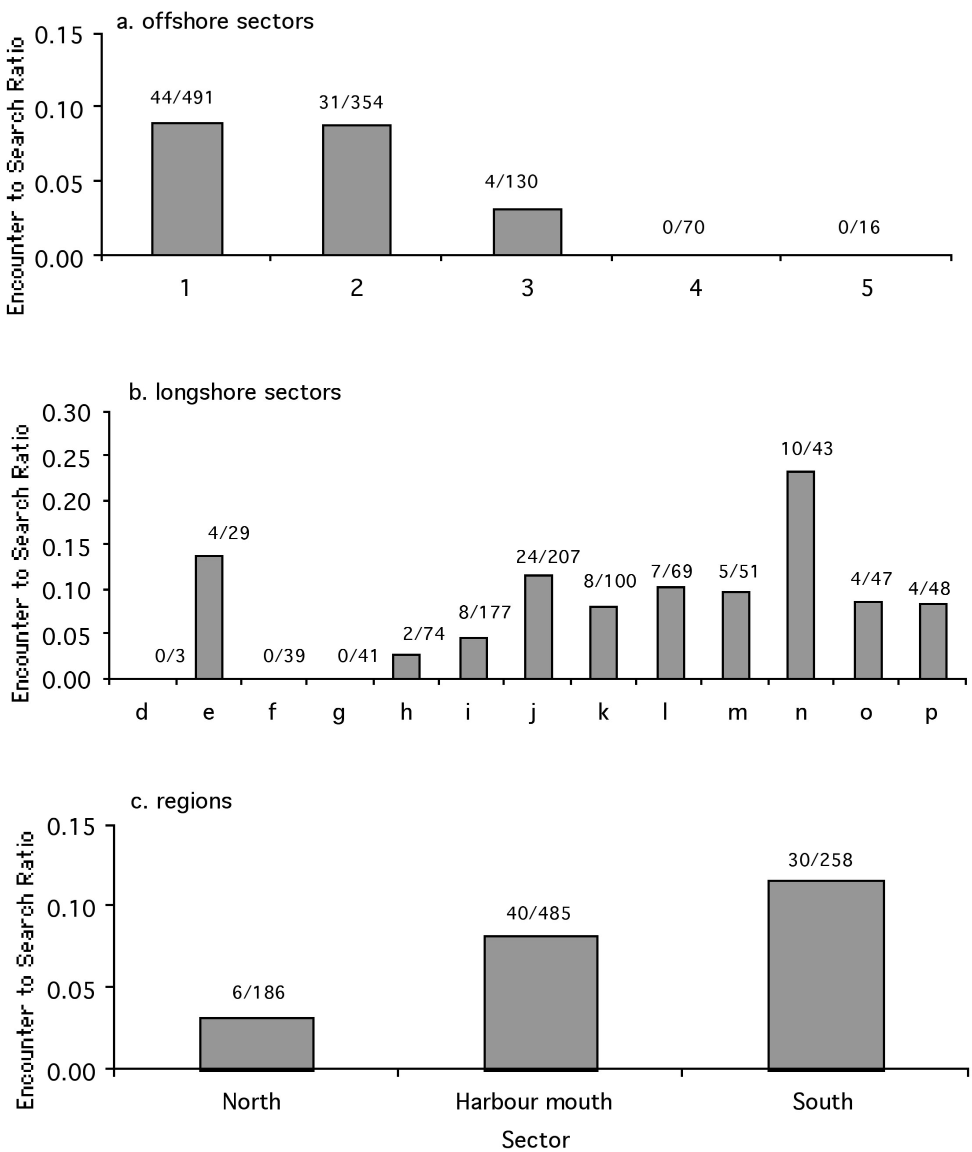

Figure 3. Encounter-to-search ratios for sectors with encounter frequency/search frequency values at the top of each bar

temperature ranged from 20.3° C (sector j) to 22.5° C (sector o). The E/S ratio was not related to surface temperature (r^2_{10} = 0.04; p>0.05), nor to subsurface temperature (r^2_{10} = 0.01; p>0.05).

Mean water visibility in the longshore sectors ranged from 2.7 (sector p) to 8.0 m (sector d). There was no significant linear relationship between water visibility and E/S ratios (r^2_{10} = 0.10; p>0.05).

Presence/Absence Analysis

During 45 follows, mean surface temperature was 20.75 ± 0.28° C and mean water visibility was 4.09 ± 0.34 m. During 50 searches when dolphins were not being followed, the mean surface temperature was 20.59 ± 0.39° C and mean water visibility was 3.50 ± 0.29 m. Neither water temperature nor water visibility differed significantly when dolphins were present or absent (temperature: t_{93}=-0.312, p>0.05; visibility: t_{93}=-1.325, p>0.05).

