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The distribution, movements and abundance of Heaviside's dolphins in the nearshore waters of the Western Cape, South Africa

By

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Abstract

Heaviside's dolphin (*Cephalorhynchus heavisidii*) is a poorly studied coastal delphinid with a limited inshore distribution off the west coast of southern Africa where it is sympatric with the similar sized dusky dolphin (*Lagenorhynchus obscurus*). It is exposed to an unknown level of bycatch particularly in near-shore set-net fisheries and is also potentially impacted by the growing boat-based whale watching industry in South Africa. In this thesis I describe the results of a study investigating the distribution, movements, behaviour and abundance of Heaviside's dolphins in the near-shore environment of the Western Cape of South Africa as a precursor to assessing its potential vulnerability to anthropogenic threats. Data were gathered using three different approaches in the field; diurnal shore based observations, boat based photo-ID surveys along ~390 km of coastline and satellite telemetry. Data were collected for dusky dolphins where feasible.

Heaviside's dolphins exhibited a strong pattern of resting inshore during daytime and foraging offshore at night that was presumed to be related to the movement of juvenile hake

(*Merluccius capensis*) closer to the surface at night. In addition, despite near-shore observations failing to indicate feeding, dolphins were consistently found to be more abundant along regions of the coast which over the long term had higher levels of small hake available offshore. In contrast the near-shore distribution of dusky dolphins varied considerably between years possibly due to the very near-shore environment being at the edge of their habitat. A tendency for dusky dolphins to move offshore during upwelling conditions was observed from shore in St Helena Bay, the site of a strong predictable upwelling cell. However this was the only location in which very large groups of animals (50-500) were seen during coastal boat surveys suggesting this pattern may have been area specific and feeding strategies may vary throughout their range. Sympatry appears to be mediated by differences in overall range and prey type and size differentiation.

Heaviside’s dolphins were found to have small home ranges and show a high degree of site fidelity over several years, at least during summer months. Dolphins fitted with satellite-linked transmitters used only limited home ranges (~876 to 1990 km^2) which scaled positively with body size within the ~50 day tracking period, while photographically identified animals did not disperse significantly further than this over 3 years. The maximum coastwise displacement observed for an individual (88.4 km after 1 year) was considerably less than the 390 km length of the overall study area, and equivalent to the maximum coastwise movement seen during satellite-tagging (83.1 km). This suggests that measured home ranges may be stable over several years, although the number of resighted individuals (n = 76) was small and (as data collection was restricted to summer months) seasonal differences in movements or migrations cannot be ruled out. Associations among photographically identified animals did not differ from a random mixing of individuals, suggesting that this species has a fission-fusion type social structure at least over the short term.

The abundance of Heaviside's dolphins was calculated from photo-ID mark-recapture data at three spatial scales using Chapman’s modified Petersen estimators. The proportion of distinctively marked individuals in this species is low (14 - 17%) reducing sample sizes and introducing a large extrapolation factor, both of which contribute to an increase in the variance of any resultant population estimate. Using resightings after one year, the total number of animals over the whole 390km study area was calculated to be 6345 (CV = 0.26, CI = 3573 – 11 267) while using same-season re-sightings the total number of animals using a 20km long section of coastline in the centre of the study area was calculated as 527 (CV = 0.35, CI = 272 – 1020). These estimates may be significantly biased downwards by the effects of heterogeneity in the capture probability of individuals which it was not possible to account for analytically due to small sample sizes.

Sympatry of Heaviside's and dusky dolphins appears to be mediated by differences in the overall range and in the type and size of prey consumed. From a conservation point of view, our findings for Heaviside's dolphins are encouraging in that they indicate a relatively large population size, although their strong site fidelity does make them more vulnerable to localised impacts than a more widely ranging species like dusky dolphins and this needs to be considered during management of the population.

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It's taken me a while to get this dissertation together and it's been a long haul since 2000 when I was the green (literally) trainee marine biologist donating my lunch to the dolphins over the side of Balaena while the rest of the Whale Unit shook their heads and wondered what they'd taken on – Desray Reeb and Meredith Thornton, thanks so much for all the help and support through the years and for putting so much time into helping collect the data, without which there would have been nothing here at all! I hope I've proved myself sufficiently over the last few years and can justifiably call myself a 'real marine biologist' now. Peter Best – thank you for giving me, a total unknown at the time, this chance in the first place and for all your guidance over the years, it's been a real experience and I've certainly learned a lot from working with you that I would never have learnt anywhere else.

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Disclaimer

This dissertation was written as a collection of five manuscripts to simplify the process of publication of these results as recommended by the Department of Zoology and Entomology. This has naturally led to some duplication between chapters, particularly in the methods and background. Literature is thus cited for each chapter independently. Chapter 5 was published in the Journal of Mammalogy in 2006, I have included a reprint from published manuscript in the Journal of Mammalogy as well as the thesis-edited version – these two versions are identical except for some minor textual corrections that have taken place subsequent to publication and a US spelling in the reprint. Chapter 1 has been subjected to peer review when it was submitted to The African Journal of Marine Science, where it was rejected but invited to be resubmitted pending extensive recommended changes which have been included in this final draft.

Declaration

I declare that the thesis that I hereby submit for the degree in PhD at the University of Pretoria has not previously been submitted by me for degree purposes at any other university.

Simon Elwen:___________________ Date:_____________________

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Two Heaviside's dolphins in St Helena Bay, 2004. Simon Elwen

Chapter 1

Near-shore diurnal movements and behaviour of Heaviside's dolphins (*Cephalorhynchus heavisidii)*, with some comparative data for dusky dolphins (*Lagenorhynchus obscurus*).

Abstract

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 such as fisheries bycatch and developing eco-tourism. Shore-based observations were made in a small bay (~1000m wide) in the Western Cape during the summer months of 1999 – 2001 to gather baseline data on their nearshore movements and behaviours. Heaviside's dolphins exhibited a diurnal onshore-offshore migration and the sighting rate varied significantly with time of day and phase of the moon, with numbers being markedly higher before 12h00 and nearer a full moon: these patterns were presumed to be tied to the vertical migration of their principal prey, juvenile hake *Merluccius spp.* and changes therein with variation in nocturnal light conditions. Heaviside's dolphins appeared to rest inshore during the day and feed offshore nocturnally. However, sightings of dusky dolphin showed no predictable variation with time of day. Dusky dolphin numbers inshore were significantly lower during winds that created upwelling conditions offshore, although this pattern may be location and season specific. No environmental factors showed significant influence on the nearshore behaviour of Heaviside's dolphins although larger groups (especially groups of 4) were more active (leaps, etc.) than smaller groups. The dissimilar responses to environmental conditions suggest that sympatry in these two species is mediated by niche as well as prey differentiation.

Introduction

Coastal regions are among the marine environments most highly impacted by human activities such as pollution and fishing. Also, coastal environments are difficult to manage as there is often considerable conflict between users with incompatible needs such as fishermen, recreational users and conservationists (Thompson et al. 2000; Hughey 2000). Owing to their nearshore distribution, coastal dolphins are among those populations most at risk from human impact. The charismatic nature of delphinids often makes them the focus of high profile conservation efforts (e.g. Hughey 2000; Reeves et al. 2006) making management of such populations particularly challenging. Central to any effective management programme is knowledge of the biology of the species being protected, which enables the risk to a population to be better quantified and ensures that management is occurring at a relevant and biologically meaningful scale. This is especially necessary for management systems involving a strong spatial component such as marine protected areas and reserves (Wilson et al 2004, Hyrenbach et al. 2006; Slooten et al. 2006). Spatially delineated protected areas are a common, simple and effective management tool in the conservation of coastal delphinids. However, to be effective, their borders need to be placed so that a sufficient proportion of the population is protected to reduce impacts to a sustainable level (Slooten et al. 2006) and a good understanding of how animals use the environment and protected area is required.

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 <100m deep, and the dusky dolphin is found from the coast to at least 500m 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, Best & Abernethy 1994).   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.) 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 (Benoit-Bird et al. 2004). The diet of dusky dolphins in South Africa includes several of the same species, but they take a more diverse range of prey including horsemackerel, hake *(M.* spp*)* lantern (*Lampanyctodes hectoris*) and hatchet fish (*Maurolicus muelleri*) (Sekiguchi et al. 1992).

The Benguela ecosystem of the west coast of southern Africa is a cold-water, wind-driven upwelling system which is well structured at a broad scale with predictable, localised upwelling cells that affect the broad-scale distribution of the cetacean fauna (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 chapter presents the results of shore-based observations of the behaviour and movements of Heaviside’s dolphins, with some appropriate data included from contemporaneous observations of dusky dolphins, and are used in an interspecies comparison to examine the way in which these sympatric predators use the nearshore environment.

Methods

Data collection

Shore-based observations of Heaviside’s dolphins were made from a temporary, gazebo structure on top of a dune approximately 5m above sea level and 100m 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 (~1 000m 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 420.6h (Table 1). Observations were discontinued if the wind exceeded ~15knots or if it was raining or foggy.

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

	Effort (mins)					
Year	Search	Track	Behaviour	Watch time (total)	First day	Last day
1999	101:16	7:28 (45)	4:46 (27)	113:30	02 February	21 March
2000	90:23	4:54 (32)	3:31 (21)	98:48	27 March	04 April
2001	190:09	13:37 (84)	4:29 (25)	208:15	12 February	17 March
Totals	381:48	25:59 (161)	12:46 (73)	420:33		

A team consisted of four observers, two on watch at a time for alternating 2h shifts, searching the bay by naked eye and with 7x35 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. There were some slight variations in field methods during watch handovers (when shifts overlapped) and observer training (when an extra, more experienced observer was also present) but this was not felt to bias data collection.

When dolphins were sighted, their numbers and group compositions were estimated. For Heaviside’s dolphins, their movements were visually tracked for 10min, with locations being recorded when at the surface, relative to prominent landmarks and a 100m 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 10min period immediately following tracking, with one observer continuing to use binoculars to monitor the dolphins while the other acted as a data recorder. No behavioural observations were made for sightings of dusky dolphins.

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 normalise 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 1h 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. Wind direction and strength were included in the analysis as wind is the principal driver of nearshore upwelling and productivity in the Benguela ecosystem, with the strongest breezes generally coming from the southerly quarter.

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).

We examined the relationship between environmental factors and the variability of the sighting rate of Heaviside's dolphins 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 / minutes ‘watching’; including tracking, searching and behavioural observations). To normalise 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 (daylight hours, in 1 hour intervals except 06h30-07h59), wind direction (N, NE, E, no wind, etc.), the presence or absence of the other species of dolphin seen and lastly the phase of the moon (less or more than half full) were included as class variables, while wind speed was included as a co-factor in the model. It was not moon phase *per se* that was felt to have potential influence on the dolphins, rather the effect that the amount of light in the night sky might have on their principal prey, hake (B. Rose, pers. comm.), hence waxing and waning moon phases were combined and analysis was limited to only more or less than half full. Heaviside's dolphins are hypothesised to spend more time offshore feeding (and thus less time inshore in the study area) when the moon is full and hake are deeper and harder to capture. Wind direction and strength were included in the analysis as wind is the principal driver of nearshore upwelling and productivity in the Benguela ecosystem, with the strongest breezes generally coming from the southerly quarter.

Although the total number of dusky dolphins observed was similar to that of Heaviside's dolphins, 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 observations in the current study were extremely skewed toward ‘slow rolls’ supporting previous reports that aerial displays by Heaviside's dolphins are comparatively rare (Best and Abernethy 1994). On account of the very low occurrences of all the other behaviours recorded, all behaviours excluding ‘slow rolls’ were summed together and divided by group size and time monitored to give a measure of ‘active behaviours’ per dolphin per minute. The second measure of behaviour analysed, was an overall index of ‘cue production’ and included all behaviours seen; 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 trackline from observer post, estimated to nearest 100m off tracking maps).

Variations in ‘evasive’ behaviour of dolphins (with respect to the 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 an average 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 2 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 (p = 0.899, F = 0.3209). 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 1.2). *Post hoc* analysis showed the sighting rate of dolphins to be higher when the moon was brighter and higher in the morning than in the afternoon for both groups and dolphins sighted per hour (Figure 1.2). 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.

Table 1.2: Results of GLM ANOVA on the effects of environmental factors affecting the sighting rates of Heaviside's dolphins measured as groups and dolphins per hour.

Variable	Groups (h^{-1})		Dolphins (h^{-1})	
	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 ½	16.47	*<0.001*	5.95	*0.015*
Wind Speed	0.03	0.864	3.08	0.079

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=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 (20m) to far offshore (1 100m), 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 200m from shore after 14:00. Correlating these data separately (Figure 1.3) shows no relationship between time and distance from shore in the morning ($r^2 = 0.018$, $p = 0.116$). However, there was 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, Figure 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, Figure 4). *Post hoc* analysis showed that the sighting rate of dusky dolphins was lower when the wind was blowing from a westerly or south-westerly 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 ever sighted from shore when the wind direction was south-westerly, 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 showing the sighting rate to be lower when the moon was brighter, this is opposite to the pattern observed for Heaviside's dolphins.

Table 13: Results of GLM ANOVA on the effects of environmental factors affecting the sighting rates of dusky dolphins measured as groups and dolphins per hour, data are shown both including and excluding the two days of anomalously high dusky dolphin sightings.

Variable	Groups (h^{-1})		Dolphins (h^{-1})	
	F	P	F	P
Including two days of high sighting rate				
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 of high sighting rate				
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

Behaviour

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 (87min) 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, df = 8) although small sample sizes during certain wind directions may weaken this analysis. However, the rate of active behaviours did vary significantly with group size (Kruskal Wallis: p = 0.007, H = 15.81, df = 5) showing a general increase in such activity with group size, but with some groups of 4 being especially active

(Figure 5), although post-hoc multiple comparisons (Statistica: multiple comparison z' values) showed no specific differences between group sizez.

The overall mean rate of cue production by 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, df = 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, df = 5, $p < 0.001$). A post hoc comparison showed the main differences occurred between sightings farther than 500m and sightings in the 100-200m and 300-400m distance strata (Tukey HSD for unequal N; p = 0.014 and 0.043 respectively). The average rate of cue production in strata less than 400m from the observer was 1.961 (SD 0.134) cues per dolphin per minute and only 0.941 (SD 0.041) in strata further than this.

In boat based observations the proportion of groups with evasive animals (Pearson: r2 = 0.685, p = 0.02155) correlated negatively with group size, while the proportion of calves in a group correlated positively with group size (Pearson: r2 = 0.7844, p = 0.007968), with more calves being seen in bigger groups.

Discussion

Shore-based observations of cetaceans have been used widely and on a variety of species, from small dolphins (Würsig and Würsig 1980, Stone *et al*. 1995) to large whales (Findlay and Best 1996, Williams *et al*. 2002) to monitor the movements and behaviour of animals. The main benefit of 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 problem with 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 indicating that 400m 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 400m 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 390km of coast (SHE pers. obs.) confirm this reduction in inshore dolphin numbers in the afternoon throughout the surveyed area. Data 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 specific movement away from the shore-based station.

The principal prey of Heaviside's dolphins is juvenile hake which was shown by Sekiguchi *et al*. (1992) to comprise nearly half (48.9%) of their diet by volume, with goby *Sufflogobius bibarbatus* the next main prey type at 13.6% of volume. 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 and Barange 1995). Goby also tend to be more prevalent near the surface at night (O'Toole 1977, this may also increase 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. A general pattern of resting inshore and feeding offshore has been observed in several other delphinids including dusky dolphins in Argentina (Würsig and Würsig 1980, Markowitz 2004) 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 though 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 south-westerly 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 south-easterly, southerly or south-westerly (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. north-westerly 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 >10kn, 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 south-western Africa or only in areas of localised 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 and 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 (~200km 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 hypothesised 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.

Behaviour and Group size observations

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 13th 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 and 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 12h30 may be associated with a motivation to disperse at that time and move offshore to begin feeding.

The behaviour of Heaviside's dolphins varied with group size, with larger groups being more active, boat friendly and containing proportionally. It is likely that protection of individual cetaceans is greatly increased in schools at least partly due to greater levels of awareness (Norris and 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 animals 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 and 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.

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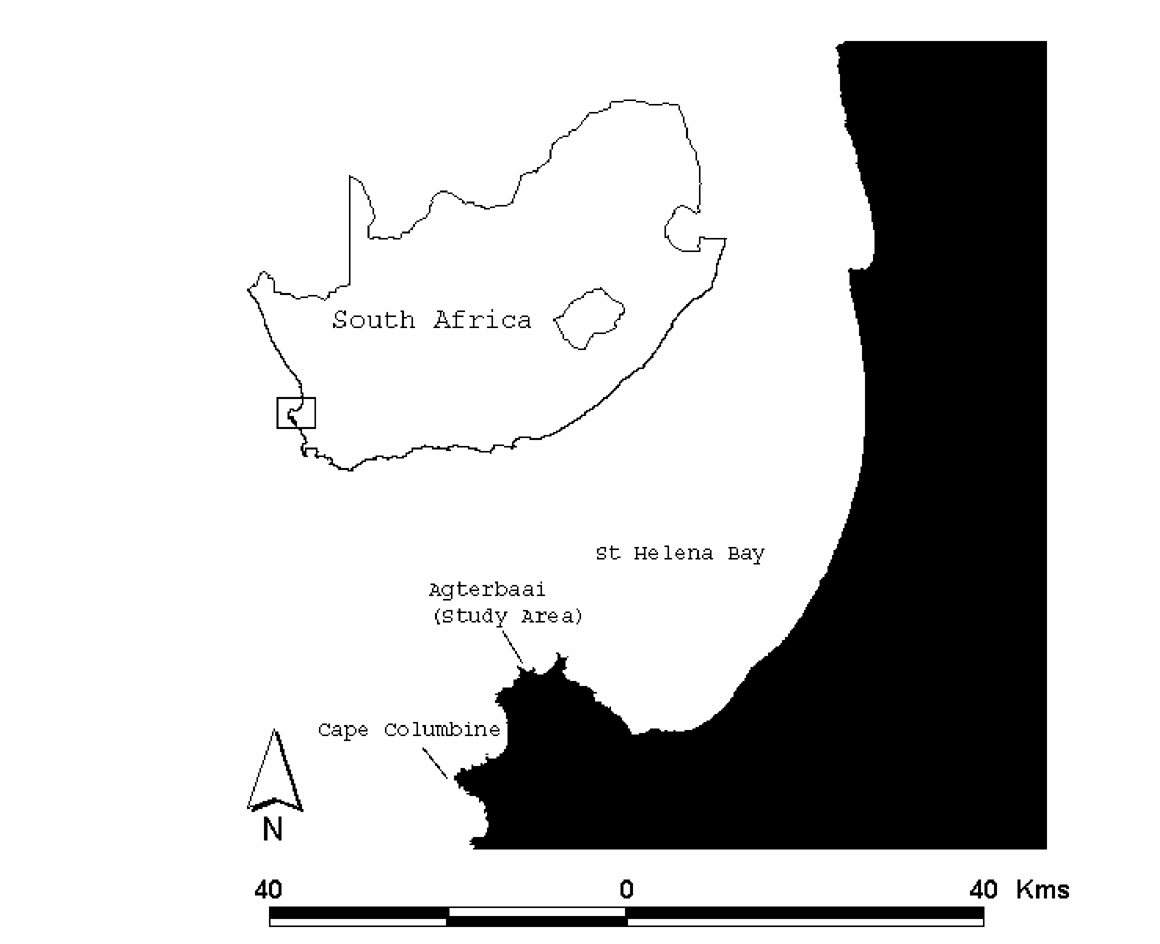

Figure 1.1. Study Area at the tip of St Helena Bay, South Africa.

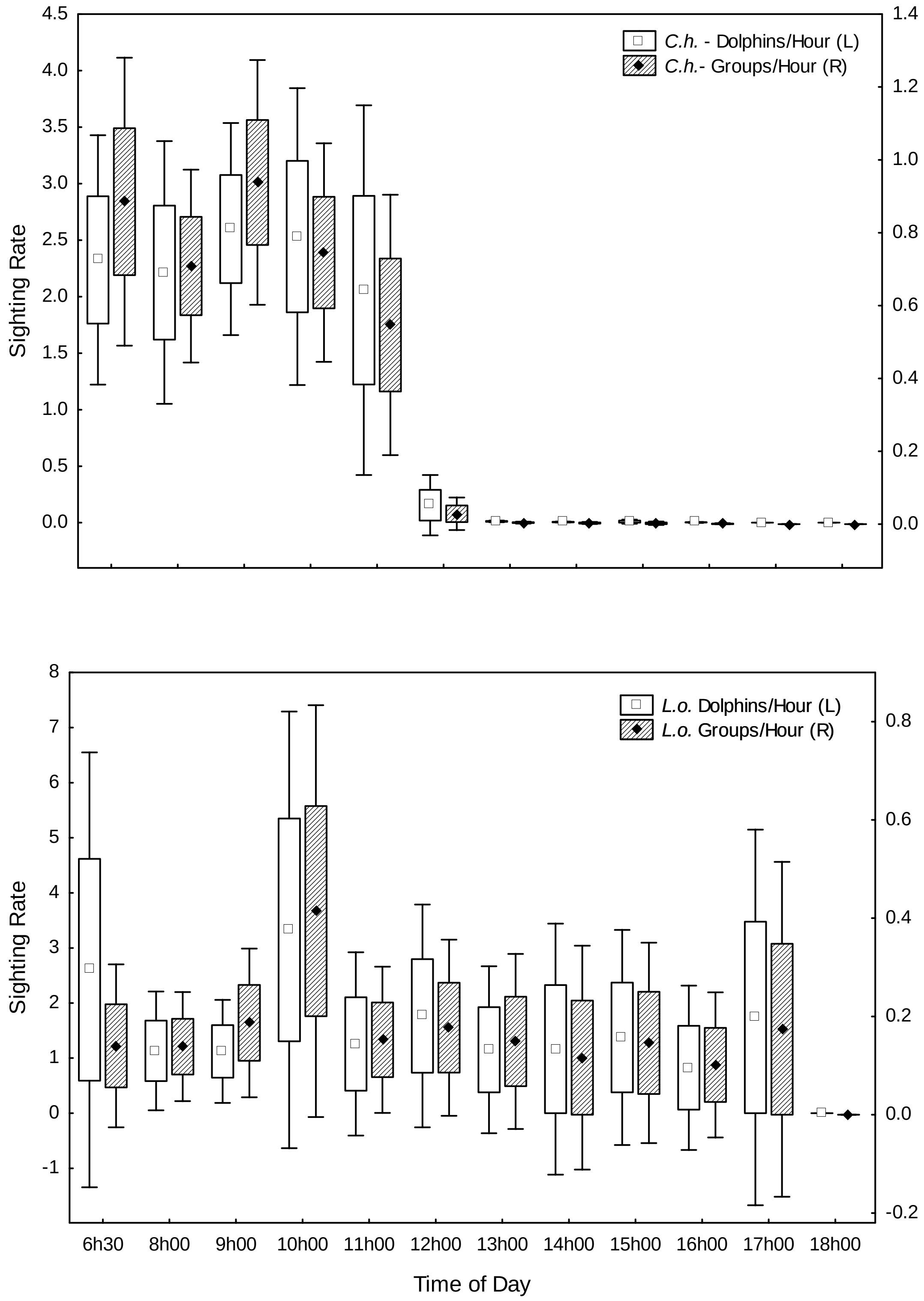

Figure 1.2. Variation in the sighting rate of individuals per hour (left axis) and groups per hour (right axis) of Heaviside's dolphins (top) and dusky dolphins (bottom) with Time of Day. Whiskers, boxes and points represent 1.96SE, SE and Means for each hourly category.

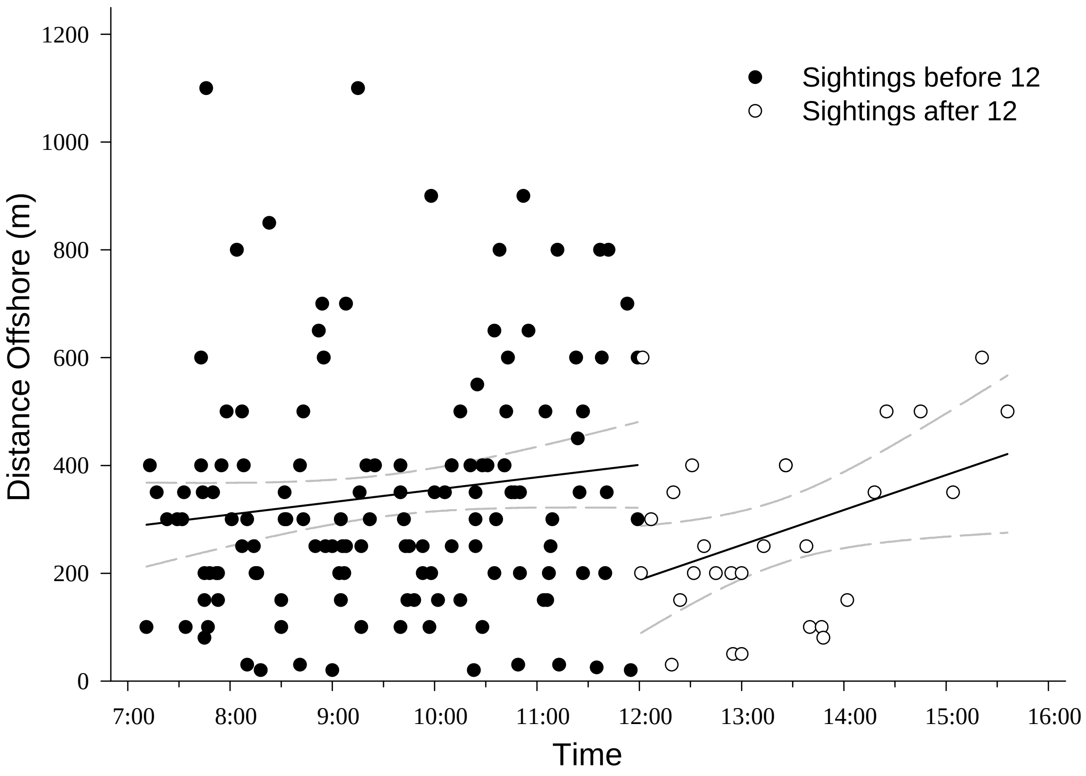

Figure 1.3. Correlation of distance offshore of tracked groups of Heaviside’s dolphins with time of day. Data and correlations split at 12h00 to show movements of animals offshore after noon.

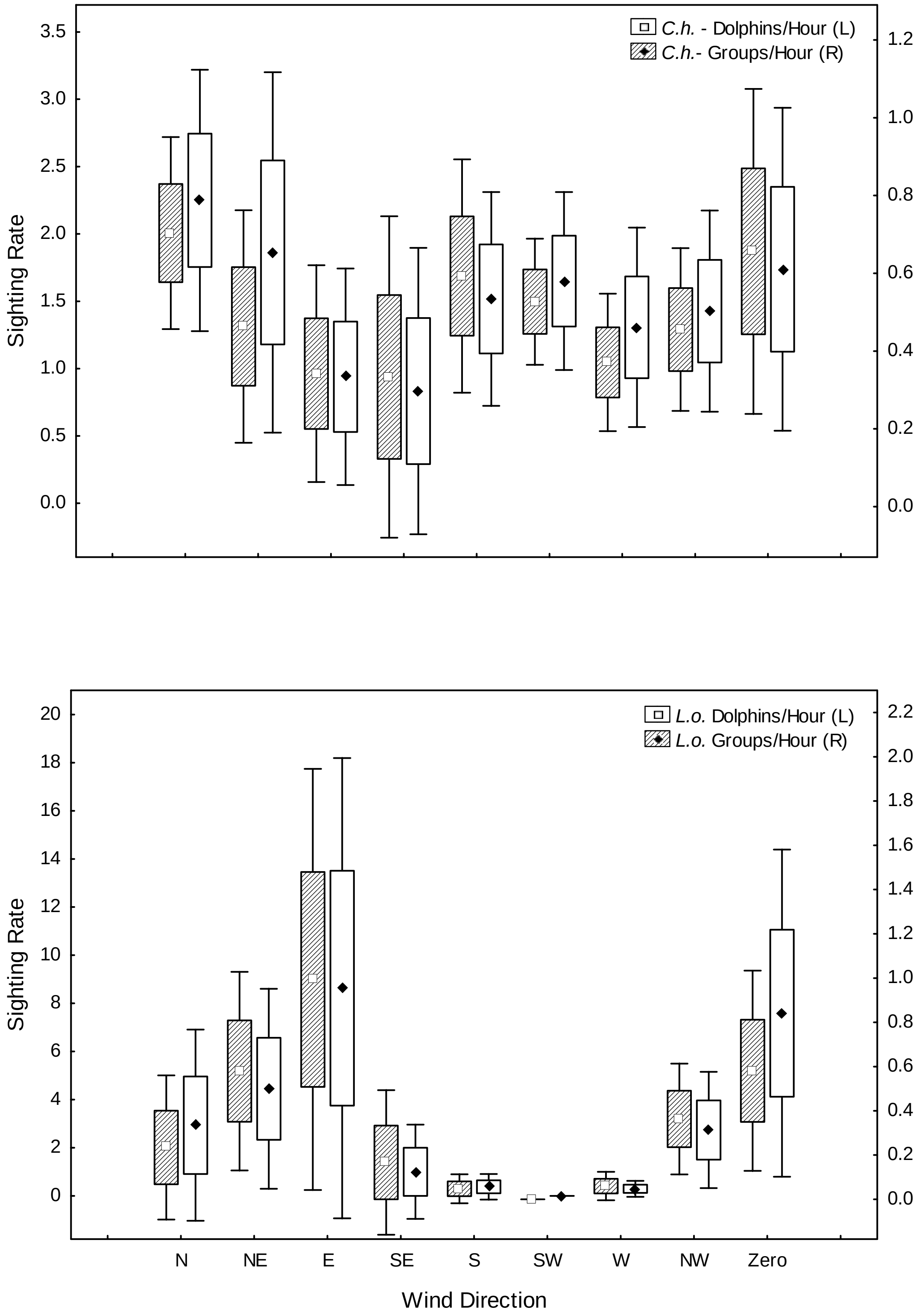

Figure 1.4. Variation in the sighting rate of individuals per hour (left axis) and groups per hour (right axis) of Heaviside's dolphins (top) and dusky dolphins (bottom) with wind direction (2 days of high dusky sightings included in this figure). Whiskers, boxes and points represent 1.96SE, SE and Means for each direction category.

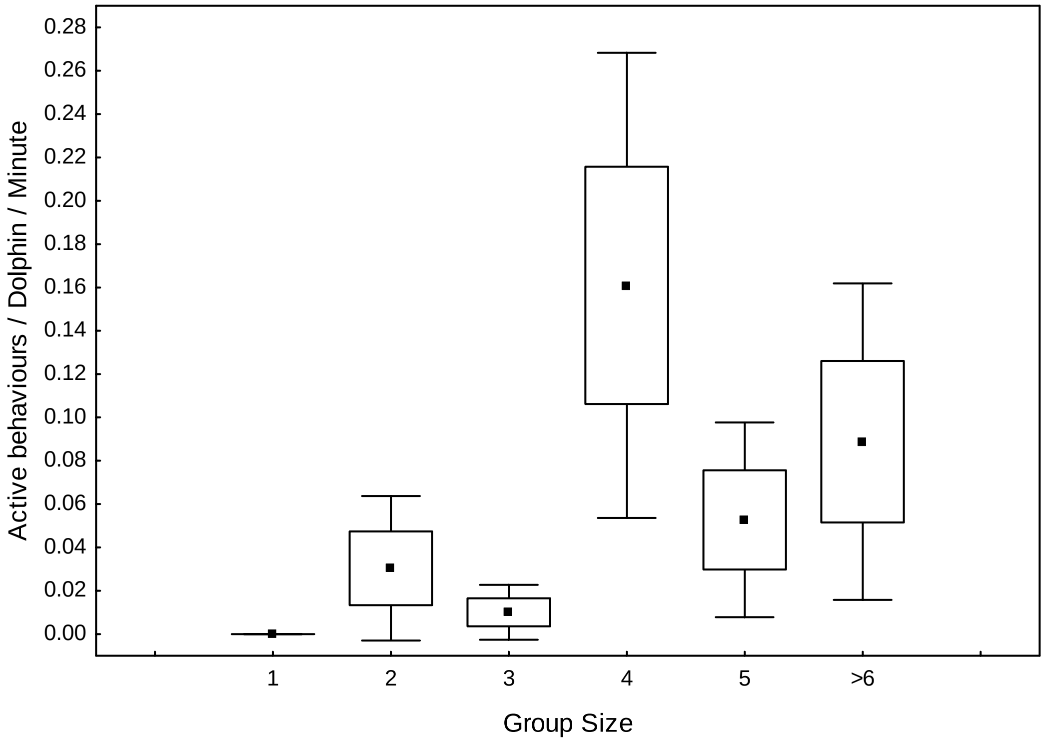

Figure 1.5. Variation in mean “Active behaviours” (per dolphin per minute) of Heaviside's dolphins with group size (the last category includes groups larger than 6). Whiskers, boxes and points represent 1.96SE, SE and Means for each direction category.

Chapter 2

Near-shore distribution of Heaviside's (*Cephalorhynchus heavisidii*) and dusky dolphins (*Lagenorhynchus obscurus*) at the southern limit of their range in South Africa, interspecific interactions and potential conflicts with fisheries.

Abstract

The range of Heaviside's dolphins off South Africa overlaps with several fisheries and the dusky dolphin. Using data collected during small boat photo-ID surveys of Heaviside's dolphins from 1999-2001 along 390km of coastline north of Cape Town (34^0S), we investigate the distribution of Heaviside's and dusky dolphins with respect to environmental conditions and inshore fishing effort. Although not feeding diurnally near-shore where data were collected, longshore concentrations of Heaviside's dolphins were consistent between years and tended to be higher adjacent to areas which over the long term had higher availability of small hake *Merluccius capensis* (their principal prey). Preference was also shown for areas of higher swell and wave activity and to some extent areas with sandy rather than rocky shores. Heaviside's dolphins were found in significantly shallower water than dusky dolphins and both species were sighted in significantly cooler waters than in the environment generally. Dusky dolphin sighting rates varied considerably between years, but were generally higher in areas with sandy shores (mostly straighter coastline). No evidence of a nursery area was found as both mixed groups and exclusively mother-calf groups were seen throughout the study area. Very large groups of 50-500 dusky dolphins were only seen in St Helena Bay, which is the site of a wind-driven upwelling zone. Very large groups were possibly aggregations of several smaller feeding groups, suggesting variability in feeding strategy throughout their range. Near-shore fishing activity (line fishing, crayfishing and set-netting) was higher in the northern half of the study area and clustered around harbours. Set netting, the most threatening fishery type for dolphins, occurred in two main areas only (Yzerfontein and St Helena Bay) but due to an industry collapse is currently thought to be a

low threat to the population. The opportunity for interactions between Heaviside's and dusky dolphins was high but those observed were usually neutral and sympatry appears to be mediated by differences in overall range and the type and size of prey species taken by the two species.

Introduction

Within the range of most species there is considerable variation in the number and density of animals at a variety of scales (Begon et al. 2005). Marine mammals are no exception and variation in their abundance has been associated with both environmental and biological influences including depth, sea floor gradient, oceanographic features, predator avoidance and competitive exclusion (Goodall et al. 1995; Tynan 1997; Davis et al. 1998; Elwen & Best 2003; Hastie et al. 2005; Heithaus & Dill 2006). The relationships between abundance and covariates may change with the scale of the study, and it is these changes which can illustrate the ecological relationships involved (Benoit-Bird & Au 2003; Johnston et al. 2005). Along the west coast of southern Africa, Heaviside's and dusky dolphins are known to be sympatric within the coastal environment but knowledge of their distribution is currently limited to broad scale descriptors. Findlay et al. (1992) describe the general range of Heaviside’s dolphins as “west of Cape Point (18.5^{0}E)… possibly into southern Angola…all sightings in waters shallower than 200m, the highest densities being inshore of the 100m isobath”, and dusky dolphins as entirely sympatric but with wider, although not entirely known limits extending to 19^{0}E (east of Cape Point into False Bay), northwards into Angola to at least 12^{0}S and offshore to at least 500m depth and possibly as much as 2000m of water. Such a broad scale overlap of ranges between potentially competing predators may be more clearly differentiated by habitat selection at finer spatial (Parra 2006; Heinrich 2006; Goodall et al. 1995) or temporal (Thompson et al. 2004) scales. To date, no studies have investigated either the environmental factors influencing niche or habitat selection or the sympatry of Heaviside’s and dusky dolphins at finer spatial scales.

Habitat or niche selection by animals is assumed to reflect the optimal choice (or compromise) of a suite of conditions, resources and influences both biotic (e.g. the distribution of predators, prey & competitors) and abiotic (e.g. depth, temperature, oceanographic features) within their potential range given the constraints of time, space and physiology. The ecological link between physical or oceanographic features and cetacean distribution patterns is frequently their association with prey which have either themselves been physically aggregated by oceanographic features or subsequently attracted to aggregations of their own smaller prey (Wolanski & Hamner 1988; Johnston et al. 2005; Tynan 1997). Heaviside's dolphins are known to move offshore at night where they are thought to feed on vertically migrating prey and to spend daylight hours (when the data used in this study were collected) closer to shore resting and not feeding (Elwen et al. 2006; Chapter 1). In animals that are not feeding, influences on distribution can be far less clear, but most evidence suggests that when resting or otherwise unengaged, cetaceans choose environments that are safe, from both predators and harsh environmental conditions (Whitehead & Moore 1982; Smultea 1994; Elwen & Best 2003; Lammers 2004, Heithaus & Dill 2006). Thus, even though Heaviside's dolphins appear to not be feeding while near shore they may still exhibit a preference for certain habitat types where predation risk is lower (inshore generally) or conditions are more conducive to resting and socialising.

A further consideration in the ecology of Heaviside's dolphins is potential competition with the slightly larger, sympatric dusky dolphin. The observable consequences of interspecific competition between sympatric predators vary from occasional harassment to potentially devastating local extinction level influences on the 'weaker' species (Linnel & Strand 2000; Creel & Creel 1996). Interactions between competing predators might not be obvious and may only be seen as avoidance by the weaker (almost always the physically smaller species, in this case the Heaviside's dolphin) of the stronger species. This may result in habitat differentiation and occasionally the counter-intuitive result of the weaker species having a higher survival rate in areas of lower prey abundance, if these areas act as refuges from competition (Linnel & Strand 2000; Durant 1998). Spatial competitive exclusion of Burmeister's porpoises has been suggested in Golfo San José, Argentina with porpoises occupying intermediate depths between the preferred ranges of dusky and bottlenose (*Tursiops truncatus*) dolphins (Goodall *et al*. 1995). Temporal (and possibly spatial) segregation of harbour porpoises (*Phocoena phocoena*) and bottlenose dolphins has been observed in areas of the Moray Firth, Scotland (Thompson *et al.* 2004). Competition between sympatric cetaceans may be mediated more subtly by resource partitioning including differences in fine scale habitat selection and prey species taken (Bearzi 2005; Heinrich 2006; Parra *et al.* 2005). There is some evidence to suggest that the two species in the current study occupy different niches as they respond to different environmental cues (Chapter 1) and eat different types and sizes of prey (Sekiguchi 1994) although there is a significant overlap of prey species taken.

