Diurnal movements and behaviour of Heaviside's dolphins, *Cephalorhynchus heavisidii*, with some comparative data for dusky dolphins, *Lagenorhynchus obscurus*

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Received 12 November 2008. Accepted 16 July 2009

The sympatric Heaviside's (*Cephalorhynchus heavisidii*) and dusky dolphins (*Lagenorhynchus obscurus*) are poorly studied in South Africa and are potentially at risk from anthropogenic threats including fisheries bycatch. As part of a larger study, shore-based observations were made in a small bay (~1000 m wide) in the Western Cape, South Africa, during the summer months of 1999–2001 to gather data on their nearshore movements and behaviour. Heaviside's dolphins exhibited a diurnal onshore–offshore migration and the sighting rate varied significantly with time of day and brightness of the moon, with numbers being markedly higher before 12:00 and nearer a full moon. These patterns were presumed to be linked to the vertical migration of their principal prey, juvenile hake *Merluccius* species and Heaviside's dolphins appeared to be resting and not feeding inshore during the day. Sightings of dusky dolphin showed no predictable variation with time of day but their numbers inshore were significantly lower when upwelling conditions existed offshore. Larger groups of Heaviside's dolphins (especially groups of four) were more active (leaps, etc.) than smaller groups, but behaviour was not linked to environmental factors. The dissimilar responses to environmental conditions suggest that sympatry in these two species is mediated by niche as well as prey differentiation.

Key words: animal behaviour, animal movements, cue production, environmental variables.

INTRODUCTION

Coastal regions are amongst the marine environments most highly impacted by human activities such as pollution and fishing. They are also amongst the most difficult environments to manage as there is often considerable conflict between users with incompatible needs such as fishermen, recreational users and conservationists (Hughey 2000; Thompson *et al.* 2000). Owing to their nearshore distribution, coastal dolphins are amongst those populations most at risk from human impact. Central to any effective management programme is a good knowledge of the biology of the species being protected and how they use the environment, which enables the risk to a population to be better quantified and ensures that management is occurring at a relevant and biologically meaningful scale.

Two species of dolphin are commonly found nearshore along the west coast of South Africa, Heaviside's dolphin (*Cephalorhynchus heavisidii*) and the similar-sized dusky dolphin *Lagenorhynchus obscurus.* Neither species has been studied in detail in the region, nor is their conservation status well known. Heaviside's dolphin is an endemic resident that occurs from the breaker zone up to 45 nautical miles offshore, but is most abundant in water <100 m deep, and the dusky dolphin is found from the coast to at least 500 m depth (Findlay *et al.* 1992). Both species are subject to an unquantified level of bycatch on account of their overlap with several commercial fisheries (Sekiguchi *et al.* 1992). They are also likely to be influenced by the growing boat-based cetacean watching industry in South Africa (Turpie *et al.* 2005), particularly the endemic Heaviside's dolphin.

Both dolphin species are predominantly piscivorous with Heaviside's dolphins being arguably the more specialist feeder of the two taking mainly small hake (*Merluccius* spp, probably shallow water hake, *M. capensis,* based on the known species distributions – F. le Clus, pers. comm.)

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Table 1. Summary of shore-based observation effort for Heaviside's dolphins at Agterbaai, South Africa, showing the time spent searching and performing tracking and behavioural observations (number of sampling events in brackets). Differences between the total sampling effort and the number of 10 min samples are due to observation sessions shorter than 5 min being discarded.

	Effort (hours)					
Year	Search	Track	Behaviour	Watch time (total)	First day	Last day
1999	101:16	7:28 (45)	4:46 (27)	113:30	2 February	21 March
2000	90:23	4:54 (32)	3:31 (21)	98:48	27 March	4 April
2001	190:09	13:37 (84)	4:29 (25)	208:15	12 February	17 March
Total	381:48	25:59 (161)	12:46 (73)	420:33		

which comprises 48.9% of their diet (Sekiguchi *et al.* 1992). Heaviside's dolphins also take goby (*Sufflogobius bibarbatus*), horse mackerel (*Trachurus trachurus capensis)* and cephalopods. The stomach contents of Heaviside's dolphins caught in the morning were greater than those caught in the afternoon and it was suggested by Sekiguchi *et al.* (1992) that they may forage nocturnally on hake as they migrate closer to the surface in the dark (Pillar & Barange 1995). Dusky dolphins are generally regarded as opportunistic feeders that alter their foraging strategies in different environments and seasons (Würsig *et al.* 2007). The diet of dusky dolphins in South Africa includes several of the same species, but they take a more diverse range of prey including horse mackerel, hake *(Merluccius* spp.), lantern (*Lampanyctodes hectoris*) and hatchet fish (*Maurolicus muelleri*) (Sekiguchi *et al.* 1992).

The Benguela current system off the west coast of southern Africa is a cold-water, wind-driven upwelling ecosystem, which is well structured at a broad scale with predictable, localized upwelling cells that affect the broad-scale distribution of the cetacean fauna in the region (Findlay *et al.* 1992). The shore-based observations in this study took place near the Cape Columbine upwelling cell which creates high productivity in the St Helena Bay area, and it is feasible that the broad-scale effects on cetacean distribution by upwelling may be apparent at a finer scale if dolphins respond to upwelling conditions.

This paper presents the results of shore and boat-based observations of the behaviour and movements of Heaviside's dolphins, with some appropriate data included from contemporaneous observations of dusky dolphins, which are used in an interspecies comparison to examine the way in which these sympatric predators use the near-shore environment.