Activity Indices

Overall, the behavioral repertoire varied significantly among the offshore sectors ($F_{15,406} = 0.802$; $p<0.01$; Figure 4). Feeding behavior decreased with distance offshore and was significantly greater in offshore sector 1 than in sector 4 (Tukey's HSD; $p<0.05$). Resting behavior showed the opposite trend, increasing significantly with distance offshore, and was significantly lower in sector 1 than in sectors 3 (Tukey's HSD; $p<0.05$) and 4 (Tukey's HSD; $p<0.01$) and was lower in sector 2 than sector 4 (Tukey's HSD; $p<0.01$). Among the longshore sectors, there was no significant difference in the overall behavior ($F_{55,841}= 0.769$; $p>0.05$; Figure 5). Among the regions, the behavioral repertoire of humpback dolphins did not vary ($F_{10,186}=0.906$; $p>0.05$; Figure 6); however, post-hoc tests revealed that the occurrence of feeding in the Harbor Mouth was significantly greater than in the North (Tukey's HSD; $p<0.05$).

Discussion

Humpback dolphins used the area within 2 km of the shore extensively. Occasionally, they used the area between 2 and 3 km from the shore, but rarely beyond 3 km. At Richards Bay, humpback dolphins occurred further offshore than has been reported in other studies in South Africa (Durham, 1994; Karczmarski et al., 1999; Saayman & Tayler, 1979) but not Australia (Corkeron, 1990; Corkeron et al., 1997). Regardless of distance off-

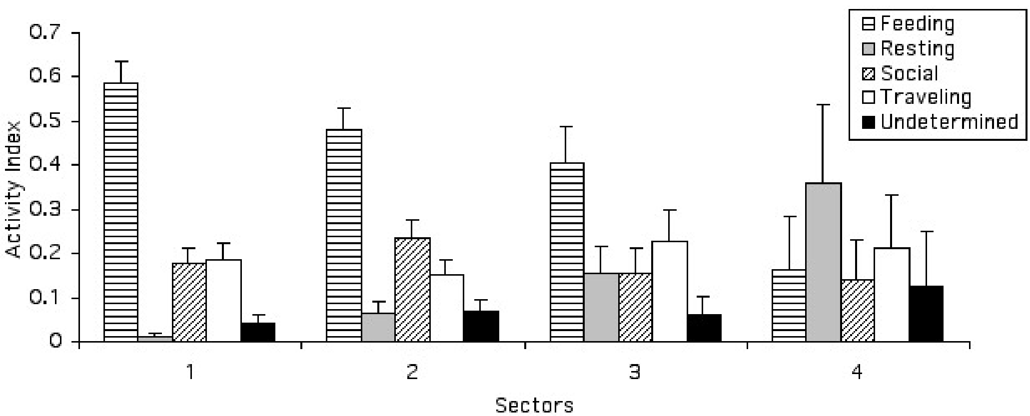

Figure 4. Mean activity indices in the offshore sectors; error bars = 1 SE of the mean

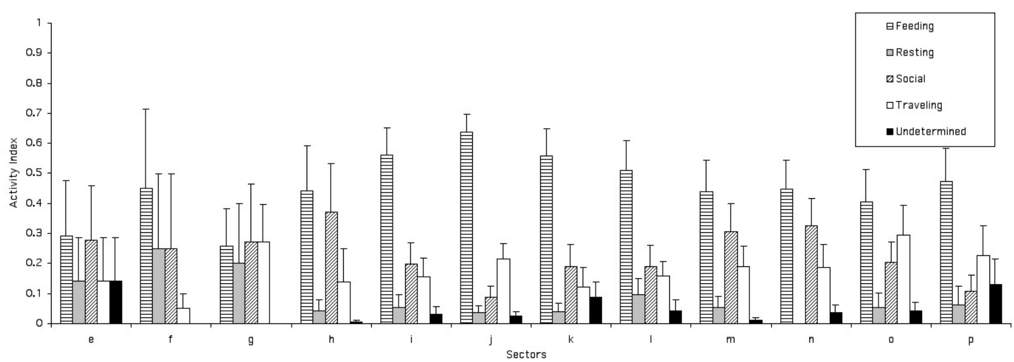

Figure 5. Mean activity indices in the longshore sector; error bars = 1 SE of the mean