In this paper we use the sightings data gathered during inshore photo-ID surveys to investigate how environmental variables affect the distribution of Heaviside's and dusky dolphins in the near-shore environment. We also investigate if their overlapping distributions (Findlay et al. 1992) are differentiated at finer scales. We further compare the observed patterns of distribution with that of near shore fishery activity observed during the same period.

Methods

Field data

The spatial data used in this study were not collected specifically to answer questions of distribution and habitat modelling but rather as a by-product of a 3 yr photo-ID survey focussed on questions of individual movements and range along the southern west coast of South Africa (Fig. 2.1). In the first year of the study 1999, effort was restricted to a 20km long stretch of coast around Britannia Bay aimed at photographically identifying all animals in the area, in the 2nd and 3rd years of the study (2000 and 2001) we searched the full ~390km study area in an effort to recapture those animals identified in the first year. Although we attempted to search as much of the coastline within the overall study area as possible, effort was uneven along the coast (Fig. 2.2) and generally higher closer to the harbours from which the research boat was launched. Also, collecting photo-ID data entails closing with a group of animals and spending considerable time with them, increasing the likelihood of seeing other animals nearby or having them attracted to the boat. Thus a varied approach was taken to analysis, with a model being generated for all sightings with all available data and a broader scale approach looking at the relationships between dolphin density and environmental factors between binned 10km sections of the coastline.

All data were collected from a 6m RIB fitted with twin 40hp outboard motors and an elevated observation platform (putting eyes at approx 3m ASL). The boat was launched daily, weather permitting and used to run coastwise searches (dependent on previously searched areas and prevailing winds), parallel to the breaker line where densities of Heaviside's dolphins are known to be highest during the day, at a search speed of 6-8kn. Upon encounter, dolphins were followed until photography was regarded as complete or until the dolphins were lost. At each sighting sea surface temperature (SST), depth (from on board fish finder) and GPS position were noted, also maximum, minimum and best group size estimates and group composition (adult or calf) as well as noting unusual behaviours (e.g. evasiveness, boat attraction, mating, inter-specific interactions). Some individuals were strongly attracted to the boat for bow-riding and when necessary, a sustained burst of speed of up to 15kn was used when moving away from a completed group to prevent them following the boat and being counted repeatedly. Such data were collected for all cetaceans encountered, but for those not part of the photo-ID study (including dusky dolphins) encounters were considerably shorter and accuracy of counts could thus be slightly affected by this. Furthermore, as group sizes were generally larger in dusky than Heaviside's dolphins, counts of very large groups were inevitably less precise than of small groups, with numbers becoming obviously rounded off above about 30 animals.

All search effort in this study occurred within a relatively narrow band close to the shore and was well defined along-shore by the collection of GPS waypoints for the start and finish of each search leg. The boat track was essentially parallel to the coast and within 1 km of it. To define the offshore limit to the study area (or "strip width") we used the furthest distance offshore of any dolphin sighting made under normal search conditions and regarded that as the furthest reasonable distance offshore that a dolphin sighting could be made, thereby defining a 2km wide strip of ocean adjacent to the shore. This 2km wide strip of coast was then split into 36 bins (or blocks) roughly 10km long each (a scale which created enough variation for differences to be seen but was not so small as to have very large variations in search effort), within which the encounter rates per kilometre searched (for groups, dolphins and calves) were calculated. A fairly fine scale digital coastline (1:150 000) was used and due to the convolutions of the coast, measuring blocks precisely 10km long was not feasible and in some instances borders were pushed slightly to align with headlands if appropriate

Environmental Data

Both depth and SST were collected (from on board fish-finder) at the site of each dolphin encounter as well as at the start and stop points of each search leg. The measured depth values were combined with data from the digitised 1:150 000 South African Naval Hydrographers navigation charts for the study region (SAN 117-119) and were used to build a TIN – a 3D sea floor model, in Arcview GIS 3.3. From this model we estimated the slope of the sea floor at each dolphin sighting and the slope and depth for large area averages. Exposure to swell was calculated using a 12 yr average (1990-2001) of offshore data (17-19^{0}E by 33-35^{0}S) collected from voluntary observer ships and kept in the CSIR EMATEK Marclim database (following Elwen & Best 2003). This average effectively represents the offshore swell climate, in the absence of any land to break it up. The majority of swell off southern Africa originates in the southwest quarter resulting in the corners of most bays on the south and west coasts being fairly protected while straight sections of coastline were mostly exposed to open ocean swell. Areas that were protected from more than 30% of this swell (east of the SSW-NNE line) were regarded as partly-protected, while areas protected from more than 60% of swell (south and east of the WSW-ENE line) were regarded as "protected". The shore type of the coast (which can be reasonably assumed to represent the near-shore substrate, Elwen & Best 2003) was defined following the Coastal Sensitivity Atlas of Southern Africa (Jackson & Lipschitz 1984); the coastline within the study area consisted of three shore types, namely “fine sandy beaches”, “wave cut rocky platforms” and “exposed rocky headlands”, with a few small sections defined as “Estuarine” (usually muddy).

Prey availability data

Hake catch data for the study area between 1990 and 2001 were available from standardised research trawls for both deep and shallow water hake (*Merluccius paradoxus* and *M capensis* respectively) performed by the South African government’s Department of Environmental Affairs and Tourism - Marine and Coastal Management. Of the two species, only the distribution of shallow water hake overlapped significantly with the known offshore range limits of Heaviside’s dolphins, so although it is not known with certitude which species Heaviside's dolphins eat, these were the data used. Sekiguchi (1994) gives the average size of hake eaten by Heaviside's dolphins as 19.5cm, with a range of 12-28cm. As the trawl data split the catches into size/age groups of 1-19cm, 20-34cm, 35-44cm etc; only the two smallest groups were deemed relevant and combined for analysis. Research trawls did not occur in the same places each year and were unfortunately limited close to shore, it being the larger hakes in deeper water that are of commercial interest. Since we were looking for longer term patterns we combined the data for all available years for analysis. Point trawls (number of fish per trawl standardised to an hour’s trawl) were then interpolated using Arcview 3.3 to allow a measurement of potentially available fish for each area offshore (Figure 2.1).

To analyse the interaction between dolphins and prey we created 20km semi-circular arcs around each 10km coastal bin, thus establishing a ‘home range’ for each segment of coast that was up to 50km long (coastwise) and 22km offshore (including the 2km width searched from the coast). This distance fell within the range limits measured for individual Heaviside's dolphins by satellite telemetry (Elwen et al. 2006) and did not exceed the observed offshore distribution of the species (Findlay et al. 1992). By measuring the amount of hake (interpolated fish/hour trawl data) within each ‘range’, we created a measure of potential prey available to a dolphin living in that region. The ‘ranges’ and the available hake therein of adjacent 10km bins clearly overlapped with potential auto-correlation problems, but since the ranges of Heaviside's dolphins apparently overlap freely (Elwen et al. 2006) we felt this to be a reasonable approximation of reality.

Unfortunately it was not possible to include any type of prey distribution data into the spatial analysis of dusky dolphin distribution as similar digitised, inshore research trawl data for horse mackerel (*Trachurus trachurus*), their predominant prey type in South Africa (Sekiguchi et al. 1992) were unavailable. However, dusky dolphins are more generalist feeders than Heaviside's dolphins locally (and diverse in their feeding strategies across the world, Würsig & Würsig, 1980; Cipriano 1992) so even though horse mackerel is the predominant prey type of dusky dolphins, it does not form as large a part of their diet as hake does for Heaviside's dolphins and a close link to a dominant prey distribution is less likely to occur.

Potential Fishery Interactions

In an effort to gain some understanding of the distribution of fishing effort within the study area and be able to highlight areas of potential human-dolphin conflict, we also collected data on all observed inshore fisheries and boating activity in the area. These were categorised by fishery type and activity (Table 2.1). We felt it most informative to split the observations by fishery type since it is the inshore set net fishery that is most likely to impact Heaviside's dolphins while other fisheries like crayfish trapping are likely to impact large baleen whales in the area, mainly the southern right whale (*Eubalaena australis*) and humpback whale (*Megaptera novaeangliae*).

Table 2.1. Categories used to describe fishing activity observed during the collection of photo-identification data on Heaviside's dolphins within 2km of the coast off the Western Cape, South Africa. Activity differentiated by fishery type.

Cray fishing	**Set Netting**	**Line fishing**	**Other**
Traps – unattended	Nets in water – unattended	Hand lining / angling from boats	Kelp gathering
Boats associated with traps (setting / hauling / hoop netting)	Boats associated with nets (setting / hauling)		Recreational boats
Transiting boats (presumed crayfishers)	Transiting boats (presumed net fishers)	Transiting boats (presumed line fishers)	

Analysis

Non-parametric correlation was used to look for a broad scale relationship between dolphin sighting rates in the 10km blocks of coast and environmental variables (average depth and slope, % sandy shore, % area exposed to swell and % area partly protected from swell) and amount of hake potentially available within 20km of each block. To investigate the stability of the distribution pattern between years, we correlated the sighting rate of groups of dolphins per block in 2000 with that in 2001.

For a finer scale investigation of the effects of environmental variables on dolphins, the raw sightings data (rank transformed group size at each sighting) were analysed using a general linear model (Proc GLM in SAS®). With categorical predictor variables for shore type (rocky or sandy), swell exposure (protected, partly protected, exposed) and region of the coast (10km bins grouped as follows: 1-8, 9-15, 16-20, 21-23, 24-26, 27-29, 30-33, 34-36 to increase sample sizes in areas of low effort) and SST and depth at each sighting analysed as continuous cofactors. Analyses such as these are inherently biased as they only include data from areas where dolphins were seen and presumably chose to be, thus we are effectively comparing degrees of favoured habitat rather than favoured with unfavoured habitat . To get some perspective into the analysis, we used the environmental data from sightings of dusky dolphins (n=207), with group size as zero, to represent ‘no dolphins seen in these conditions’ in the GLM. Post hoc analyses to more closely investigate relationships between factors were done using Least Squares Means (categorical predictors) and correlations (continuous predictors). Dusky dolphin sightings were similarly analysed, with the environmental data from Heaviside's dolphin sightings acting as the ‘no dolphins sighted in these conditions’ entries.

To investigate possible niche selection or differentiation within the environment and differences between the two study species, we also compared the depth and SST values measured at each sighting between the two species as well as with the SST measures available for the environment generally. We did not measure environmental SST specifically (i.e. at either random or regular points) but measurements were taken at the beginning and end of every search leg during the day. These measures were taken irrespective of dolphin presence and usually in their absence, thus we felt comfortable using them as indicators of SST measures for the environment “generally”.

Results

Heaviside’s dolphins

The sighting rate of groups of Heaviside's dolphins per kilometre searched in each bin is remarkably similar between 2000 and 2001 and was strongly correlated ($r^2 = 0.605$, $p < 0.001$) despite varied search effort in each bin and season (Fig 2.2 and 2.3). We analysed the relationship between the density of Heaviside's dolphin along the coast and environmental factors separately for 2000 and 2001 as effort differed slightly between years with very limited or no effort in bins 1-7 in 2001 (Fig. 2.2). In both years, the sighting rate of dolphins was positively correlated with the amount of hake potentially available within 20kms of the inshore bins, for all three measures of dolphin density (Table 2.2). Bins with high exposure to swell and those with predominantly sandy shores also showed a significant positive correlation with some measures of sighting rate but differed between years, suggesting that although there is probably some relationship, it is weak at this scale.

Table 2.2. Results of Spearman Rank correlations between sighting rates of Heaviside's dolphins (number of groups, dolphins and calves seen per km searched) and environmental variables in each ~10km block of coast (n=36 blocks). R values with asterisk are significant at the 5% level (Statistica 7.0)

	% Exposed coast	% Partly exposed coast	Average Slope in Bin	Average Depth in Bin	% Sandy shore in Bin	Hake within 20km of Bin
2000						
Groups	0.144	-0.057	-0.094	-0.043	0.452*	0.390*
Dolphins	0.121	-0.031	-0.069	-0.052	0.418*	0.344*
Calves	0.330	-0.225	0.011	-0.097	0.266	0.424*
2001						
Groups	0.356*	-0.193	-0.228	0.028	0.311	0.577*
Dolphins	0.324	-0.151	-0.272	-0.035	0.321	0.519*
Calves	0.252	-0.161	-0.227	0.050	0.138	0.400*

The general linear model of Heaviside's dolphin sightings was significant overall and region, swell exposure, depth and SST significantly influenced the group size of sightings (Table 2.3). Post-hoc least squares mean analysis showed blocks 24-26 (the corner of St Helena Bay) to have the lowest mean group size (3.66) and number of sightings (n=3), this area was significantly different to all the other areas in the analysis. The areas with the largest group size are blocks 21-23 (4.69; Britannia Bay and surrounds), 1-8 (4.65; Cape Town to south of Yzerfontein) and 27-29 (4.61; the open exposed side of St Helena Bay). Group size may be influenced by the attraction of dolphins toward the boat if they join to form larger groups, this is more likely to occur in areas of higher density. Dolphin groups were significantly larger in areas partly protected from swell (mean 4.97, n = 215) than in areas exposed to swell (mean 4.29, n = 677). Depth had an overall (slightly) negative relationship with sightings (fewer dolphins as depth increased) and SST had an overall slightly positive relationship.

Table 2.3. Results of Proc GLM of Heaviside's dolphin sightings along the southern west coast of South Africa in 2000 and 2001. Overall model results at top and break down by parameter below, significant results marked with an asterisk.

Source	DF	Sum of Squares	Mean Square	F Value	p
Model	14	93.32	6.67	7.11	<.0001
Error	1312	1229.88	0.94		
Corrected Total	1326	1323.1907			

R-Square	Coeff Var	Root MSE	Mean
0.070523	-418230	0.97	-0.0002

Source	DF	Type III SS	Mean Square	F Value	p
Block	7	51.83	7.40	7.90	<.0001*
Shore Type	1	0.29	0.29	0.31	0.58
swell	2	7.07	3.53	3.77	0.02*
Shore x swell	2	0.50	0.25	0.27	0.77
Sst	1	5.12	5.12	5.46	0.02*
Depth	1	11.83	11.83	12.62	0.00*

Dusky dolphins

Dusky dolphins were seen less regularly than Heaviside's dolphins, but generally in larger groups (all groups observed, Heaviside’s dolphins: mean = 4.53; mode = 2; median = 4; dusky dolphins: mean = 17.15; mode = 4; median = 6) and occasionally in very large groups of up to 500 animals. Notably, these very large groups (>50 animals estimated) were only sighted within St Helena Bay (Fig. 2.4) from block 22-29. Also, dusky dolphins occasionally formed nursery groups (never seen in Heaviside's dolphins), consisting almost exclusively of multiple mother-calf pairs, although calves were also seen in mixed groups with adults and juveniles where adults significantly outnumbered calves. Figure 2.4c/d show the distribution of these two group types along the coast, compared to Fig. 2.4a/b for distribution of all groups (differentiated by group size). Groups containing dusky dolphin calves, both mixed and nursery groups, were sighted throughout the study area in both years, and there is no evidence of any kind of nursery area.

The sighting rates of dusky dolphins were far more variable than the sighting rates observed for Heaviside's dolphins (Fig. 2.2) and did not correlate at all between years ($r^2 = 0.02$, $p = 0.44$). For example, during a 2 week field trip based from the Yzerfontein harbour in 2000, only 3 groups of 10 dolphins were seen, whereas during an identical two week field trip in 2001, 19 groups of 108 dusky dolphins were seen; compared to the very similar 90 groups of 428 Heaviside's dolphins in 2000 and 116 groups of 481 Heaviside's dolphins in 2001.

However, in both years, all three sighting rates measured (groups, dolphins and calves seen per km searched) were significantly positively correlated with the percentage of sandy shore in each bin (Table 2.4). In the study area, sandy beaches generally occur along long straight sections of coastline running north-south, while rockier coastline tends to be more convoluted and often forms headlands and bays. In 2000 the sighting rate of calves was higher in bins with partial protection from swell and lower in bins that were deeper on average (depth used as a positive number in analysis), however these patterns were not evident in the 2001 data set nor in any other sighting rate used.

Table 2.4. Non-parametric Spearman rank correlations between sighting rates of dusky dolphins (calculated as the number of groups, dolphins and calves seen per km searched in each 10km bin) and environmental variables in each bin (calculated as either an average or percentage for each bin). R values marked with asterisk are significant at the 5% level (Statistica 7.0)

	%Exposed coast	%Partly exposed coast	Average Slope in Bin	Avg Depth in Bin	%Sandy shore in Bin
2000					
Groups	-0.124	0.232	-0.180	-0.136	0.397*
Dolphins	-0.136	0.269	-0.224	-0.213	0.390*
Calves	-0.204	0.347*	-0.285	-0.393*	0.332*
2001					
Groups	0.231	-0.046	0.046	-0.028	0.394*
Dolphins	0.079	0.085	-0.078	-0.157	0.471*
Calves	-0.017	0.085	-0.089	-0.107	0.360*

The general linear model of dusky dolphin sightings was significant overall but only area significantly influenced sightings (Table 2.5). Post-hoc least squares mean analysis showed blocks 24-26 (St Helena Bay) to have significantly larger group sizes than any of the other areas. The average group size of dusky dolphin sightings is more than 20 for all the blocks around St Helena Bay (Blocks 21-23: 20.42; Blocks 24-26: 38.52; Blocks 27-29: 26.05), more than twice as high as any other region along the coast (Blocks 1-9: 9.0, Table Bay) due to the occurrence of very large groups of more than 50 animals only being seen in this region.

Table 2.5. Results of Proc GLM of dusky dolphin sightings along the southern west coast of South Africa in 2000 and 2001. Overall model results at top and break down by parameter below, significant results marked with an asterisk.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	14.00	69.57	4.97	5.31	<.0001*
Error	1233.00	1154.55	0.94		
Corrected Total	1247.00	1224.12			
R-Square	Coeff Var	Root MSE	cbbest Mean		
0.06	-9258.11	0.97	-0.01		

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Block	7	60.16	8.59	9.18	<.0001*
Shore	1	0.02	0.02	0.02	0.89
Swell	2	3.63	1.81	1.94	0.14
Shore x Swell	2	1.74	0.87	0.93	0.39
Sst	1	0.34	0.34	0.36	0.55
Depth	1	2.93	2.93	3.13	0.08

Interspecies comparisons

The two most precise and contemporaneous factors in which the two species could be compared were the sea surface temperature and depth at each sighting. The SST did not differ significantly between the two species, although in general Heaviside's were in slightly colder water than dusky dolphins (Fig. 2.5). Both species however were found in significantly colder water than the general temperature in the study area (measured at the beginning, end and various stop points of each search leg) see Table 2.6. Dusky dolphins were found in deeper water than Heaviside's dolphins in all years, significantly so in 2 years and when all years were grouped together (Table 2.6).

Table 2.6. Results of Student's t-tests comparing the SST and depth at sightings of Heaviside's dolphins (*C.h*) and dusky dolphins (*L.o*) for each of the study years and all together, as well as the comparison between all dolphins and 'randomly' collected SST values in the environment (see text).

	SST		Depth	
	T	P	T	P
All Years grouped	-1.05	0.29	-4.89	*<0.001*
1999	-0.81	0.42	-4.17	*<0.001*
2000	-0.41	0.68	-0.89	0.374
2001	-0.58	0.56	-4.34	*<0.001*
All *C.h* versus Environ	-5.78	*>0.001*		
All *L.o* versus Environ	-3.15	*0.002*		

Due to the closing mode nature of the data collection (spending time with groups of animals and potentially allowing for previously unsighted animals to approach or be sighted) and the focus on Heaviside's dolphins it was not possible to do a detailed analysis of co-variation in the sightings of the two species with time and space both included simultaneously. Although Heaviside's dolphins were seen on effectively every day at sea (109 of 110, see Table 2.7 and notes therein), dusky dolphins were only seen on 65 of 110 (59.1%) sea days. However, when we did see dusky dolphins, 30.5% of the sightings (54 of 177), also contained Heaviside's dolphins. Since we were focussed on photographing Heaviside's dolphins and not dusky dolphins it is perhaps better to word it conversely; 30.5% of dusky dolphin groups were seen with or near enough to a group of Heaviside's dolphins to be considered as one sighting.

Table 2.7. Frequency of the number of groups of Heaviside's and dusky dolphins sighted on any given sea day.

Number Groups Seen on Day	Frequency (Dusky)	% Dusky	Frequency (Heaviside's)	% Heaviside's
0	45	40.9	1*	0.9
1	29	26.4	2	1.8
2	11	10.0	2	1.8
3	4	3.6	6	5.5
4	7	6.4	3	2.7
5	2	1.8	6	5.5
6	4	3.6	9	8.2
7	1	0.9	6	5.5
8	2	1.8	6	5.5
9	1	0.9	9	8.2
10	1	0.9	9	8.2
11	1	0.9	6	5.5
12	0	0.0	11	10.0
13	1	0.9	5	4.5
14	0	0.0	10	9.1
15	0	0.0	5	4.5
16	1	0.9	3	2.7
17	0	0.0	3	2.7
18	0	0.0	2	1.8
19	0	0.0	1	0.9
20	0	0.0	1	0.9
21	0	0.0	0	0.0
22	0	0.0	2	1.8
23	0	0.0	2	1.8
Total Number of Sea Days	110		110	

** This day was aborted after only a few minutes due to adverse weather, thus effectively we saw Heaviside's dolphins on every working sea day*

Potential cetacean- fisheries conflicts.

Although search effort varied along the coast within and between years (Fig. 2.2), it is still possible to identify areas where certain fisheries are more active and areas where they are not. Firstly, it is clear from figure 2.6 that all fishing effort tended to cluster around the launch sites available at harbours along the coast and that fishing effort at all levels was considerably higher north of Saldanha Bay than between Cape Town and Saldanha Bay; this is largely due to the distribution of the (mostly subsistence) fishermen themselves.

Inshore line fishing, either hand line or rod fishing, is not felt to offer any great threat to cetaceans other than the possible risk of boat collisions and will not be discussed further here. Crayfish on the west coast are caught commercially using two methods, hand-lining with hoop nets from small open dinghies which proffers very little risk for cetaceans and secondly, traps which are set from larger boats and left unattended on buoys for extended periods (but usually less than 24 hours). These traps are unlikely to affect dolphins but are a significant entanglement threat to large whales, especially humpback and right whales which are increasingly common in this area. Some trapping and hoop-netting activity was seen in both years in blocks 18 (just north of Danger Bay) and 22 (Seal Rocks) but the most extensive crayfishing occurred in the Lamberts Bay region, where set traps were regularly seen close to shore (the highest number of trap-buoys counted was 60 in one location). In some parts of the world dolphins have been targeted for use as bait in crab fisheries (Lescrauwaet & Gibbons 1994); this practise does not apparently occur in South Africa although in the past some targeted harpooning of dolphins for human consumption has occurred from these crayfishing vessels (Best and Abernethy 1994).

Set nets and their associated boats were primarily seen in 2 regions, very near to the Yzerfontein harbour mouth (this was primarily one local fisherman seen regularly when we were launching) and around block 26 (just north of the Laaiplek launch harbour in the Berg river mouth), which consisted mainly of a St Joseph’s shark (*Callorhinchus capensis*) fishery.

Currently, the fishery in this area is felt to be potentially the most threatening to Heaviside's dolphins due to the high number of nets with a large mesh size. There are currently (late 2006) 80 fishing rights holders in the area between Cape Columbine and Rocherpan (a few kms north of Laaiplek), who are each allowed to use 2 St Joseph gillnets (178 mm mesh, 75 m long) and 2 harder (*Liza richardsonii*) gillnets (48-64 mm mesh, 75 m long) (info: Marine and Coastal Management). This fishery allocation area has recently been reduced in size disallowing fishing in the area between Cape Columbine and Saldanha Bay to reduce the illegal take of elasmobranchs, and future St Joseph's net exclusion zones may be put in place in the current area. Since 2003, both legal fishing levels and the instances of unattended St Joseph nets have been drastically reduced. Of greater concern is the high number of illegal set nets in the area principally used to catch smooth hound sharks (*Mustelus mustelus)*; these nets are often 400-700m long, up to 10 per boat and sunk beneath the surface and often set for a day or more (Steven Lamberth, Marine & Coastal Management pers. comm.). Mortalities of cetaceans and sea birds in these nets are thought to be high, but are currently unquantified.

During the 3 seasons of field work involved in this project, only one dolphin entrapment was observed. At Yzerfontein harbour two Heaviside's dolphins swam rapidly toward our research vessel as its engines were started upon launching, they swam into and became entangled in a short set net just outside the harbour. The accompanying fisherman released both animals alive within minutes.

Discussion

Our data show that the inshore density of Heaviside's dolphins varied along shore within their overall range but was spatially consistent between the 2 years of the study. Heaviside's dolphins were seen more regularly adjacent to regions where juvenile hake is likely to be regularly more abundant immediately offshore and to a lesser extent, more regularly in regions with sandier shores and higher exposure to swell. Dusky dolphins within the study area had a less predictable distribution pattern than Heaviside's dolphins and the sighting rate varied considerably along the coast and was not similar between years, except that the formation of the very largest groups (50-500) of animals only occurred in the St Helena Bay area. Dusky dolphins showed a markedly different social structure to Heaviside's dolphins, forming much larger groups on average, including nursery groups of multiple mother-calf pairs.

Bays on the west coast of South Africa are given their logarithmic spiral shape by the predominant south-westerly swell which results in their generally having an exposed open end with larger swell and a protected corner with very little swell (Bremner 1991). At sea observations suggested that Heaviside's dolphins were seen more frequently at the exposed end of bays where the swell was large. In these areas dolphins were frequently first sighted while exiting the back of waves and heading toward the boat at high speed to bow-ride it. This pattern was not very clear at the broader scale analysis of 10km bins and a significant positive correlation with swell exposure in bins only occurred for group sighting rate in 2001, although the general linear model showed group sizes to be significantly bigger in areas of higher swell. The relationship with swell size is possibly somewhat underestimated in the analysis as search effort was limited in the largest, most protected area, the corner of St Helena Bay (blocks 24-26), an area with almost permanently flat sea in summer. Prior work in St Helena Bay (MRI unpublished data) had shown so few sightings of dolphins that in the interests of maximising the collection of photo-ID data (the principal aim of the project), the bay was only searched once. This pattern of very low density in protected areas was also observed in the smaller protected corner of Table Bay at the south of the survey region and Saldanha Bay in the centre.

Barring the very low densities in the most protected areas of the coast (St Helena and Saldanha Bays), Heaviside's dolphins had a continuous distribution within the study area and apparently throughout their entire range (Findlay et al. 1992), which is reflected by a lack of phylogeographic population structure (Jansen van Vuuren et al. 2002). This contrasts markedly with the closely related Hector’s dolphin of New Zealand which has a distinctly patchy distribution throughout its range which, combined with very limited dispersal in this species, has resulted in distinct genetic differences between populations as little as 500km apart (Pichler et al. 1998). Habitat openness (open ocean or straight coastline) has been linked with home range in delphinids, with dolphins in more open habitats (Defran et al. 1999) ranging considerably further than dolphins in more closed, estuarine or coastal island type habitats (Gubbins 2002, Heinrich 2006). The relative straightness of the southern African west coast, in comparison with the New Zealand coastline, might be a contributing factor to the differences in the range of the two species. From a conservation perspective, the more continuous distribution and lack of genetic differentiation of the Heaviside's dolphin makes it potentially more resilient than the Hector’s dolphin, populations of which are known to be at serious risk due to anthropogenic factors (e.g. Slooten & Lad, 1991; Slooten et al. 1992).

The very similar longshore distribution pattern of Heaviside's dolphins between years and its strong correlation with the amount of hake potentially available nearby suggests that both species might have relatively stable distribution patterns. Unfortunately the commercial and thus scientific interest in hake is primarily in the bigger animals further from shore, so that the available data on inshore juvenile hake distribution is limited. It is worth noting that two areas of higher hake density highlighted in this study (approximately off Lamberts Bay and Yzerfontein) are also obvious in Payne’s (1989) figure of the distribution of all shallow water hake made using a similar but older data set to the one in this study. Unfortunately, no published explanation for these apparent hotspots in hake numbers can be found. However, the southern Benguela current system is a fairly structured wind-driven upwelling current system in which changes in bottom topography and longshore wind stress can result in locally enhanced and predictable upwelling cells (Pitcher et al. 1992). Two of the strongest upwelling cells in the region occur off the Cape Peninsula and Cape Columbine, roughly 60 km to the south of the dolphin 'hot spots' at Yzerfontein and Lamberts Bay respectively. It is feasible that the higher density of dolphins and hake in these areas are later steps in a trophic cascade resulting from the increased phyto- and zooplankton associated with these upwelling cells with the whole drifting northwards in the current. Shallow water hake is considerably more common in Namibian waters (Payne 1989) than in South African waters and a comparison of Heaviside's dolphin diets, distribution and movement patterns in the two areas would be informative.

Dusky dolphins were not the focal species in this study and were seen in lower numbers inshore than Heaviside's dolphins, although in larger groups. Dusky dolphins showed much greater variation in their numbers and location throughout the study area and varied considerably between years. They were observed more regularly in areas with sandy rather than rocky shores and in 2000 the sighting rate of calves suggests a preference for shallower more protected areas of coast and in the field dusky dolphins were rarely seen in the breakers. Because the range of dusky dolphins extends further from shore than that of Heaviside's dolphins (Findlay et al. 1992) it is likely that sightings occurring very close to shore as here are effectively at the edge of their range and thus probably not fully representative of dusky dolphin habitat. Analysis of 32 dusky dolphin stomachs collected off southern Africa indicated feeding on either pelagic fish (maasbanker, pilchard and anchovy) or mesopelagic fish (myctophids and hatchet fish), suggesting the exploitation of two alternative resources (Best, 2008)

Dusky dolphins are known to use a variety of feeding strategies in other parts of their range. In Peninsula Valdez, Argentina, several medium-size groups of dolphins aggregate to form very large schools (20-300) while surface feeding on large schools of anchovy (*Engraulis anchoita*) in summer, but this changes seasonally and very large groups are far more rare during the winter months when the anchovy move offshore (Würsig & Würsig 1980). At Kaikoura canyon, New Zealand dusky dolphins in winter form much larger groups and remain offshore and feed all day, while in summer they show a pronounced onshore-offshore movement pattern and feed nocturnally on animals associated with the deep scattering layer (Markowitz 2004, Benoit-Bird et al. 2004). Further highlighting the individual flexibility of dusky dolphin foraging techniques, some of the same photo-identified animals that feed nocturnally on DSL organisms at Kaikoura move hundreds of kilometres north in winter to feed in small groups during the day on surface schooling fish in the shallow inshore waters of Marlborough Sound (Benoit-Bird et al. 2004).

We do not know if there is a seasonal shift in the predation strategies of dusky dolphins in South Africa, but our data suggest that there may be a spatial variation, at least inshore since very large groups of dusky dolphins were only observed in St Helena Bay, very close to the site of a strong, regular upwelling plume enriching the area. Shore based observations in the same area, showed dusky dolphins to apparently move offshore during conditions that were likely to cause upwelling offshore (Chapter 1). We do not know if the species of fish being taken by dolphins in these upwelling areas is different to those in non-upwelling areas, but schooling fish such anchovy *Engraulis capensis* and sardines *Sardinops ocellatus* do form a part of the dusky dolphin diet in the study area. It is the high activity levels associated with feeding on surface schooling fish such as the presence of leaping dolphins and diving birds that may act as a visual cue for nearby smaller schools of dolphins to home in on, thereby resulting in a large aggregation of dolphins (Würsig & Würsig, 1980).

Interspecies interactions

Interspecific interactions between odontocetes vary from indifferent (bottlenose and dusky dolphins largely avoid or ignore each other in Argentina, Würsig & Würsig 1980) through potentially symbiotic (a common dolphin apparently providing parental care for a bottlenose dolphin calf while its mother was feeding, Bearzi 1996), commensal (nocturnal spinner dolphins resting by day with more alert diurnal spotted dolphins, Scott & Cattanach 1998), to aggressive (bottlenose dolphins killing harbour porpoises in Scotland, Patterson et al. 1998) and predatory/kleptoparasitic (Weller et al. 1996; Palacios & Mate 1996). With 30% of sighted dusky dolphin groups seen with or in close proximity to Heaviside's dolphins, the opportunity for interactions between the two species must occur regularly in the inshore waters of the study area. The only agonistic behaviours observed however were jostling between individuals of both species for space on the survey vessel’s bow wave (which the larger, faster dusky dolphins invariably won). No feeding interactions were observed, and most cases of proximate sightings passed with groups not apparently interacting (although we were not making formal behavioural observations during encounters). Single dusky dolphins were twice sighted with groups of from 3 – 7 Heaviside’s dolphins and single Heaviside's dolphins were seen swimming with two groups of roughly 30 and 500 dusky dolphins. Currently we can only conclude that, at least in inshore waters where feeding for one of the species is apparently limited, dusky and Heaviside's dolphins are not apparently avoiding or attracted to each other and interactions between the species are generally neutral.

Competition between sympatric species may be mediated by resource partitioning, spatial heterogeneity (Chesson 1985) or competitive exclusion (Durant 1998). The data presented in this study do not allow us to fully investigate the ecological interaction between the two species, but it is clear that some degree of prey partitioning occurs (Sekiguchi et al. 1992), there is some differentiation in habitat (mainly depth and distance from shore, shore type and slope but possibly also water temperature) and there is some spatial heterogeneity in dusky dolphin feeding strategies. These mechanisms may have been sufficient to mediate any direct inter-specific competition.

Fisheries Conflicts

Currently, due to a low level of set netting in the region, potential negative impacts of fisheries on Heaviside's and dusky dolphins appear to be limited within the study area. The entire range (~2900km) of Heaviside's dolphins is sparsely populated with Cape Town, at the very southern limit of their range, being the biggest human concentration, but with limited near shore fishing in Cape Town opportunities for direct conflict here are limited. The human population gets sparser north of Lamberts Bay (northern end of our study area), with only a few coastal towns or cities throughout the remaining range of the species (Port Nolloth in South Africa and in Namibia, Oranjemund, Lüdertiz, Walvis Bay and Swakopmund). However, we can not draw any conclusions about human-dolphin conflict outside of our current study area without direct knowledge of the inshore fishing activities occurring in these areas,

Bycatch in inshore set-netting is the principal concern for Heaviside's dolphin conservation. Within the study area netting was observed to occur mainly around Yzerfontein (block 12) and just north of Laaiplek. Eighty fishermen hold rights to set net between Cape Columbine and just north of Laaiplek, but it is the illegal fishery that is of most concern currently. Besides an estimate of this possible bycatch, future research should focus on getting a good population estimate of dolphins in the area as an important step in managing and understanding the impacts of all fishing activity of Heaviside’s dolphins in the Western Cape.

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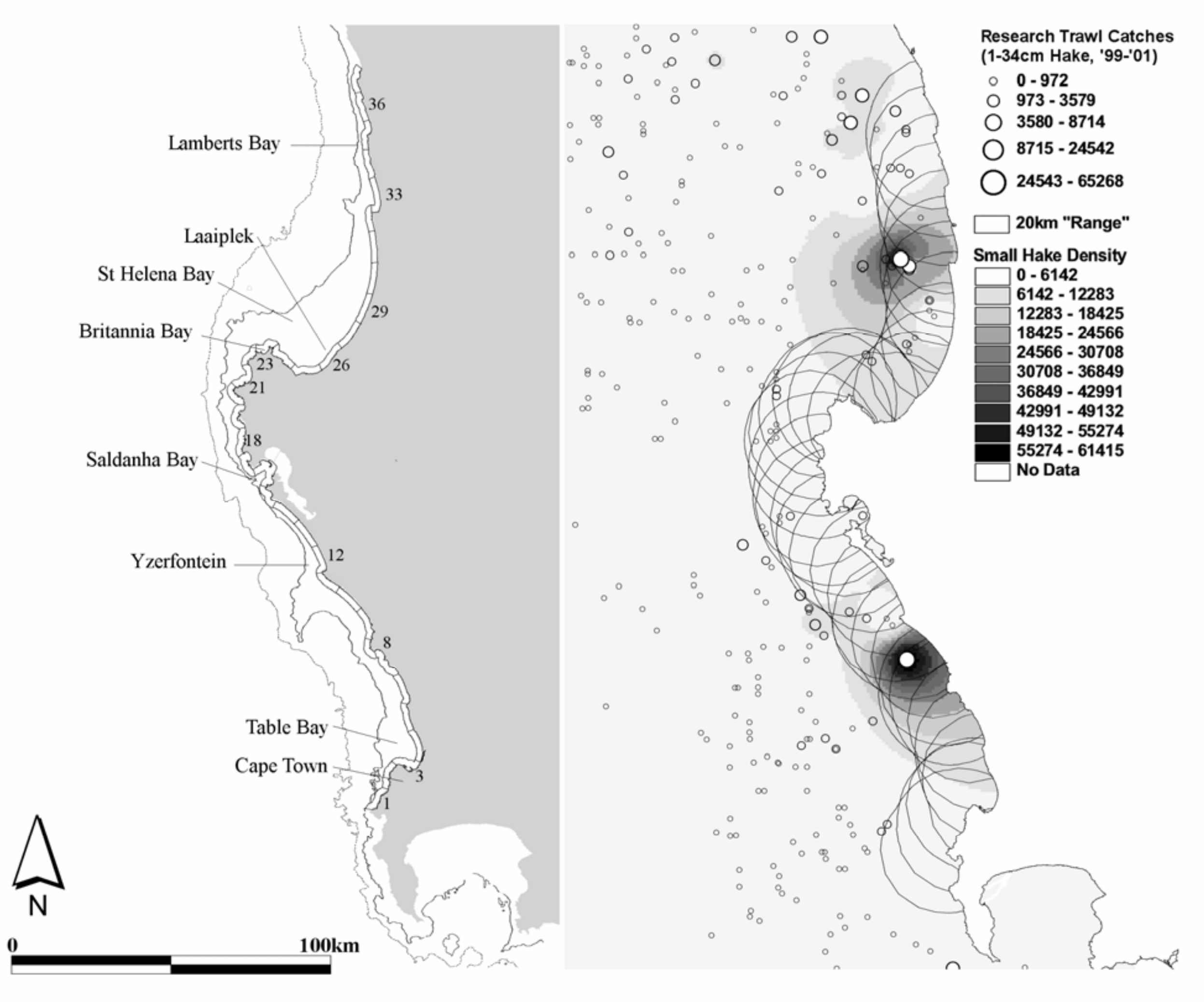

Figure 2.1. a) Study area on the southern west coast of South Africa, showing bathymetry and places mentioned in the text as well the 10km long bins used to defined search effort along the coast (numbered from south to north 1-36) and b) interpolated research trawl data of number of small (1-34cm) shallow water hake caught per hour, shown as raw trawl counts (circles) and interpolated values (solid colour) for data from 1990 to 2001. Overlain on trawl data are the 20km ‘search ranges’ from each 10km bin along the coast used to calculate the amount of hake potentially available to dolphins in those bins.