METHODS

Data collection

Both shore-based and boat-based research was conducted. Shore-based observations of Heaviside's dolphins were made from a temporary, gazebo structure on top of a dune approximately 5 m above sea level and 100 m back from the high-water mark, at Agterbaai, on the west coast of South Africa (Fig. 1). The bay was chosen because it is small enough (~1000 m wide) for dolphin movements to be followed throughout, boat traffic is minimal, and it is an area known to be well frequented by Heaviside's dolphins. The bay is north-facing, so it is largely sheltered from the southwesterly winds that are prevalent in summer. All fieldwork took place between early February and early April in 1999, 2000 and 2001 and was timed to take advantage of optimal weather conditions during the summer and occurred in conjunction with a boat-based photo-ID project. Effort was partly dependent on the number of volunteers available because boat-based work took priority and the shore-based observations were curtailed if insufficient manpower was available to staff both projects. Observations were made for all possible daylight hours, weather permitting, for a total of 420.6 h (Table 1). Observations were discontinued if the wind exceeded ~15 knots or if it was raining or foggy.

Some data collected from the concurrent boat surveys were used as a comparison with the data collected from the shore station. The boat was used to run searches parallel to the shore usually just behind the breaker line where the density of Heaviside's dolphins is thought to be highest during the day. Upon encounter, dolphins were followed until photography of the group was regarded as complete or until the dolphins were lost. Estimation of group size was problematic, as

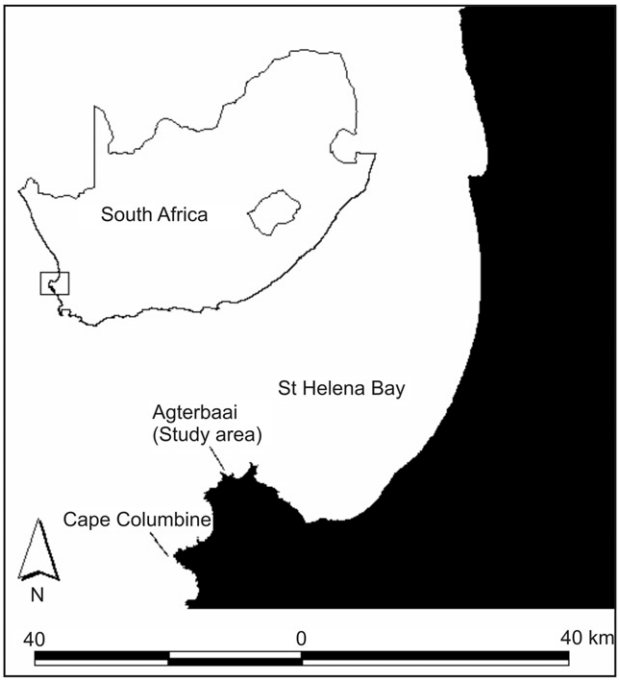

Fig. 1. Study area at the tip of St Helena Bay, South Africa.

some individuals were attracted to the boat and tended to follow it from one sighting to the next, biasing counts. Only sightings where this did not occur and counts regarded as 'confident' are used here. Dolphins response to the boat was noted if obvious as 'evasive' (animals continuously moving away from the boat despite repeated approaches) or 'boat friendly' (animals approaching boat and/or bow riding boat).

A team consisted of four observers, two on watch at a time for alternating 2 h shifts, searching the bay by naked eye and with 7 × 35 binoculars. Environmental variables (cloud cover, Beaufort scale, wind strength and direction, swell height, percentage glare) were recorded hourly or if a noticeable change in conditions occurred. An index of overall sightability (from 1–5; very poor to excellent), encompassing all the above conditions, was recorded at the same time. Some slight variations in field methods occurred during watch handovers (when shifts overlapped) and observer training (when an extra, more experienced observer was also present). However, because of overall standardization of techniques, it was our judgement that these slight variations did not bias data collection due to the presence of experienced observers and brevity of the periods of overlap.

When dolphins were sighted, the numbers of adults and calves (animals roughly 70% or less than the size of adults) in the group were estimated. Groups were defined as aggregations of individuals within 20 m of each other. For Heaviside's dolphin schools that were close enough to shore, their movements were visually tracked for 10 min when at the surface, with approximate locations being estimated relative to prominent landmarks and a 100 m square grid marked on a map of the bay. Although fairly widely used in similar studies on account of its generally greater precision, a theodolite was not used during this study owing to the poor accuracy it would have attained from such a low observation platform (Würsig *et al.* 1991) and the need to train new observers every two weeks. Behavioural observations were recorded for a further 10 min period immediately following tracking, with one observer continuing to use binoculars to monitor the dolphins while the other acted as a data recorder. Since dolphins sometimes moved out of sight before or during this period, there were fewer behavioural sessions than tracking sessions. Because they were not the target species for the study, behavioural observations were not undertaken for dusky dolphins.

During behavioural observation sessions ($n = 73$), all behaviours observed for a group of dolphins were recorded for a 10 min period. In the field,

behaviours were recorded as precisely as possible with nine behaviours that were differentiated (slow roll, spy hop, chin out, tail out, lob tail, chasing, noisy jump, vertical jump and horizontal jump – Slooten, 1994). Because observations were extremely skewed toward normal surfacings ('slow rolls' – 95.4%), all behaviours excluding 'slow rolls' were summed together and referred to as 'active behaviours'. To avoid the bias caused by end effects (*i.e.* starting or ending the observation period to coincide with particular events, such as high activity or being submerged / surfaced), periods of observation began at a set time independently of the actual behaviours at the time, and ended 10 min later. Behavioural observations were attempted on each group sighted, but the dolphins were sometimes lost before the full 10 min period had passed. Although such 'losses' could conceivably represent prolonged submergences rather than actual departures from the field of view, it was considered inappropriate to include data from sessions of less than 5 min owing to the small number of behavioural observations therein. In total, 70 sessions of behavioural observations were available for analysis.