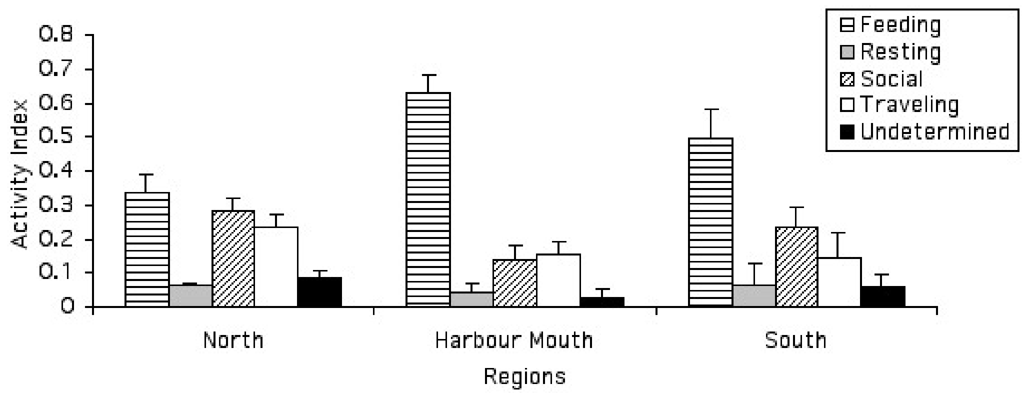

Figure 6. Mean activity indices in the three regions; error bars = 1 SE of the mean

shore, most reports stated that humpback dolphins occurred in depths of less than 20 m (Corkeron, 1990; Durham, 1994; Jefferson, 2000; Jefferson & Karczmarski, 2001; Karczmarski et al., 1999; Ross et al., 1994), and this is also true in the present study since all encounters (and most follows) occurred in water that was less than 20 m deep. Water depth may be the main factor limiting the distribution of humpback dolphins (Karczmarski et al., 1998).

Humpback dolphins used the area south of the Harbor Mouth most extensively. All five of the longshore sectors south of the Harbor Mouth had average or higher than average probabilities of finding dolphins and included sector n, with the highest E/S. The opposite was true north of the Harbor Mouth where the probability of finding dolphins was very low. Sector e was unusual, however, and the probability of finding dolphins here was high. The reason for this is unknown as this sector was not particularly warm or cold, shallow or deep, clear or turbid. One noticeable difference in the bathymetry between these two regions is the steepness of the slope. In the North, the 20-m isobath was 2 to 3 km from the shore, whereas in the South this isobath was 4 to 5 km from the shore (Figure 1).

The chance of finding dolphins in the Harbor Mouth, in longshore sectors i, j, and k was variable. Since every search began and ended at the Harbor Mouth, effort was greatest here. In sector j, the probability of finding humpback dolphins was higher than average. This sector contained two breakwaters that define the Harbor Mouth entrance, is the mouth of the estuary, and appears to be an important feeding area (see below). The chance of finding dolphins in sector i was low, but, because of the presence of the shark nets, effort here was high. The low E/S may be an indication that the dolphins avoid this area to some degree; however, it seems more likely that the E/S is deflated due to the elevated search effort at the shark nets.

Along the shore, none of the environmental factors were correlated with the chance of finding humpback dolphins. The mean depth of the longshore sectors close to shore where the dolphins were found did not appear to affect the spatial distribution of the dolphins. Within 2 km of the shore, all the longshore sectors were within the preferred depth (20 m) reported for humpback dolphins (Corkeron, 1990; Durham, 1994; Jefferson, 2000; Jefferson & Karczmarski, 2001; Karczmarski et al., 1999; Ross et al., 1994), which may account for a lack of a demonstrable effect of depth on spatial distribution along the shore.

Along the shore, the spatial distribution of humpback dolphins was apparently unrelated to water temperature, possibly because the variation between the mean longshore sector temperatures was so small (0.5° C). Sea temperatures at Richards Bay are warm and relatively constant compared to Algoa Bay, South Africa, where the range was between 16.5 and 21.3° C, and surface temperature was positively correlated with the temporal distribution of humpback dolphins (Karczmarski et al., 1999).

The spatial distribution of humpback dolphins at Richards Bay appeared to be unrelated to water visibility. This was contrary to expectation since Durham (1994) found a strong (negative) correlation between water visibility and humpback dolphins sighting rate. The range measured here (2.7 to 8.0 m), however, was much smaller than that (2 to 15 m) measured by Durham (1994). On the other hand, Karczmarski et al. (2000) found that water visibility had no affect on humpback dolphin distribution in

Algoa Bay nor in Plettenberg Bay, South Africa, where humpback dolphins can be found in very clear water (up to 24 m visibility) (Saayman & Tayler, 1979). Water visibility might not influence humpback dolphin distribution, but, rather, the relative density of humpback dolphins (Durham, 1994). The importance of water visibility to humpback dolphins is unresolved, but it did not appear to influence their spatial distribution at Richards Bay.