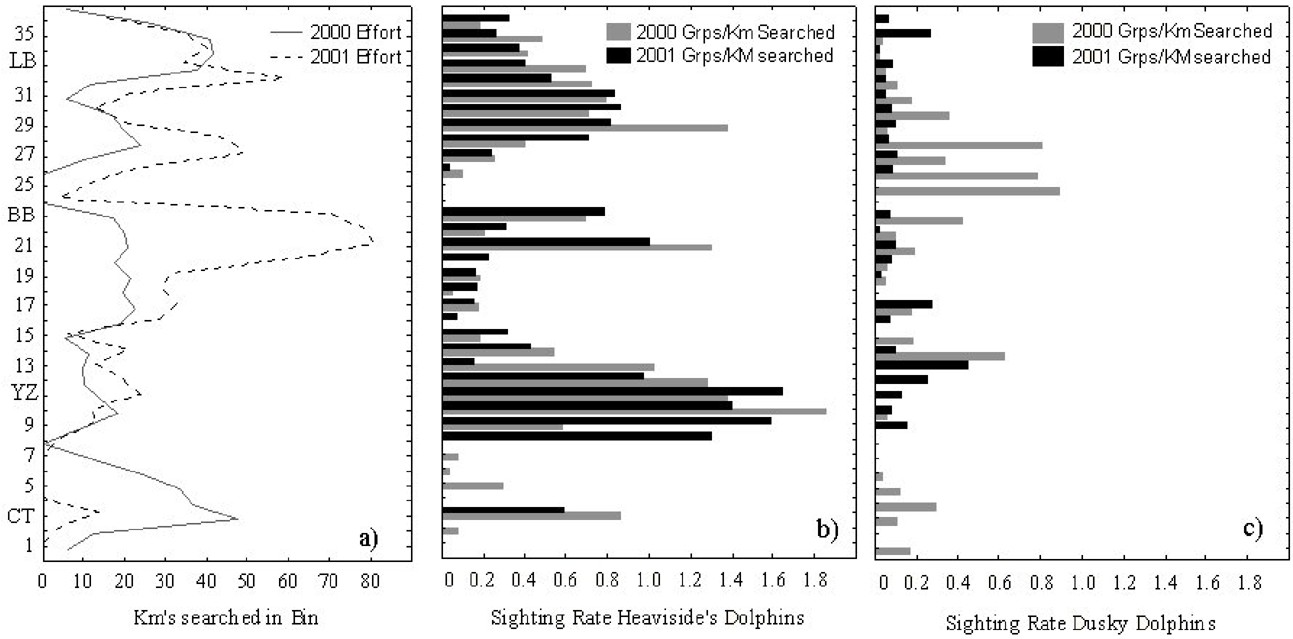

Figure 2.2. Figure oriented with north at the top and south at the bottom, with the bins containing Cape Town (CT), Yzerfontein (YZ), Britannia Bay (BB) and Lamberts Bay (LB) shown by letters. a) Number of km's searched in each ~10km long bin along the southern west coast of southern Africa in 2000 and 2001, b) number of groups of Heaviside's dolphins seen per km searched in each bin in 2000 and 2001, c) number of groups of dusky dolphins seen per km searched in each bin in 2000 and 2001.

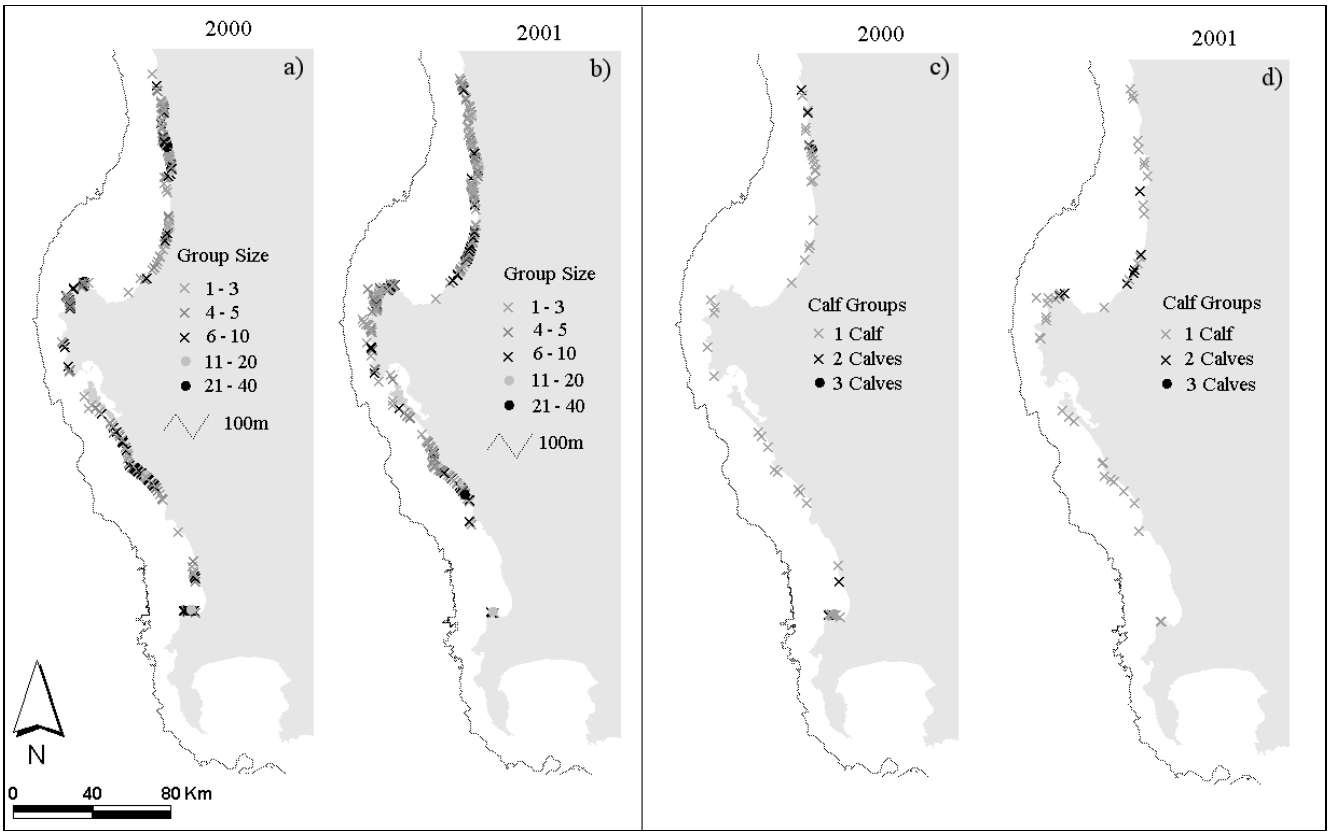

Figure 2.3. a) and b) Distribution of all Heaviside's dolphins sightings in 2000 and 2001 respectively, colours show variation in group sizes; c) and d) show the distribution of groups of Heaviside's dolphins containing calves in 2000 and 2001 respectively. All maps shown with the 100m contour as a dotted line.

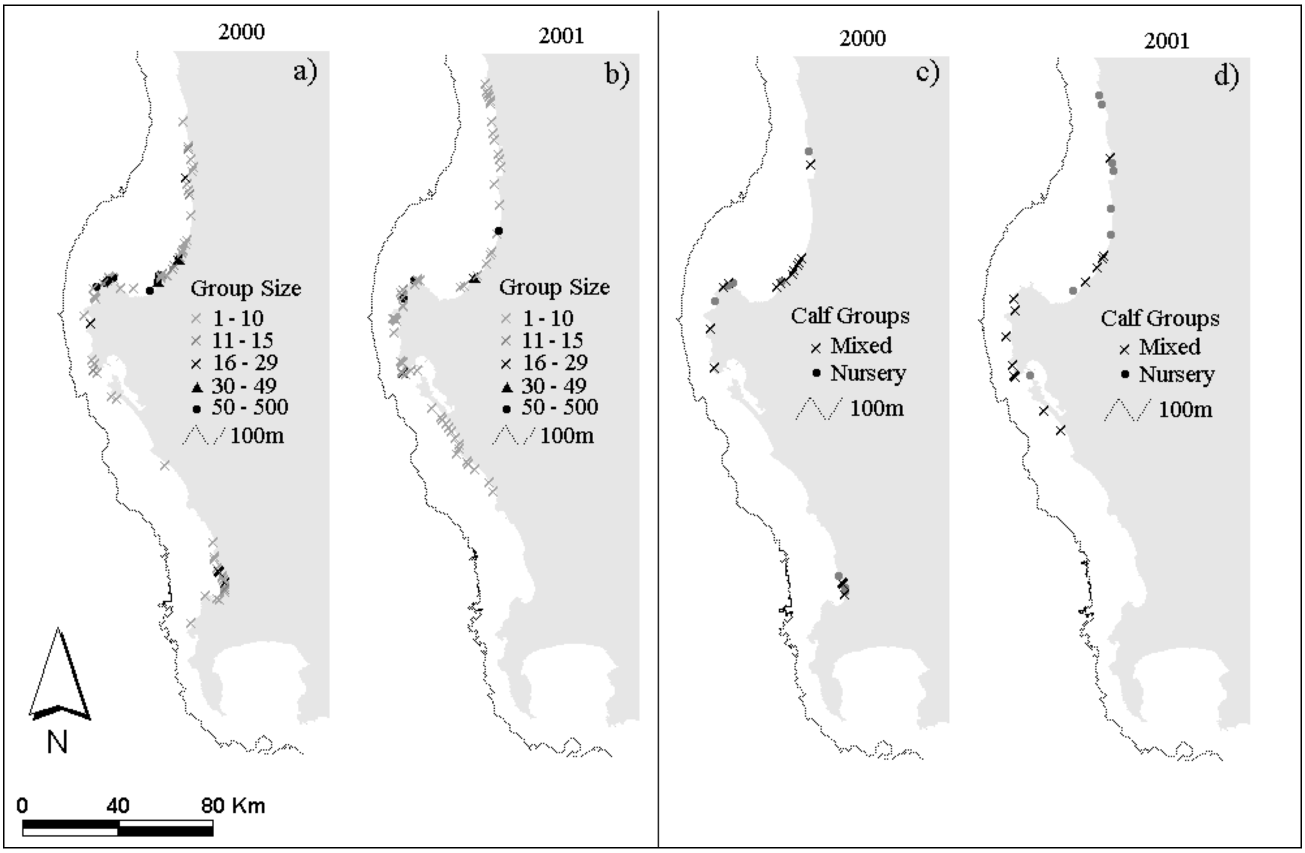

Figure 2.4. a) and b) Distribution of all dusky dolphin sightings in 2000 and 2001 respectively, colours show variation in group size; c) and d) the distribution of the two types of groups containing dusky dolphin calves 2000 and 2001 respectively (mixed groups containing adults, juveniles and calves and nursery groups of mothers and calves only). All maps shown with the 100m contour as a dotted line.

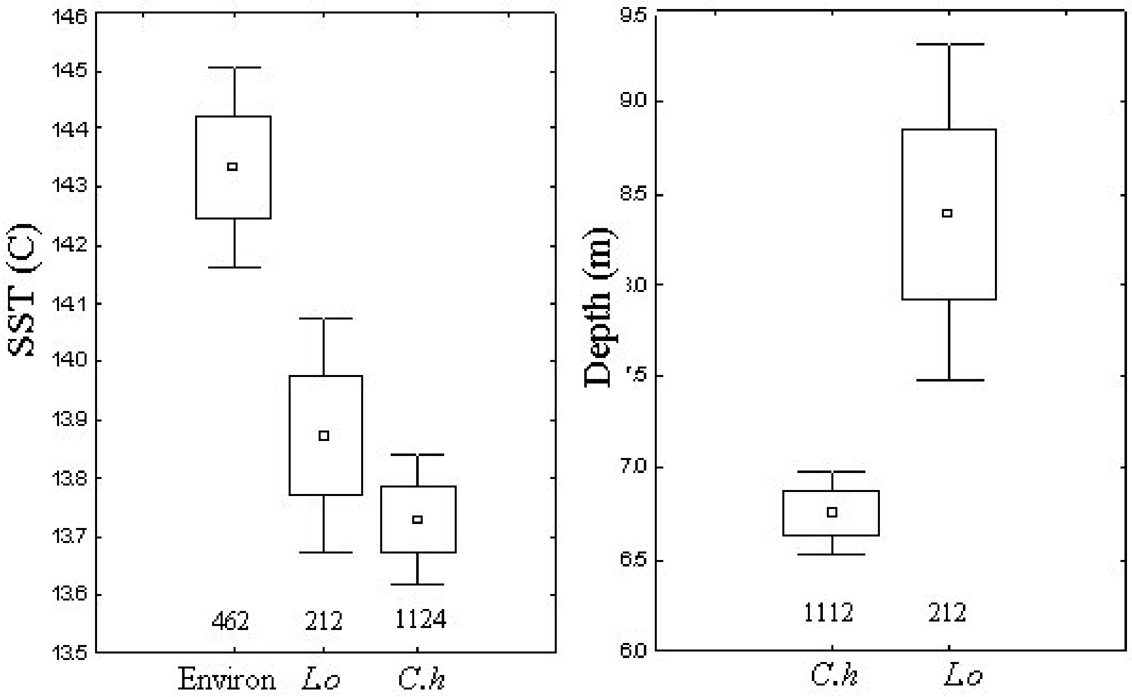

Figure 2.5. Box plots (point: mean, box: SE, whiskers: 1.96SE) showing (left) the mean sea surface temperature at sightings of Heaviside's (*C.h*) and dusky dolphins (*L.o*) and in the environment generally and (right) the mean depth measured at the beginning of each dolphin sighting.

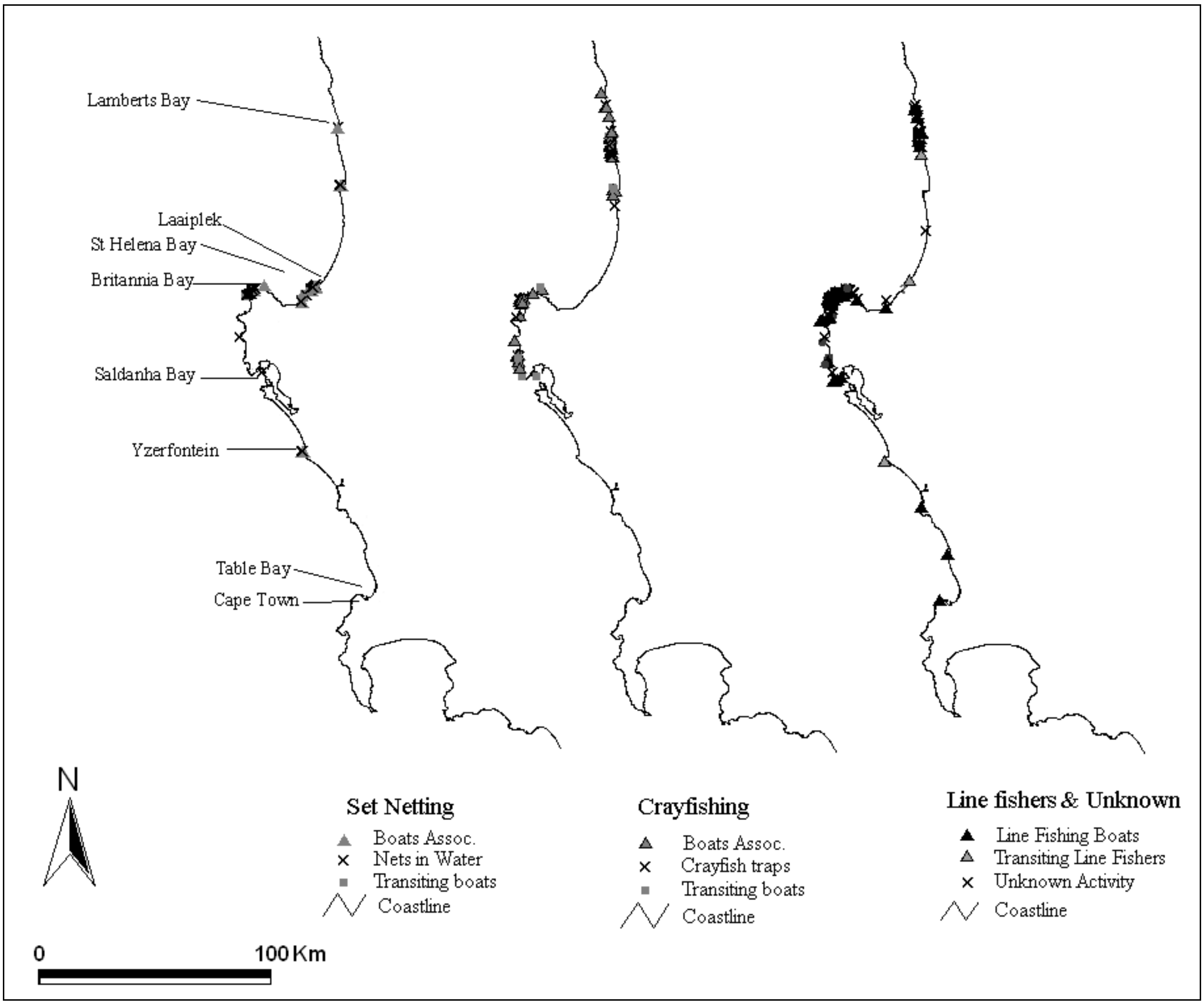

Figure 2.6. Maps showing the distribution of fishing effort observed during field work, split into the set netting (left), crayfishing (centre) and line fishing and unknown vessel (right) operations, showing the positions of traps/nets and boats associating therewith.

Chapter 3

Site fidelity in a dynamic environment: range, dispersal and social structure of Heaviside's dolphin *Cephalorhynchus heavisidii*.

Abstract:

We investigated the dispersal of individually identified Heaviside's dolphins from a central location over 3 years, with the principal aims of measuring the alongshore range as a proxy for their home range and investigating the degree of site fidelity of individuals. Data were collected during the late summer (Jan-Apr) along the southern west coast of South Africa. Resighting rates were low throughout most of the study area but movements of individuals were spatially limited, and considerably smaller (maximum = 88.4km after 1 year) than the ~390km length of the full study area. Several animals showed very fine scale site fidelity and were observed within 2km of their original sighting even after 2 years at large, and >50% of movements at all time scales were <20km from the original sighting. Residence patterns, modelled using lagged identification rates (the probability of resighting individuals after various time lags) were difficult to interpret due to the strong spatial and temporal patterns in our raw data, but are consistent with a pattern of short term residency within seasons with at least some animals being resident over the longer term. Inter-animal associations were calculated for data from a single season and locality, and did not differ from a random mixing of individuals, suggesting that this species has a fission-fusion type social structure over the short term. We conclude that the site fidelity observed from over ~50 days of satellite telemetry of 5 female Heaviside's dolphins (Elwen et al. 2006) is a stable pattern and continues over at least 3 years, although a seasonal migration or variation in home range size cannot be ruled out as data were only available from summer. The apparently high degree of site fidelity observed over long periods in this species is inconsistent with the more transient movements expected from delphinids living on an open dynamic coastline and feeding in

open waters. However, if their demersal prey source (juvenile hake, *Merluccius spp*) is equally unpredictable throughout their environment, dolphins may choose to stay in an area with which they are familiar, rather than risk moving to a novel location. Phylogeny may also play an important role in limiting dispersal in this species, since high site fidelity is apparent in at least 2 of the 3 congener species.

Introduction

'*Despite the simplicity of the concept, studies of dispersal cover many different subjects and it has been described as the 'glue' linking ecology, population genetics, ethology and evolution*' (Stenseth & Lidicker 1992). Studies to increase our understanding of the motives and scale of animal movement have a strong applied value as such movements influence the size and efficacy of marine reserves and management areas (Hyrenbach et al. 2006), the effect of both localized and broad scale anthropogenic impacts (Bräger et al. 2002) and even the level of interaction between different populations of a species including potential speciation events (Serrano & Tella 2003; Belliure et al. 2000).

Heaviside's dolphin is a coastal delphinid endemic to the west coast of southern Africa; it is relatively abundant with several thousand animals in the southern part of their range (Chapter 4), and although probably not of a high level (Best & Abernethy 1994), anthropogenic impacts on the population, such as fisheries bycatch, remain unquantified. The species has a near-shore distribution and satellite telemetry has shown females to be resident in ranges <2000km^2 over at least a 50-day period (Elwen et al. 2006), with the ranges of individual animals overlapping to a high degree. The fidelity to small home ranges over several years of the closely related Hector's dolphin in New Zealand (Bräger et al. 2002) is thought to be the main cause of the high genetic differentiation of that species and has profound implications for both speciation and conservation (Pichler et al. 1998; Baker et al. 2002). In contrast, Heaviside's dolphins show little genetic differentiation across a significant part of their range (Jansen van Vuuren et al. 2002), despite the high short-term site fidelity of at least females (Elwen et al. 2006). Although they apparently occur continuously throughout their range (Findlay et al. 1992) and there are no obvious physical barriers to their movements along what is essentially a long straight coastline, the lack of genetic differentiation seems incompatible with the high level of site fidelity observed over the short term. It seems likely that some greater degree of movement may take place by at least some members of the population at some time in their life cycles, most likely males or juveniles. Alternately, the population's history may have been too short for genetic differentiation to have developed in this environment.

This study was specifically designed to investigate the dispersion of Heaviside's dolphins over 1 and 2 years from a central location with the principal aim of measuring the alongshore range of individuals as a proxy for their home range. St Helena Bay was selected as the central location for the study for logistic reasons and because of a potentially high (but unmeasured) point source of by-catch in an inshore set net fishery for St Josephs shark *Callorhinchus capensis* in the bay. Knowledge of how many animals were likely to interact with the fishery, how those animals dispersed along the coast and over what time frame, is important for management purposes.

Methods

Data collection

In the first year of the study, a core area (~20km coastwise, centred at 32.7deg S) was saturated with photographic effort in 26 worked sea days over two months, split over three 2 week field trips a week apart in an attempt to 'capture' all the dolphins in the area photographically. In the following two years, effort (four 2 week field trips operating in adjacent areas) was spread along the coast line between Cape Town (~34.0S) and just north of Lamberts Bay (~31.9S) including the original core area, in an effort to resight individuals as they dispersed over time (Fig. 3.1). A similar pattern of data collection occurred in 2001, although two trips took place in the central area (to facilitate concurrent shore based observations) and only one day was worked out of Cape Town. The temporal nature of the data collection becomes important during the analysis of time lags between sightings. In total, 109 sea days were worked in four adjacent areas over 22 summer weeks in 3 years. All data were collected from the research unit’s 6m RIB fitted with twin 40hp 2-stroke outboards, with an elevated observation platform (putting eyes at approx 3m ASL). The boat was launched daily, weather permitting and used to run coastwise searches (dependent on previously searched areas and prevailing weather), usually just behind the breaker line where numbers are known to be highest during the day, at a search speed of 6-8kn. Upon encounter, dolphins were followed until photography of the group was regarded as complete or until the dolphins were lost; an effort was made to photograph all animals in the group and not bias attention towards those observed to be marked. At each sighting SST, depth (from on board fish finder) and GPS position were noted. Due to the nature of the Western Cape coastline and the limitations of weather, boat launches were limited to available harbours, consequently effort tended to be higher near harbours with less effort at the extremes of the search ranges from each harbour. Photography was with manual focus Nikon F301 and Minolta F300s cameras, using Kodak T-Max 400 film; in 1999 only one photographer was used but in 2000 and 2001, two photographers took pictures of each group concentrating on opposite sides of the boat to help increase the capture probability and speed up encounters. Some dolphins were prone to follow the boat, if this was noticed in the field the boat would speed up after finishing with a group to 12-15 knots in an attempt to lose the dolphins. This was not always successful in high-density areas and some individuals were seen in several subsequent sightings; when this occurred only the first sighting of the individual that day was used.

Spatial data processing

The GPS locations recorded for all groups encountered were entered into a GIS database (Arcview 3.3) for analysis. The distance between resightings of individuals was measured in the GIS using the ‘shortest straight swim’ distance (i.e. across bays but around headlands). In the majority of the study area where the coastline was straight, this measure did not differ much from a ‘coastwise’ movement; only across St Helena Bay were the distances much different. However based on knowledge of animal movements from satellite telemetry

(Elwen et al. 2006) and dolphin distribution in the bay (Chapter 2) a direct swim across the bay was felt to be more realistic than measuring distance around the coast.

Our survey effort covered ~390km of coastline from just south of Cape Town to north of Lamberts Bay and was effectively one dimensional (all sightings within 2.2km of shore) with animals being resighted either north (+) or south (-) of their original sighting. Distances between sightings were calculated from the 1st sighting of an animal to all subsequent sightings within a year, and to the first sighting in each year for inter-year sightings. The coastline was divided up into 36 blocks 10km long coastwise following the methods in Chapter 2 which were used to describe location and broad scale movements. Where appropriate, we have structured the data into three different spatial scales, the full 390km study area (Cape Town to north of Lamberts Bay), the ‘central area’ (~150km of coast) and the ‘core area’, which constitutes only that ~30km of coast searched during 1999. The ‘central area’, including St Helena Bay and extending southwards to Saldanha Bay, was the area straddling the 1999 core area that was searched within single 2 week field trips in 2000 and 2001, the majority of data in this study was collected within this central area due to higher overall effort here.

Photographic data processing

Black and white negatives were examined for quality and distinctiveness using a variable magnification dissecting microscope (up to 32x magnification) over a light table to allow for maximum observational power. At the highest magnification of the microscope the film grain was discernible, thus negatives were studied to their maximum information content. Images containing well marked fins and of usable quality were scanned in and matched on screen to the catalogue. Photographs were rated for quality out of 6 (1- barely identifiable; 2 – very poor; 3 – contains information but is not good; 4 – can make out small marks but edges not clear; 5 – good; 6 – excellent, big, focussed, well lit, perpendicular to camera) and animals were rated for distinctiveness (1 – no mark; 2 – small single notch/marking; 3 – 2 or more marks of reasonable size or a fairly unique marking; 4 – several, obvious markings, unique shapes; 5 – extremely obvious mutilations), based on as many photos as possible to minimise the relationship between photographic quality and ability to observe distinctiveness. Both rating systems were subjective but the ratings were checked several times by a single observer to increase consistency within the database. Factors affecting photo quality were investigated separately and fin size, focus and parallax were found to be most influential on overall quality. Distinctiveness is a quality that not only reflects the observability of the markings (size relative to the fin) but to some extent, their rarity, as in general Heaviside's dolphins are not well marked animals and markings tend to be small and relegated to the trailing edge; shape and colouring were not usable and scarring was not useful for long term matching. Only photos of PQ≥4 and animals of D≥3 were used in the analyses of residency and association indices as an assumption of equal capture probability is required where the entire database was analysed as a whole. However, conditions were relaxed somewhat when only individual movements were being described, in the interest of getting as much information on individual animal movements as possible: in some cases we used images that were below the selection criteria if we were confident of the match.

Analysis

The proportion of the population that was distinctively marked was fairly low (14-17%, Chapter 4) which, combined with a large population, the relatively short time frame of the data and its broad spatial spread resulted in a low number of individual resightings. To best overcome this, a multi-faceted approach to analysis has been used.

Firstly, a ‘proportion of resightings at centre, over time’ approach following Attwood and Cowley (2005) was used. If a population of animals is dispersing randomly (diffusing), then at release (time *t*) all animals will be at the release location, at time *t+1*, animals will have spread out and fewer will be near the release point and at time *t+2* even fewer will be at the release point. Conversely, if animals are showing site fidelity to their original point of capture then the proportion of animals remaining near there will remain constant over time. The data were summarised into 3 time lags to group movements observed within a year (2000 and 2001 only), after 1 year (animals sighted in 1999 and 2000 and resighted in 2000 and 2001 respectively) and after 2 years (animals sighted in 1999 and resighted in 2001). Resightings made within 1999 were excluded due to the small size of the study area in this year preventing observation of movements longer than ~20km. The field season in all years was from late January to early April, so movements "within a year" are for this time period only.

Since our data set was relatively small and had a strong spatial and temporal structure, the observed time lags (in days) between all the resightings of individuals seen more than once were compared to the pattern of time lags that were possible given the temporal structure of the field work. For those individuals seen 3 or more times, we calculated the observed time lags for all combinations of sightings of those individuals (e.g. 1st-2nd, 1st-3rd, 2nd-3rd etc).

The residence time of individuals was calculated as "lagged identification rate" (LIR), using the movement module in the compiled version of SOCPROG 2.2 (Whitehead 2005). The LIR is the probability that if an individual is sighted in the study area at time zero, it will be re-identified in the study area some time lag later (Whitehead 2001). LIRs were calculated at two spatial and temporal scales, the full data set from the whole study area (blocks 1-36) and secondly the central area (blocks 16-29) where the majority of data were collected. For both spatial scales, LIRs were calculated firstly for the entire duration of the study (no maximum lag set), and secondly by setting a maximum time lag of 150 days which is longer than the field season but shorter than the period between years and effectively calculates the LIR within seasons, "averaging" (the term is used loosely) resightings within this time period, across the 3 years of data.

Models of residency were fitted to the LIR data using likelihood methods, with the best fitting models judged using the Akaike Information Criterion (AIC) (Whitehead 2005) which accounts for both model fit and the number of parameters allowing for comparison between different models. Errors for both the data and models were calculated using bootstrap methods. The terminology of the fitted models can not be taken literally and must be placed into context; 'emigration' for example means emigration from the database not necessarily the study area, we have no way of knowing whether animals actually died, left the area or were simply not seen again due to chance The LIR is calculated using the sighting histories of all animals (including those only seen once) and thus to some extent represents an 'average' residency rate for all animals included in the analysis; if there are distinct strategies employed by different groups of animals within the overall population (e.g. males/females, transients/residents) then the LIRs would be most informative if the data set were structured appropriately (Letteval et al. 2002; Whitehead 2001). Unfortunately (apart from a few cows with neonates) males and females could not be differentiated in the field, so these analyses are performed on all animals grouped together.

The social structure of Heaviside's dolphins was investigated using only the data collected in 1999 where sufficient resightings of animals were made over a short enough period to allow for analysis. Coefficients of association were calculated for all animals sighted more than once (35 animals in 91 sightings) using the simple ratio of association which describes the associations observed without attempting to correct for unknown biases in the data (Ginsberg & Young 1992) and is probably the most appropriate for investigating association within groups (Whitehead 2005). Permutation tests were performed in SOCPROG 2.2 to test whether observed association patterns were greater than expected from a randomly permuted set of associations between the same individuals following the Manly-Bejder procedure modified by Whitehead et al. (2005). Animals were defined as associated if they were seen in the same sighting; however some sightings consisted of multiple sub-groups from which the photographs could not be differentiated, which may skew or weaken the analysis to some extent.

Even within a population, different measures of association between individuals can vary greatly, depending on the index used, the size of the population being sampled, group size, proportion of well marked animals, whether groups are fully sampled or not and the selection criteria used to include animals in the analysis (usually the number of times each animal has been sighted). Due to the low mark rate and number of resightings, this analysis is effectively only performed on a small portion of the animals in the area and no groups were regarded as fully sampled (i.e. all individuals in the group identified photographically). The ranging patterns of animals also has an influence on their social structure by limiting the potential number of associates that an animal can have and if individuals show high site fidelity they are likely to associate more often with their close neighbours or animals with overlapping home range (e.g. Rossbach & Herzing 1999).

Results

Both the temporal (2 week field sessions separated by a week) and spatial structure (12 of the 22 weeks of effort were in or included the central core area) of our field effort clearly affected our overall sighting patterns; of the 393 sightings of 263 individuals in 109 sea days, nearly half (179 sightings and 105 individuals) were made in the central 20km long core area used in 1999. In total there were 263 dolphins identified and 76 resighted at least once during the 3 years of surveys (Table 3.1, Fig. 3.2)

Table 3.1. The number of photographically identified and resighted Heaviside's dolphins seen during the summer months of 1999-2001 on the west coast of South Africa. Resightings within a year include multiple resightings of those animals first identified in previous years.

Photographed in	Total identified (new animals)	Number resightings of individuals		
		1999	2000	2001
1999	67 (67)	30	4	9
2000	120 (116)		22	10
2001	99 (80)			16

Recapture data suggest there is to some extent a split in the population around Saldanha Bay with only one animal being resighted both north and south of this bay (Fig. 3.3). Although sightings of dolphins and marked animals regularly occurred either side of the bay (Blocks 14, 15, 17, 18), they were generally fewer in number here than in areas farther north (Paternoster and Britannia Bays) and south (near Yzerfontein) of this area (Chapter 2), while in Saldanha Bay itself (Block 16) there were only 2 sightings of 7 animals during our 5 searches of the northern half of the block during 2000 and 2001.

Dispersal – Proportion at 'centre' over time

To increase the sample size in this analysis, several well marked, but poorly photographed animals were included, as measurements were made of individual animals and were independent of each other. The greater the amount of time lapsed between sightings of an animal, the further it could potentially have moved. The shortest straight swim distance between the extremes of the full area studied in 2000 or 2001 was 240km (~390km coastwise). However, all observed movements within 2 years (n = 9) were made within 50km of the original sighting (Figs 3.4 and 3.5) and only 3 of the 21 sightings made 1 year apart and 1 of the 55 observed movements within a year exceeded this measure (the maximum observed distance between any 2 sightings of an individual was 88.4km). More than 50% of observed movements in all three time intervals were made within 20km of the original sighting. Strikingly, many individuals were resighted very close to their original sighting location, several within 2km of the original sighting even after a year (n= 6/21) or two (n=2/9) ‘at large’ suggesting that at least some dolphins are showing a degree of site fidelity at a scale of essentially a few hundred metres (at least at this time of year). Larger moves were observed after 1 year than after 2 yrs, but we feel that this is probably an artefact of the smaller number of animals seen after 2 years.

Observed frequency of time lags between sightings

As a preliminary to calculating the lagged identification rate (residency) using SOCPROG, we plotted the time lags that were potentially possible given the distribution of our data collection efforts and number of resightings and compared them to the observed time lags between sightings. The 2 weeks on – 1week off temporal structure of the field trips is clearly evident in the pattern of the expected (“possible”) number of time lags that could be observed, creating peaks and troughs representing time lags with more and less effort respectively (Fig. 3.6). For example, in 1999 the maximum time lag that could be observed between two sightings of an individual was 52 calendar days but this could only occur for animals seen on both the very first and last sea days of the season, similarly, the low number of working sea days 31-34 days apart resulted in very little opportunity for animals to be resighted after this time period, however there was ample opportunity to resight animals after shorter periods 1-3 days apart (Fig. 3.6). The low sample sizes did not allow for statistical comparison of the observed and expected time lags between sightings; we discuss some of the data below.

The pattern of resighting-lags also reflects the spatial structure of the data collection, in that the longer spent in a single area the more resightings of individuals were made. Given the distribution of effort, the observed number of resightings of individuals in 1999 is slightly higher than might be expected for short time lags (1-3days), markedly higher for long lags

(45-50days) and generally lower in between, possibly suggesting some kind of cyclic movement pattern over this time scale. Observed lags from 2000 (only one trip per area) are only higher than expected for intervals less than 10 days (within a field trip) and in 2001 for 1-7 days and 18-26 days (within one and two field trips apart) reflecting the 2 consecutive trips based in the central region in that year. In all three years, the most frequent time gap between resightings of individuals occurred 1-5 days apart, suggesting that dolphins are more likely to be resighted over short time periods than longer ones and in 2000 and 2001, no resightings were observed more than 41 days apart, even though the field seasons were twice as long.

Residency, using Lagged Identification rates

Although the maximum likelihood approach of the LIR technique was specifically designed to analyse data that are non-uniform and non-random both spatially and temporally (Whitehead 2001), it still requires "large" data sets to work properly. Our data set is relatively small and has strong spatial and temporal structuring evident throughout (Fig 3.6). Reasonable model fit could not be attained at the largest spatial scale (full study area) for either the full study period or the within-season approach and there was strong overdispersion of the data (variance inflation factor >4). For the central study area at the full time scale, the LIR was best described by a model of emigration and reimmigration, although a goodness of fit test showed the model to be significantly different from the data (Table 3.2, Fig. 3.7a). When limiting the time frame to 150 days to model the LIR within-seasons, a considerably better fit to the data were achieved (Table 3.2, Fig. 3.7b), with a goodness of fit test showing the best fitting model to not differ significantly from a model describing a population with emigration, re-immigration and mortality. Although the LIR initially drops toward a lower level after a short residence period, indicating emigration, there is an increase in the probability of resighting at ~45days evident in the raw data at both time scales and the model fit within seasons (Fig. 3.7b) which is most likely driven by the peak in resightings after that time lag in the 1999 data set (Fig. 3.6). The estimated residence time within the study area of

5.78 days (±1.6SE) is similar to the period in which a high number of resightings can be observed in the raw data (Fig. 3.6). The spatial scale of the central area covers roughly one home range to either side of the 1999 core area, and with the small movements made by this species we might expect animals identified in 1999 to be effectively resident within this stretch of coastline, although literal emigration and re-immigration are likely to occur especially near the edges. This analysis is weakened by the low resighting rate of known individuals during the study period which is largely a result of the low effort relative to the large population size in the area (3429 animals, 95%CI = 1721 – 6828, calculated with the same data set for the same area, Chapter 4) and the low mark rate of this species (~14-17% of animals). The clear effect of the spatio-temporal pattern of the raw data on these model results suggests that the data set is perhaps too small to effectively use this type of analysis.

Table 3.2. Estimated residency parameters (±SE) for individual Heaviside's dolphins in the central study area for the full duration of the study (3 years) and within seasons (<150 days). These results were calculated from 231 sightings of 139 Individuals on 51 days at sea.