Data analysis

Although observations were stopped when sighting conditions became too poor, detectability could still have been influenced by varying conditions within the search time. We therefore compared the rate of dolphin sightings between hours of 'worse' sightability (1–3; poor to moderate) and 'better' sightability (4–5; good to excellent).

The relationship between environmental factors and the variability of the sighting rate of Heaviside's dolphins was examined using a general linear model (Proc GLM in SAS®). Dolphin presence was expressed as the sighting rate of (a) dolphins per hour, and (b) groups per hour (number of groups seen per total minutes observing; which included tracking, searching and behavioural observations). To normalize the residuals, the sighting rates of Heaviside's dolphins were rank-transformed, ties were broken by adding a small random number and then Blom transformed (Blom 1958) to decrease the inequality of the variances. *Post-hoc* testing was performed using least squares means. Time of day (*i.e.* daylight hours, in 1 h intervals except 06:30–07:59), wind direction (N, NE, E, etc. or no wind), the presence or absence of dusky dolphins and lastly the brightness of the moon (less or more than half full) were included as class variables. Wind speed was included as a co-factor in the model. Waxing and waning moon phases were combined and analysis was limited to more or less than half full.

The total number of dusky dolphins observed was similar to that of Heaviside's dolphins, but there was higher variation in group sizes and timing of sightings. Dusky dolphin sighting rates were strongly influenced by the sighting of several hundred animals in multiple groups over two consecutive days. This created a strong bias in the analysis toward the environmental factors prevalent on those two days, thus potentially masking any possible relationships during the majority of days with much lower sighting rates. The analysis of variance was thus performed both with and without the data from these two days. The dusky dolphin sighting rate data were transformed as were the Heaviside's dolphins' to attain normality and the same factors were included in the model with the presence of Heaviside's dolphins replacing the presence of dusky dolphins in the previous analysis.

Behavioural data were analysed using a) 'active behaviours' per dolphin per minute and b) using an overall index of 'cue production' per dolphin per minute which included all behaviours seen, and is useful for calculating sightings probabilities for, for example, line transect surveys. Variation in both the rates of active behaviours and cue production was compared independently to wind strength, direction and moon phase as well as time of day, group size and distance from the observers (average distance of track line from observer post, estimated to nearest 100 m off tracking maps).

Variations in 'evasive' behaviour of dolphins (with respect to the boat crew's attempt to close with the group for photography) and calf number were analysed with respect to group size.

RESULTS

In total, 54 days were worked in the field, during which 616 Heaviside's dolphins were seen in 203 groups, with a mean group size of 3.3 (range = 1–10, mode = 3). In all, 660 dusky dolphins in 75 groups were seen at an average group size of 7.9 (range = 2–50, mode = 10). If the two days of very high sightings were excluded, 131 animals in 25 groups were seen. The size of tracked groups of Heaviside's dolphins did not vary with distance from shore ($n = 161$, $P = 0.899$, $F = 0.3209$) when distance was categorized as 100 m bins from 0–500 m (with observations >500 m clumped,

n = 10). Neither the sighting rates of Heaviside's dolphins (P = 0.51, t = –0.66) nor the observed group size (P = 0.41, t = 0.82) varied significantly between worse (152:52 hours) and better (267:41 hours) sighting conditions. This confirms that field observations were curtailed before the quality of data collection was compromised by sighting conditions, and overall sighting conditions can be considered as an essentially random variable.

The sighting rate of Heaviside's dolphins was significantly related to both time of day and brightness of the moon when measured as either groups per hour or dolphins per hour (Table 2). *Post hoc* analysis showed the sighting rate of dolphins to be higher when the moon was brighter (0.35 *vs* 0.71 groups per hour and 0.94 *vs* 2.36 dolphins per hour for darker and brighter moons respectively), and higher in the morning than in the afternoon for both groups and dolphins sighted per hour (Fig. 2). It is noteworthy that only two groups (five individuals) of Heaviside's dolphins were ever spotted after 16:00 despite 61:16 h on watch in this period. The presence of dusky dolphins influenced the sighting rate of dolphins per hour but not groups per hour, with *post hoc* analysis showing the rate to be higher when dusky dolphins were present. This suggests that the presence of dusky dolphins in the bay may influence the group size, if not the overall number of groups of Heaviside's dolphins seen.

To examine the pattern of movement offshore with time of day in more detail, the starting time of all tracked sightings of Heaviside's dolphins (n = 161) was correlated against each track's mean distance from shore. While there was no relationship in the overall spread between the data (r^2 = 0.005, P = 0.954), the pattern after noon appeared different to that before noon. Sightings in the morning were spread throughout the bay from close inshore (20 m) to far offshore (1100 m), whereas the dolphin sightings were less spread out in the afternoon, being close to the breakers around noon, then increasing in distance from shore during the afternoon, with no sightings within 200 m from shore after 14:00. Correlating these data separately (Fig. 3) shows no relationship between time and distance from shore in the morning (r^2 =0.018, P = 0.116) but a positive correlation in the afternoon (r^2 = 0.158, P = 0.037) suggesting that dolphins move farther offshore as the afternoon progresses.