Richards Bay is known to be an area in KZN that is preferred by humpback dolphins (Durham, 1994). It seems likely then that most of the environmental conditions are suitable for humpback dolphins and that our measurements were within the range of those preferred by humpback dolphins; therefore, the relationships between environmental conditions and spatial distribution may have been masked.

Close to the shore, feeding behavior was most important, and resting behavior hardly occurred. With increasing distance offshore, feeding behavior was infrequently recorded, and resting became more important. Distance from shore did not appear to influence social and traveling behavior.

No trends were detected in the behavior of humpback dolphins along the shore. Almost invariably, the predominant behavior was feeding. Often, the next most predominant activity was social behavior, but occasionally it was traveling. Resting was only observed for a small proportion of the time. In Algoa Bay, feeding behavior was predominant in only half of the sectors, while in the other half, the predominant behavior was traveling (Karczmarski et al., 2000).

It is interesting that in most of the longshore sectors (76.9%), all four of the behavioral categories were recorded; and in the remainder, three of the four behavioral categories were recorded. The situation in Algoa Bay was a little different, with all four behaviors recorded in half of the sectors, and in 16% of the sectors only one behavior, traveling, occurred (Karczmarski et al., 2000). The Algoa Bay study area includes stretches of rocky shore, shallow reefs, and sandy areas, and Karczmarski et al. (2000) reported that behavior patterns were correlated with bottom topography. A similar situation, with site-specific behaviors, was recorded off Plettenberg Bay, another region with variable bottom topography (Saayman & Tayler, 1979). The Richards Bay area is without rocky outcrops, and the seabed has been classified as sandy and muddy (McClurg, 1998). The habitat at Richards Bay could be considered homogenous, possibly explaining why almost all the behaviors were recorded in all the longshore sectors, unlike the site-specificity of humpback dolphin behavior reported in Algoa Bay and Plettenberg Bay (Karczmarski et al., 2000; Saayman & Tayler, 1979).

When the longshore sectors were combined to form regions, some differences in behavior became apparent. Although the behavioral repertoire was essentially the same in all three regions, feeding occurred more in the Harbor Mouth region than it did in the North. Humpback dolphins feed on reef-associated, estuarine and demersal fish, as well as cephalopods (Barros & Cockcroft, 1991, 1999; Ross et al., 1994). The Harbor Mouth region is a wide entrance to the Richards Bay Harbor, which is a dredged estuary. The Harbor Mouth entrance is defined by two breakwaters totaling about 1.2 km in length, which may act as artificial reefs (Fennessy et al., 1998). The estuary and artificial reefs may attract humpback dolphin prey, and this might explain the very high proportion of time spent feeding in the Harbor Mouth. In the South, the mouth of the Mhlatuzi Estuary opens to the sea, and feeding occurred at high levels in this area. In contrast, there are neither estuaries nor major artificial reefs in the North, which would explain the lower levels of feeding in this area.

Shark nets are placed about 500 m offshore in the Harbor Mouth region, where humpback dolphins were frequently observed feeding. This suggests that the shark nets have been placed in a humpback dolphin feeding area. It is possible that feeding dolphins may be prone to entanglement (Goodson et al., 1994), though there are other explanations for their capture in the nets (Dawson et al., 1998). Goodson et al. (1994) stated that feeding bottlenose dolphins target their prey and suppress sonar echoes from objects other than the target, implying that during feeding, nets are unlikely to be detected. If humpback dolphins behave similarly, they might not detect the shark nets while feeding. It may be worth testing if moving the shark nets away from the feeding areas at the Harbor Mouth will reduce the mortality rate. We realize that the presence of beach infrastructure in the immediate area makes this suggestion impractical, although adding devices to the nets that alert the dolphins to the presence/dangers of the nets may also be an option. They would have to override the echo-suppression that may occur during feeding, however.

In conclusion, humpback dolphins at Richards Bay were usually found within 2 km of the shore. Along the coastline, the chances of finding humpback dolphins varied but their presence in one sector, n, was particularly high. In general, humpback dolphins were most likely to be found in the South and least likely to be found in the North. None of the environmental factors measured was related to the longshore spatial distribution, but this is considered to be due to the fact that most of the variables measured were within the preferred range of humpback dolphins. In terms of the spatial distribution of behavior, there was a reciprocal relationship between feeding and resting, with feeding more likely to occur close to shore and resting further offshore. Along the shore, no particular behavior was predominant; however, feeding occurred at an elevated rate in the Harbor Mouth compared to the North. The shark nets are set at the Harbor Mouth in what appears to be a humpback dolphin feeding area, and this may be important with respect to humpback dolphin capture in the Richards Bay shark nets.

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