Model	Population size	Time in	Time out	Mortality	AIC	GOF (p)
			FULL PERIOD			
Emigration & Reimmigration	68.69 (±14.44)	125.14 (±87.85)	689.162 (very large)	NA	1873.96	*0.0130*
			WITHIN SEASONS			
Emigration & Reimmigration	39.41 (±12.41)	4.24 (±2.89)	5.64 (±7.37)	NA	1327.66	*0.013*
Emigration, Reimmigration & Mortality	43 (3.81)	5.78 (1.6)	49.23 (1698.09)	-0.04 (0.03)	1314.51	0.913

Association patterns

Of the 30 identified animals seen more than once in 1999, only 7 (2 dyads and a triad) were seen together on more than one occasion and all of those animals were seen ‘unassociated’ on at least one other occasion. None of these animals were believed to be adult females accompanied by dependent offspring. All the sightings between which associations of these animals occurred were considerably larger (12-42 animals) than the average group size for Heaviside's dolphins reported from unbiased shore based observations in the same area (mean 3.3, range 1-10; Chapter 1) and all consisted of several undifferentiated subgroups of dolphins rapidly aggregating into one sighting, so the associations observed are not strictly at the ‘group’ level.

The mean number of associations observed per dyad was 0.082 and per individual 2.8. Neither the mean association index of individuals (including zeroes) nor its SD differed from a random data set with 20 000 permutations (Table 3.3) suggesting that the associations observed between individuals in 1999 were essentially random in nature and at this scale Heaviside's dolphins have a fission-fusion type social structure. Due to the apparently high site fidelity of individuals, data collected over a longer period would likely result in more observations of associations and may result in preferential associates or avoidances being observed. This type of analysis is greatly weakened by the low mark rate of this species and is best performed on groups of animals in which all members can be identified (Chilvers & Corkeron 2002)

Table 3.3. Results of a permutation test for preferential companionship amongst Heaviside's dolphins photographically identified within a season (1999), showing the means of average association indices, standard deviation, CV's and p-values for the observed data (all and non-zero associations shown separately) and a data set randomised with 20 000 permutations.

	Mean	SD	CV	Non zero proportion	Non-zero Mean	Non-zero SD	Non-zero CV
Observed	0.018	0.071	4.017	0.072	0.247	0.121	0.490
Random	0.017	0.067	3.829	0.077	0.229	0.102	0.444
P values	0.90	0.974	0.982	0.023	0.984	0.959	0.864

Discussion

For an animal to have a measurable home range it must be sighted several times throughout its range and show some degree of site fidelity to an area causing the size of the observed range to asymptote over time, which it would not do if its movements were entirely random in nature (Crook 2004; Spencer et al. 1990). The number of sightings required to accurately define the home range of individuals varies between species, populations and study methods with at least 20 sightings being regarded as a minimum (e.g. Gubbins 2002; Heinrich 2006) with 50 – 100 sightings more likely for an accurate estimate (Urian 2002). Heaviside's dolphins range from the breaker zone to roughly the 100-200m isobath (Findlay et al. 1992) or 20-30km offshore (Elwen et al. 2006) and use different parts of this range at different times of the day, being close to shore in the mornings and generally offshore in the afternoon and at night, making it all but impossible to intercept them for photo-ID throughout a significant part of their home range. Further, they tend to be far more difficult to find and approach when not inshore (pers obs.), limiting the area in which photo-ID techniques could be effectively applied to the inshore zone during daylight hours. Thus, we have made no attempt to define a "home range" in this study, rather we have used an alongshore range, but due to the straight nature of the majority of the coastline, these two measures are closely related (Elwen et al. 2006) and we are confident that conclusions drawn from along-shore ranges can be interpreted in light of theories applying specifically to “home range”.

If animals are transient, do not have a limited range or territory and the direction of their movements is effectively random, then the movements of individuals after a point release can usually be described by a simple diffusion model (Turchin 1998). The same diffusion pattern applies to a range limited animal ‘filling up’ its home range over time. If there are sufficient observations then the diffusion growth pattern should reach an asymptote when the animal has been observed throughout its home range. Elwen et al. (2006) suggested that the 5 female Heaviside's dolphins fitted with satellite tags in their study reached this asymptote and occupied more or less their entire home range during the 45-55 days of transmitter attachment and had alongshore ranges in the region of 39 – 83km. Even after a full year only one movement observed in this study exceeded this distance (88km), while observed movements 2 years apart were even smaller supporting the hypothesis of Heaviside's dolphins showing long term site fidelity to limited ranges; and no movement observed in this study exceeds the distance that a dolphin can swim in a single day[1].

At a broader scale (using data collected predominantly offshore) Heaviside's dolphins have an effectively continuous distribution throughout their ~2500 km range from the Cape Peninsula to southern Angola (Findlay et al 1992; J-P Roux, pers comm). Finer scale spatial analysis of the same inshore data used in this study highlighted areas of higher and lower density along the coast, correlated with the offshore distribution of juvenile shallow water hake, higher wave activity and sandier shores (Chapter 2). However, no consistent discontinuities or potential sub-populations in the distribution were identified based on the distribution of sightings alone (Chapter 2). Nevertheless, one interpretation of the movements of individually

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[1] Based on the 2.5m/sec (9km/hr) ‘maximum traveling speed’ used in Elwen et al 2006, to filter satellite telemetry data, a dolphin can swim 216km in a 24hr day, although this level of speed is unlikely to be sustained for long periods.

identified animals in this chapter would be that mixing of animals appears to be limited between the northern and southern parts of the study area, with the break point roughly at Saldanha Bay. Extensive shore based tracking work based on the northern headland of Saldanha Bay, as well as the associated boat based intercepts of humpback and right whales over the three years subsequent to this study, rarely encountered Heaviside’s dolphins in Saldanha Bay (J Barendse pers comm.). The mouth of Saldanha Bay is a deep channel forming the entrance to a commercial harbour; this deep-water habitat near shore may be unattractive to the dolphins. Differences in ranging patterns can affect the social structure of a population (Lusseau et al. 2005; Rossbach & Herzing 1999) and dolphins that are spatially separated are less likely to interact with each other, potentially creating distinct “communities” of individuals which can have potentially important conservation and management implications (Wilson et al. 1997; Heinrich 2006). However, genetic analysis of Heaviside's dolphins does not show any longshore population differentiation even at a much larger spatial scale (Jansen van Vuuren et al 2002) and although possibly restricted, dispersion is likely to occur across such low density regions. Genetic mixing throughout the range of the species with be enhanced by the apparently high social fluidity, continuous population structure and overlapping home ranges.

Animals sighted only once provide limited and confusing information in a study such as this as they could be transients passing through, have ranges barely overlapping the study area, be behaviourally less likely to be captured, have died, emigrated or simply have not been resighted due to limited search effort in that area. In some studies, animals seen only once are regarded as transients (Pocock et al. 2005) and there are mixed strategies of “residence” and “transience” within some delphinid species (Ford et al. 1998) and even mixed strategies within a population in a single area (Gubbins 2002; Hubard et al. 2004; Barco et al. 1999; Wilson et al. 1997). Further, in promiscuous mating systems, males are expected to range more widely than females in search of receptive mates (MacDonald 1983; Wells et al. 1987; Wauters & Dhondt 1992; Owen et al. 2002) which may lead to an appearance of different ranging strategies unless males and females are differentiated. Although the sexes were not differentiated in this study, very few of the movements observed exceeded the short term ranges of female Heaviside's dolphins measured with satellite telemetry (Elwen et al. 2006) and the smooth continuum and broad spread of observed movements showed no obvious differences (e.g. a bimodal distribution pattern) that might lead to a definition of resident or transient strategies or major differences between males and females. We interpret the increase in resightings that occurred with time spent in an area and the lack of dispersion or spread of animals across the study area over the 3 years of the study to be indicative of active site fidelity and that Heaviside's dolphins remain in relatively defined home ranges for extended periods. Although we have no data outside of summer months, a winter migration as seen in some delphinids (Gubbins 2002) is less likely to occur in this environment as the oceanography of the west coast of Southern Africa is dominated by the wind driven, Benguela upwelling system in which seasonal temperature variation is relatively low, at least in the southern part (Shannon 1989).

Due to their high energetic demands and low energy reserves, the movements of small delphinids in cold water environments are expected to be closely related to those of their prey (Koopman 1998, Johnston et al. 2005) especially for females that have the added costs of pregnancy and lactation (Read 2001). The positive relationship between home range size and body size of female Heaviside's dolphins (Elwen et al. 2006) provides some confirmation that their use of space is metabolically linked to food and feeding. The ultimate size of a home range is influenced by among other factors, the density, dispersion and predictability of food resources (MacDonald 1983) with home range size generally increasing with the decreasing predictability and density of prey. There is some evidence to support this amongst coastal delphinids. Those species living on convoluted coastlines which tend to have predictable prey hotspots such as tidal races and reefs often have smaller home ranges (Gubbins 2002; Heinrich 2006) than those species which live on exposed coastlines and presumably feed more on shoaling fish and open water prey (Defran et al. 1999; Read & Westgate 1997).

Despite their coastal distribution, Heaviside's dolphins feed well offshore on non-schooling demersal prey (predominantly hake and secondly goby, *Sufflogobius bibarbatus*), which cannot be regarded as a predictable resource on the same scale as species associated with tidal races or reefs. Given the degree of mobility of the species and the ecology of their environment, an open coastline with no resources predictable at a small spatial scale, we might expect Heaviside's dolphins to either have much larger ranges than they do or show only temporary site fidelity linked by larger exploratory or seasonal movements (the general model of 'transient' delphinids, Hubard et al. 2004; Defran et al 1999) rather than the apparently high site fidelity observed.

Site fidelity in most animals is related to holding a territory, nest or mate defence (Brashares & Arcese 2002; Burrows et al. 2004), past reproductive success (Switzer 1997) or predictably located food resources (Hastie et al. 2004; Atkins et al. 2004; Ingram & Rogan 2002). Site fidelity in the absence of any spatial 'anchors' is rare and the only equivalent examples we can find are in non-territorial coastal fish (Burrows et al. 2004), which show some homing abilities when translocated from their original ranges. In an environment with abundant resources and no aggressive, territorial neighbours, animals tend to use only as much space as they need (King 2002) and to stay in areas familiar to them rather than risk moving to novel areas, even if they are more productive (Switzer 1993). If resources are evenly spread throughout an environment, animals usually spread evenly as well and if those resources are defendable, territoriality is often the result (Emlen & Oring 1977). In unpredictable environments, if all 'sites' are equivalently unpredictable, modeling has shown fidelity to be a more beneficial strategy than changing sites (Switzer 1993). Although unpredictable at a fine scale (10s to 100s of meters), demersal prey of Heaviside's dolphins are arguably equally unpredictable everywhere at this scale, thus effectively forming an evenly dispersed, undefendable resource. The fidelity of southern elephant seals (*Mirounga leonina*) to particular foraging areas of highly variable productivity even during lean years, has been shown to have potential long term benefits when those areas are more productive in the long run (Bradshaw et al. 2004). Heaviside's dolphins have been shown to be more abundant on stretches of coast (10s of km) which show higher hake abundance over the long term (Chapter 2). This combination of fine scale unpredictability with broad scale predictability of prey abundance may make site fidelity the optimal strategy for Heaviside's dolphins in this environment. Phylogenetic effects might also play an important role in determining the home range size and site fidelity of Heaviside's dolphins as it seems to be a common trait throughout the genus *Cephalorhynchus*; both Hector’s and Chilean dolphins exhibit strong site fidelity (10s of km) over several years (Bräger et al. 2002; Heinrich 2006). Only Commerson’s dolphins have been observed to make longer seasonal movements (>200km) which may be related to seasonal variation in food supply (Coscarella 2005). Our data set, particularly per dolphin, is small and covers a relatively short period in summer months only so we certainly can not exclude the possibility that ranges of individuals might shift or drift over time (Doncaster & MacDonald 1991), or with changes in reproductive status (Read 2001), age (Owen et al. 2002) or seasons. Finally, our data only concern well-marked individuals which may or may not be representative of the population as a whole. However, over the 3 year period of this study, all observed Heaviside's dolphins showed a strong tendency for site fidelity at a scale similar to that observed for other *Cephalorhynchus* dolphins.

Animals with small ranges and high site fidelity are naturally more susceptible to localised impacts since at an individual level they are likely to be exposed to risk more often, while at a population level the impact is likely to be higher since it focuses on a single discrete group with a more limited ability for repopulation than if animals were ranging widely. Localised population impacts can be further exacerbated if social communities of individuals within a single area are not recognised and treated appropriately (Lusseau et al. 2005), and in a species showing high site fidelity, even short distances between groups of animals can result in a separation of communities (Heinrich 2006). The large numbers, high density and fluid social structure of Heaviside's dolphins and their near-continuous distribution throughout their range will to some extent mitigate any localized impacts on the population but a better understanding of the levels and effects of human activities affecting this population is needed and a cautionary approach to management is recommended.

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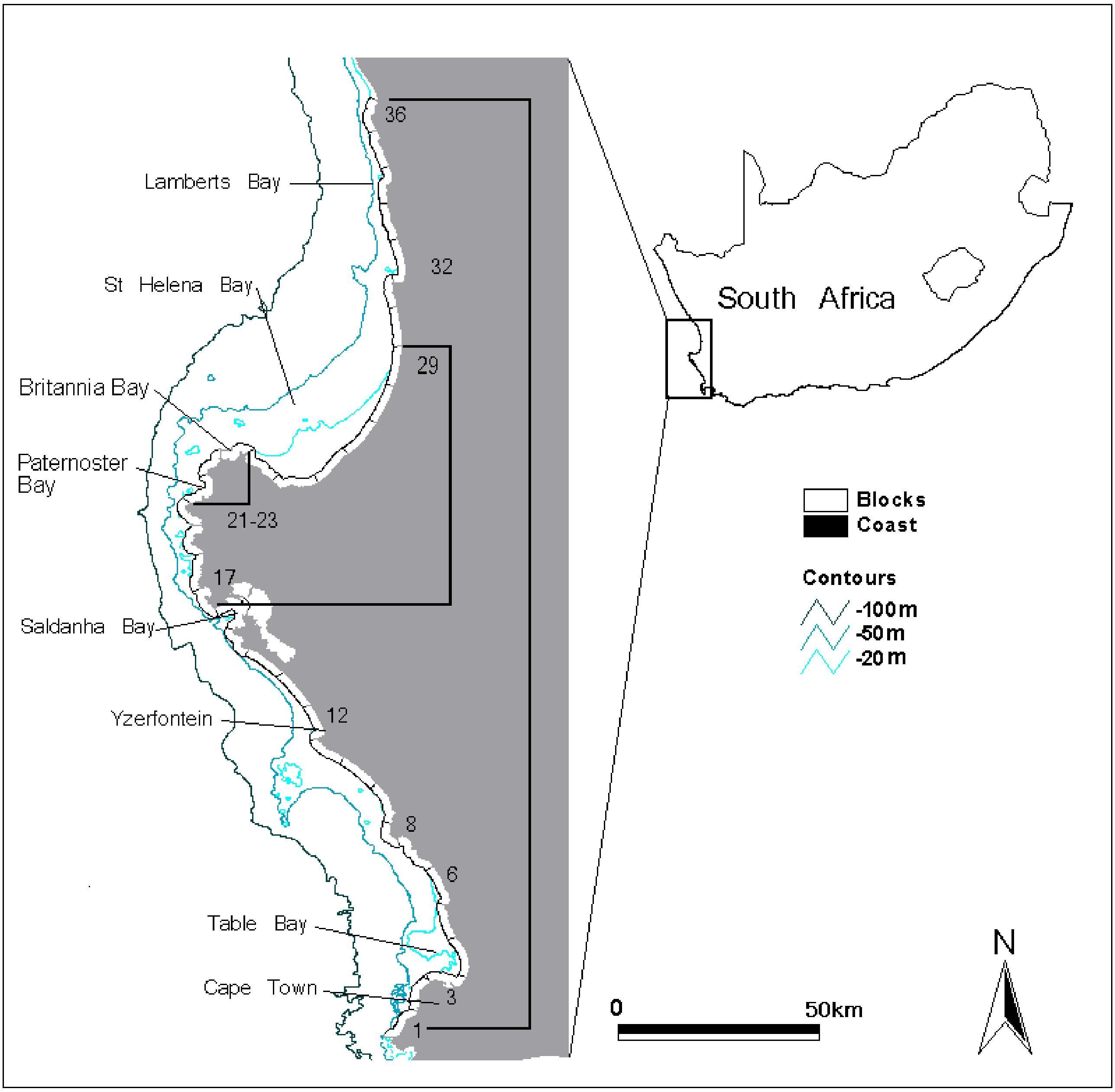


Figure 3.1. Map showing study area and place names mentioned in text. The area searched is within the blocks close to shore. The full study area includes all blocks from 1-36, the ‘central area’ blocks 17-29 and the ‘core area’ blocks 21-23.

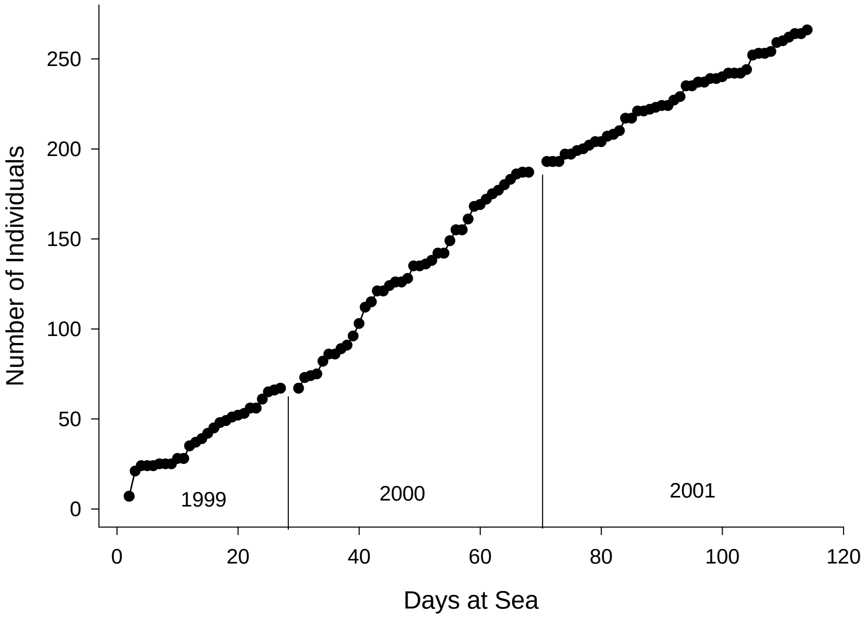


Figure 3.2. Discovery curve (number of new animals discovered per survey day) of well marked Heaviside's dolphins photographed off the west coast of South Africa in 1999, 2000 and 2001.

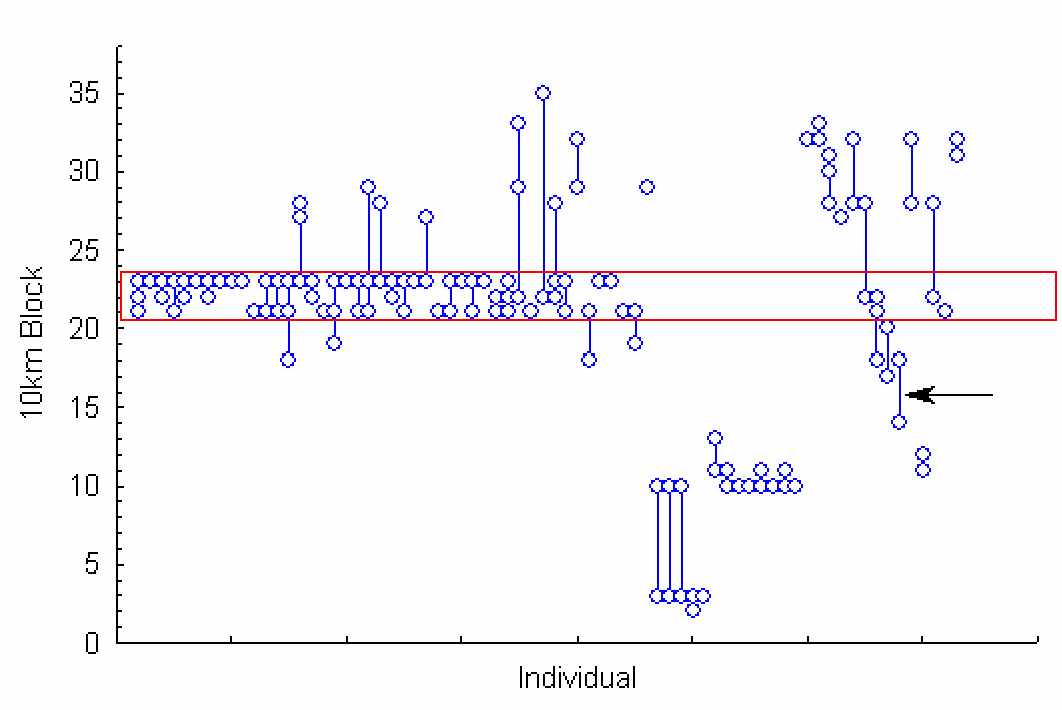


Figure 3.3. Figure showing the along shore range of Heaviside’s dolphin movements (summarised by 10km block of coastline) for all individuals seen more than once. Animals first sighted in 1999 are only shown if they were seen in a later year to prevent domination of the figure by the geographically limited 1999 data set. Each vertical line represents one animal’s movements but each point may represent more than one sighting in that block. The box outlines the three block of the 1999 study area and the arrow indicates the single animal observed to cross block 17, which contains Saldanha Bay mouth and is the region of a putative split in the population.

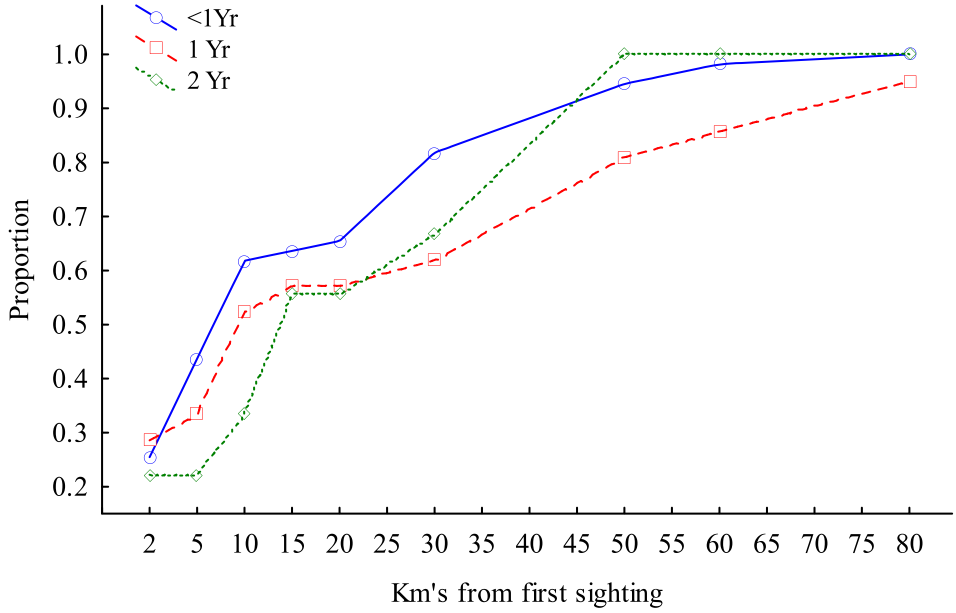


Figure 3.4. Cumulative proportion of Heaviside's dolphin movements (Y axis) occurring within a given distance (X axis) from the 1st sighting of the animal, shown separately for movements observed within one year (2000 and 2001 only), after one year and after two years at large. Observed movements were largest and most spread after one year

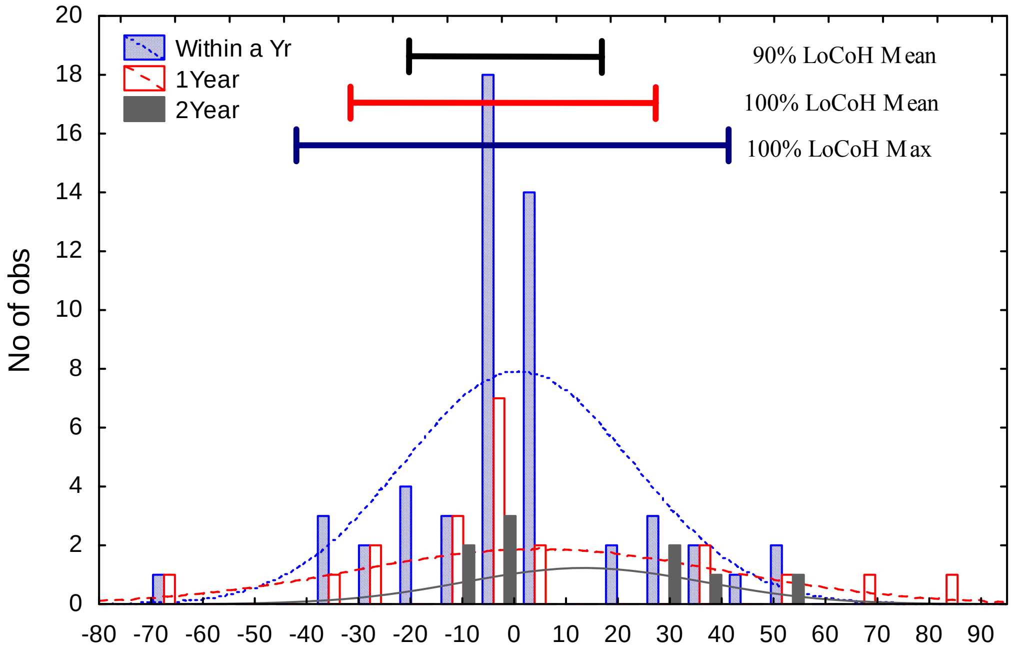


Figure 3.5. Histogram of coastwise movement vectors of all resighted individual Heaviside's dolphins from their first sighting, north as positive and south as negative. Bars across the centre line represent the alongshore ranges calculated from the 90% (mean) and 100% (mean and maximum) isopleths of the local convex hull home ranges (Getz & Wilmers, 2004) of 5 female dolphins fitted with satellite transmitters for up to 55 days (Elwen et al, 2006). With the size of the study area, animals could theoretically have been sighted as much as 240km apart.

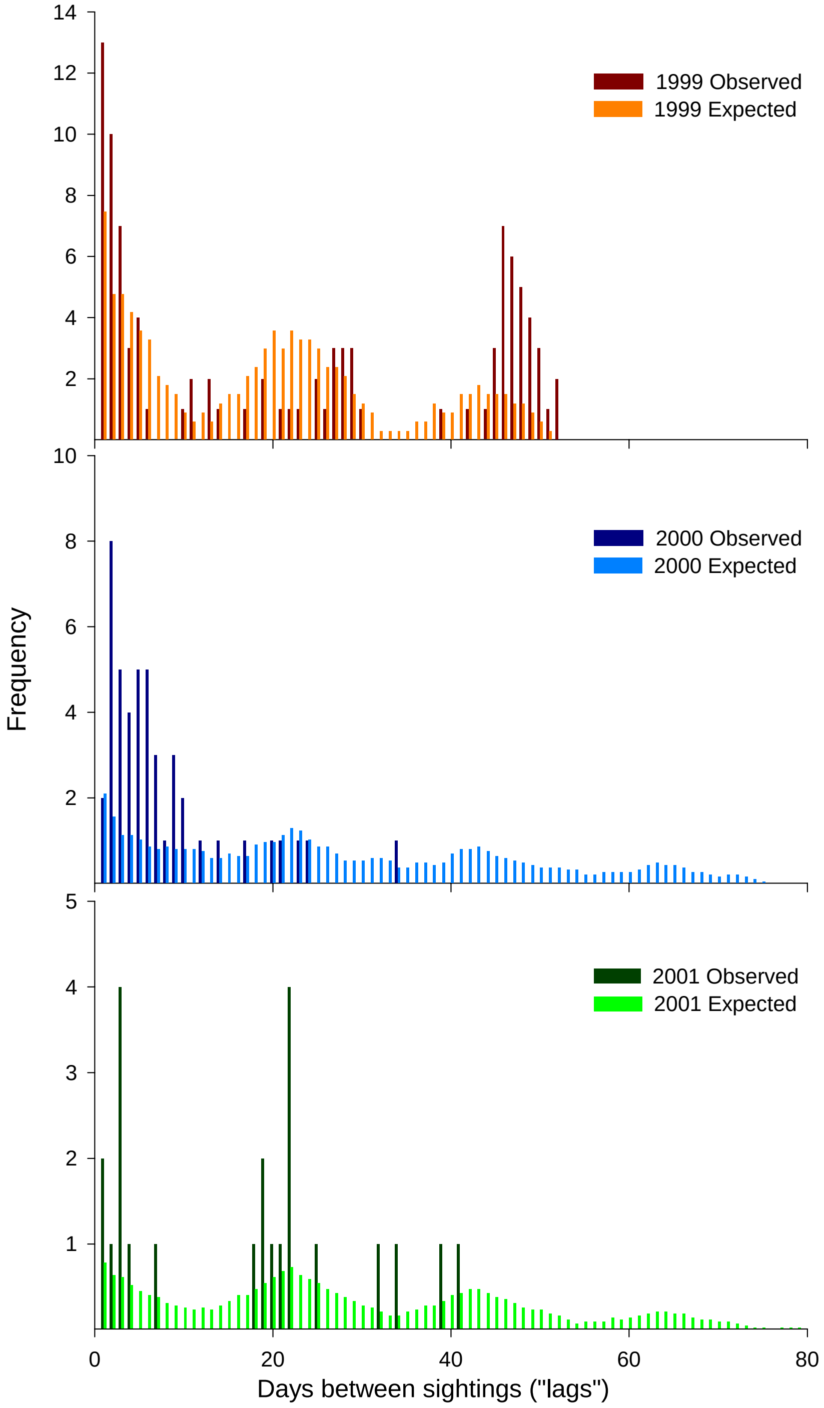
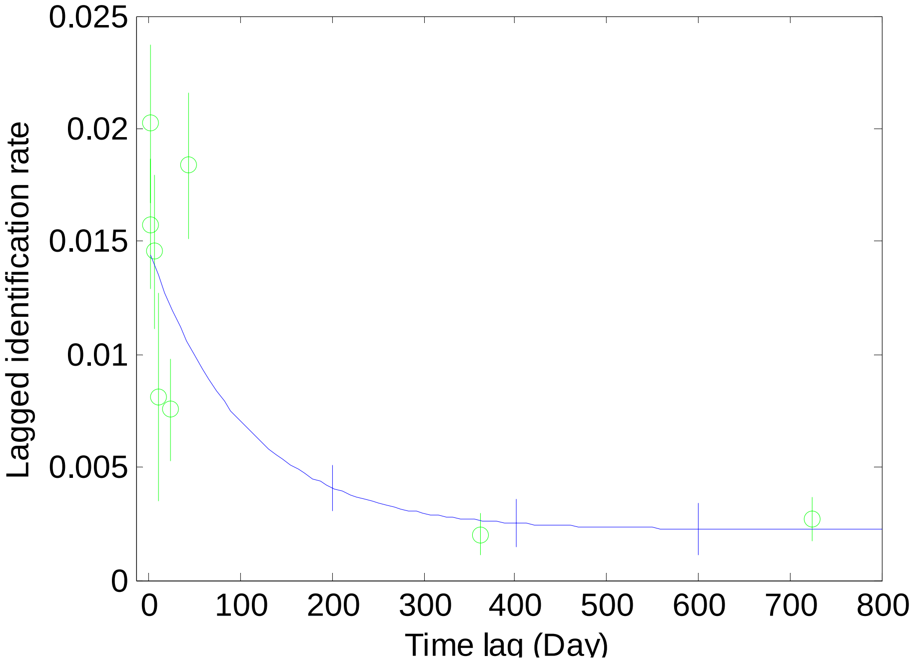


Figure 3.6. Time lags in days between resightings of individual Heaviside's dolphins seen more than once in the study period. Peaks and troughs in the expected values are caused by the 2 weeks on – 1 week off structure of the field work. Observed time lags between sightings were calculated between all combinations of sightings of individuals not only consecutive or from the 1st sighting. Expected time lags are calculated using the same sample size as the observed number of resightings. Although shorter than the other field seasons, 1999 was the only year where all the effort took place in the same area (Blocks 21-23, Fig 3.1).



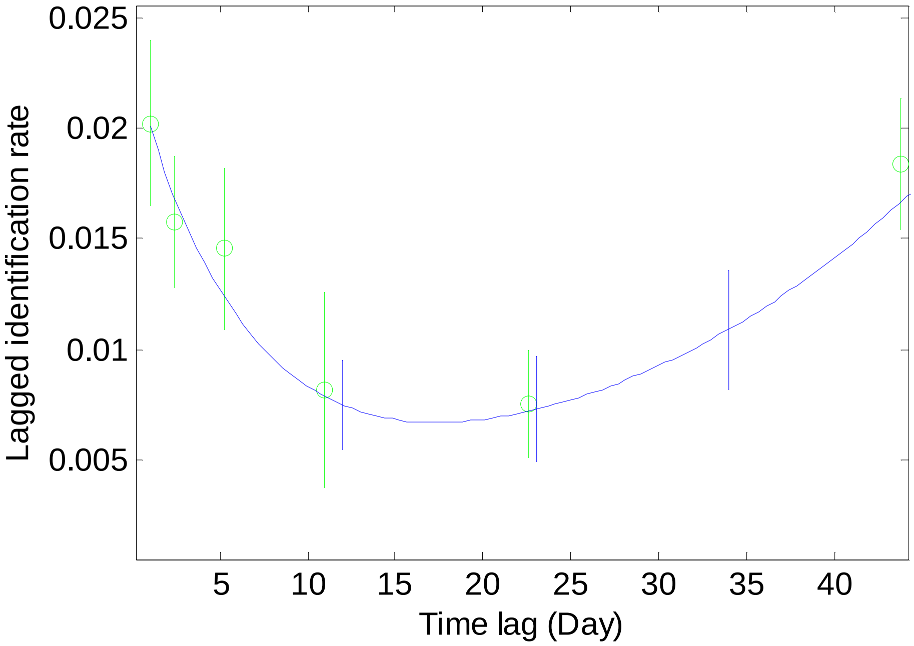


Figure 3.7. Calculated lagged identification rates (the probability of resighting an individual over time) with bootstrap errors of Heaviside's dolphins for the Central Area of the study site with best fit models (Socprog 2.3). Top: results for the full time period (~800 days) with fitted model of emigration and reimmigration. Bottom: results of the 'within seasons' analysis (maximum analysed lag set at 150days) with the best fitting model of emigration, reimmigration and mortality

Chapter 4

A population estimate of Heaviside's dolphins in the southern end of their range.

Abstract

Heaviside’s dolphins are endemic to south western Africa, where they have a near shore distribution and are exposed at an unknown level to anthropogenic threats such as inshore set netting. Using photo-ID data collected over 3 years we calculated Chapman’s modified Petersen abundance estimates at three spatial scales. Sample sizes were small and recapture rates low resulting in high variance; inter-year estimates of marked animals using the full (390km, 2 years) study area and central study area (~150km, 3 years) were 1007 (CV= 0.25, 95%CI = 625-1623) and 532 (CV= 0.29, 95%CI = 305-929) respectively. An ‘instantaneous’ estimate of the number of marked animals using the ~30km long core study area in 1999 was 87 (CV= 0.13, 95%CI = 68-112). Mortality between yearly samples was a known and correctable bias; unfortunately no estimates of survival rates are available from Heaviside's dolphins so a 0.914 (0.01SD) survival rate available from the closely related Commerson’s dolphin was used where appropriate. The proportion of distinctively marked individuals in this species is low and varied over both time and area. Using the most appropriate data to calculate the specific mark-rates for each scale (14 - 17%) resulted in total population sizes of 6345 animals (CV = 0.26, CI = 3573 – 11 267) in the full study area, 3429 animals (CV = 0.36, CI = 1721 - 6828) in the central study area and 527 animals (CV = 0.35, CI = 272 – 1020) in the 1999 study area. Heterogeneity of recapture probability is a potentially serious problem in mark-recapture studies, and in a species showing high site fidelity such as this may be principally caused by differential use of the study area. Analysis of the movements of 5 female Heaviside's dolphins fitted with satellite transmitters in 2004 showed their use of the inshore area where mark-recapture data was collected, to vary from 39.5 – 94.7% of their transmission days (38 – 51 total) suggesting at least one possible source of capture heterogeneity which would bias our estimates downwards, but due to small sample sizes it was not possible to account for this analytically.

Introduction

Heaviside's dolphins are coastal delphinids distributed along the inshore waters of the west coast of southern Africa. The coastal nature of their distribution brings them into close contact with potential anthropogenic impacts; fortunately the coastline along which they occur is sparsely populated and current impacts are thought to be low, although not as yet quantified and general knowledge of the species remains poor. An integral part of any effective management plan, and essential in assessing the impact of any human activities, is knowledge of the size of the population.

Due to the inaccessible nature of their environment and the small proportion of the time spent at the surface, estimating the abundance of cetaceans is invariably challenging. Line transect surveys from ships or aircraft are a powerful method to estimate the abundance of individuals within a defined survey area, and can also provide a measure of the relative density of animals in different environments or parts of the survey area, but make no assumptions of the number of animals outside that area and generally cover only a brief temporal window so are best suited to use on populations in which the entire range is known and their movement patterns well understood (Hammond 1986). Capture-mark-recapture (CMR) techniques use data on the number of animals marked (individually identifiable from photographs) and the proportion of those resighted in subsequent samples to estimate several population parameters including abundance (Seber 1982). Rather than the spatially restricted, instantaneous sample of a line transect, CMR methods result in an estimate of the number of animals using the study area over a series of sampling periods, even if not all those animals are in the area at all times. If the study period is long enough, photographic mark-recapture also allows for the collection of data on important population parameters such as birth rates and inter-animal associations (Whitehead et al. 2005) as well as mortality (Hammond 1986), residency (Whitehead 2001; Karczmarski et al. 2005) and individual movement patterns (Chapter 3; Whitehead 2001).

Within the overall range of the species (west coast of Africa from ~16^0 - 34^{0}S) the distribution of Heaviside's dolphins is apparently continuous (Findlay et al. 1992) although with areas of higher and lower density associated mainly with overall prey abundance (Chapter 2). Within that range, individual animals show site fidelity to particular areas (<80km alongshore) and their home ranges overlap extensively (Elwen et al. 2006). Although Heaviside's dolphins are regarded as having a coastal distribution and are found concentrated close to shore near the breakers in the morning where they are apparently resting but not feeding (Chapter 1), they disperse several kilometres offshore in the afternoons (Elwen et al. 2006) to feed on demersal prey, predominantly juvenile hake (*Merluccius spp*) (Sekiguchi 1994) which migrate closer to the surface in the dark (Pillar and Barange 1995). When moving offshore, animals become more evasive and less likely to approach the boat and are correspondingly more difficult to photograph (Chapter 1), limiting the effective collection of photo-ID data to inshore waters, usually in the morning. This diurnal pattern to the movement and 'catchability' of dolphins has implications for photographic mark-recapture studies since animals are potentially not always available for recapture, a prerequisite condition of most mark-recapture models. In 2004 (3-5yrs post photo-ID) 5 female Heaviside's dolphins were fitted with satellite transmitters in St Helena Bay (roughly the centre of the photo-ID study area) to investigate their home range and movement patterns (Elwen et al. 2006). We use these data here to investigate how the 'true' movements of individuals compare with and potentially affect the results from the photographic mark-recapture, since the low number of resightings observed in this study seems at odds with the evidence of high site fidelity observed from satellite telemetry (Elwen et al. 2006) and photo-ID data (Chapter 3).