The movements of dusky dolphins were markedly different from those of Heaviside's dolphins; they were seen less frequently and tended to be in larger groups. Occasionally groups of up to several hundred animals were observed (the largest group of Heaviside's dolphins observed during contemporaneous observations at sea was 40 animals and consisted of several subgroups). The principal factor influencing the sighting rate of dusky dolphins was not time of day (dolphins were seen with equal probability throughout the day, Fig. 2) but the direction of the wind which showed a significant relationship with the sighting rate of dolphin groups per hour in both the full data set and the data set where the two very high sightings days were removed (Table 3, Fig. 4). *Post hoc* analysis showed that the sighting rate of dusky dolphins was lower when the wind was blowing from a westerly or southwesterly direction (242:36 watch hours), than when the wind blew from a north to easterly direction (59:42 watch hours). It is noteworthy that no dusky dolphins were sighted from shore when the wind direction was southwesterly, despite nearly 130 watch hours during those conditions. The brightness of the moon appeared to have little effect on the sighting rate of dusky dolphins, as a significant effect was only seen on the sighting rate of groups when the two days of very high sightings were removed. *Post hoc* analyses showed the sighting rate to be lower when the moon was brighter; this is opposite to the pattern observed for Heaviside's dolphins.

Table 2. Results of GLM ANOVA on the effects of environmental factors affecting the sighting rates of Heaviside's dolphins in Agterbaai, South Africa, measured as groups and dolphins per hour.

Variable	Groups/h		Dolphins/h	
	F	*P*	*F*	*P*
Overall	3.04	0.001	3.13	<0.001
Time of day	3.27	0.001	4.10	<0.001
Wind direction	0.93	0.488	1.19	0.305
Dusky dolphins	2.09	0.149	5.97	0.015
Moon phase	16.47	<0.001	5.95	0.015
Wind speed	0.03	0.864	3.08	0.08

Behaviour

A total of 73 behavioural observation sessions were available for analysis from three years. Given the low resighting rate in photo-identification studies (Elwen *et al.* 2009) and high turnover of group membership (Elwen 2008), it is likely that these groups consisted of different animals and no

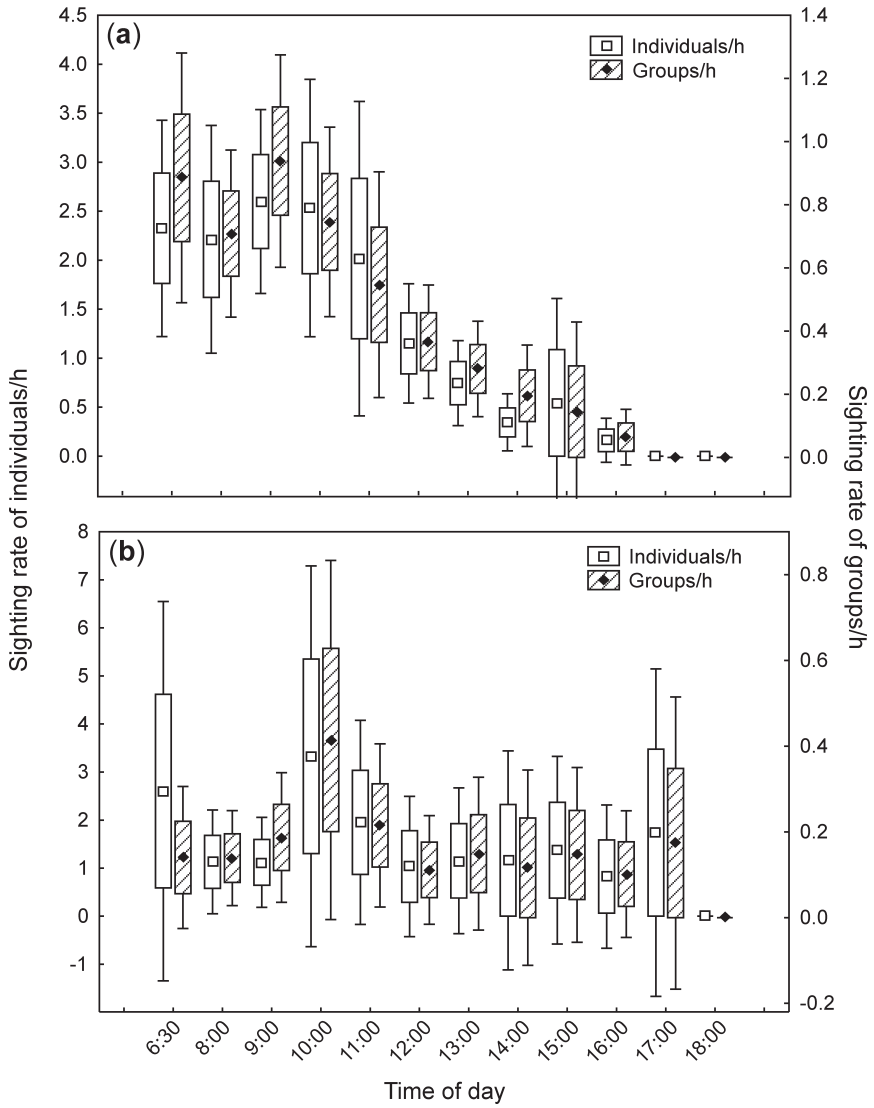

Fig. 2. Variation in the sighting rate of individuals per hour and groups per hour of Heaviside's dolphins (**a**) and dusky dolphins (**b**) in Agterbaai, South Africa, with time of day. Whiskers, boxes and points represent 1.96 S.E., S.E. and means for each hourly category. Calculated as rates per clock hour on watch. Sample sizes in each category exceed 30 hours except 17:00 (n = 15) and 18:00 (n = 2).