In this paper we use photo-ID data collected as part of a larger project investigating the dispersal characteristics and range of individual dolphins, to generate an abundance estimate for the southern part of the species' range, and use satellite telemetry data of individual dolphins to shed light on the observed patterns and to better select the scale at which we perform future analyses.

Methods

Field techniques

Data were collected over three years during the summer months along the southern west coast of South Africa. During the first year of the study (1999) 6 weeks of effort (26 sea days) were expended extensively covering a ~30km section of coast (Fig 4.1), the core study area, in an attempt to photographically identify all the animals using that area. In year 2 and 3 of the study (39 and 44 sea days respectively), we searched the full ~390km of our study area launching from 6 different harbours and searching coastwise to cover the entire region in an attempt to recapture the animals identified in year 1; as a result, our effort was spatially broad, but relatively limited temporally and in most areas did not cover more than two weeks of effort within each study year.

All data were collected from the research unit’s 6m RIB fitted with twin 40hp 2-stroke outboards, with an elevated observation platform (putting eyes at approx 3m ASL). The boat was launched daily, weather permitting and used to run coastwise searches (dependent on previously searched areas and prevailing winds), usually just behind the breaker line where numbers are known to be highest during the day, at a search speed of 6-8kn. Upon encounter, dolphins were followed until photography of the group was regarded as complete or until the dolphins were lost. Photography was with manual focus Nikon F301 and Minolta F300s cameras using Kodak T-Max 400 film; in 1999 only one photographer was used but in 2000 and 2001 two photographers took pictures of each group concentrating on opposite sides of the boat. An effort was made to photograph all animals in the group and not bias attention towards those observed to be marked, however it was still possible that this bias occurred and it is felt to be a potentially significant problem in photo-ID studies of this kind. In an attempt to gain some perspective on the degree of potential bias, after each encounter both photographers independently recorded their estimate of how many ‘marked’ animals were seen in the group and how many they had photographed. Some dolphins were prone to following the boat; if this was noticed in the field the boat would speed up after a group to 12-15kn in an attempt to escape following dolphins.

Lab techniques: photographic data processing

Black and white negatives were examined for quality and distinctiveness using a variable magnification dissecting microscope (up to 32x magnification) over a light table to allow for maximum observational power. At the highest magnification of the microscope the film grain was discernible, thus negatives were studied to their maximum information content. Marked fins of usable quality were scanned in to digital format and matched on screen to the existing catalogue: if a match was not found animals were given a unique number and added to the catalogue. Photographs were rated for quality out of 6: 1- barely identifiable; 2 – very poor; 3 – contains information but is not good; 4 – can make out small marks but edges not perfectly clear; 5 – good; 6 – excellent (big, focused, well lit, perpendicular to camera), and animals were rated for distinctiveness (see appendix 1): 1 – no mark; 2 – small single notch/marking; 3 – 2 or more marks of reasonable size / fairly unique marking; 4 – several, obvious markings, unique shapes; 5 – extremely obvious mutilations; based on as many photos as possible to minimise the relationship between photographic quality and ability to observe distinctiveness (Read et al. 2003; Friday et al 2000). Both rating systems were effectively subjective but are well accepted within the field and the ratings were checked several times by a single observer to increase internal consistency within the database. Factors affecting photo quality were investigated separately and fin size, focus and parallax were found to be most influential on overall quality. Distinctiveness is a quality that not only reflects the obviousness of the markings (size relative to the fin) but to some extent, their rarity. In general Heaviside's dolphins are not well marked animals and markings tend to be small and relegated to the trailing edge; shape and colouring were not usable and scarring was deemed to be not useful for long term matching. Only photo's of PQ>=4 and animals of D>=3 were used for mark-recapture analyses. It was not considered feasible to relax these criteria any further without compromising the reliability of the results.

Analysis: mark-recapture estimates

The number of recognizable individuals within the study area was calculated using a series of Chapman's modified Petersen estimates (hereafter CMP estimate) (Seber 1982), which is a generally robust abundance estimator that can be modified to control for the violation of some of its key assumptions (Hammond 1986). The CMP estimator assumes that all individuals have an equal probability of being captured in the first sample, that the second sample is random and there is complete mixing of the population between samples, that marking does not affect the catchability of the animal, that marks do not change between samples and are correctly reported upon sighting and that there are no births or deaths between samples (Seber 1982).

Three abundance estimates were calculated at different scales from the available data; firstly, a two sample estimate of the number of animals using the full study area from Cape Town to Lamberts Bay was calculated using the geographically comparable data collected in 2000 and 2001. Secondly, because home range estimates from satellite telemetry data (Chapter 5, Elwen et al. 2006) and analysis of the current data set with respect to dispersal patterns (Chapter 3) have shown that Heaviside's dolphins are faithful to ranges at a much smaller scale than our full study area; that there might be a degree of separation between animals in the northern and southern parts of our study area (roughly either side of Saldanha Bay) and that edge effects are a concern at the northern limit of the study area, a separate abundance estimate was calculated for the central section of our study area using only data collected in the St Helena Bay region. It was felt this cropping of the data set would increase the robustness of the analysis since the majority of the data (~50%) were collected in this central section over the 3 years of the study, and it is a length of coast (~155km) roughly one 'home range' to the north and south of the core area worked in 1999 and so was likely to be more geographically 'closed' than the full study area. Further, this part of our study area overlaps almost precisely with a single consolidated fisheries management unit (Areas 8-11) in which Marine and Coastal Management (South African Department of Environmental Affairs and Tourism) control the inshore subsistence fisheries, including those set net fisheries thought to present a potentially significant bycatch threat to Heaviside's dolphins. Lastly, the abundance of animals was calculated using the core area worked in 1999 using the three 2 week field trips as samples. This estimate provides an 'instantaneous' sample of the number of animals using a small stretch of coastline (~20km) and is a relevant management scale for boat based dolphin watching and small area developments such as harbour development (a potential issue at Sandy Point adjacent to the east of this region). Recapture rates within 1999 are further compared to data from satellite monitored animals in the region to investigate patterns of resighting and aid in future data collection design.

The abundance of well marked animals $\widehat{N}$ for all three scales was calculated using the Chapman's modified Petersen estimate:

Eq 1

$$\widehat{N} = \frac{(n_1 + 1)(n_2 + 1)}{m_2 + 1} - 1$$

where

n_1 = number of well-marked animals identified in the first sample

n_2 = number of well-marked animals identified in the second sample

m_2 = number of well-marked animals identified in both samples

Variance for the estimate is calculated as:

Eq 2

$$\operatorname{var}(\widehat{N}) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - m_2)(n_2 - m_2)}{(m_2 + 1)(m_2 + 2)}$$

As unmarked animals are not included in either n_1 or n_2, the estimate must apply only to the number of well-marked animals.

Analysis: meeting assumptions of mark-recapture analysis.

Violating the assumptions of mark-recapture analyses can greatly affect both the accuracy and precision of the results (Hammond 1986). The types of fin mutilations and injuries used to differentiate between individuals in cetacean studies are generally regarded as permanent (Lockyer & Morris 1990), so mark loss *per se* is not an issue, but it is possible for marks to alter to the point where a previously identified animal becomes unrecognizable (Gowans & Whitehead 2001) and it will be incorrectly assigned a new identity in the catalogue thereby falsely increasing the resulting estimate by the incorrect addition of animals to the catalogue and the consequent decrease in the number of resightings recorded (m_2 in Eq 1 and 2). As with other studies of this kind (Wilson et al. 1999; Read et al. 2003), we have used only well marked animals and good quality photographs to maximize the accuracy of identifications since any changes to marks were likely to be noticed and we feel that the relatively short period of the study (~800 days) and degree of “distinctiveness” used for photographic selection and identification makes this a relatively minor concern.

It is unlikely that the assumption of equal capture probability of all individuals is ever truly upheld by a natural population due to underlying variability at the individual level (Hammond 1986; Durban & Elston 2005). In this type of study, such individual variation may be apparent as attraction toward the boat for bowriding or an avoidance of the boat by some individuals, for instance mothers with calves. A further consideration in this study is the degree of site fidelity and the small home ranges of Heaviside's dolphins, thus for any location along the coast the animals in that region may have ranges entirely overlapping the study area or barely touching it, in which case their probabilities of being resighted are likely to differ. In 2000 and 2001 we made an effort to search the entire length of our study area to reduce the probability of missing or over-sampling animals due to their site fidelity and we have only used geographically equivalent areas for calculations at different scales. Photograph quality and individual distinctiveness also affect the catchability of individuals, a problem which is at least partially mitigated by using only high quality images and highly distinctive animals (Heinrich 2006). If the assumption of equal capture probability is violated, it will result in an underestimated population size (Hammond 1986); due to the nature of our data (broadly spread along the coast and with a low resighting rate) it was not possible to attempt to account for capture heterogeneity using modelling techniques for which a large sample size and multiple recapture occasions are required (White et al. 1982).

The CMP estimate assumes demographic (no births or deaths) and population (no emigration and immigration) closure. The scale of our overall study was considerably larger than that of the home ranges of individual animals (Chapter 3; Elwen et al. 2006). Given the apparent site fidelity of the species, any mark-recapture data collected within a set area should deal with a ‘closed’ set of animals that may use that area frequently or occasionally (affecting capture probability). We only used geographically similar areas for samples in each analysis and thus feel that an assumption of geographic closure was reasonable at all three scales at which estimates were calculated.

When demographic turnover occurs, Hammond (1986) has shown that the resulting population estimate tends to be overestimated by roughly the inverse of the survival rate. Other studies using the Chapman’s modified Petersen estimator on large whales have ignored the influence of mortality on the resulting estimates due to the small influence thereof relative to their long lives and high survival rate (Stevick et al. 2001). However, dolphins in the genus *Cephalorhynchus* are relatively short lived and due to the duration of this study and the use of years as samples, the assumption of demographic closure is unlikely to have been upheld. Unfortunately there is currently no estimate for the survival or birth rates of Heaviside's dolphins available, however since the influence of mortality is a known error in this type of analysis we feel that including a less accurate correction factor is considerably better than applying no correction at all. Lockyer et al. (1988) calculated the survival rate of the closely related Commerson's dolphin from incidentally caught animals for 4 different age classes: 0-18yr, 1-18yr, 1-5yr and 5-18yr old dolphins, of which we felt the 0.914 (0.01SD) calculated for adults only was the most appropriate, as studies such as this based on natural markings are most likely to be capturing adults. No *a priori* reason existed to expect an increasing or decreasing population, and recruitment to the marked population is likely to be equal to losses from mortality. Subsequently we have addressed the violation of demographic closure in those calculations using multi-year samples in this study by adjusting the final abundance estimates using the survival rate available from adult Commerson's following the technique of Hammond (1986).

Analysis: estimating the percentage of marked animals in the population

The proportion of the population that was distinctive enough to be used in mark-recapture estimates is referred to as θ. The accuracy of θ is of particular concern in this study because the mark-rate is low and the extrapolation from the number of marked animals to the total population size is greater than in most other delphinid studies (Wilson et al. 1999; Parra et al. 2005; Heinrich 2006). In the recent literature several studies have taken the approach of calculating θ from photographs on a per sighting or daily basis and then averaging across the season to calculate a representative mark rate (Williams et al. 1993; Wilson et al. 1999; Chilvers & Corkeron 2003; Heinrich 2006). Due to the low mark rate of Heaviside's dolphins and our large proportion of poor images we were not able to use this approach as on several days at sea, no dolphins were photographically identified. Thus, θ was calculated from all images of sufficient quality from a relevant area or period, pooled together. However, values of θ calculated only from photographs may be potentially inflated by the bias of photographers in the field toward capturing more distinctively marked animals (particularly in a poorly marked species such as this), even though every effort was made to avoid this and to photograph every member of a group regardless of observed markings. To gain some insight into possible biases in the estimate of θ, we compared the values calculated from well marked animals in good quality photographs (θ_1) to those estimated in the field by photographers, for which 2 values were recorded, the proportion of marked animals seen (θ_2) and the number thought to have been photographed (θ_3). Data for both photographers was combined for values of θ_2 and θ_3. Values were compared for each of the 2 week field trips worked in different parts of the study area, using for θ_1 at least 100 randomly selected good quality images for each trip. The recording of marked animals seen and photographed in a group was only implemented in the 2nd two years of the study.

We attempt to tease out which measure of θ is most correct by comparing the three different mark rates and how they varied with group size. We could not use the standard measure of θ, the “percentage of good quality images containing distinctively marked fins” for this analysis as it was not possible to effectively differentiate by group size. Instead we have used “percentage identified of seen” referred to as $\theta_{1'}$ (theta-one-prime), which is the percentage of distinctive animals finally identified and catalogued of the total number of animals seen in the field in that group size category. This value is thus lower than the proportion of marked animals calculated from good quality photos only as we have effectively included in the denominator all those groups seen in the field which were not well photographed, or contained no marked animals. We know that the ‘time per dolphin’ of a sighting decreases as group size increases and that smaller groups (1 or 2 animals) tend to be more evasive than larger groups making them more difficult to approach and photograph (Chapter 1). On the other hand, very large groups of animals frequently consisted of several subgroups, which might arrive at or leave the boat at slightly different times and move around and mix, making it more difficult to get full photographic coverage: thus medium sized groups are likely to be the optimal ones to photograph.

Analysis: estimating the total population size.

Since θ calculated from photographs varied both spatially and temporally, only relevant data (i.e. only photographs taken during those field trips) were used to calculate a value of θ for each abundance estimate by using the average value and error from 50 random samples of 100 good images (multiple samples of 50 images used for the smaller 1999 data set) taken from the total set of good quality images from the relevant field trips (n = 1071; 835 and 396 usable images for the full study area, central study area and 1999 area respectively). Estimates for each spatial scale were combined with an inverse CV-weighted average and scaled for the 0.914 (0.01SD) bias of mortality per year. To cross-validate the abundance estimate, we further calculated an estimate of the number of individual animals encountered in the field for the 1999 data set (in which the most recaptures occurred) by adjusting the total number of animals seen (sum of 'best' field estimates for all groups encountered) by the frequency of resighting of marked animals, on the assumption that the frequency of resighting of marked and unmarked animals will be similar. This approach was not feasible for 2000 and 2001 as very few animals were seen more than once (19% and 16% of catalogued animals respectively). Theoretically, the distribution of animals seen once, twice, thrice etc can be extrapolated to estimate the number of animals seen zero times, the 'uncaptured' animals, using for instance the Poisson distribution (Baker & Herman 1987; Dalebout et al. 2002). However, we did not feel that this method of estimating the total population size was as powerful or flexible as the mark-recapture estimates used and regard it as a useful way to ground-truth our mark-recapture estimates but not as a substitute thereof.

Total population size was then calculated by:

$$\mathrm{N}_{\mathrm{total}} = \frac{\widehat{N}}{\theta}$$

With the variance calculated by the delta method (Wilson et al. 1999):

$$Var(\widehat{N}_{total}) = \widehat{N}^{2}_{total}\left(\frac{\operatorname{var}\widehat{N}}{\widehat{N}^{2}} + \frac{1-\hat{\theta}}{n\hat{\theta}^{2}}\right)$$

where n is the total number of fins from which θ was calculated

and the CV for the total population expressed as terms of the CV's of the CMP estimate and θ:

$$CV(\widehat{N}_{tot}) = \sqrt{\left(CV\left(\widehat{N}\right)\right)^2 + \left(CV\left(\widehat{\theta}\right)\right)^2}$$

The log normal Confidence Interval (recommended by Burnham et al. 1987 to avoid an unrealistic lower confidence interval below zero) was calculated using the formula:

$$r = \exp\left(1.96\sqrt{\ln\left(1 + (CV(N_{total}))^2\right)}\right)$$

With the lower confidence interval calculated as N/r and the upper limit as N*r.

Comparison with satellite and field observations

In 2004, 5 female Heaviside's dolphins were fitted with satellite transmitters, and we use the telemetry data here as prepared in Elwen et al. (2006) to analyse the proportion of time in which these individuals were potentially available for photographic capture given the field protocol used in 1999-2001. We present the number of received locations in total for each tag, as well as those received in "daylight" (defined as 07h00-16h00 to be roughly equivalent to boat based photo-ID work), and those daylight locations in the inshore study area searched for dolphins (defined in Chapter 2 for habitat modelling purposes as from the coast to 2km from shore). The position of these locations are not independent within a day as the tags were sending locations with high frequency (every ~2hrs), therefore we have summarised the data to a daily level to represent the number of days in which the animals were located inshore and potentially available for photographic capture.

Results

Petersen estimates of the number of well marked individuals

Since this study was primarily designed to investigate dispersal of individuals, survey effort was focused in a small area in 1999 to photographically capture as many animals as possible and subsequently spread broadly, albeit thinly along the coast in both 2000 and 2001. The discovery curve of new animals identified per survey (Fig 4.2) shows that with usually only 2 weeks in each quarter of the study area in 2000 and 2001 and even with the six weeks of focused effort in 1999, we did not manage to capture all the identifiable animals in any part of the study area. One result of an ‘unsaturated’ population is that the number and identity of animals recaptured between samples is far more random and generally, as here, there is a low recapture rate (m_2 in Eq 1), which translates into a larger variance in the abundance estimates (Eq 2 and Table 4.1).

Chapman’s modified Petersen abundance estimates of the number of well marked Heaviside's dolphins off the southern west coast of South Africa are presented in Table 4.1 for the three spatial scales at which they were calculated. The estimates using inter-annual samples (Full Coast and Central Area) are not corrected at this stage for the upward bias caused by mortality between samples. The results compare favourably with the spatial scale at which the data were collected as the estimate for, and area of, the full study area is roughly double that of the central region. The ~30km long 1999 study area is smaller than the known along-shore ranges of this species (Chapter 3; Elwen et al. 2006); since the CMP estimate calculates the number of animals using the study area over the period of the study, it is thus likely that animals captured in this region were ranging over a considerably larger area. All three sampling trips in 1999 occurred within February and March and were considered to be sufficiently close together in time to not be affected by issues of mortality and mark loss. To increase the number of abundance estimates calculable from these data all combinations of the 3 field trips/sampling periods (1&2, 2&3, 1&3) were used and not only sequential trips.

The first two estimates are very similar but the third (trip 1 – trip 3) is considerably smaller, largely due to a higher number of resightings that occurred between these samples, which equated to about 45-50 days in the area. This series of resightings may be due to a cyclical movement pattern by dolphins returning to the area, or due to chance alone; it is not likely to be caused by any communal or associative movement of a specific group of individuals as inter-animal associations in this species are apparently random (Chapter 3).

Table 4.1: Chapman's modified Petersen estimates of the population size of well marked Heaviside's dolphins ($\hat{N}$) on the west coast of South Africa, presented with Standard Deviations, CV's and 95% log-normal confidence intervals for each estimate. Calculations shown for the 3 scales a) Full coast (~390km, 2 yrs) b) Central area only (~155km, 3 yrs) and c) 1999 study area (~30km, 3 2-week sampling trips) and averaged using the inverse CV-weighted mean.

Area	*Period*	n_1	n_2	m_2	$\hat{N}$	*SD* ($\hat{N}$)	*CV* ($\hat{N}$)	*95%CI*
Full coast	2000-2001	120	99	11	1007	248.9	0.25	625-1623
Central Area	1999-2000	67	34	3	594	242.95	0.41	275-1284
	2000-2001	34	53	3	472	191.36	0.41	219-1013
	Inv CV mean				532	154.35	0.29	305 - 929
1999 Area	1 – 2	26	26	3	181	69.43	0.38	88-374
	2 – 3	26	35	5	161	49.29	0.31	78-333
	1 – 3	26	35	14	64	8.25	0.13	31-132
	Inv CV mean				87	11.15	0.13	68 - 112

Investigations of theta - the mark rate of animals.

The three estimates of θ were compared for each 2 week field trip and in 7 out of 8 cases; θ was higher when measured from the photographs than from field estimates (Table 4.2), although the three values of θ were closely correlated (θ_1 - $\theta_{2:}$ $r^2 = 0.747$; θ_1- θ_3, $r^2 = 0.847$, both significant at the 5% level). There are two possible and contradictory causes for this pattern; firstly it is quite possible that despite our best efforts not to, we may have been biased toward photographing marked animals more extensively than unmarked animals or groups containing marked animals for longer periods, thereby inflating our estimate of θ from photographs. Conversely, field estimates of mark rate made by eye may have been underestimated or under reported since marks are small, on small fast moving animals which did not always come very close to the boat and were made by photographers who were generally looking at the dolphins through a camera lens.

Table 4.2. Table showing a break down of the percentage of well marked Heaviside's dolphins (θ) by area (St Helena Bay, Yzerfontein, Lamberts Bay and Cape Town) and field trip (a,b,c). The three measures of θ presented are θ_1 – the % of good quality fin images containing well marked animals (n = the number of photos from which θ_1 was calculated), θ_2 – the percent of marked animals seen and θ_3 – thought to have been photographed in the field (this was only recorded in the 2nd and 3rd years of the study).

			PHOTOGRAPHS	FIELD ESTIMATE	
			% Images	% Seen	% Photo'd
	n photos	Area	θ_1	θ_2	θ_3
1999	100	StH a	25	-	-
1999	102	StH b	14.7	-	-
1999	194	StH c	12.9	-	-
1999-ALL	396		16.41		
2000	105	CT	23.8	17.0	14.1
2000	129	YZ	18.6	16.4	11.9
2000	141	LB	16.3	14.9	11.2
2000	145	StH	11.0	9.8	8.5
2000-ALL	519		16.76	14.2	11.1
2001	115	LB	8.7	8.5	7.2
2001	131	StH	18.3	10.7	9.1
2001	163	StH	7.9	8.0	6.8
2001	108	YZ	16.67	11.5	9.8
2001	35*	CT	34.28*	14.8	13.6
2001-ALL	534		13.29	9.8	8.4

* Only one day was worked out of Cape Town harbour in 2001

In an attempt to gain further insight into factors affecting our measures of mark rate, we broke down the three measures by group size (θ_{1}·, the percent of animals seen in a particular group size class ultimately catalogued, θ_2, and $\theta_{3,}$ the two field estimates of mark rate). The highest mark rates were seen in the field in groups of 3-5 animals in 2000 and in groups of 1-2 animals in 2001. A decrease of θ with increasing group size is seen in both years (Fig. 4.3) and is likely to have been caused by a lessened ability to spot and photograph all marked animals in large groups, or the pattern may be a result of a variation in social structure with group size, such as the higher proportion of (relatively poorly marked) calves observed in larger groups (Chapter 1). However, due to the high turnover of group membership (Chapter 3) and the low percentage of calves in the data set (3.6%) it seems likely that the observed decrease is more likely to be due to an inefficiency of capture rather than a social effect. This inefficiency is also reflected in the photographic coverage of groups since θ_1` also shows a general decrease with increasing group size and the ratio between θ_2 and θ_3 seems to increase with increasing group size. Small groups of Heaviside's dolphins tended to be more evasive toward the boat in the field (Chapter 1) and are thus more difficult to approach, photograph and assess for marks. The observed relationship between the three θ values in the smallest group class differed between the two years: in 2000 a higher proportion of animals were successfully photographed than were seen in the field, while in 2001 the converse is true. Unfortunately, conclusions are limited in this size class as relatively few small groups were seen (Fig 4.3). However, it is clear that there was a degree of under-reporting of marked animals in the field and a decreased efficiency of capture as group size increased. The value of θ calculated from good quality photographs only (θ_1) is to some extent less biased in this regard as it is calculated only from images taken and is independent of capture rate. Any bias by photographers in the field towards focusing on marked animals is likely to act in the opposite direction to any inefficiency and we thus feel that θ_1 is the most representative measure available.

A further complication arises in that θ_1 varied with location (as did θ_2 and θ_3), showing a general decrease with distance northwards from Cape Town (Table 4.2, Figure 4.4) and being generally lower in 2001 than in 2000. The highest mark rate, from Cape Town in 2001, needs to be treated with caution as only one day was worked in the area in this year. This aside, the geographic pattern is consistent between years, but with only 2 samples from each location we must be cautious in interpreting these patterns. The only area for which multiple samples exist is St Helena Bay, which shows considerable variation in the measured mark rate even between trips within the same year, suggesting that any other patterns aside, there is considerable stochasticity in the measure of θ, which is at least partly attributable to the high turnover of animals being sighted. To control for these variations somewhat, θ_1 was calculated separately for each abundance estimate using only data from the relevant area and time periods. Total extrapolated population estimates for each spatial scale are presented below (Table 4.3) for both the simple and the mortality corrected estimates.

Table 4.3. Total population sizes (N_{tot}) of Heaviside's dolphins on the west coast of South Africa at three different spatial scales. N_{tot} extrapolated from Chapman's Modified Petersen estimates of the number of marked animals ($\widehat{N}$) using the proportion of well marked animals in the photographic sample (θ_1). Estimates for the Full study area and the Central Area using inter-annual samples are also shown corrected for the upward bias caused by population turnover following Hammond (1986) using the survival rate (0.914, SD0.01) of the closely related Commerson's dolphins (Locker et al 1988).

			No Mortality correction			Mortality corrected		
Area	θ_1	CV θ_1	N_{tot}	CV	95% CI	N_{tot}	CV	95% CI
Full coast 2000-2001	14.51	0.23	6942	0.24	3989 – 12 082	6345	0.26	3573 – 11 267
Central Area Inv CV mean	14.19	0.27	3751	0.29	1920 – 7326	3429	0.36	1721 - 6828
1999 Area Inv CV mean	16.62	0.37	527	0.35	272 – 1020	n/a		

In 1999, 68 animals were identified from good quality photographs, 54% (n = 37) of which were only seen once, 19% twice and three times (n = 13 each), 1% seen four times (n = 1), 4% five times (n = 3) and 1% (n = 1) six times. In the field, 1342 animals were seen, which when adjusted by the observed resighting distribution, results in approximately 964 individual dolphins being encountered in the 26 worked days in the field, which is considerably higher than the extrapolated mark-recapture estimate using the same data.

Interpretations of relevant satellite tag data.

The transmitter life on the satellite tagged females in 2004 (up to 51 days), was very similar in duration to the length of the 1999 field season (52 days, 04 February to 27 March) and occurred in the same study area (St Helena Bay), making for very comparable data, albeit with a 5 year time lag and the addendum that there is no telemetry data from male dolphins. Photo-ID studies on this species are logistically limited to near-shore waters in daylight hours, predominantly in the mornings when animals are close to shore, easily detectable and approachable. Given these limitations to data collection, the strong diurnal movement pattern observed during shore based observations of Heaviside's dolphins, where the inshore presence dropped off rapidly after midday from more than 2 dolphins per hour in the mornings to effectively zero after 4pm (Chapter 1), is particularly relevant. This observed pattern was assumed to represent a general offshore movement of all individuals associated with nocturnal feeding offshore (Chapter 1), and was confirmed by the more detailed movement data available from satellite transmitters (Chapter 5; Elwen et al. 2006). However, closer investigation of the movement patterns from the telemetry data over the 24hour cycle shows that some dolphins would occasionally spend several days at a time either in deeper water offshore, or in shallower water closer to shore (although probably beyond the limited viewing range from land): it is these periods spent in the unworkable offshore environment that are of concern for photo-id studies. The breakdown of the number of satellite locations received during daylight hours (07h00-16h00) clearly shows that the 5 tagged dolphins varied considerably in the amount of time they spent in the inshore area where photo-ID data were collected (2km from shore, Chapter 2) (Table 4.4, Fig. 4.5), that these periods tended to be temporally clumped over several days and at least one animal (Dolphin 5) spent more time in the unavailable offshore environment than inshore.

Table 4.4. The number of locations received from Heaviside's dolphins fitted with satellite transmitters while they were potentially available to be photographed using the techniques used in this study, given the logistic restrictions of the study area. Survey area is defined as within 2km from the shore and daylight hours as 07h00-16h00.

Dolphin	Total Locations	No. Daylight locations	No. Daylight locations in survey area	% Daylight locations in survey area	Days in survey area in daylight (total tag-life*)	% Days of tag-life in survey area in daylight
Dolphin 1	428	165	66	40	23 (41)	56.1
Dolphin 2	313	116	40	34.5	27 (42)	64.3
Dolphin 3	578	207	100	48.3	36 (51)	70.6
Dolphin 4	490	171	124	72.5	36 (38)	94.7
Dolphin 5	693	233	51	21.8	17 (43)	39.5

* excluding the initial 72-120hrs post tagging when dolphins behaviour was considered to be potentially affected by the capture and tagging process (Elwen et al. 2006)

Discussion

A population estimate is fundamental to any conservation project and ecologically effective management program to enable the degree of risk to a population by any anthropogenic impact to be quantified, as well as to understand the magnitude of the role of that population in the ecosystem. Prior to this study there has been no substantiated estimate of the abundance of Heaviside’s dolphin in any part of its range and although variance is high in the estimates at all three spatial scales investigated, our results clearly show that Heaviside's dolphins are reasonably abundant within the area studied and number in the order of thousands of animals.

To address the assumptions of mark-recapture estimates, it is ideal to explicitly control for them in the initial study design (e.g. Wilson et al. 1999). The data analyzed in this study were collected to investigate individual dispersal patterns from a ‘point source’ (the 1999 study area) across a large spatial scale over the 3 yrs of the project, so our surveys were focused on maximizing area coverage and not specifically on generating a population estimate and thus have some short comings. In retrospect, this study would have benefited from a longer field season or longer periods within the same areas to increase the recapture rate of animals, which would probably have gone some way toward increasing the precision of our estimates and allowed us more flexibility to investigate biases including capture heterogeneity and survival rates.

Mortality and recruitment within a population cause a known and measurable bias in the Chapman’s modified Petersen estimate, which assumes a demographically closed population, but these biases are relatively easily calculated, understood and accounted for (Hammond 1986). We thus felt it was appropriate to make some effort to account for this bias in our estimates, and in the absence of the relevant data from Heaviside's dolphins have elected to use data from the closely related Commerson’s dolphin. Unfortunately, this estimate was based on animals found beach cast and presumed to have been killed in the local gillnet fishery (Lockyer et al. 1988) and it is thus likely that this population will have a lower survival rate than a non-impacted population. Although the level of human induced mortality on Heaviside's dolphins is not currently known, it is thought to be lower than that on either Commerson’s (Lockyer et al. 1988) or Hector’s dolphins (Slooten et al. 1992) due to the low density of human habitation throughout the majority of their range, the associated low level of inshore fishing effort (Chapter 2) and the fortuitous lack of overlap in both prey size (Sekiguchi et al. 1992) and distribution (F Le Clus pers. comm.) with the commercial hake fishery which targets larger fish offshore. The use of the adult survival rate of Commerson's dolphin for correcting population estimates may therefore exaggerate the inter-year mortality of Heaviside's dolphins.

A further bias that affects almost all mark-recapture studies and one of the most difficult to avoid logistically (Wilson et al. 1999) is heterogeneity in the capture probability of individual animals which, when it occurs, will result in an underestimated population size (Hammond 1986; Whitehead & Wimmer 2005). It is likely in this type of study to arise from two main sources – animals behaving differently toward the research boat and animals using the environment differentially. In studies where animals are physically captured and handled, an aversion to capture or an attraction to the bait may occur, neither of which are likely in photographic mark-recapture which takes place more remotely. A developed attraction or aversion to the boat is possible but in most studies of this kind is regarded as unlikely (Wilson et al. 1999; Heinrich 2006) due to general habituation to boat traffic and specific attempts by researchers to minimise negative impact by cautious approaches, although a recent study by Bejder and colleagues (2006) cautions us in this regard – they showed that long term exposure to boat based ecotourism (with presumably similarly cautious approaches) caused some individuals to emigrate from the impacted area, a behaviour which would have consequences for long term mark-recapture abundance estimates if not noticed and accounted for. However, with the low resighting rate observed in this study, it seems unlikely that such acquired behaviours would have developed enough to influence the overall results. Of greater concern is variation at the individual level, as in the field dolphins were noted to vary considerably in their reaction toward the boat with some animals persistently following the boat to bowride it, despite attempts to avoid them, while others were distinctly evasive and difficult to close with for photography. Such evasive behaviour was noted to occur much more frequently in small groups and single animals (Chapter 1) suggesting that group size could play a role in capture probability, but due to the high turnover of group membership in this species (Chapter 3) this should not in reality affect capture probability if sample sizes are high enough. However, if a tendency toward evasion or attraction is a stable characteristic of individual dolphins, then not only will it introduce heterogeneity into the capture probability, thereby negatively biasing the results, but it is possible that some animals are effectively uncatchable and will not be included in the abundance estimate at all.

Although possible, accounting for capture heterogeneity at the analysis stage requires large sample sizes and multiple recapture occasions (White et al. 1982) to enable effective differentiation between emigration, temporary emigration, mortality, heterogeneity and simple probability. The most effective way to minimise heterogeneity in a data set is to maximise the capture rate so that there is little chance that any individual is undetected in the population (Cooch and White[1]). Unfortunately, due to this study's primary focus on dispersal and distribution rather than abundance, the low mark rate of Heaviside's dolphins and the large population, our sample size was not big enough to allow for an effective analytical approach to account for heterogeneity. When heterogeneity is known to occur most common abundance estimators tend to underestimate the true population size, sometimes significantly so. In Carothers' (1973) study of a 'population' of taxi-cabs in Edinburgh with known parameters he showed that in the event of capture heterogeneity, the Chapman's modified Petersen estimate could result in an underestimate of as much as 30%. Given the high likelihood of heterogeneity in the capture probabilities of Heaviside's dolphins our calculated population sizes using the Chapman's modified Petersen estimate are likely to be lower than the true population sizes for all estimates, which is at least partly supported by the estimate of the number of animals encountered in the field. In 1999, arguably our strongest data set, the number of animals encountered was estimated to be nearly twice that of the mark-recapture estimate (n = 964 and 526 respectively), although still within the 95% CI (272 - 1020). Since this frequency calculation does not extend to an estimate of the number of animals not encountered (although it theoretically includes those encountered but not well photographed)

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[1] E. Cooch and G. White (Eds) "Programme MARK: a Gentle Introduction", 5th Edition. http://www.phidot.org/software/mark/

it is also likely to underestimate the true population size, suggesting that for the 1999 data set at least, our CMP estimates may have considerably underestimated the true population of animals using the study area.

Data from satellite telemetry on this species have provided some insight into at least one source of capture heterogeneity, the differential use of the inshore environment where photo-ID data can be effectively collected, with the number of days on which the 5 female dolphins fitted with satellite transmitters in 2004 were potentially catchable varying from 39 to 95% of their transmission periods. Due to their along shore site fidelity and use of sub areas within their home ranges (Elwen et al. 2006), a similar degree of individual variation in capture probability will also likely occur in a longshore direction as for any given area along the coast, the ranges of some animals may be only partially overlapping the study area reducing the amount of time they are available to be captured. Although not an insurmountable problem, these so-called ‘edge effects’ do affect mark-recapture estimates and need to be specifically accounted for if possible by knowledge of how distance from the study edge affects capture probability (Boulanger & McLellan, 2001). All 5 animals fitted with satellite tags were caught near shore; given the differences in the time spent inshore by these animals, it is possible that some animals in the population effectively never come close enough to shore to be captured photographically, in which case their numbers would not be reflected in these population estimates.

Results of the satellite telemetry data also have implications for the choice of sampling occasions. An approach used in some mark-recapture studies of inshore delphinids is to use single days as the capture events in a modelling approach (e.g. Read et al 2003; Chilvers and Corkeron, 2003) on the assumption that each survey day is a random and representative sample of the population. This approach would not be appropriate for Heaviside's dolphins using our sampling methods as the satellite data indicate that their presence inshore (or not) tended to be clumped into periods of several days, so a sampling period of a about a week is probably the minimum length that should be used to allow for full mixing of individuals within the area.

The low mark rate (θ) of Heaviside's dolphins is one of the biggest challenges in the application of mark-recapture techniques to this species. Values of θ used to extrapolate a mark-recapture estimate to the total population size are usually considerably higher than the ~14-17% used in this study and typically at least half the population is considered "marked" (0.53-0.75 in *Stenella longirostris*, Karczmarski et al. 2005; 0.56-0.68 in *Tursiops truncatus*, Wilson et al. 1999; 0.44 *Tursiops aduncus*, Chilvers & Corkeron 2003; 0.63-.78 in *Orcaella heinsonhi* and 0.66-0.79 in *Sousa chinensis*, Parra et al. 2005). Even within the same genus, mark rates may be at least double that of Heaviside's dolphins, 0.33-0.74 in *Cephalorhynchus eutropia* (Heinrich 2006) and 0.36 in *Cephalorhynchus hectorii* (Bejder & Dawson 2001). The low mark rate in this population requires an inflation factor of roughly 7 times and its accuracy is thus of considerable importance as any biases in the estimates would be similarly inflated. Attempts to calculate independent estimates of θ using estimates made by eye in the field were not completely successful but were valuable in providing a lower bound and suggested that field estimates tended to underestimate the number of marked animals present in a group. Although arguably not perfect, estimation of mark rate from photographs was considered the most effective method available.

Values of θ showed considerable variation across the study area (from 7.9 to 25% of animals), as well as over time, at least in St Helena Bay for which multiple samples were available. Some of this variation may be due to chance, since all samples were relatively small, the population was far from saturated and the apparent reduction in mark rate from 2000-2001 is difficult to explain. Why the mark-rate in this species should be so low is not clear, although their small triangular dorsal fins may be more robust than the taller falcate fins of most dolphins reducing the number of injuries resulting in permanent markings. The relatively low fishing effort and boat traffic throughout the study area may also play a role in reducing the scarring from anthropogenic causes such as net or pollution entanglement (e.g. packing tape) or direct boat injury in comparison with many other studied populations. Reduction in mark rate with distance northward from Cape Town (by far the largest human habitation throughout the species range, not just the study area) is suggestive that anthropogenic causes do play a role in creating scarring. Although commercial and recreational traffic is probably higher around Cape Town, the distribution of inshore fisheries (particularly set-nets) thought to pose a threat of injury or death to dolphins are in fact biased away from Cape Town with the majority of inshore set nets within the study area being found in St Helena Bay (Chapter 2), an area where the mark rate is intermediate and showed great variation between sampling trips. Lastly, we did not capture the entire population of marked animals within the study area, and this may also have played a role in the high variation seen in the mark rate between field trips. It is difficult, given the information at hand to fully understand all the influences affecting the mark rate of Heaviside's dolphins but there is some evidence to suggest that there is an anthropogenic link as well as purely natural causes.