pseudo-replication occurred. The rate of active behaviours per dolphin per minute in Heaviside's dolphins was not significantly correlated to the brightness of the moon (Mann Whitney *U*-test, z = –0.266, P = 0.79) or time of day (ANOVA: P = 0.84, F = 0.448) and, although sample sizes in the afternoon were small, no active behaviours at all were seen in the nine sampling events (87 min) occurring after 12:30. Further, the rate of active behaviours was not correlated with wind speed (Spearman rank order correlation; r_s = 0.047, P > 0.05) or wind direction (Kruskal Wallis: P = 0.43, H = 8.08, d.f. = 8) although small sample sizes during certain wind directions may weaken this analysis. However, the rate of active behaviours showed a general increase with group size (Kruskal Wallis: P = 0.007, H = 15.81, d.f. = 5), but with some groups of four being especially active (Fig. 5); although *post-hoc* multiple comparisons (Statistica: multiple comparison z' values) showed no specific differences.

The overall mean rate of cue production by

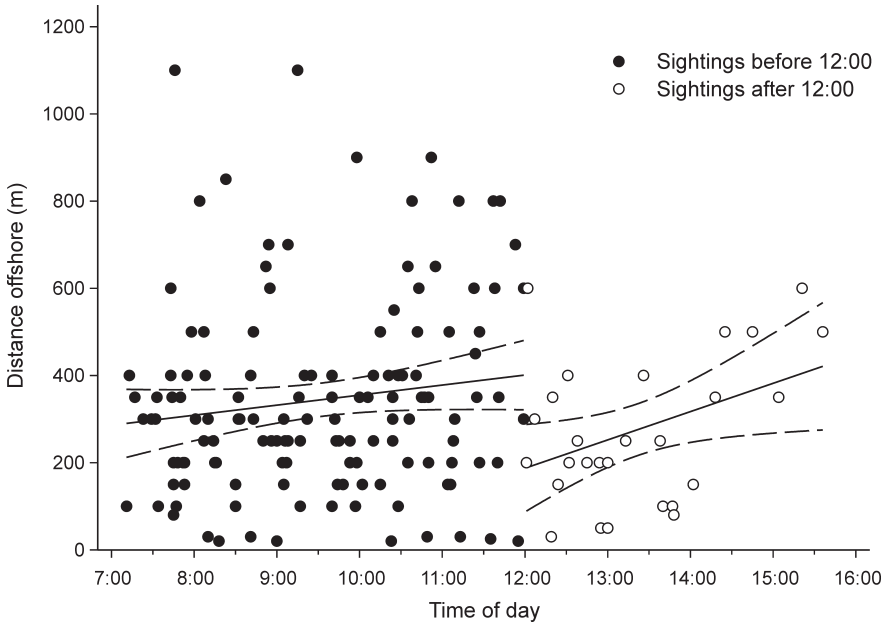

Fig. 3. Regression (with 95% confidence intervals) of distance offshore of tracked groups of Heaviside's dolphins in Agterbaai, South Africa, with time of day. Data and correlations split at 12:00.

Heaviside's dolphins was 1.79 cues per animal per minute (range: 0.22–4.03, n = 70). Variation in the cue production rate was not correlated with either wind speed (Pearson: $r^2 = 0.013$, $P = 0.337$), moon brightness (r^2 = 0.012, P = 0.341) or group size (ANOVA; $F = 0.461$, d.f. = 5, $P = 0.803$). However, cue production rate decreased significantly throughout the day (Pearson: r^2 = 0.093, P = 0.007) (although there was only one sample after 14:30) and with distance from the observer (ANOVA: $F = 5.00$, d.f. = 5, $P < 0.001$). A *post hoc* comparison showed the main differences occurred between sightings farther than 500 m and sightings in the 100–200 m and 300–400 m distance strata (Tukey HSD for unequal n; P = 0.014 and 0.043, respectively). The mean rate of cue production in strata less than 400 m from the observer was 1.961 (S.D. = 0.134) cues per dolphin per minute and only 0.941 (S.D. = 0.041) in strata further than this.

Table 3. Results of GLM ANOVA on the effects of environmental factors affecting the sighting rates of dusky dolphins in Agterbaai, South Africa, measured as groups and dolphins per hour: data are shown both including and excluding the two days of very high sighting rates.

Variable	Groups/h		Dolphins/h	
	F	*P*	*F*	*P*
Including two days with high sighting rates				
Overall	1.80	0.017	1.03	0.428
Time of day	0.32	0.975	0.21	0.996
Wind direction	2.03	0.042	1.65	0.108
Heaviside's	3.45	0.064	0.66	0.417
Moon phase	0.43	0.511	1.41	0.235
Wind speed	3.86	0.050	0.16	0.686
Excluding two days with high sighting rates				
Overall	1.78	0.018	1.20	0.243
Time of day	1.14	0.332	0.77	0.657
Wind direction	2.04	0.041	1.70	0.097
Heaviside's	0.00	0.976	0.01	0.927
Moon phase	6.95	0.009	0.42	0.518
Wind speed	0.03	0.871	1.63	0.203

In boat-based observations, group size was negatively correlated with evasive behaviour (Pearson: r^2 = 0.685, P = 0.022) and positively correlated with the proportion of calves in a group (Pearson: $r^2 = 0.7844$, $P = 0.008$), with more calves being seen in bigger groups.