Where it is not possible to account for biases in analysis, it is at least preferable to know in which direction they are likely to occur. The data collected in this study suffered primarily from being too small and spread too thinly given the number of animals, and the subsequent shortfall in population ‘saturation’ has had the principal effect of increasing variance in the resulting estimates and magnifying the role of capture heterogeneity. Biases were due principally to (a) violation of population closure due to natural mortality and population turnover between years, (b) a possible systematic bias in photographing distinctive versus non-distinctive animals and (c) heterogeneity of capture probability. We have made some efforts to account for (a) which would tend to inflate population estimates, by applying a mortality rate estimate derived from a related species. If (b) is a real effect, it would tend to bias total population estimates downward, but although a comparison with visual field estimates is suggestive of such an effect, it seems that the visual estimates themselves may be biased downwards to some degree, leaving θ as the best available estimate of the proportion of distinctive animals. Capture heterogeneity (c) will result in a (sometimes considerable) downward bias in the population estimate (Hammond 1986; Whitehead & Wimmer 2005) and the spatially and temporally limited nature of the data collection process in this study is potentially vulnerable to such a bias. Overall, given the known biases, our population estimates are likely to err on the low side, possibly substantially, but more data are urgently needed to gain a more accurate and precise population estimate.

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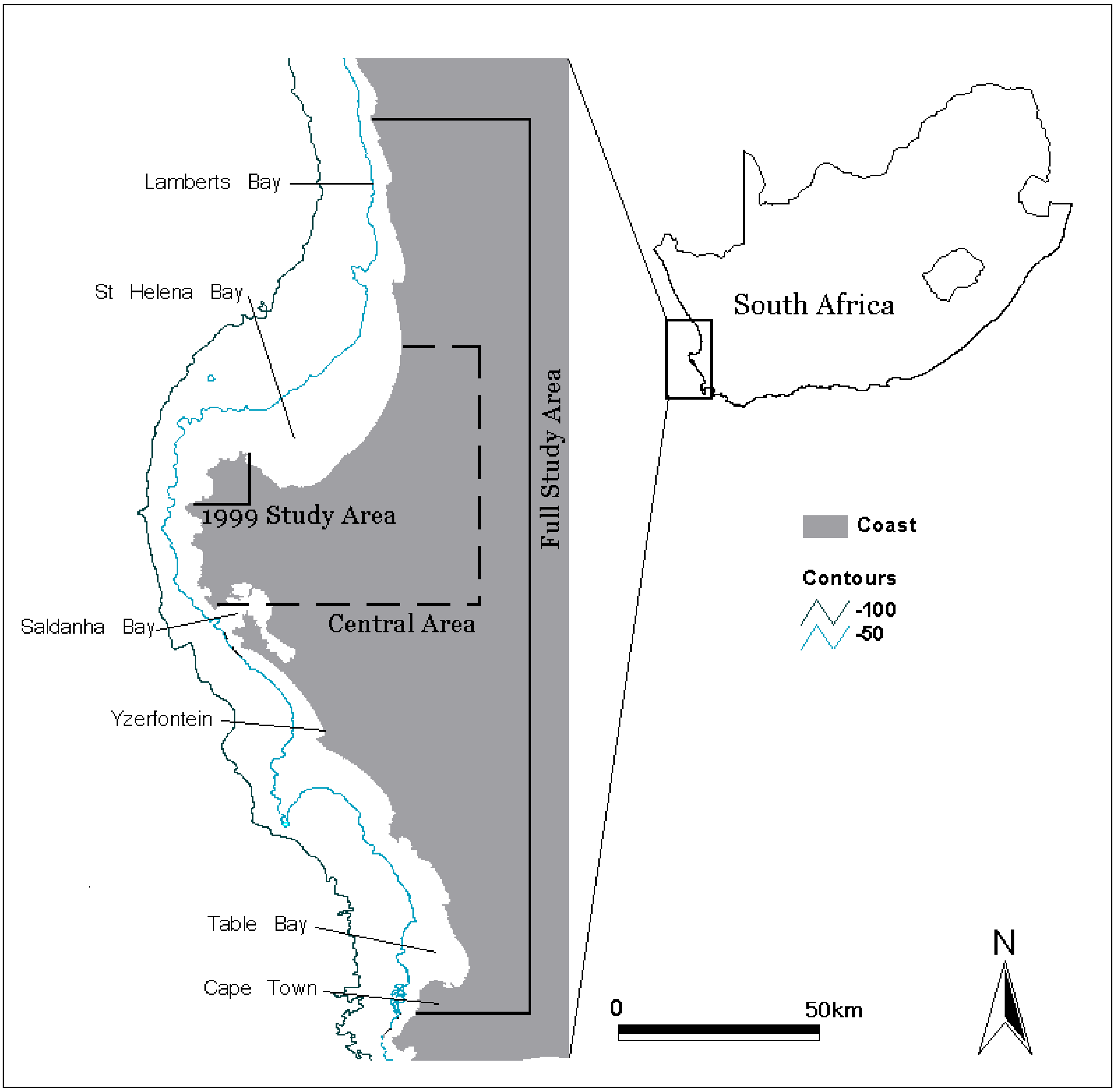


Figure 4.1. Map of study area showing three spatial scales at which abundance estimates were calculated, the full study area from 2000 to 2001, the central study area for 1999-2000-2001 and the 1999 core study area.

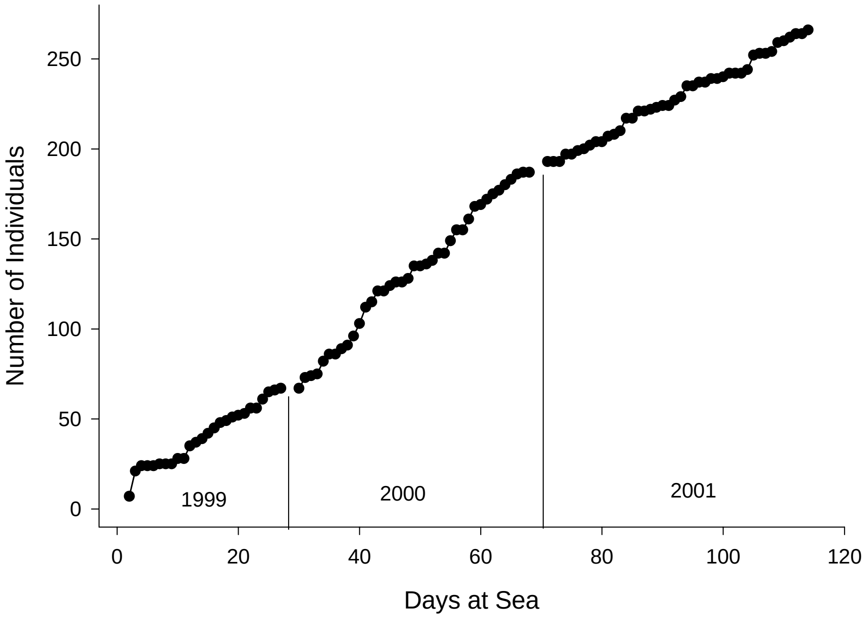


Figure 4.2. Discovery curve (number of new animals discovered per survey day) of well marked Heaviside's dolphins photographed off the west coast of South Africa in 1999, 2000 and 2001.

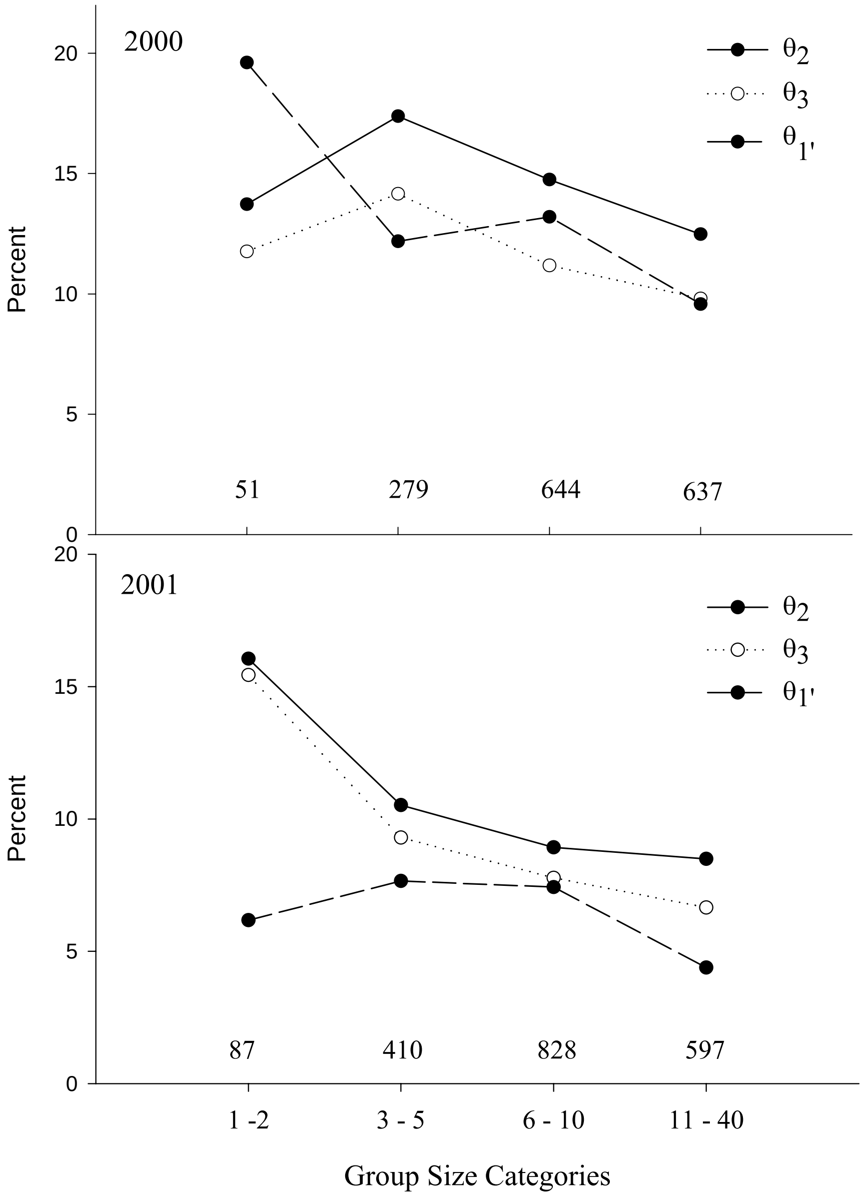


Figure 4.3. Figure showing the variation with observed group size of the three different measures of the mark rate of Heaviside's dolphins calculated for the 2000 and 2001 field seasons. The percent of marked animals seen (θ_2) and photographed (θ_3) in the field, and the percent of catalogued animals of the total number of animals in that group ($\theta_{1'}$). Values under points are the number of animals seen in that group size category.

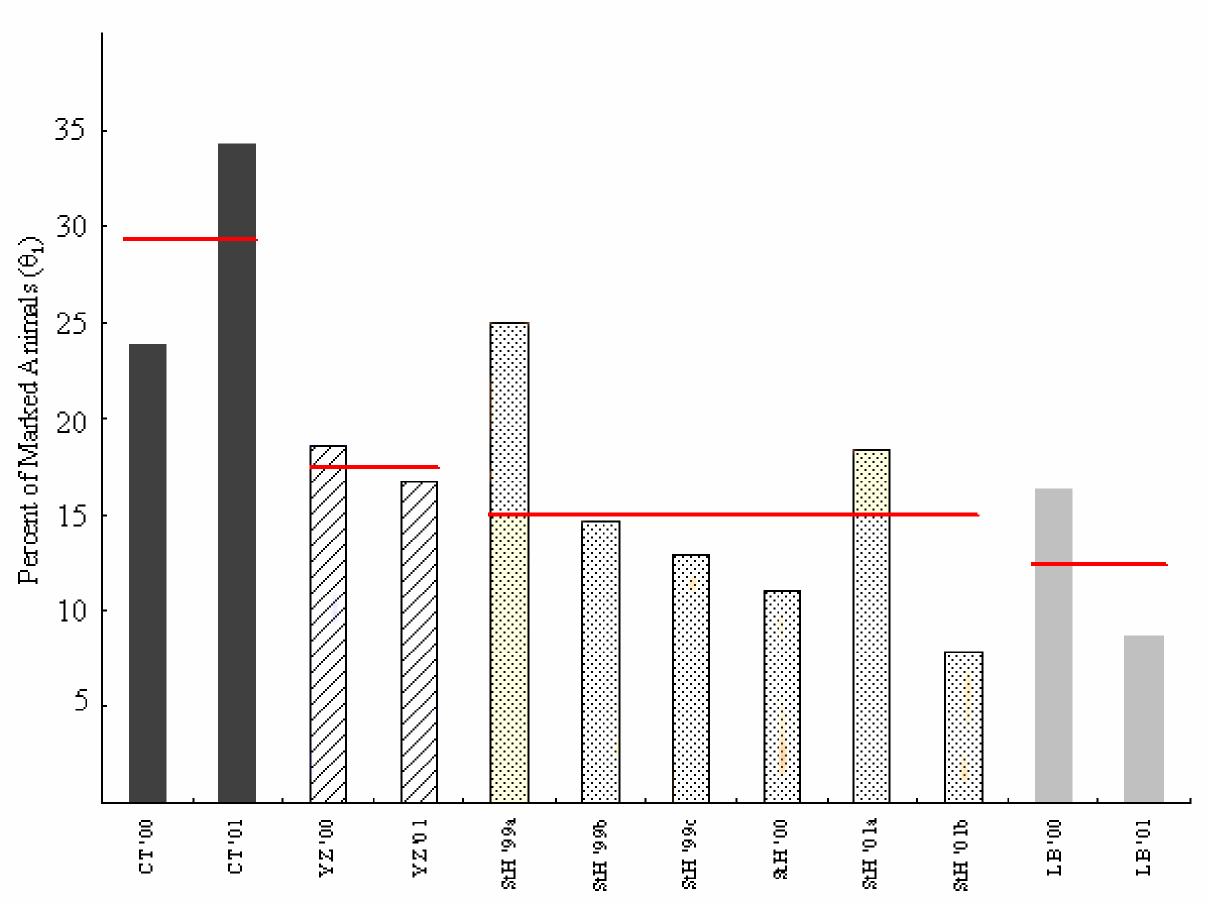


Figure 4.4. Variation in θ_1 (the percent of good quality images containing distinctive individuals) with area (CT – Cape Town, YZ – Yzerfontein, StH – St Helena Bay, LB – Lamberts Bay) and field trip (a/b/c) for all three study years ('99-'01). The 4 regions of the study area are represented geographically from south to north as left to right in the figure. Values were calculated from at least 100 photographs randomly selected from each field trip (except CT '01, where only 35 photographs were selected from the 59 good quality images available from the single day in the field there that year). Solid horizontal lines are the averages for each location.

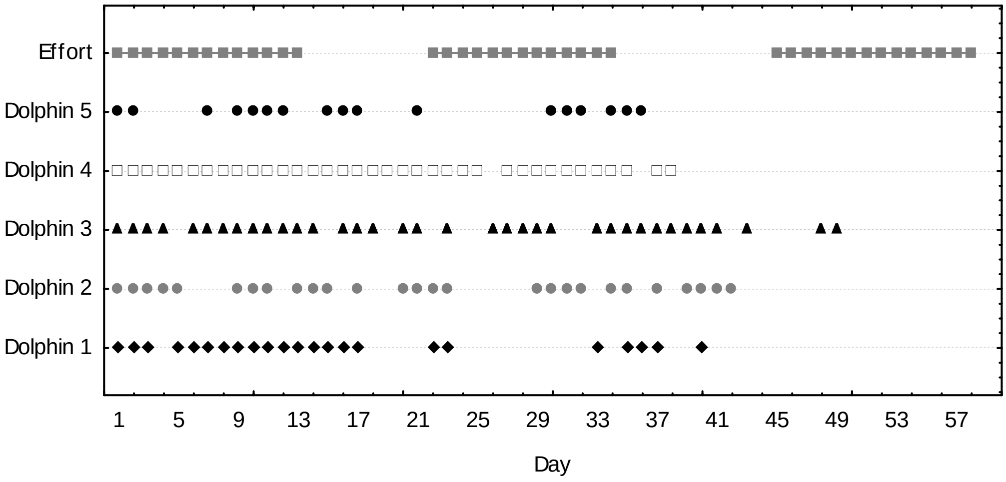
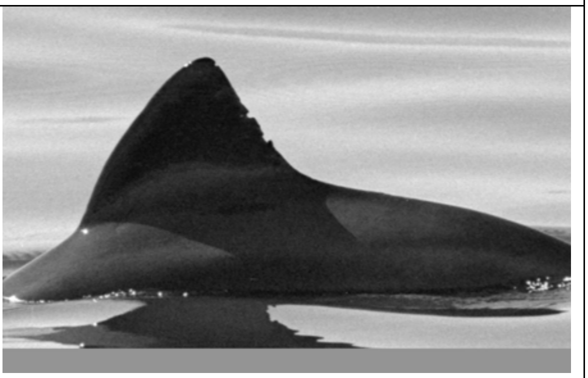
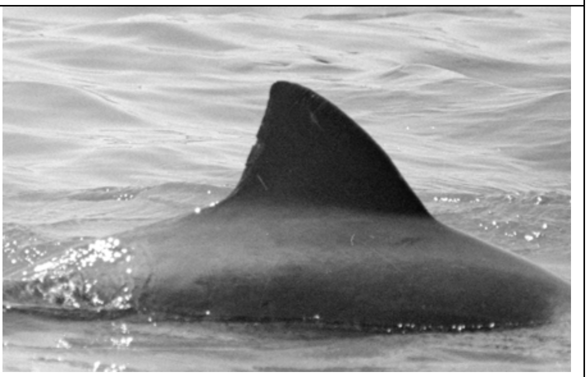


Figure 4.5. Figure showing the days from the first usable day of data transmission on which satellite tagged dolphins were inshore (<2km) during daylight hours (07h00-16h00) and theoretically available to be found and captured photographically by the methods employed in this study. The effort (top) represents the temporal pattern of boat based photo-ID data collection in 1999: three 2wk periods of field work in the same area separated by a single week, although days not worked due to bad weather conditions are not represented.

Appendix 1

Markings of Heaviside’s dolphins used in mark-recapture, showing rating for Distinctiveness as described in text.

 D5	 D4
 D4	 D3
 D3	 D3
 D3	 D3

Chapter 5

Range and movements of female Heaviside’s dolphins *Cephalorhynchus heavisidii*, as determined by satellite-linked telemetry.

Abstract

Heaviside's dolphin *Cephalorhynchus heavisidii* is a coastal delphinid with a limited inshore distribution off the west coast of southern Africa. Knowledge of its habitat usage is an essential precursor to assessing its potential vulnerability to fisheries interactions. Six Heaviside's dolphins (1 male, 5 females) were fitted with satellite-linked transmitters in 2004, and tracked for up to 54 days. The five tags fitted to female dolphins transmitted continuously, allowing for analysis of movements at a fine temporal scale. Four dolphins showed an initial avoidance of the capture site by moving over a wider area in the first 2-5 days post-tagging than later in the deployment period. All dolphins had used their full home ranges (determined as 100% minimum convex polygons) 5 – 20 days prior to tag failure, suggesting measured home ranges were stable at this temporal scale. Home range estimates using local convex hulls, ranged from 301.9 to 1027.6 km^2 (90% isopleths) and 875.9 to 1989.6 km^2 using the 100% isopleths and scaled positively with body size but varied in shape, usage and number of core use areas. Although the distance from shore and depth at which individual dolphins moved varied greatly, all dolphins showed a strong onshore-offshore diurnal movement pattern, generally being closest inshore between 06h00 and noon, and furthest offshore between 15h00 and 05h00. This pattern is assumed to be related to the movements of their principal prey, juvenile shallow-water hake (*Merluccius capensis*), which migrate into the upper water column at night. Movements inshore may be associated with rest, socializing and predator avoidance.

Introduction

Published information on the distribution of Heaviside's dolphins (*Cephalorhynchus heavisidii*) is limited but suggests that individuals have a restricted range and are likely to be resident year round within a certain area (Best and Abernethy 1994; Rice and Saayman 1984). The closely related Hector's dolphin (*C. hectori*) has been shown to have a high degree of site-fidelity over more than a 10 year study period (Bräger et al. 2002), and mitochondrial DNA studies show a high genetic diversity over a relatively small geographic range suggesting a low dispersal rate at least for female Hector's dolphins (Pichler et al. 1998). A slightly shorter term study at Isla Chiloé, Chile found Chilean dolphins (*C. eutropia*) also exhibit a high degree of site-fidelity between years (Heinrich 2006); thus it seems likely from phylogenetic evidence that Heaviside's dolphins will have relatively small ranges and show high site fidelity over long periods.

Considering the known and potentially devastating effect of bycatch on *Cephalorhynchus* dolphins in general (e.g. Dawson et al. 2001; Slooten and Lad 1991; Lockyer et al. 1988) and the known, although not yet quantifiable, risk to Heaviside's dolphins from mid-water trawls, purse seines and particularly beach seines and set-nets (Best and Abernethy 1994), it is prudent that we gain a better understanding of the range and site-fidelity of these animals if the impact of such mortalities is to be evaluated. This paper describes the results of a satellite telemetry study, designed to obtain detailed records of the diurnal movements and range of Heaviside's dolphins over a period of 6-8 weeks.

Methods

Capture and Transmitter details

Six Heaviside's dolphins were captured in two trips off the west coast of South Africa in August and November 2004 (Table 5.1, Fig. 5.1) five were female and one a male. Dolphins were captured from a 6m semi-rigid inflatable boat using either a tethered head net or tail grab (dolphin 4 was caught with a head net from the 42m research vessel RV Sardinops and retrieved immediately by the small boat), a diver was put in the water to hold the animal’s head clear of the surface and to guide it into a stretcher; on most occasions animals were transferred to a larger vessel (RV Sardinops) for tag attachment. We used 2 types of satellite linked radio transmitters, Telonics (Argos linked transmitter, model ST-18, Telonics, Inc., Mesa, Arizona) and HABIT (Argos linked transmitter, HABIT Research, Victoria, BC, Canada). Transmitters were attached to the dorsal fin of dolphins through holes drilled in the fin with a modified electric drill, using 3 Delrin (a type of hard wearing plastic) pins for the Telonics transmitters or 2 nylon coated stainless steel pins for the HABIT transmitters, with corrodible nuts to allow the tag to fall off the animal after the appropriate period. Contact time (capture to release) varied from 23 to 29 min and dolphins were on deck from 17 to 25 min (Table 5.1). Time on deck consisted of letting the dolphins become settled, examination by the attendant veterinarian or veterinary-nurse, application of anaesthetic to the drill site, sexing and measurement of as many standard measures as could be achieved with minimal disturbance to the animal, tag insertion and bolting, final check and release. The HABIT tags were set to transmit for 8 hours followed by 12 hours off to save battery life and were expected to last up to 12 months. The Telonics tags were set to transmit continuously with an expected battery life of up to 3 months, but they varied in age so transmission duration was an unknown factor.

This work was conducted under a permit issued to PBB in terms of the Marine Living Resources Act (Act 18 of 1998) of South Africa; approved by the Ethics committee of the

University of Pretoria (AUCC 040405-010b Conservation of Heaviside’s dolphin) and followed the relevant ASM animal care and use guidelines.

Table 5.1 Transmitter type, capture information and biological details for Heaviside’s dolphins caught off the coast of west South Africa for fitting with satellite linked transmitters in 2004. All dolphins were fitted with Telonics ST18 transmitters except dolphin 6 with a HABIT transmitter.

Dolphin number	Transmitter number	Date of Capture	Contact time (mins)		Sex	Body length (cm)	Method of capture
			Total	On Deck			
6	10015	12 Aug 2004	29	24	Male	148	Head net
1	17229	18 Aug 2004	23	17	Female	159	Tail grab
2	14066	20 Nov 2004	27	25	Female	165	Tail grab
3	24274	20 Nov 2004	28	25	Female	163	Tail grab
4	16204	21 Nov 2004	26	22	Female	149	Head Net
5	24276	21 Nov 2004	25	22	Female	143	Tail grab

Telemetry Data, Location Filtering

The location of the transmitters was determined by triangulation of their signals from polar orbiting satellites operated by Service Argos (Ramonville, Saint-Agne cedex, France). Diagnostic software files received from Service Argos were imported to Arcview 3.3 for manipulation and analyzed using the Argos Tools® extension. Diagnostic files included a location, with an associated time-date stamp and a quality index for the accuracy of the location; standard locations (location class LC 3, 2, 1, 0) have a theoretical precision while auxiliary locations (location class A and B) do not. However some studies have shown that there can be significant error in all location classes (Le Boeuf et al. 2000, Vincent et al. 2002) and we thus chose to use all location classes and filter them using the measured swimming speed between received locations using the Argos Tools® 3 point running average speed filter to remove locations that resulted in implausible ground speeds (the middle location of the 3 is removed if the average speed of both legs exceeds the filter threshold). Since no prior, independent measure of swimming speeds existed for Heaviside's dolphin, we used only the highest quality points (classified as quality 1-3 by Service Argos) of several dolphins to calculate the travel speed, of which the 95th percentile was about 2.5m/s (9 km/h) for all dolphins with speeds above this tending toward the ridiculous (>20km/h), and thus 2.5m/s was used as the maximum plausible speed for the filtering process.

The data for the 5 females was filtered down to 35–76% of the original number of locations in the pre-filtered data file (Table 5.2), which compares favourably with other studies using satellite linked transmitters in the marine environment (Austin et al. 2003). The data for the male dolphin was not filtered because only 55 locations were received over 11 days, the vast majority of which were in realistic locations (i.e. only 3 were over land, 1 of those by a mere 350m, another of which was the first position received possibly while the tag battery was still de-ionising); thus some interpretations from these data can still be made. Note also that the 5 Telonics tags had been stored for some time prior to deployment and the older tags (chiefly on animals 2 and 4) under-performed in comparison to the newer tags with regards to accuracy of locations (number of points over land post filtering) and percentage of standard locations received (Table 5.2).

Table 5.2. Table shows information on the collection and filtering of location data from satellite linked transmitters on Heaviside's dolphins off the west coast of South Africa, including transmitter life span, number of data points collected (raw data), number of points used after data were filtered, and number of points erroneously appearing to be on land.

Dolphin number	Transmission of location data		Number of data points			Raw data in LC 1-3	Points appearing to be on land	
	Duration (Days)	Duty Cycle (h)	Total (Raw)	After filtering			No.	%
				Number Used	% rejected			
6	11	8 on, 12 off	55	n.a	n.a	26	3	6
1	44	24	923	470	48	17	16	3
2	45	24	950	338	65	10	29	9
3	54	24	958	620	35	33	61	9
4	55	24	858	536	38	37	89	16
5	49	24	1013	768	24	61	16	2

Tag Effects

Only one animal (6) was resighted post tagging, thus limiting our investigation into the influence that the tag may have on the animal or its behaviour to interpretation of the tag location data itself. The 24-hour constant transmission of the Telonics tags allowed for analysis of movements at a fairly fine temporal scale. Therefore, we compared the movements, swimming speed and distance from shore for the first 72hrs post tagging (in 24 hour periods), using t-tests (or Mann-Whitney tests where normality could not be achieved by transformation), to the remainder of the data set. This period was chosen based on observations from the data and the literature (Geertsen et al. 2004); we refer to this as the ‘impact period’ for the remainder of this paper. Anomalous movement behaviours that might be expected are a) fast directed movement away from tagging site (in either distance covered or distance offshore) (Geertsen et al. 2004), b) very slow or little movement as the animal habituates to the feel of the tag (Geertsen et al. 2004), or c) a movement inshore, or rather a lack of movement offshore, if the animal feels vulnerable, since some small cetaceans are thought to move inshore to shelter from predators (Würsig and Würsig, 1979).

Movements

Heaviside’s dolphins have been observed by us (SE, PBB, MT) to be close inshore in the mornings but move away, presumably offshore, from noon onwards. Thus, we expected the dolphins to be closest to shore in the daylight hours of the morning and furthest from shore and in deepest waters at night with transitory periods between. We hypothesize that speed of movement would be lowest during the presumed resting and socializing period inshore and during feeding offshore when animals might be expected to feed in a fairly localized region for a night, with travel speeds being greatest during the movements between resting-socializing and feeding grounds. To analyze this pattern more closely we looked at the variation of mean depth (limited to the area between 0m at the coast and 100m isobath for which we had good bathymetry data; some points falling outside this area were lost to analysis) and distance from shore, as well as mean speed between successive locations for each hour of the day. Due to the observed impact on behaviour post tagging, we did not include the first 72 hours of data post tagging (120 hours for dolphin number 5). Longer-term movements and distribution patterns are also discussed where relevant.

Home range

The calculation of a home range for individual animals is challenging as there is no single correct or best way to describe an animal’s area usage nor can we ever hope to track every movement an organism might make throughout its life, and indeed for most questions we need to ask, this would not be necessary. However, it is important to scale the temporal and spatial aspects of data collection to the appropriate scale for the question being asked, and conversely to limit interpretations of the data to the relevant scale both temporally and spatially. Due to the tag programming parameters, data in the current study has a high temporal density, allowing for analysis of movements within a day, but none of the tags transmitted for more than 2 months, thus limiting conclusions beyond this period.

Several methods exist of describing an animal's home range; we have chosen the local convex hull (LoCoH) home range (Getz and Wilmers 2004), which seems to be more powerful than kernels at estimating home range size and area, especially in environments with corners or holes in the distribution (e.g. in fenced reserves or around lakes or islands). The local convex hull method generates density contours (isopleths) around all known locations to give a realistic idea of an animal's home range and area usage therein. We have also used the minimum convex polygon (MCP) method, in which the smallest possible convex polygon is drawn around the known locations, for some analyses. Minimum convex polygons are extremely sensitive to outliers in distribution, but this artefact can be used to some extent as a tool to highlight changes in movement or ranging behaviour.

A particular characteristic of this data set is that the proximity of the dolphins to shore much of the time makes errors in the received locations very obvious. It could be argued that since the locations over land are obviously incorrect, by deleting them we could only increase the accuracy of the dataset as a whole and indeed, the maps would certainly look "less incorrect". However, the location accuracy errors occur in all directions not just onshore and vary between tags and dolphins (due to differences in construction and behaviour respectively); deleting only the onshore locations is an effectively arbitrary procedure and non-repeatable across animals or tags and provides the reader with the tacit assumption that all locations at sea are 100% correct (when this is obviously not the case). Moreover, it would limit the comparability of our data with other studies where perhaps the study animal occurs further from shore and such an arbitrary filtering procedure cannot be performed. To aid in any future comparisons with data from other species that may not be constrained by a coastline, we felt it constructive to effectively ignore the coastline and the obviously incorrect points for some of the analyses. Although the minimum convex polygon method is particularly sensitive to outliers such as those on land, the local convex hull method gives much better results, particularly the 90% isopleth (which we regard as being probably the most realistic home range estimator to use). This is highlighted clearly by comparing the performance of the two methods for animal 1 whose range extended around a headland, the local convex hull method did a reasonable job at getting around the corner (Fig. 5.3), while the minimum convex polygon cut the corner across the headland (Fig 5.2).

To determine if the home ranges measured during this study were representative of the “maximum” long-term home ranges of the animals, we plotted growth of the home range in 5 day increments on the assumption that if the home range was still growing at the end of the tag’s transmission life, then the dolphin had not yet covered its entire range. We chose to use the 100% minimum convex polygon home range rather than the LoCoH home range since the MCP method is more likely to overestimate the actual range by including both ARGOS inaccuracies and long range movements, thus making the calculation of time to full usage more conservative.

Along-shore Range

Human impact on Heaviside's dolphins is highest near to shore where there is some risk of being caught in an inshore set net fishery for St Joseph’s sharks (*Callorhinchus capensis*) (Best & Abernethy 1994). Understanding the range of dolphins along the shore and the way this relates to their full home range will be informative in assessing risk to the population from localized by-catch; it will have the added benefit of enabling us to compare our results here with data generated from inshore photo identification mark-recapture studies of both this and other species where effort is limited to the near shore. We calculated the ‘along-shore distance' between the furthest points of the 90% and 100% LoCoH's for each dolphin, using a smoothed line 500m from shore for the 'distance traveled'.

Results

Tag effects. behaviour in the first 3 days post release

Our investigation into the reaction of dolphins to capture and tagging was limited to interpretation of the positions received from the transmitters via the Argos system, with all the errors associated therewith. We interpreted large movements away from the tagging site, especially those outside the area occupied during the remainder of the tagging period as 'capture site avoidance', and although much more difficult to interpret, extended periods of little movement may indicate a period when dolphins are adjusting to the feeling of having the tag attached (Geertsen et al. 2004; Irvine et al. 1982). We present the movements during the first 72 hours after tagging (120hrs for dolphin 5) as lines in Figure 5.2 overlain on the 95% and 100% minimum convex polygons calculated for every other location after this period. Because minimum convex polygons include all points within their boundaries they generally overestimate home range, making any movements outside this area even more striking. It is clear from Figure 5.2 that dolphins 4, 5 and 1 all moved outside of the area covered by the minimum convex polygon. Further, it is constructive to compare these movements with the calculated LoCoH home ranges of Figure 5.3 to highlight the distance dolphins moved outside of their main usage areas.

Dolphin 2 showed no movements that we interpreted as either capture site avoidance or an adjustment period. It showed no significant variation in speed during the impact period; however during the 1st and 3rd 24 hours periods, this dolphin was significantly closer to shore than on average (Table 5.3), although this is not clear from visual analysis of the data. It must be born in mind that this tag produced the worst locations in terms of location class and number of points on shore.

After release, dolphin 1 moved offshore, then to a small area approximately 12x6km in the far east of its range where it remained for the period 9-46hours post tagging, indicating a possible adjustment period. During the impact period, the dolphin showed no significant differences in speed or distance from shore than during the remainder of the transmission time (Tables 5.3 and 5.4). This animal was tagged in Britannia Bay and regularly frequented that bay during the remainder of the tag-life, suggesting that the inferred avoidance was temporary.

During the impact period dolphin 3 did not leave the greater home range area (MCP) covered by it during the remainder of the tagging period, but it did move to the far south-west of its range, to a lesser used area where it spent considerable time (39-72 hrs post release) moving around significantly further offshore than normal (Table 5.3). Although, no significant variations in speed were observed (Table 5.4), the movement to the southern subregion seems to indicate some degree of capture site avoidance.

The distribution of dolphin 4 was generally much closer to shore than that of the other dolphins. The animal was significantly further from shore than normal during the first 24hours post release, spent a 10 hour (21-31 hours post release) possible adjustment period very close to shore in a small localized area (approximately 4km along shore) to the south of the minimum convex polygon region and then moved even further offshore (significantly so, Table 5.3) and southwards into the central offshore area of St Helena Bay. The dolphin moved significantly faster than normal in the 48-72hour post release period (Table 5.4), when it moved rapidly from the southern offshore region to the far north of its range before returning southwards toward the centre of its utilized range. The animal’s movements well outside even the MCP area, suggest a reasonably strong avoidance of the capture site.

Dolphin 5 showed the strongest reaction to the tagging procedure in that it was the only animal that showed possible range shift as a response and took more than 72 hours to settle down. After being released the animal moved offshore and southwards into the central reaches of St Helena Bay, during which it covered nearly 25km in 8 hours, and moved significantly faster (but not further from or closer to shore) than average (Tables 5.3 and 5.4). Although after 72 hours the dolphin had returned to within about 10km of its capture location it continued moving northwards ending in Elands Bay, the northern most point reached by this dolphin and well outside the main range. Only on the 5th day after capture did the dolphin move southwards, ending in the centre of the area used during the remainder of the monitoring period. Due to the large area covered and fast swimming speeds recorded from this animal over the first 5 days, we felt that it was appropriate to remove the first 120 hours of data post tagging for home range analysis.

Dolphin 6 only transmitted data for 11 days, which is unfortunate as it was the only male caught and tagged in this project. The reason for transmitter failure is unknown but possibly caused by the aerial breaking as this was thought to be a potential weak spot in the transmitter design. The first transmissions were only received on the night following the morning of capture (this tag transmitted for 8 hours and was inactive for 12 hours) and indicate the animal was 16km offshore due north of the tagging position. The dolphin lingered offshore in this region for 5 days after tagging. Few locations were received from this animal per day but during the last few days of the transmission the animal started a slow directed southward movement, passing Shelley Point, North West Bay and the last locations were received from offshore of Saldanha Bay.

Table 5.3. Comparisons of distances offshore (m) during the first 72 h after being fitted with satellite transmitters to the mean distance offshore for the remainder of the transmission period for each Heaviside’s dolphin (distance values are back transformed for analyses requiring transformed data). Values that differ significantly from the remainder of data are in italics and are marked with asterisks (* $P< 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Dolphin number	Remainder of transmission time		1-24 hours		24-48 hours		48-72 hours	
	N	mean	n	mean	n	mean	n	mean
1	428	11282.8	13	9854.9 ns	13	8528.4 ns	16	*5286.4* *
2	313	8897.1	5	*4065.9* *	9	4860.9 ns	11	*6870.7* **
3	578	8162.8	14	5893.8 ns	15	9751.9 ns	13	*13567.7***
4	490	3433.5	17	*6594.2* **	13	*8180.9* ***	17	3548.3 ns
5	693	7567.8	14	9519.8 ns	15	7173.9 ns	15	7333.2 ns

Table 5.4. Comparisons of speeds (m/s) during the first 72 h after being fitted with satellite transmitters to the mean speed for the remainder of the transmission period for each Heaviside’s dolphin (values for speeds are back transformed for analyses requiring transformed data). Values that differ significantly from the remainder of data are in italics and are marked with asterisks (*** $P < 0.001$).

Dolphin number	Remainder of transmission time		1-24 hours		24-48 hours		48-72 hours	
	n	mean	n	mean	n	mean	n	mean
1	428	0.959	12	0.927 ns	13	0.814 ns	16	1.07 ns
2	313	1.299	4	1.005 ns	11	0.984 ns	7	1.337 ns
3	578	0.942	13	0.932 ns	15	1.079 ns	13	0.981 ns
4	490	0.821	16	1.057 ns	13	0.934 ns	17	*1.479****
5	693	0.736	13	*1.075* ***	15	0.732 ns	15	0.890 ns

Diurnal Movements

All five animals on a continuous transmission cycle showed a clear inshore-offshore movement pattern, being significantly closer to shore and in significantly shallower water in the morning hours (primarily 5am to 1pm) and moving offshore usually just after noon and remaining in deeper waters until around 3am (Table 5.5 and Fig. 5.4). Clarity of these results is slightly reduced due to the dolphins being in a large bay, since movement away from one shore may bring them closer to another. The hypothesized reduction in travel speed during feeding and resting periods was not as clear as the onshore-offshore movement; only 3 of the 5 animals showed significant variation in speed over the day (Table 5.5) and post hoc tests (Tukey HSD) were not particularly informative. All dolphins exhibited two periods of reduced speed at similar times (see means in graphs), first between midnight and 0500 h then again from the late morning (1000 h or 1100 h) into the afternoon (between 1400 h and 1700 h; Fig. 5.4).

Table 5.5. Kruskal-Wallis ANOVA results for the diurnal variation (by hour of the day) in the distance from shore, depth, and speed of travel of Heaviside’s dolphin carrying satellite-linked transmitters. Data from the first 72 hours after tagging (or first 120 hours for dolphin number 5) omitted from analysis, degrees of freedom is 23 for all analyses. Italics indicate analyses in which there was significant variation in values across the 24 hour daily cycle.

Dolphin number	Shore distance		Depth		Speed	
	H	p	H	p	H	p
1	67.0	*<0.0001*	68.41	*<0.0001*	31.55	0.109
2	72.55	*<0.0001*	72.50	*<0.0001*	49.25	*0.0012*
3	207.55	*<0.0001*	263.92	*<0.0001*	35.06	0.0514
4	112.02	*<0.0001*	116.7	*<0.0001*	40.06	*0.0152*
5	52.85	*0.0004*	96.25	*<0.0001*	65.28	*<0.0001*

Home range and Along-shore range

Along shore range was not easy to measure in this study as 3 of the 5 dolphins (1, 3, 5) had ranges that extended out into St Helena Bay that did not readily yield to the measure; these animals had generally longer along-shore ranges than the two dolphins on the straight coastline (Table 5.6).

The growth of home ranges (measured as 100% MCP) in 5-day increments (Fig 5.5) showed some degree of tapering off before the end of transmissions, with dolphins 5 and 4 having the most stable ranges and dolphin 2 the least stable. The low density of locations beyond the 90% LoCoH isopleth is largely due to location inaccuracies (especially those on land) and the occasional foray by dolphins beyond their main areas of occupancy (see details of dolphin 1 in ‘movements’ section below). The observed degree of stability in the measured home ranges indicates that they are probably representative over this time scale, at least for females of the species.

Table 5.6. Along-shore distances (km) of the 90% and 100% local convex hull (LoCoH) home ranges of Heaviside’s dolphins studied off the west coast of South Africa.

Dolphin number	90% LoCoH	100% LoCoH
1	43.7	83.1
2	37.3	46.8
3	43.4	62.5
4	33.3	38.8
5	25.4	68.0
Mean ± *SD*	36.6 ± 7.6	59.8 ± 17.5

Local Convex Hulls

The local convex hull method (Getz and Wilmers 2004) is analogous to calculating and combining many small minimum convex polygons for sequential (overlapping) subsets of locations, where the number of locations (k) in each subset is chosen to minimize holes or gaps in the resulting home range that can not be justified by known geography (such as those that would occur for lakes, islands or headlands). The local convex hull home range effectively covers the minimum area needed to encompass all the location points (and thus fits inside the MCP borders, Fig. 5.5), and indicates density isopleths within the area used (Table 5.7 and Fig. 5.3).

We feel the 90% isopleth (i.e. covering 90% of the locations) best represents the main area used by each dolphin and is the most realistic measure of area usage for comparison between individuals, since none of the 90% isopleths cover much land and are more independent of outliers from both actual movements and Argos locations. The 100% isopleth area, which takes into account all the remaining locations, is indicative of the region that may be covered by each dolphin on occasional forays. The borders of both the polygon methods used (minimum convex polygon and local convex hull) end abruptly at the outermost location point, thus defining them as the furthest point a dolphin will ever move. With the apparent absence of any territorial conflict and an effectively borderless environment, we feel that the abrupt borders delineated by the methods used are not entirely representative. The area extending beyond the 90% isopleth out to the 100% isopleth border (and probably the 100% MCP border and possibly a little way beyond) should instead be regarded as an area in which the probability of occupation by the animal is gradually reduced, but not zero. In general, we are satisfied with the local convex hull method to describe home range usage by Heaviside’s dolphins. Its only real drawback being that there is no temporal component in the description of HR and this needs to be analyzed separately and is done below in the ‘movements’ section. We conclude that the home ranges used by these five animals ranged from 301.9 to 1027.6 km^2 (90% LoCoH isopleths) and 875.9 to 1989.6 km^2 using the 100% LoCoH isopleths.

Table 5.7. Size of the area covered (km^2) by the each of the 10, 20, 50, 90 and 100% isopleths (indicating decreasing density and increasing coverage of received, filtered locations) of the local convex hull home ranges of Heaviside's dolphins fitted with satellite linked transmitters off the west coast of South Africa, as well as the value of k (number of nearest neighbour locations) used to calculate local convex hull home ranges.

Dolphin Number	K	Area covered by Isopleths (km^2)				
		10%	20%	50%	90%	100%
1	15	8.53	22.96	149.31	728.41	1723.15
2	13	11.82	32.14	148.08	653.52	1299.73
3	14	18.58	45.43	239.49	1027.62	1989.61
4	15	5.83	16.69	72.49	301.97	973.82
5	15	5.02	14.35	61.65	301.97	875.96

Home range and body size

Not all dolphins could be weighed but their body mass in kg was estimated from their total body length in meters (Weight = 17.59 × Length$^{2.66}$; Best and Abernethy 1994) and correlated against the home range size (km^2) of each animal (Fig. 5.6). The measured home ranges generally increased with body size as predicted (Fig. 6.6) but are 11-20 time larger than those predicted for a terrestrial carnivore of the same mass ($\text{Area}_{ha} = 170\text{Mass}^{1.03}$; Lindstedt et al. 1986). The exact relationship varied with the measure of home range used: 100% MCP = $20.297M^{2.2167}$; 95% MCP = $26.127M^{2.0435}$; 100% LoCoH = $94.619M^{1.7884}$; 90% LoCoH = $0.5428M^{2.8495}$.

Longer term movements and distribution patterns

No measure of home range currently takes into account the temporal aspect of an animal's area usage. We have given some idea of the movements of individual dolphins on a daily time scale, but longer term movement in the order of several days are not conducive to any form of statistical analysis and we are therefore reduced to describing any interesting anomalies from the raw data itself and contrasting the behaviours of individuals. The instrument on animal 2 had the oldest battery and consequently was the least precise and least informative of the animals, while dolphin 6 (11 days transmission, 12-22 Aug 2004) was discussed in the Impacts section of the paper. Here we briefly discuss the movements of dolphins 3 and 4 and then contrast the movements of 1 and 5 in slightly more detail to better highlight some individual differences that may impact on any future surveys or population estimates.

The area used most by dolphin 3 was near shore south of Elands Bay; it also had a slightly higher usage area in the south of its range with a ‘corridor’ between (Fig. 5.3). It used both areas throughout the tagging period and exhibited the general onshore-offshore diurnal movement fairly predictably.

Dolphin 4 had the most near shore distribution of all the tagged dolphins, hardly ever even crossing the 50m depth contour (Fig. 5.3). Although it did exhibit the onshore-offshore diurnal movement, this was not as pronounced as in the other animals (see diurnal movements section). This animal had two high usage areas, in the north and centre of the LoCoH range. Other than tending toward the northern part of its range during the early part of the tagging period and toward the south in the second part, the dolphin used its whole range throughout the tagging period.

The local convex hull range of dolphin 1 shows two areas of higher use, an area very close to shore in and around Britannia Bay (area A) and an offshore area roughly 22km north-north west of the inshore area (area B) (Fig. 5.3). For the first 5 days of the data set, the dolphin moved between this inshore ‘resting area’ and the offshore ‘feeding area’ on the diurnal cycle shown previously. It then moved south along the coast and spent 4 days (26-30 August) in the western most section of its home range (showing normal onshore-offshore diurnal movements) in the region due west of area A. The dolphin then moved back to the Britannia

Bay area where it then spent 5 days very close (<5km) to shore, not moving offshore at all. It resumed the ‘normal’ onshore-offshore movement between areas A and B for 9 days, after which it made a one day (12 September) foray around the coast to the most southerly point it reached, near Saldanha Bay. The dolphin then moved north to Area B and spent 11 days in a scattered region centred on area B staying at least 5km offshore all this time. During the last 8 days of transmission it returned to the diurnal movement between areas A and B.

Dolphin 5, despite a high degree of range overlap, shows quite different movements to animal 1. Where the main centre of distribution of animal 1 was actually within Britannia Bay, the centre of animal 5’s distribution was roughly 5 km offshore off the bay (Fig. 5.3) and in general this animal had far fewer received locations close to shore, and did not generally range as far offshore as dolphin 1. It must be noted that while dolphin 1 was captured within the area regarded as the post-impact home range, dolphin 5 was captured well outside its post-impact range (~10km from LoCoH border and ~40km from the highest density LoCoH region), and it was the only animal that was felt to be impacted for more than 72 hours by the tagging procedure. When in the main area of distribution, area A, this animal stayed within about 12km of the coast all the time, although it still had a clear onshore offshore diurnal movement. After spending two days in area A it moved to the more offshore area B for 2 days, almost in the centre of the bay before returning to area A where it spent almost a month with the occasional foray into the 100% Isopleth region. In late December, animal 5 spent 5 days out in area C, an area it had barely touched upon before this, 15-20km from area A and 15km from the nearest coast. After this period the dolphin returned to a distribution centred on area A again (although slightly on the west side of the highest density area) with occasional forays into the 100% isopleth region, including a trip to the most northern edge of its range.

Discussion

Satellite telemetry provides a very powerful tool for studying the movements of individual cetaceans and is the only available method for studying an animal's movement 24 hours a day for long periods, and as such can sometimes produce surprising results. Read and Westgate (1997) found satellite tagged harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy-Gulf of Maine area moved much greater distances than previously thought, and occupied previously unrecognized feeding areas with implications for the population's management regime. Suydam et al. (2001) found beluga (*Delphinapterus leucas*) whales in the eastern Chukchi Sea to be using a previously unrecognized offshore deep-water habitat. In contrast, the telemetry results from this study did not show any unpredicted movements or behaviours but gave very good support of our two main hypotheses; that Heaviside's dolphins exhibit some degree of site fidelity (or have a limited home range), at least over the 2 months of the study period and that the onshore-offshore diurnal movement observed by us was shown by all the tagged dolphins. The fine scale of our results do however highlight the high degree of variability between individuals in both behaviour and home range sizes, a pattern frequently observed in studies focusing on single animals both those using telemetry (Read & Westgate 1997; Suydam et al. 2001) and photo-identification (Odell and Asper 1990).

Diurnal movement patterns

The pattern of diurnal onshore-offshore movement was common to all the tagged dolphins and the overriding behavioural pattern observed, although significant individual variation was observed. Dolphin 4 stayed closest to shore of all the tagged dolphins (within 6km from shore) and rarely crossed the 50m depth contour, dolphin 5 also stayed largely within the 50m depth contour but further offshore, while dolphin 1 with an overlapping distribution moved large daily distances up to 22km from within Britannia Bay to offshore waters 100m deep; yet despite these large variations in range, depth and general distance from shore, all the dolphins tended to exhibit the inshore-offshore diurnal movement suggesting that it is very closely tied to the ecology of the species.

The offshore movement of Heaviside's dolphins at night is felt to be strongly linked to the vertical migration of one of their main prey species, juvenile hake (probably shallow water hake *Merluccius capensis*) (Sekiguchi et al. 1992) which are known to migrate vertically in the water column on a diurnal scale (Pillar & Barange 1995), coming closer to the surface to forage when it's dark. A similar pattern of offshore movement to feed on fish associated with the vertical migration of the deep scattering layer was observed by Würsig et al (1991) for dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand and by Norris and Dohl (1980) and Lammers 2004 for Hawaiian spinner dolphins (*Stenella longirostris*). The associated period of inshore movement of Heaviside's dolphins is thought to be for rest, socialising and a potentially reduced level of predation near shore as in spinner dolphins (Lammers, 2004)

The variation in speed of movement throughout the day is not as clear as the daily variation of depth and distance from shore. In general, all the tagged dolphins exhibited two minima in speed of movement, in the early afternoon (roughly 1100 h - 1500 h) and from midnight to early morning (0000 h to 0500 h). This pattern suggests that after a 'high speed' active morning inshore, the dolphins move offshore slowly then seem to speed up possibly while searching for prey and/or feeding, then slow down again after midnight, either while feeding in a fairly localized area or moving slowly back inshore. With the current data set it is not possible to say exactly when the dolphins were feeding, and future studies should include time depth recorders and temperature sensors to investigate this aspect of their ecology in greater detail.

Home range, Along-shore Range and Movements

Few published examples of a full home range exist for small cetaceans; most work on individual distribution and site fidelity has been done with photo-identification or similar boat-based work (Bräger et al. 2002; Odell and Asper 1990; Würsig and Harris 1990) limited to working in daylight hours, usually close to shore. Due to the relatively low number of known individual locations (at least compared to satellite telemetry studies) authors tend to define ‘along-shore ranges’ (e.g. Ballance 1992; Bräger et al. 2002) rather than home ranges per se. Our measure of along-shore range as well as a full home range in this study allows for comparisons with other and future studies using primarily photo-identification techniques.

Ecological theory predicts that in general home range size should increase with body size (Lindstedt et al. 1986; Buskirk 2004) and, due to the reduced cost of locomotion for swimming animals, dolphins should have larger home ranges than terrestrial animals of the same body size (Connor 2000). As predicted, Heaviside's dolphins have a much larger home range than that predicted by Lindstedt et al’s (1986) model for terrestrial carnivores, however for all measures of home range used, the relationship between the two is well above the ¾ power expected from metabolic requirements or the linearity more commonly observed (Lindstedt et al. 1986). Larger territorial mammals require a home range that is larger than predicted from metabolic needs alone because they share resources with their neighbours more than smaller animals do (Jetz et al. 2004; Buskirk 2004); perhaps it is the large degree of home range overlap and the associated ‘sharing with the neighbours’ that causes range size to increase so rapidly with body size in Heaviside’s dolphin. However samples sizes are small and we only have good data from female dolphins. The relationship linking body size to home range size in odontocetes seems to break down in interspecies comparisons. Although the along-shore ranges measured in this study were of the same order and tended to be slightly larger that those measured for the closely related and slightly smaller Hector’s dolphins (average 31.0km long, SE = 2.43; Bräger et al. 2002), satellite monitored harbour porpoises in the North Sea (Teilmann et al. 2004) and in the northeastern US (Johnston et al. 2005) have far larger ranges (7738-11 289km^2) and are far more transitory (although over 3-4 times the monitoring period) than the slightly larger Heaviside's dolphins in this study. Evidence from different populations of bottlenose and dusky dolphins suggests that ecology and habitat type (particularly ‘openness’) may override body size as the determining factor in home or along shore range size. The minimum linear home ranges of bottlenose dolphins in a protected, inshore, closed habitat in the Indian and Banana river systems in Florida vary from as little as 1.8km to as much as 100km (Odell & Asper 1990) while on the west coast of the USA bottlenose dolphins in a very open habitat are thought to be essentially transient along the Californian coast with very low site fidelity (Defran & Weller 1999). Dusky dolphins living in a shallow bay and feeding on schooling fish in Argentina differed in their ranging behaviour and degree of site fidelity to dusky dolphins living in deeper, open water in New Zealand and feeding on vertically migrating prey (Würsig et al. 1991). The small sample sizes in this study and the large amount of variation within and between species somewhat limits comparisons made at this level but the evidence suggests that as for group size (Gygax 2002), home range size in delphinids may be influenced by both phylogeny and habitat openness. However none of these populations are reported to exhibit any territoriality, and despite varying degrees of site fidelity, ranges appear to overlap freely.

With respect to range and movements, the most important results from this study are that all tagged Heaviside's dolphins showed a clear onshore-offshore movement pattern on a daily scale, had a spatially limited range and exhibited some degree of site fidelity. Home ranges showed considerable variation between individuals where they varied in their size, shape and proximity to shore and even at the individual level movements varied considerably and single animals both ranged widely, presumably in search of food, and remained in a fairly localized region for several days. Both these latter traits may influence attempts to count the dolphins.

These conclusions are limited to the 5 female dolphins for the period of monitoring in this study; male dolphins might be expected to range more widely and even female home ranges would probably increase to some extent with a much longer monitoring period, but we feel that the ranges presented here are probably representative and certainly of the correct magnitude, unless the species exhibit some kind of as yet unsuspected seasonal movement.

Tagging and effects thereof

The frequency of the locations received allowed us to examine in reasonable detail the movements of the animals post tagging. We interpreted the large movements away from the tagging site by some of the animals to be an initial avoidance of the tagging site as observed in harbour porpoises (Geertsen 2004; Teilmann 2000), which returned after ‘several days’. Only one animal (dolphin 5) did not return to the tagging site in this study suggesting it was more disturbed or more sensitive than the other dolphins: nothing abnormal occurred during the capture or tagging of this animal and we must assume that the apparently greater reaction to tagging was due to higher individual sensitivity of this dolphin. Interpretation of this ‘reaction’ in terms of home range estimation is difficult; avoidance of the tagging site could mean underestimation of the existing range (e.g. dolphin 5) or extension of the normal range. Animal 6 was the only dolphin resighted post capture and was swimming normally with 3 other animals (normal group size for Heaviside's dolphins) 8 days after capture and did not avoid the boat at all when approached (when initially released back into the water it had actually attempted to bow ride the capture boat). The tag on this animal was seated as attached and no obvious movements or injury could be discerned.

A dramatic increase in logging behaviour (lying still at the surface) of a captive harbour porpoise on the day of tagging as well as the longer surfacing rolls observed (Geertsen et al. 2004) and a sinking backwards behaviour (after breathing, rather than a normal forward dive) observed in both harbour porpoises (Teilmann 2000) and bottlenose dolphins (Irvine et al. 1982) was thought to be a behavioural adaptation to the discomfort of the tagged fin striking the air-water interface. We could not observe such fine scale behaviours with the data set used in this study, but the periods of localized movements of some of the animals (particularly 1 and 4) could represent a period when the dolphin was moving slowly and spending extended periods at the surface while adjusting to the feel of the tag.

In conclusion our results suggest that researchers should be wary of the impact period of the tagging process on cetacean behaviour and movements. We agree with Geertsen at al (2004) that more focused study is needed on all the potential impacts of tagging on cetaceans over both the short and longer term.

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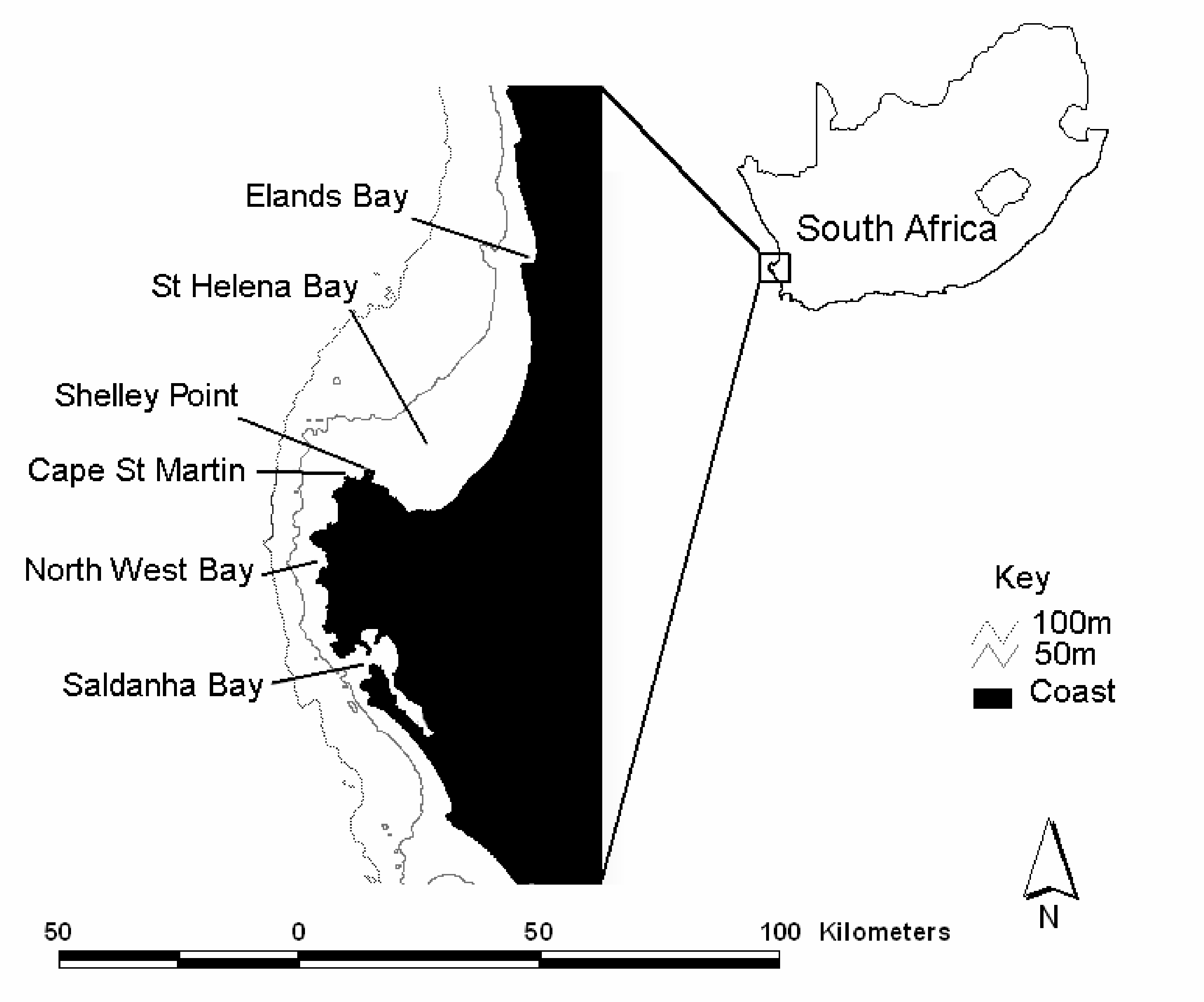

Figure 5.1. Study area and place names mentioned in the text.

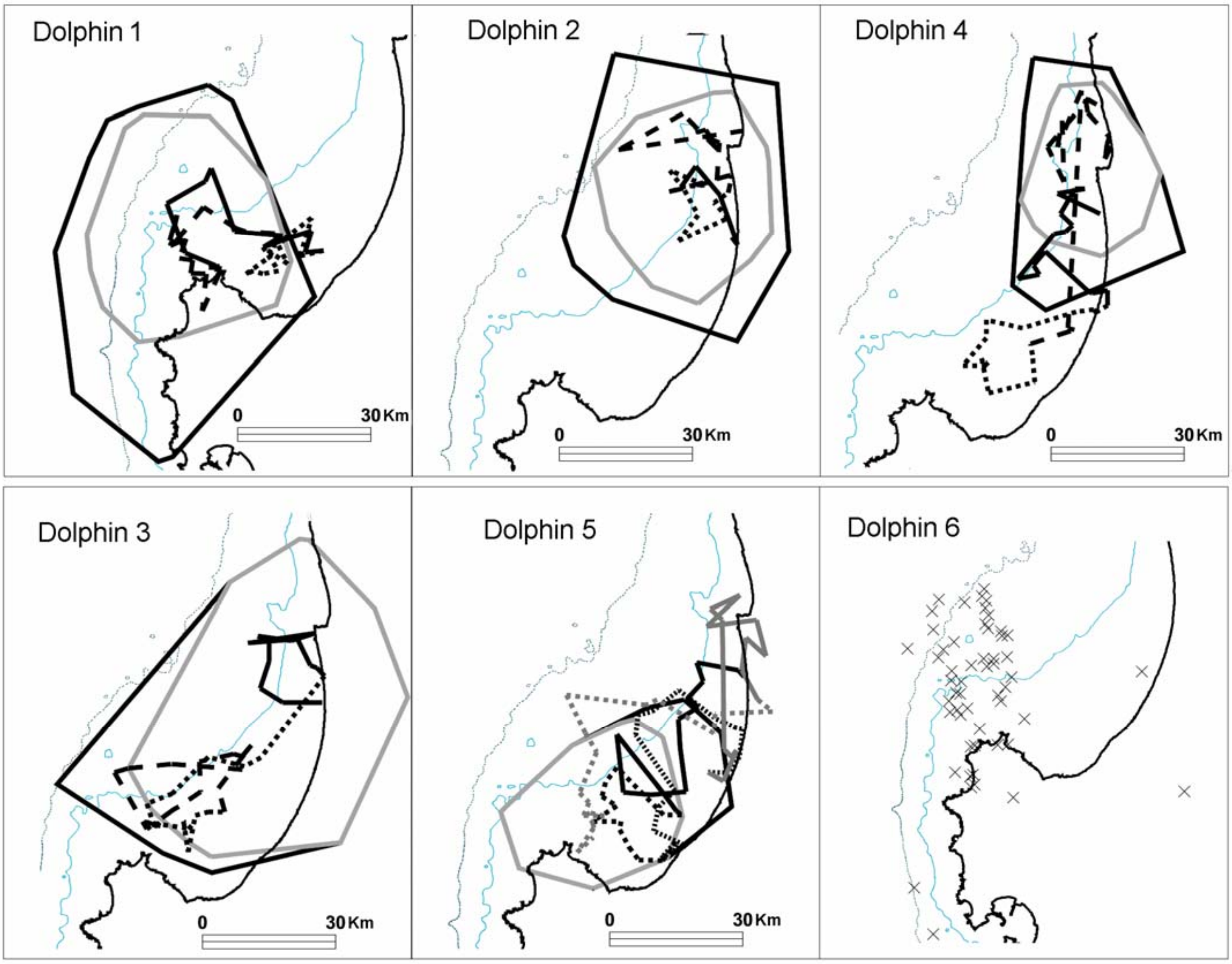

Figure 5.2. Series of maps showing home range as 100% (solid bold black line) and 95% (solid gray line) minimum convex polygons of 5 female Heaviside’s dolphins fitted with satellite-linked transmitters off the coast of South Africa. These ranges were calculated without the initial ‘‘impact period’’ (first 72 h posttagging except 120 h for dolphin 5). This period is shown as a line starting from capture site, solid for 1–24 h, short-dashed for 24–48 h and long dashed for 48–72 h. The additional days for tag 5 are shown as 72–96 h ¼ solid gray; 94–120 h ¼ dashed gray. Because of the short transmitter life and high accuracy of received locations, all the received locations from the only male dolphin (dolphin 6; unfiltered) are shown. Contours shown are the 50- and 100-m depth.

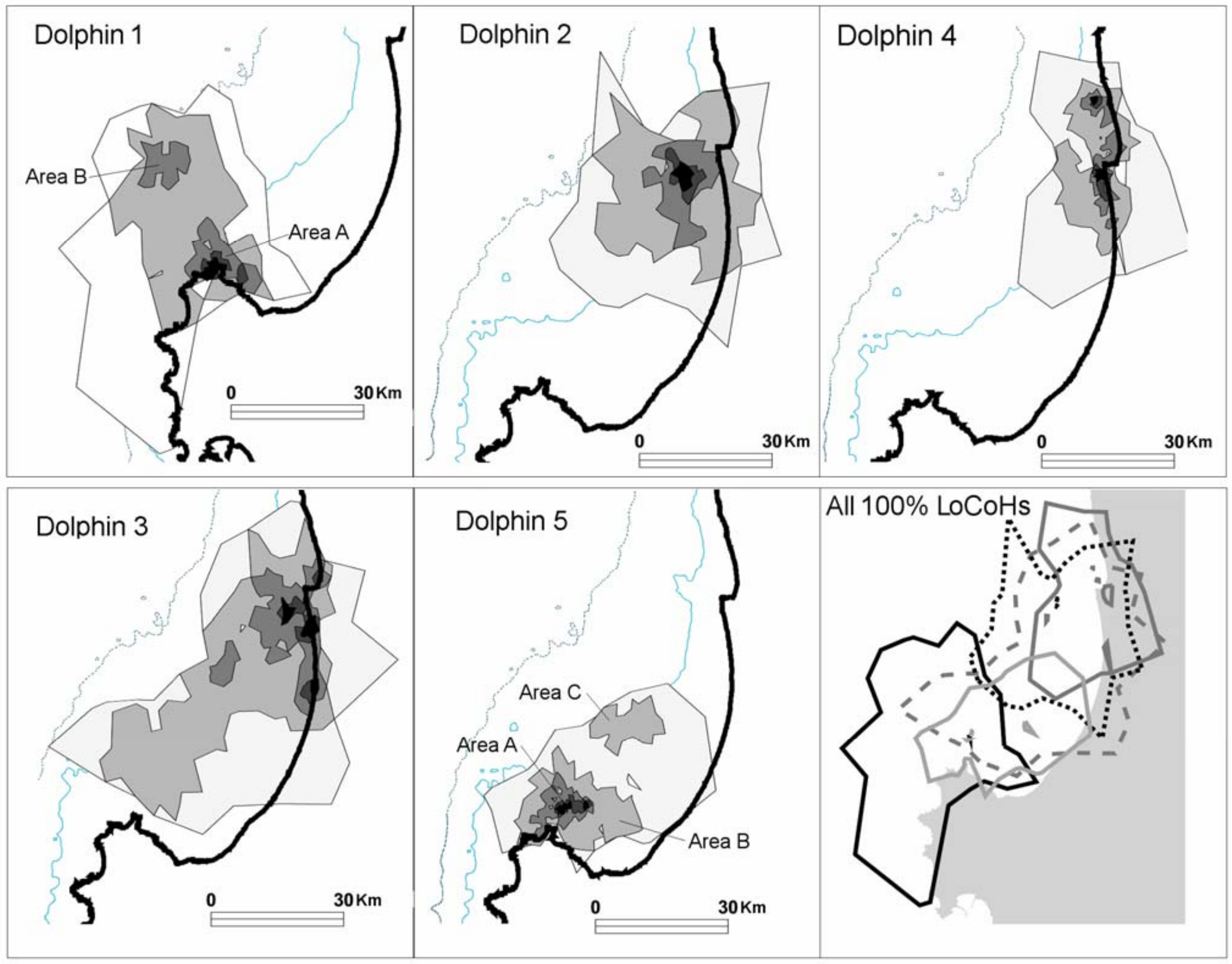

Figure 5.3. Series of maps showing home ranges as local convex hull (LoCoH) polygons with density isopleths (Getz and Wilmers 2004) for 5 female Heaviside’s dolphins fitted with satellite transmitters off the west coast of South Africa. Contours shown are the 50-m and 100-m depth. Isopleths shown are 100% (lightest shading), 90%, 50%, 20%, and 10% (darkest gray shading). The bottom right figure shows the 100% LoCoH isopleths for all dolphins.

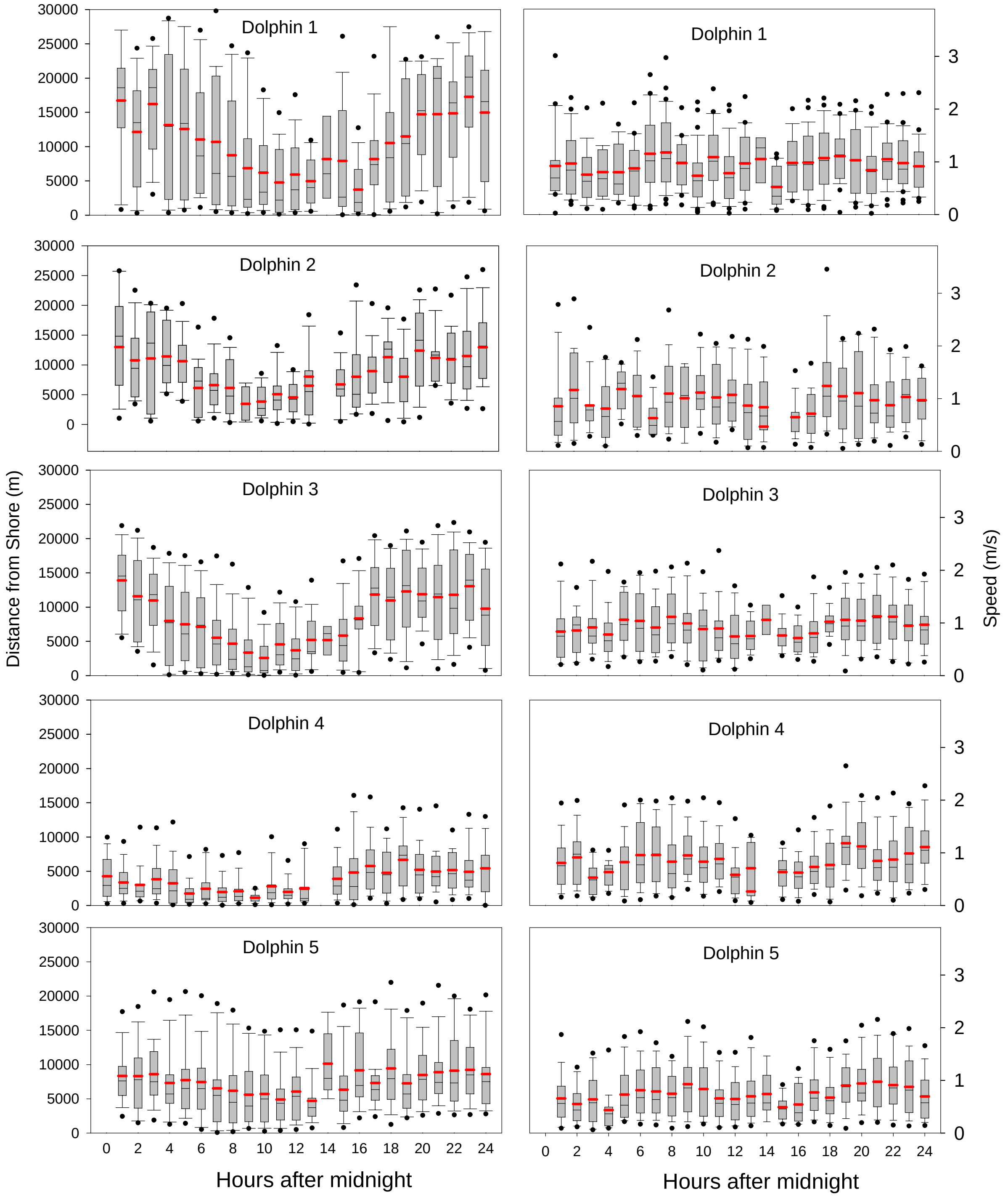

Figure 5.4. Distance from shore (m) on left and speed (m/s) on right of Heaviside's dolphins fitted with satellite transmitters off west South Africa. Means are shown as thick lines, medians as thin lines within boxes. Points, whiskers, and boxes represent the 5th, 10th, 25th, 75th, 90th, and 95th quartiles, respectively.

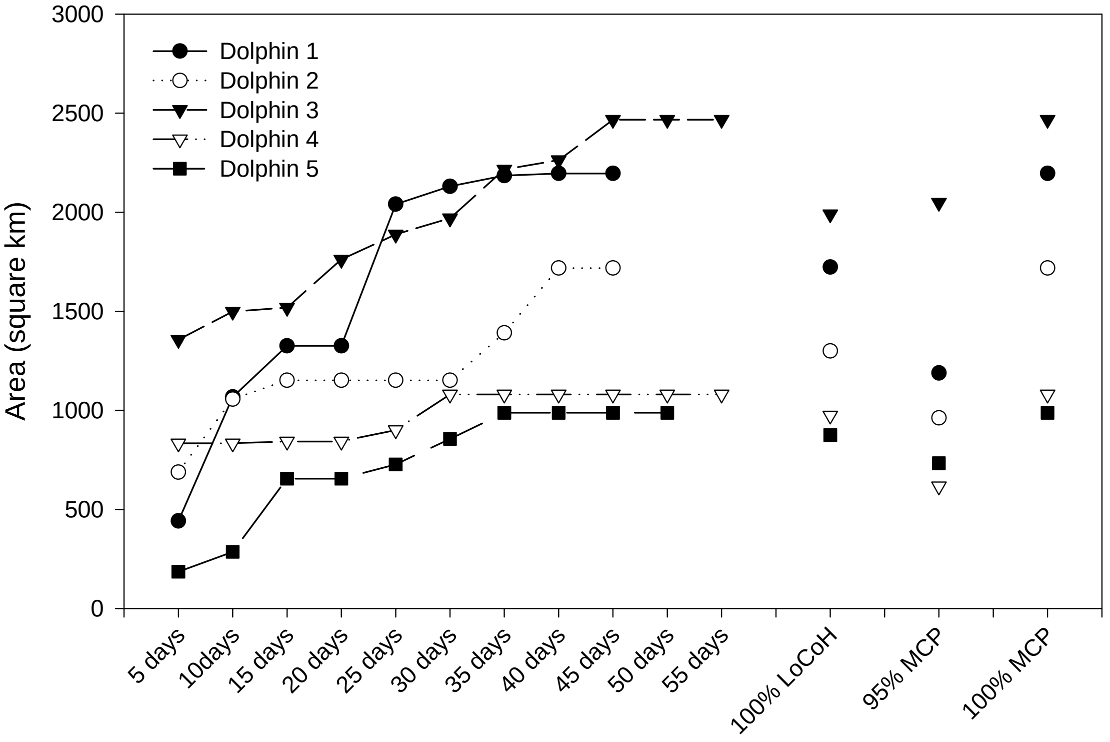

Figure 5.5. Minimum convex polygon (MCP) home-range growth in 5-day increments (area as km2) of Heaviside's dolphins starting afterimpact period (72 or 120 h postrelease). Full 90% and 100% LoCoHs and 95% MCPs shown on right of graph for comparison.