DISCUSSION

Shorebased observations of cetaceans have been used widely and on a variety of species, from small dolphins (Würsig & Würsig 1980; Stone *et al.* 1995) to large whales (Findlay & Best 1996; Williams *et al.* 2002) to monitor the movements and behaviour of animals. The main benefit of

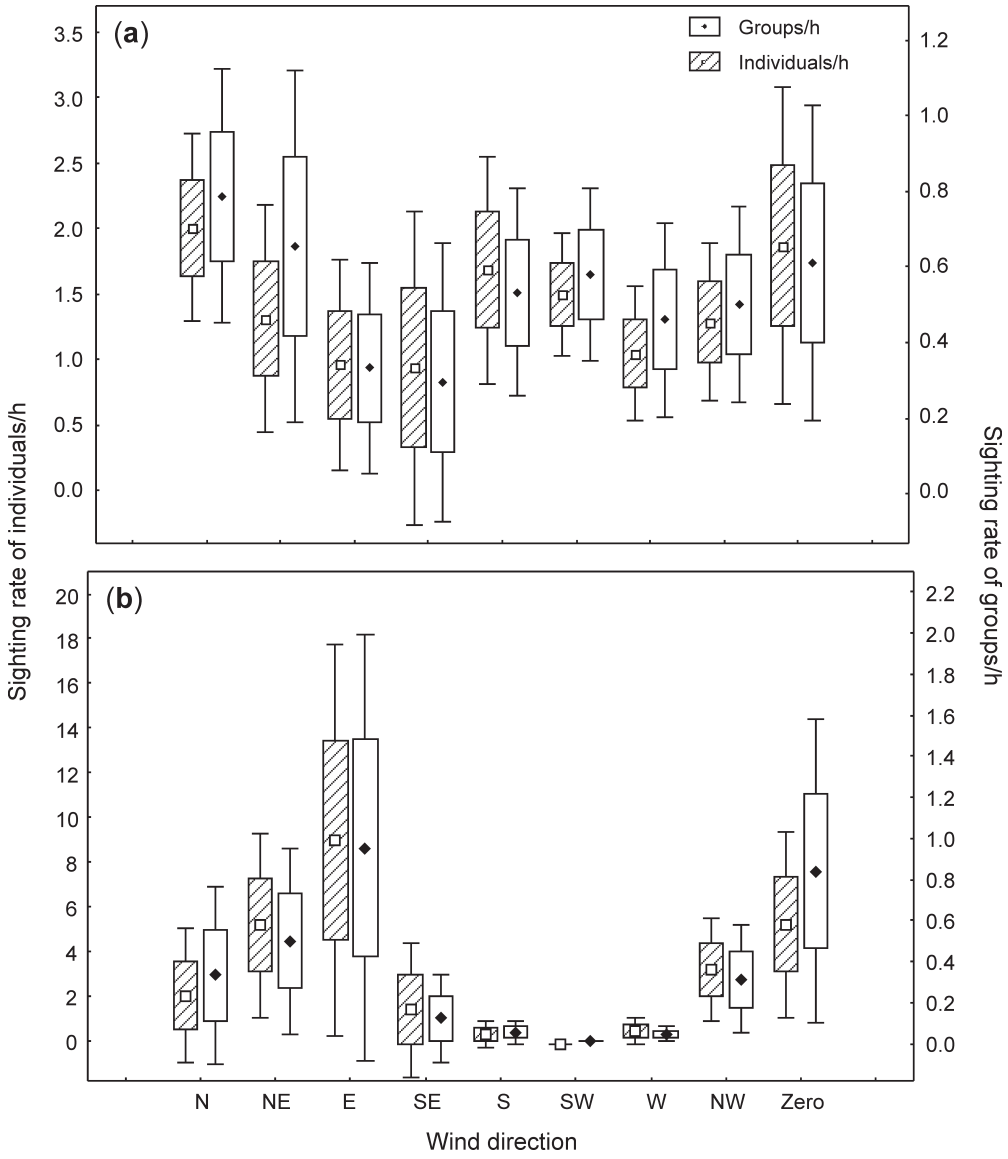

Fig. 4. Variation in the sighting rate of individuals per hour and groups per hour of Heaviside's dolphins (**a**) and dusky dolphins (**b**) in Agterbaai, South Africa, with wind direction (two days with high dusky dolphin sightings included in this figure). Whiskers, boxes and points represent 1.96 S.E., S.E. and means for each direction category. Sample sizes for each wind direction as shown in the figure are: 22, 18, 19, 6, 45, 149, 121, 53, 32 hours on watch.

shore based observations is that they do not interfere with the behaviour of the subject animal. For example, boat attraction or avoidance may take place at or beyond the visual range of observers, with profound implications for line transect data (Dawson *et al.* 2003) and behavioural observations. Shore based observations of dolphin movements, numbers, group composition and behaviours can provide a control for similar boat based observations. Probably the main drawback of shore based studies is the inability to control the distance between observer and animal, so that range becomes an important factor in establishing species identity, estimating group size, and observing behaviour patterns.

In this study, the recorded rate of cue production by Heaviside's dolphins dropped off significantly with increased distance from the observer, indicat-

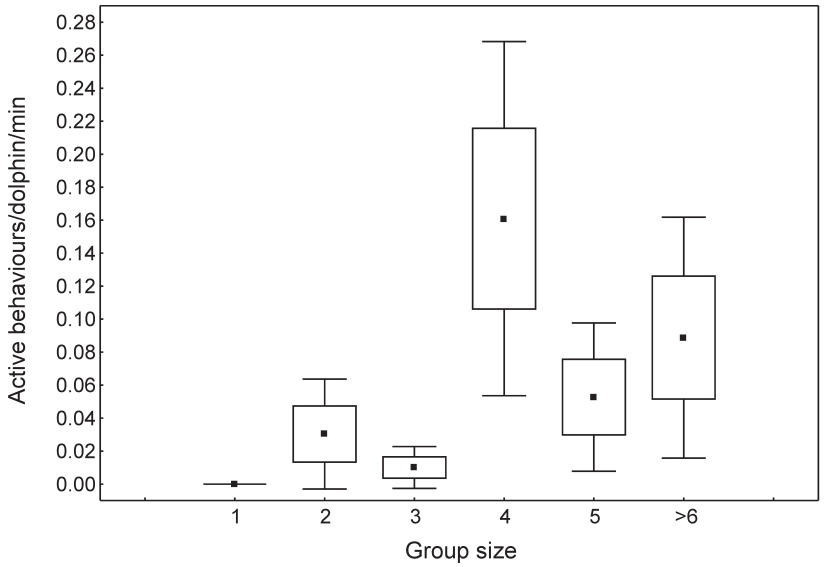

Fig. 5. Variation in rate of production of 'active behaviours' of Heaviside's dolphins with group size, Agterbaai, South Africa. Whiskers, boxes and points represent 1.96 S.E., S.E. and means for each group size (samples sizes from left to right: 3, 14, 28, 16, 11, 5).

ing that 400 m was the farthest distance at which dolphin surfacings could be detected without a significant bias, at least from the low observation platform used here. However, the size of observed groups did not vary significantly with distance from the observer, suggesting that although the ability to see surfacing cues lessened with distance, the proportion of animals seen did not differ within and beyond 400 m in the study site.

The sympatric Heaviside's and dusky dolphins in this study appeared to respond to different environmental cues. The most obvious behavioural pattern exhibited by Heaviside's dolphins was the diurnal variation in their numbers inshore. The total number of observed dolphins reduced greatly after noon, and those groups that were tracked were seen farther from shore as the afternoon progressed. Observations of Heaviside's dolphins made at sea during the concurrent boat-based photo ID work over 390 km of coast (S.E., pers. obs.) confirm this reduction in inshore dolphin numbers in the afternoon throughout the surveyed area. From satellite tagging of five female dolphins in the St Helena Bay area, Elwen *et al.* (2006) showed that, although there was variation between the animals in the distance moved from shore, and sometime several days could be spent either inshore or offshore, all five animals showed a clear diurnal inshore–offshore movement pattern throughout the transmission period of their tags (up to 54 days). These dolphins were closest to shore between about 05:00 and 13:00. It is therefore reasonable to assume that there is a general offshore movement throughout the species' range rather than a localized movement away from the shore-based station.

Dolphins caught early in the day (07:00–10:00) had fuller stomachs than those caught in the afternoon and Sekiguchi (1994) proposed that Heaviside's dolphins feed at night and in the early mornings when hake migrate vertically into midwater (Barange *et al.* 1994; Pillar & Barange 1995). Goby also tend to be more prevalent near the surface at night (O'Toole 1977), which may add to the motivation to move offshore to feed nocturnally. The movements of Heaviside's dolphins observed in this study are consistent with the hypothesis of a nocturnal feeding excursion to exploit the vertical migration from deeper water of their dominant prey species. An inshore resting and offshore feeding pattern has been observed in several other delphinids including dusky dolphins in Argentina and New Zealand (Würsig & Würsig 1980; Markowitz 2004, respectively) and Hawaiian spinner dolphins (*Stenella longirostris*) (Würsig *et al.* 1994). Both of these species nocturnally exploit prey species associated with a vertically migrating scattering layer and are thought to move inshore when not feeding due to a reduced predation risk in shallower water where sharks and killer whales

(O*rcinus orca*) are less prevalent. Although killer whales are rarely sighted along the west coast of southern Africa (Findlay *et al.* 1992), several Heaviside's dolphins have been seen bearing scars consistent with shark bites (Best & Abernethy 1994). Predator avoidance may therefore also play a role in the movements of Heaviside's dolphins, in particular the choice to move inshore when not feeding rather than remain offshore.

Although hake and vertically migrating mesopelagic fish such as lantern and hatchet fish (Prosch *et al.* 1989) form a large part of the dusky dolphin diet (33% by modified volume combined (Sekiguchi *et al.* 1992), the sighting rate of dusky dolphins showed no predictable variation with time of day. However, their presence inshore appeared to be related to wind direction; the absence of dusky dolphins inshore when the wind was southwesterly is particularly noteworthy given that this was the predominant direction from which the wind blew during the study. The larger area in which the study site was located (St Helena Bay) has a regular, predictable, wind-driven upwelling plume off Cape Columbine (Shannon 1989). Upwelling in this region occurs when the wind is southeasterly, southerly or southwesterly (generally an offshore direction at the study site but an alongshore direction to the majority of the coast) but not when the wind is from the opposite directions, *i.e.* northwesterly to easterly. Our data show a potential link between the absence of dusky dolphins inshore and strong upwelling offshore that merits further investigation. It is possible that in the study area, dusky dolphins may use wind strength as a cue to move offshore, since during watch hours when the wind blew >10 knots, only 1% of those occurred from a 'non-upwelling' direction.

It is not known if dusky dolphins exhibit a similar relationship with wind direction or upwelling in other parts of their range in southwestern Africa or only in areas of localized upwelling, as observations in this study are limited to St Helena Bay and summer months only. However, dusky dolphins are adaptable predators that use different foraging strategies throughout their range. In the deep canyon habitat of Kaikoura, New Zealand, they exhibit a strong diurnal migration pattern of resting inshore during daylight hours and moving offshore in the late afternoon to feed on vertically migrating organisms associated with the deep scattering layer (Cipriano 1992). In shallow-water bays in both New Zealand (Markowitz *et al.* 2004) and Argentina (Würsig & Würsig 1980) scattered groups of dolphins feed diurnally on schooling fish near the surface. There is some evidence to suggest that dusky dolphins in South African waters use different feeding strategies. Two animals caught in a beach-seine net early in the morning in Hout Bay (~200 km south of St Helena Bay) had eaten mesopelagic lantern fish and were thus thought to have been feeding on the continental shelf over night and subsequently moved inshore to rest (Sekiguchi 1994). Thus, although the observed relationship between dusky dolphins and upwelling conditions is reasonably clear from the data collected in this study, these observations must be placed in the broader context of the environment as a whole and the flexible foraging habits of the species, as the observed relationship may be both area and season specific.

Variation in dolphin numbers and behaviours with regard to the brightness of the moon was examined on the grounds that the vertical migration behaviour of many fish species is affected by the light intensity in the sky, including moonlight (Woodhead 1966), with fish not migrating as close to the surface under brighter light conditions.

Heaviside's dolphins were hypothesized to spend more time offshore feeding (and thus less time inshore in the study area) when the moon is brighter and hake are deeper and theoretically harder to capture. However, the opposite pattern was observed and Heaviside's dolphins were seen in higher numbers inshore during the brighter full moon. Two alternate hypotheses exist although neither can be tested in this context: either the dolphins do not move offshore to hunt when foraging is sub-optimal, or they may shift prey type.

The Heaviside's dolphins in the bay generally exhibited slow movement, sometimes milling and in specific directions, but high activity and speed were rare. During the more than 400 h of shore-based observations and the 110 days of concurrent boat-based operations, there was only a single observation of obvious feeding behaviour by Heaviside's dolphins. On 13 February 2001, a group of five Heaviside's dolphins was seen harassing a single cormorant (probably white breasted *Phalacrocorax carbo*) until the cormorant released the fish that it had just caught. Although it is not known if the dolphins then ate the fish, this same group of dolphins was described as 'feeding with the cormorants' by the observers on watch at the time. Our observations of the timing, behaviours and movements of the dolphins, combined with the general lack of feeding observed, all add

support to the theory that Heaviside's dolphins rest inshore between offshore nocturnal foraging bouts.

Resting or non-feeding behaviour is difficult to interpret because it is inherently undirected. Würsig *et al.* (1994) describe Hawaiian spinner dolphins (*Stenella longirostris*) as bunching more closely and becoming much less active when resting inshore during the day. Aerial behaviour observed in Hector's dolphins was associated with sexual and aggressive behaviours and not feeding behaviour, but in that particular population feeding appears to occur throughout the day (Slooten & Dawson 1994). In this study, no predictable variations in the active behaviours of Heaviside's dolphins were noted with wind direction, speed or brightness of the moon; and although not statistically significant, the lack of any active behaviours observed after 12:30 may be associated with a motivation to disperse at that time and move offshore to begin feeding.

Heaviside's dolphins were more active in larger groups, and during the concurrent boat-based work, smaller groups and particularly individuals acted evasively toward the boat. Conversely, larger groups contained proportionally more calves than smaller groups. It is likely that protection of individual cetaceans is greatly increased in schools at least partly due to greater levels of awareness (Norris & Dohl 1980; Markowitz 2004). Activity levels of Atlantic white-sided dolphins (*Lagenorhynchus obliquidens*) have been observed to increase with group size (Weinrich *et al.* 2001). Slooten (1994) found much higher rates of sexual behaviour and associated active behaviours (such as jumps) in groups of 11–15 Hector's dolphins than in either larger or smaller groups, and for the level of sexual behaviours to increase when two groups fused. Increased school size presumably creates greater opportunities for social interactions, and hence is likely to lead to a higher incidence of behaviours other than 'slow rolls'.

In conclusion, these first shore-based observations of Heaviside's dolphins in South Africa have provided some support for previous hypotheses on the diurnal movement and feeding pattern of this species (Best & Abernethy 1994; Sekiguchi 1994), as well as providing some baseline data on their inshore behaviours and how they may vary with environmental and social influences. Concurrent observations of dusky dolphins show that, at least in St Helena Bay, they respond to different environmental cues, which may be indicative of the two species employing different foraging strategies as a result of niche differentiation between similar-sized competitors.

ACKNOWLEDGEMENTS

We would like to thank Rina Owen and Jackie Grimbeek of the University of Pretoria Statistics department for their invaluable help with statistical analyses. We would also like to thank Colleen Moloney and John Field for other statistical advice. These data could not have been collected without the aid of all the Earthwatch Institute volunteers in 1999, 2000 and 2001 who put in many long hours in the sun searching for dolphins, even when they were not there to be found: Cressida Bainton, Jane de Jarnette, Annie Evans, Jennifer Leishmann, Todd Pusser, Betsy Schwarz, Shaun Dillon, Patrick Foster, Pearl Jordan, Alexandra du Sold, Shirley Einarsson, Lynn Heidler, Jackie Bishop, Darrell Blandford, Hilary Waite, Robyn Aiton, Janet Chriest, Cindee Dickens, Gill Hayward, Kimberly Martin, Alun Rees, Jo Culf, Ursula Daniels, John Decosta, Beverly Brown, Toni Goodley, Roger Johnson, Kay Swann, Laurie Tiller, Jane Cheetham, Gillian Clarke, David Hawker, Betty Lee, Joanne Thompson, Julie Wittrock, Craig Blackwell, Roger Sparrow, Keith Thomson, Tanja Thomson. This material is based on work supported by the National Research Foundation (South Africa) under grant number 2034991.

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Corresponding Editor: M.N. Bester