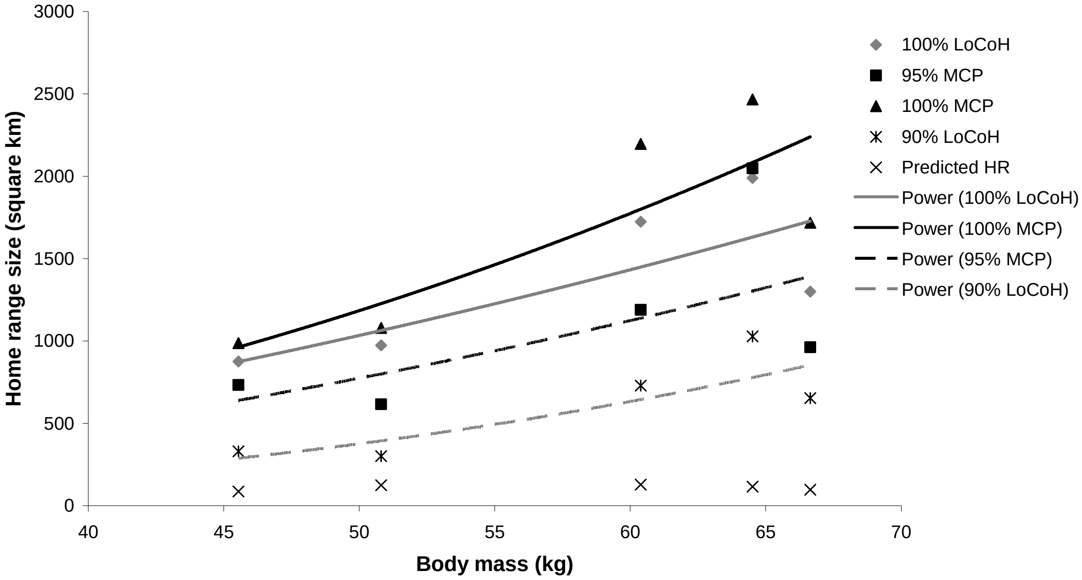

Figure 5.6.—Relationships between body size (using mass estimated from total length) and home-range size (km2) for 4 measures of home range; local convex hulls (LoCoHs) and minimum convex polygons (MCPs). Compare with Table 5.1, which gives body length. Power curves were fitted for each measure of home range. Predicted home-range sizes are from Lindstedt et al (1986) based on terrestrial carnivores.

Chapter 6

Synthesis

Prior to this study, very little was known about the ecology of Heaviside's dolphins, beyond their diet (Sekiguchi 1994) and broad scale distribution (Findlay et al. 1992), although studies of morphology (Best 1988), taxonomy (Pichler et al. 2001) and genetic variation (Jansen van Vuuren et al. 2002) were more advanced. Heaviside's dolphins were known to occur in the shelf waters of the Benguela current region from the coast to roughly 200m depth (Findlay et al. 1992), with an apparently continuous distribution throughout their range and no meaningful genetic differentiation between Namibia and South Africa (Jansen van Vuuren et al. 2002). From stomach content analysis they were known to feed on a variety of fish and cephalopods but predominantly juvenile hake (Sekiguchi 1994). Fortuitously, they did not seem to overlap with the commercial hake fishery in either prey size taken (Sekiguchi et al. 1992) or spatial range as the commercial fishermen are targeting larger fish in deeper water (F. le Clus pers. comm.).

One interpretation of the genetic data available was that despite its restricted range, the population might be reasonably large and healthy (Jansen van Vuuren et al. 2002). However, some fisheries bycatch was known to occur, particularly in near-shore fisheries (Best & Abernethy 1994) and a major motivation for this study was an unknown but potentially serious risk of bycatch in the inshore set-net fishery in St Helena Bay. This was particularly concerning because of circumstantial evidence suggesting that Heaviside's dolphins have small ranges and exhibit some degree of site fidelity (Rice & Saayman 1984), a characteristic which is though to have played a pivotal role in the isolation and high genetic differentiation of populations of the con-generic Hector’s dolphin (Pichler et al. 1998). A further consideration which has arisen since 1999 when the project began, is the rapid development of the boat based whale watching industry in South Africa, which although primarily focused on large whales also includes a dolphin watching component, particularly in the out-of-season summer months. Although arguably of little impact in comparison to fisheries bycatch in which animals are killed, the persistent harassment of dolphins by boats is likely to affect many more individuals at a lower level and may result in broad scale behavioural changes throughout the population with potentially serious although subtle effects (e.g. Williams et al. 2006; Bejder et al. 2006). From a management point of view a better understanding of the ecology and natural behaviours of these coastal dolphins was long overdue. For management to be effective, to be able to understand the degree of impact likely to be caused by either bycatch or dolphin watching, we need to know the number of animals in the population, the range and movements of individuals and how they are using their environment.

The principal objective of this study was to describe the alongshore distribution, range and dispersal of individual Heaviside’s dolphins using mark-recapture techniques, in order to determine if a ‘point’ source of bycatch such as was potentially occurring in St Helena Bay was likely to be affecting a localized or wide spread subset of the total population. Secondary objectives were to (i) investigate the usefulness of photo-ID to provide data for other studies on the species such as an abundance estimate or investigations of social structure and (ii) through analysis of our sightings data and concurrent shore based observations, to increase the general knowledge of environmental factors influencing the movements and distribution of Heaviside's dolphins. The limitations of the data and the relevance of our findings have been placed in the context of other studies and ecological theory in greater detail within each chapter, so in this conclusion I will try to synthesize the major findings of the study within a management framework.

Summary of main findings

The pattern of diurnal resting and nocturnal foraging offshore was consistent with both observations from shore (Chapter 1) and from the movements of the 5 female dolphins fitted with satellite transmitters (Chapter 5). We concluded that this movement offshore is almost certainly to exploit the vertical migration from deeper water of their principal prey, juvenile hake. Furthermore, variations in the along shore density of dolphins were positively correlated with the long term abundance of small hake available nearby (Chapter 2). Together, these findings suggest that the ecological link between Heaviside's dolphins and juvenile hake is a close and important one, at least in the Western Cape. Upwelling zones create seasonal and spatial structure within the Benguela current system (Shannon 1989), affecting the abundance and stock structure of hake along the coast, including known spawning grounds where juveniles are particularly abundant (O'Toole 1977). These variations are reflected both spatially and temporally in the opportunistic diet of fur seals in Namibia which forage on whatever is most abundant in their local environment at the time (Mecenero et al. 2006a, b) to the extent that the diet of seals in any year predicted the cohort strength of hake measured a year later in demersal research trawls (Mecenero & Roux 2002). Although the South African hake stock is currently well managed and certified by the Marine Stewardship Council, similar data on spatio-temporal variation in the diet and foraging strategies of Heaviside's dolphins would be informative as to likely scenarios in the event of a fishery collapse or significant environmental change. Dietary analysis could conceivably be investigated using fatty-acid and stable isotope analysis from biopsied tissue (Budge et al. 2006; Borrel et al. 2006).

High site fidelity of Heaviside's dolphins was suggested from two different approaches, over shorter periods by those animals fitted with satellite transmitters and over longer periods (up to 3 years) by those animals photographically re-identified. This supports earlier suggestions of site fidelity based on more circumstantial evidence (Rice & Saayman 1984; Best & Abernethy 1994). Although our data collection was largely confined to the summer months and we cannot rule out a seasonal migration or variation in range size, the pattern is clear enough that a conclusion of general site fidelity appears reasonable, although it seems in contrast to the genetic homogeneity observed (Jansen van Vuuren et al. 2002). This finding has important management implications: site fidelity limits the number of animals being affected by a localized threat but increases the risk at the individual level. It also creates the opportunity for community substructure (e.g. Heinrich 2006; Lusseau et al. 2005; Wilson et al 1997) which can split a population and reduce the rate of repopulation if one community is reduced by some impact such as localised bycatch. If animals are socialising widely and indiscriminately, the highly fluid social structure we described in chapter 3 may to some extent, act to counter any geographic structure such as the putative split which we identified in the Saldanha Bay area. However both these analyses were strongly affected by the low proportion of identified animals in the population and these results must be treated with caution until further data confirms the findings. Although the large population size and the seemingly fluid social structure of Heaviside’s dolphins are likely to play a role in the lack of phylogeographic structure observed as well as mediate the effects of any anthropogenic impacts on this population, both set-net bycatch (as shown in chapter 2) and boat based whale watching encounters are likely to be localised impacts affecting a limited pool of individuals and the site fidelity of these animals must still be considered in their management.

Since photo-ID had not been previously attempted on Heaviside's dolphins, an evaluation of its applicability to the species was a secondary goal of the project. Sufficient natural markings of the dorsal fin of Heaviside's dolphins occur to enable the identification and importantly, re-identification of individual animals, the minimum requirements for any capture-mark-recapture (CMR) study. Using photographic identification we were able to describe the movements of individuals, their residency patterns and to some extent the social structure of the population as well as generating an abundance estimate. However, the major drawbacks to using CMR techniques on this species are that the population is large and the proportion of marked animals is very low, the lowest of any cetacean studied to date. These two factors combine to result in fewer identified animals and fewer re-sightings of individuals per unit effort, as well as producing a marked potential for interaction between image quality and animal distinctiveness. These factors in turn led to high variance in our abundance estimates, low sample sizes for movement analyses and incomplete group membership description weakening the analyses of social interactions considerably. Photographs for this study were taken with older model manual focus film cameras; the use of more modern digital cameras with rapid auto-focus is likely to considerably improve the applicability of photo-ID techniques to this species by improving the overall quality of images taken, thereby potentially broadening the spectrum and subtlety of marks that are available for identification and thus the proportion of marked animals in the population. Future studies, particularly those requiring a high proportion of animals in a group to be identified, might focus in areas where the proportion of marked animals is higher, for instance near Cape Town, or use a different technique such as microsatellite analysis. Due to the low efficiency of mark-recapture over broad scales on Heaviside's dolphins, we would recommend researchers investigate other available methods such as telemetry, fatty-acid and isotope analysis and genetics and take into consideration the relative costs and benefits of each method per unit data gathered.

Dusky dolphins were known from studies in other parts of their range to be generalist feeders that use a variety of foraging strategies (Würsig & Würsig 1980). Current evidence suggests that South African dusky dolphins are similarly opportunistic and flexible; dietary analysis has indicated that foraging may occur in different habitats in different seasons (Sekiguchi 1994) while results from this study provide some evidence of spatial variation in foraging strategies. During the boat based work, very large groups of animals (n>50) were only encountered in St Helena Bay suggesting that the strong association with upwelling conditions we observed from shore may be specific to this area and potentially other areas of strong upwelling. Heaviside's dolphins were the priority during this study and data from dusky dolphins were collected more opportunistically. More data are needed to better understand the ecological interactions of dusky and Heaviside's dolphins but it is clear from the data available that foraging strategies and social structure differ between the two species and such differences need to be taken into account for management purposes.

Closing words

In this study, we have provided baseline data on several different aspects of the ecology of Heaviside's dolphins in the southern part of their range, although all conclusions must be tempered by the relatively short and seasonal nature of the data collection. We have confirmed, using shore based observations and satellite telemetry, the diurnal movement pattern of inshore resting and offshore nocturnal foraging of Heaviside’s dolphins originally suggested by Sekiguchi (1994), and at least for the summer season and particularly for female dolphins, the small ranges and high site fidelity suggested by Rice & Saayman (1984). In addition, we have confirmed the large population size suggested by the high genetic diversity (Jansen van Vuuren et al. 2002) and we have provided some preliminary data on how environmental factors influence their distribution, movements and behaviour inshore, as well as on the ranging behaviours and residency of individuals. Our findings suggest that despite being sympatric, Heaviside's and dusky dolphins have evolved different strategies for co-existence, and encouragingly, both species were encountered in large numbers in the field and anthropogenic threats are currently felt to be reasonably low.

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RANGE AND MOVEMENTS OF FEMALE HEAVISIDE'S DOLPHINS (*CEPHALORHYNCHUS HEAVISIDII*), AS DETERMINED BY SATELLITE-LINKED TELEMETRY

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Heaviside's dolphin (*Cephalorhynchus heavisidii*) is a coastal delphinid with a limited inshore distribution off the west coast of southern Africa. Knowledge of its habitat usage is an essential precursor to assessing its potential vulnerability to fisheries interactions. Six Heaviside's dolphins (1 male and 5 females) were fitted with satellite-linked transmitters in 2004, and tracked for up to 54 days. The 5 tags fitted to female dolphins transmitted continuously, allowing for analysis of movements at a fine temporal scale. Four dolphins showed an initial avoidance of the capture site by moving over a wider area in the first 2–5 days posttagging than later in the deployment period. All dolphins had used their full home ranges (determined as 100% minimum convex polygons) 5–20 days before tag failure, suggesting measured home ranges were stable at this temporal scale. Home-range estimates using local convex hulls ranged from 301.9 to 1,027.6 km^2 (90% isopleths) and 875.9 to 1,989.6 km^2 using the 100% isopleths and scaled positively with body size but varied in shape, usage, and number of core-use areas. Although the distance from shore and depth at which individual dolphins moved varied greatly, all dolphins showed a strong onshore–offshore diurnal movement pattern, generally being closest inshore between 0600 h and noon, and farthest offshore between 1500 h and 0500 h. This pattern is assumed to be related to the movements of their principal prey, juvenile shallow-water hake (*Merluccius capensis*), which migrate into the upper water column at night. Movements inshore may be associated with rest, socializing, and predator avoidance.

Key words: Argos, *Cephalorhynchus heavisidii*, Heaviside's dolphin, home range, satellite telemetry

Published information on the distribution of Heaviside's dolphins (*Cephalorhynchus heavisidii*) is limited but suggests that individuals have a restricted range and are likely to be resident year-round within a certain area (Best and Abernethy 1994; Rice and Saayman 1984). The closely related Hector's dolphin (*C. hectori*) has been shown to have a high degree of site fidelity over a more than 10-year study period (Bräger et al. 2002), and mitochondrial DNA studies show a high genetic diversity over a relatively small geographic range, suggesting a low dispersal rate at least for female Hector's dolphins (Pichler et al. 1998). A slightly shorter-term study at Isla Chiloé, Chile, found Chilean dolphins (*C. eutropia*) also exhibit a high degree of site fidelity between years (Heinrich 2006); thus it seems likely from phylogenetic evidence that Heaviside's dolphins will have relatively small ranges and show high site fidelity over long periods.

Considering the known and potentially devastating effect of bycatch on *Cephalorhynchus* dolphins in general (e.g., Dawson et al. 2001; Lockyer et al. 1988; Slooten and Lad 1991) and the known, although not yet quantifiable, risk to Heaviside's dolphins from midwater trawls, purse seines, and particularly beach seines and set-nets (Best and Abernethy 1994), it is prudent that we gain a better understanding of the range and site fidelity of these animals if the impact of such mortalities is to be evaluated. This paper describes the results of a satellite telemetry study, designed to obtain detailed records of the diurnal movements and range of Heaviside's dolphins over a period of 6–8 weeks.

MATERIALS AND METHODS

Capture and transmitter details.—Six Heaviside's dolphins (5 females and 1 male) were captured in 2 trips off the west coast of

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TABLE 1.—Transmitter type, capture information, and biological details for Heaviside's dolphins caught off the coast of west South Africa for fitting with satellite-linked transmitters in 2004. All dolphins were fitted with Telonics ST18 transmitters except dolphin 6, which was fitted with a HABIT transmitter.

Dolphin no.	Transmitter no.	Date of capture	Contact time (min) Total	On deck	Sex	Body length (cm)	Method of capture
1	17229	18 August 2004	23	17	Female	159	Tail grab
2	14066	20 November 2004	27	25	Female	165	Tail grab
3	24274	20 November 2004	28	25	Female	163	Tail grab
4	16204	21 November 2004	26	22	Female	149	Head Net
5	24276	21 November 2004	25	22	Female	143	Tail grab
6	10015	12 August 2004	29	24	Male	148	Head net

South Africa in August and November 2004 (Table 1; Fig. 1). Dolphins were captured from a 6-m semirigid inflatable boat using either a tethered head net or tail grab (dolphin 4 was caught with a head net from the 42-m research vessel *RV Sardinops* and retrieved immediately by the small boat), a diver was put in the water to hold the animal's head clear of the surface and to guide it into a stretcher; on most occasions animals were transferred to a larger vessel (*RV Sardinops*) for tag attachment. We used 2 types of satellite -linked radiotransmitters, Telonics (Argos-linked transmitter, model ST-18; Telonics, Inc., Mesa, Arizona) and HABIT (Argos-linked transmitter; HABIT Research, Victoria, British Columbia, Canada). Transmitters were attached to the dorsal fin of dolphins through holes drilled in the fin with a modified electric drill, using 3 Delrin (a type of hard-wearing plastic) pins for the Telonics transmitters or 2 nylon-coated stainless steel pins for the HABIT transmitters, with corrodible nuts to allow the tag to fall off the animal after the appropriate period. Contact time (capture to release) varied from 23 to 29 min and dolphins were on deck from 17 to 25 min (Table 1). Time on deck consisted of letting the dolphins become settled, examination by the attendant veterinarian or veterinary nurse, application of anesthetic to the drill site, sexing and measurement of as many standard measures as could be achieved with minimal disturbance to the animal, tag insertion and bolting, final check, and release. The HABIT tags were set to transmit for 8 h followed by 12 h off to save battery life and were expected to last up to 12 months. The Telonics tags were set to transmit continuously with an expected battery life of up to 3 months, but they varied in age so transmission duration was an unknown factor.

This work was conducted under a permit issued to PBB in terms of the Marine Living Resources Act (Act 18 of 1998) of South Africa, was approved by the Ethics Committee of the University of Pretoria (AUCC 040405-010b Conservation of Heaviside's dolphin), and followed the relevant animal care and use guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

Telemetry data and location filtering.—The location of the transmitters was determined by triangulation of their signals from polar-orbiting satellites operated by Service Argos (Ramonville, Saint-Agne Cedex, France). Diagnostic software files received from Service Argos were imported to ArcView 3.3 (ESRI, Redlands, California) for manipulation and analyzed using the Argos Tools extension. Diagnostic files included a location, with an associated time–date stamp and a quality index for the accuracy of the location; standard locations (location classes 3, 2, 1, and 0) have a theoretical precision whereas auxiliary locations (location classes A and B) do not. However, some studies have shown that there can be significant error in all location classes (Le Boeuf et al. 2000; Vincent et al. 2002) and we thus chose to use all location classes and filter them using the measured swimming speed between received locations using the Argos Tools 3-point running average speed filter to remove locations that resulted in implausible ground speeds (the middle location of the 3 is removed if the average speed of both legs exceeds the filter threshold). Because no previous, independent measure of swimming speeds existed for Heaviside's dolphin, we used only the highest-quality points (classified as quality 1–3 by Service Argos) of several dolphins to calculate the travel speed, of which the 95th percentile was about 2.5 m/s (9 km/h) for all dolphins with speeds above this tending toward the ridiculous (>20 km/h), and thus 2.5 m/s was used as the maximum plausible speed for the filtering process.

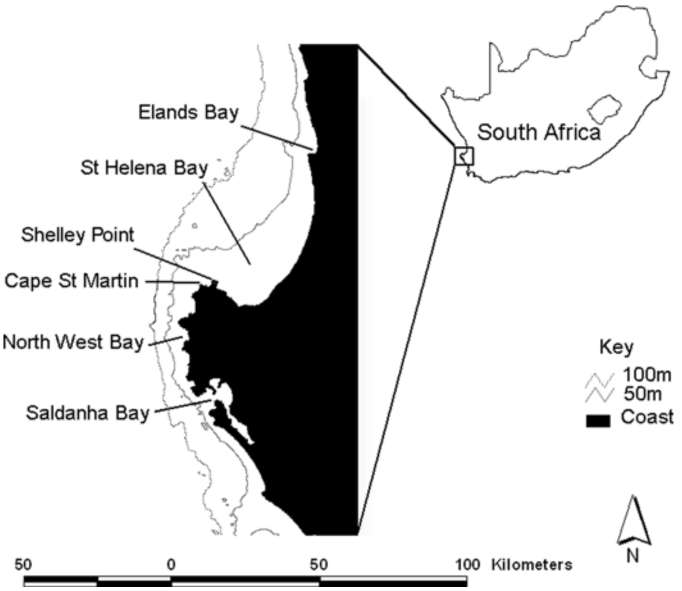

FIG. 1.—Study area and place names mentioned in the text.

The data for the 5 females were filtered down to 35–76% of the original number of locations in the prefiltered data file (Table 2), which compares favorably with other studies using satellite-linked transmitters in the marine environment (Austin et al. 2003). The data for the male dolphin were not filtered because only 55 locations were received over 11 days, the vast majority of which were in realistic locations (i.e., only 3 were over land, 1 of those by a mere 350 m, another of which was the 1st position received possibly while the tag battery was still deionizing); thus some interpretations from these data can still be made. Also note that the 5 Telonics tags had been stored for some time before deployment and the older tags (chiefly on animals 2 and 4) underperformed in comparison to the newer tags with regard to accuracy of locations (number of points over land post-filtering) and percentage of standard locations received (Table 2).

Tag effects.—Only 1 animal (dolphin 6) was resighted posttagging, thus limiting our investigation into the influence that the tag may have on the animal or its behavior to interpretation of the tag-location data themselves. The 24-h constant transmission of the Telonics tags allowed for analysis of movements at a fairly fine temporal scale. Therefore, we compared the movements, swimming speed, and distance from shore for the first 72 h posttagging (in 24-h periods), using *t*-tests (or Mann–Whitney tests where normality could not be achieved by transformation), to the remainder of the data set. This period was chosen based on observations from the data and the literature (Geertsen et al. 2004); we refer to this as the "impact period" for the remainder of this paper. Anomalous movement behaviors that might be expected are fast,

Table 2.—Information on the collection and filtering of location data from satellite-linked transmitters on Heaviside's dolphins off the west coast of South Africa, including transmitter life span, number of data points collected (raw data), number of points used after data were filtered, and number of points erroneously appearing to be on land after data filtering.[a]

			No. data points					
	Transmission of location data			After filtering		Raw data in LCs 1–3	Points appearing to be on land	
Dolphin no.	Duration (days)	Duty cycle (h)	Total (raw)	Number used	% rejected		Number	%
1	44	24	923	470	48	17	16	3
2	45	24	950	338	65	10	29	9
3	54	24	958	620	35	33	61	9
4	55	24	858	536	38	37	89	16
5	49	24	1,013	768	24	61	16	2
6	11	8 on, 12 off	55	NA	NA	26	3	6

[a] LC = location class; NA = not applicable.

directed movement away from tagging site (in either distance covered or distance offshore—Geertsen et al. 2004); very slow or little movement as the animal habituates to the feel of the tag (Geertsen et al. 2004); or a movement inshore, or rather a lack of movement offshore, if the animal feels vulnerable, because some small cetaceans are thought to move inshore to shelter from predators (Würsig and Würsig 1979).

Movements.—Heaviside's dolphins have been observed by us (SE, PBB, and MT) to be close inshore in the mornings but move away, presumably offshore, from noon onward. Thus, we expected the dolphins to be closest to shore in the daylight hours of the morning and farthest from shore and in deepest waters at night with transitory periods between. We hypothesize that speed of movement would be lowest during the presumed resting and socializing period inshore and during feeding offshore when animals might be expected to feed in a fairly localized region for a night, with travel speeds being greatest during the movements between resting–socializing and feeding grounds. To analyze this pattern more closely we looked at the variation of mean depth (limited to the area between 0 m at the coast and 100 m isobath, for which we had good bathymetry data; some points falling outside this area were lost to analysis) and distance from shore, as well as mean speed between successive locations for each hour of the day. Because of the observed impact on behavior posttagging, we did not include the first 72 h of data posttagging (120 h for dolphin 5). Longer-term movements and distribution patterns are also discussed where relevant.

Home range.—The calculation of a home range for individual animals is challenging because there is no single correct or best way to describe an animal's area usage nor can we ever hope to track every movement an organism might make throughout its life, and indeed for most questions we need to ask, this would not be necessary. However, it is important to scale the temporal and spatial aspects of data collection to the appropriate scale for the question being asked, and conversely to limit interpretations of the data to the relevant scale both temporally and spatially. Because of the tag programming parameters, data in the current study have a high temporal density, allowing for analysis of movements within a day, but none of the tags transmitted for more than 2 months, thus limiting conclusions beyond this period.

Several methods exist of describing an animal's home range; we have chosen the local convex hull (LoCoH) home range (Getz and Wilmers 2004), which seems to be more powerful than kernels at estimating home-range size and area, especially in environments with corners or holes in the distribution (e.g., in fenced reserves or around lakes or islands). The LoCoH method generates density contours (isopleths) around all known locations to give a realistic idea of an animal's home range and area usage therein. We have also used the minimum convex polygon (MCP) method, in which the smallest possible convex polygon is drawn around the known locations, for some analyses. MCPs are extremely sensitive to outliers in distribution, but this artifact can be used to some extent as a tool to highlight changes in movement or ranging behavior.

A particular characteristic of this data set is that the proximity of the dolphins to shore much of the time makes errors in the received locations very obvious. It could be argued that because the locations over land are obviously incorrect, by deleting them we could only increase the accuracy of the data set as a whole and indeed, the maps would certainly look less incorrect. However, the location accuracy errors occur in all directions not just onshore and vary between tags and dolphins (because of differences in construction and behavior, respectively); deleting only the onshore locations is an effectively arbitrary procedure and nonrepeatable across animals or tags and provides the reader with the tacit assumption that all locations at sea are 100% correct (when this is obviously not the case). Moreover, it would limit the comparability of our data with other studies where perhaps the study animal occurs farther from shore and such an arbitrary filtering procedure cannot be performed. To aid in any future comparisons with data from other species that may not be constrained by a coastline, we felt it constructive to effectively ignore the coastline and the obviously incorrect points for some of the analyses. Although the MCP method is particularly sensitive to outliers such as those on land, the LoCoH method gives much better results, particularly the 90% isopleth (which we regard as being probably the most realistic home-range estimator to use). This is highlighted clearly by comparing the performance of the 2 methods for animal 1, whose range extended around a headland. The MCP cut the corner across the headland (Fig. 2), whereas the LoCoH method did a reasonable job at getting around the corner (Fig. 3).

To determine if the home ranges measured during this study were representative of the ''maximum'' long-term home ranges of the animals, we plotted growth of the home range in 5-day increments on the assumption that if the home range was still growing at the end of the tag's transmission life, then the dolphin had not yet covered its entire range. We chose to use the 100% MCP home range rather than the LoCoH home range because the MCP method is more likely to overestimate the actual range by including both Argos inaccuracies and long-range movements, thus making the calculation of time to full usage more conservative.

Along-shore range.—Human impact on Heaviside's dolphins is highest near shore where there is some risk of being caught in an inshore set-net fishery for St. Joseph's sharks (*Callorhinchus capensis*—Best and Abernethy 1994). Understanding the range of dolphins along the shore and the way this relates to their full home range will be informative in assessing risk to the population from localized bycatch; it will have the added benefit of enabling us to compare our results here with data generated from inshore photo

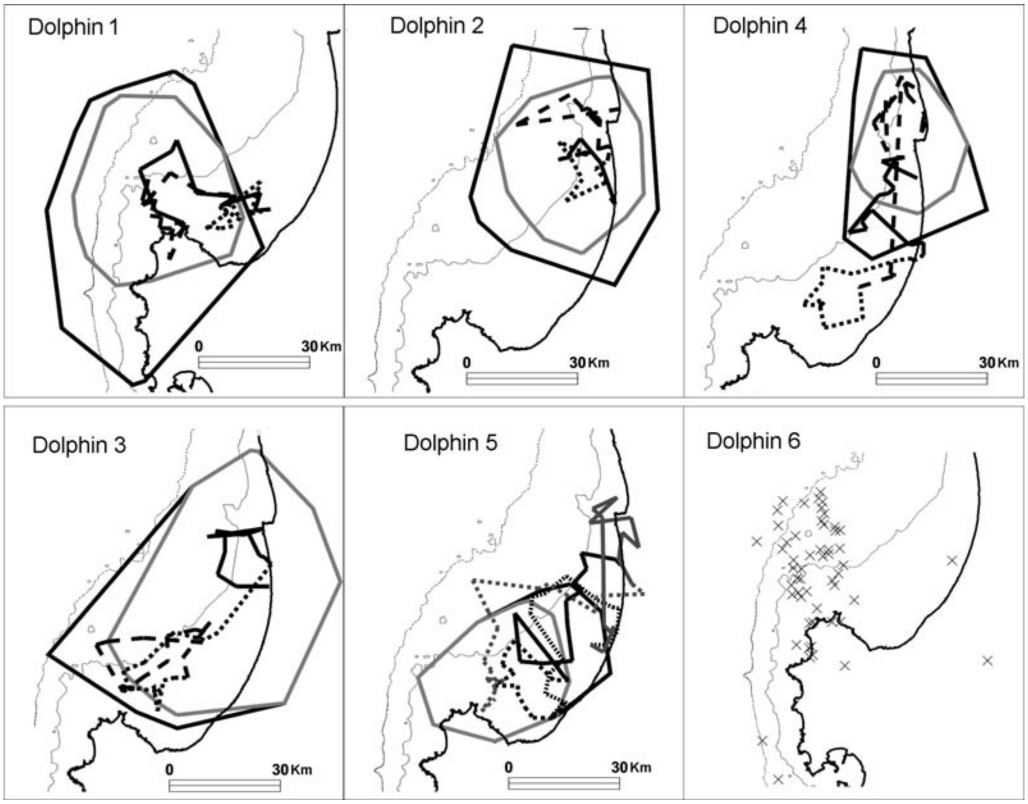

Fig. 2.—Series of maps showing home range as 100% (solid bold black line) and 95% (solid gray line) minimum convex polygons of 5 female Heaviside's dolphins fitted with satellite-linked transmitters off the coast of South Africa. These ranges were calculated without the initial "impact period" (first 72 h posttagging except 120 h for dolphin 5). This period is shown as a line starting from capture site, solid for 1–24 h, short-dashed for 24–48 h and long dashed for 48–72 h. The additional days for tag 5 are shown as 72–96 h = solid gray; 94–120 h = dashed gray. Because of the short transmitter life and high accuracy of received locations, all the received locations from the only male dolphin (dolphin 6; unfiltered) are shown. Contours shown are the 50- and 100-m depth.

identification mark–recapture studies of both this and other species where effort is limited to the nearshore. We calculated the along-shore distance between the farthest points of the 90% and 100% LoCoHs for each dolphin, using a smoothed line 500 m from shore for the distance traveled.

RESULTS

Tag effects: behavior in the first 3 days postrelease.—Our investigation into the reaction of dolphins to capture and tagging was limited to interpretation of the positions received from the transmitters via the Argos system, with all the errors associated therewith. We interpreted large movements away from the tagging site, especially those outside the area occupied during the remainder of the tagging period as capture-site avoidance, and although much more difficult to interpret, we believe that extended periods of little movement possibly indicate a period when dolphins are adjusting to the feeling of having the tag attached (Geertsen et al. 2004; Irvine et al. 1982). We present the movements during the first 72 h after tagging (120 h for dolphin 5) as lines in Fig. 2 overlain on the 95% and 100% MCPs calculated for every other location after this period. Because MCPs include all points within their boundaries they generally overestimate home range, making any movements outside this area even more striking. It is clear from Fig. 2 that dolphins 4, 5, and 1 all moved outside of the area covered by the MCP. Further, it is instructive to compare these movements with the calculated LoCoH home ranges of Fig. 3 to highlight the distance dolphins moved outside of their main usage areas.

Dolphin 2 showed no movements that we interpreted as either capture-site avoidance or an adjustment period. This animal showed no significant variation in speed during the impact period; however, during the first and third 24-h periods, this dolphin was significantly closer to shore than on average (Table 3), although this is not clear from visual analysis of the data. It must be borne in mind that this tag produced the worst locations in terms of location class and number of points on shore.

After release, dolphin 1 moved offshore, then to a small area approximately 12 × 6 km in the far eastern part of its range where it remained for the period 9–46 h posttagging, indicating a possible adjustment period. During the impact period, the dolphin showed no significant differences in speed or distance from shore than during the remainder of the data set (Tables 3 and 4). This animal was tagged in Britannia Bay (between Cape St. Martin and Shelley Point) and regularly frequented that bay during the remainder of the tag-life, suggesting that the inferred avoidance was temporary.

During the impact period, dolphin 3 did not leave the greater home-range area (MCP) covered by it during the remainder of

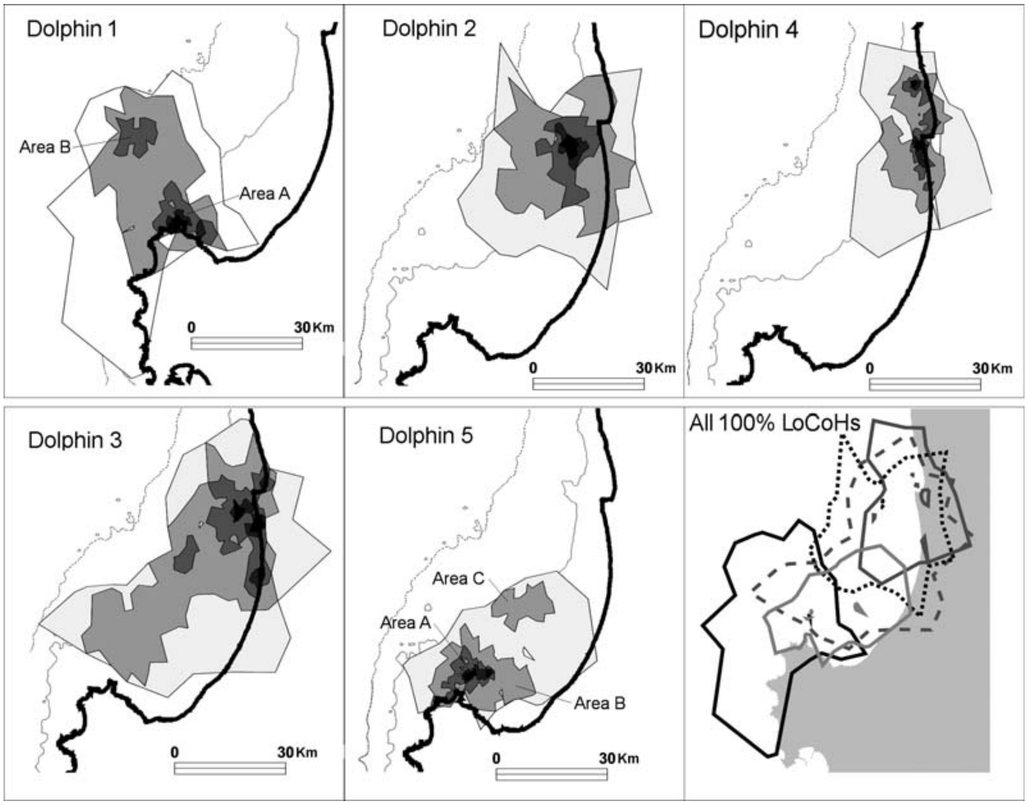

FIG. 3.—Series of maps showing home ranges as local convex hull (LoCoH) polygons with density isopleths (Getz and Wilmers 2004) for 5 female Heaviside's dolphins fitted with satellite transmitters off the west coast of South Africa. Contours shown are the 50-m and 100-m depth. Isopleths shown are 100% (lightest shading), 90%, 50%, 20%, and 10% (darkest gray shading). The bottom right figure shows the 100% LoCoH isopleths for all dolphins.

the tagging period, but it did move to the far southwestern part of its range, to a lesser-used area where it spent considerable time (39–72 h postrelease) moving around significantly farther offshore than normal (Table 3). Although no significant variations in speed were observed (Table 4), the movement to the southern subregion seems to indicate some degree of capture-site avoidance.

The distribution of dolphin 4 was generally much closer to shore than that of the other dolphins. The animal was significantly farther from shore than normal during the first 24 h postrelease, spent a 10-h (21–31 h postrelease) possible adjustment period very close to shore in a small localized area (approximately 4 km along shore) to the south of the MCP region, and then moved even farther offshore (significantly so; Table 3) and southward into the central offshore area of St. Helena Bay. The dolphin moved significantly faster than normal in the 48- to 72-h postrelease period (Table 4), when it moved rapidly from the southern offshore region to the far

TABLE 3.—Comparisons of distances offshore (m) during the first 72 h after being fitted with satellite transmitters to the mean distance offshore for the remainder of the data for each Heaviside's dolphin (distance values are back-transformed for analyses requiring transformed data). Values that differ significantly from the remainder of data are in italics and are marked with asterisks (ns not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Dolphin no.	Remainder of transmission time		1–24 h		24–48 h		48–72 h	
	n	$\bar{X}$	n	$\bar{X}$	n	$\bar{X}$	n	$\bar{X}$
1	428	11,282.8	13	9,854.9 ns	13	8,528.4 ns	16	*5,286.4**
2	313	8,897.1	5	*4,065.9**	9	4,860.9 ns	11	*6,870.7***
3	578	8,162.8	14	5,893.8 ns	15	9,751.9 ns	13	*13,567.7***
4	490	3,433.5	17	*6,594.2***	13	*8,180.9****	17	3,548.3 ns
5	693	7,567.8	14	9,519.8 ns	15	7,173.9 ns	15	7,333.2 ns

TABLE 4.—Comparisons of speeds (m/s) during the first 72 h after being fitted with satellite transmitters to the mean speed for the remainder of the data for each Heaviside's dolphin (values for speeds are back-transformed for analyses requiring transformed data). Values that differ significantly from the remainder of data are in italics and are marked with asterisks (ns not significant, *** $P < 0.001$).

Dolphin no.	Remainder of transmission time		1–24 h		24–48 h		48–72 h	
	n	$\bar{X}$	n	$\bar{X}$	n	$\bar{X}$	n	$\bar{X}$
1	428	0.959	12	0.927 ns	13	0.814 ns	16	1.07 ns
2	313	1.299	4	1.005 ns	11	0.984 ns	7	1.337 ns
3	578	0.942	13	0.932 ns	15	1.079 ns	13	0.981 ns
4	490	0.821	16	1.057 ns	13	0.934 ns	17	*1.479****
5	693	0.736	13	*1.075****	15	0.732 ns	15	0.890 ns

northern part of its range before returning southward toward the center of its utilized range. The animal's movements well outside even the MCP area suggest a reasonably strong avoidance of the capture site.

Dolphin 5 showed the strongest reaction to the tagging procedure in that it was the only animal that showed possible range shift as a response and took more than 72 h to settle. After being released the animal moved offshore and southward into the central reaches of St. Helena Bay, during which it covered nearly 25 km in 8 h, and moved significantly faster (but not farther from or closer to shore) than average (Tables 3 and 4). Although after 72 h the dolphin had returned to within about 10 km of its capture location it continued moving northward, ending in Elands Bay, the northernmost point reached by this dolphin and well outside the main range. Only on the 5th day after capture did the dolphin move southward, ending in the center of the area used during the remainder of the monitoring period. Because of the large area covered and fast swimming speeds recorded from this animal over the first 5 days, we believed that it was appropriate to remove the first 120 h of data posttagging for home-range analysis.

Dolphin 6 only transmitted data for 11 days, which is unfortunate because it was the only male caught and tagged in this project. The reason for transmitter failure is unknown but possibly caused by the aerial breaking. The 1st transmissions were only received on the night after the morning of capture (this tag transmitted for 8 h and was inactive for 12 h) and indicate the animal was 16 km offshore due north of the tagging position. The dolphin lingered offshore in this region for 5 days after tagging. Few locations were received from this animal per day but during the last few days of the transmission the animal started a directed southward movement, passing Shelley Point and North West Bay, and the last locations were received from offshore of Saldanha Bay.

Diurnal movements.—All 5 animals on a continuous transmission cycle showed a clear inshore–offshore movement pattern, being significantly closer to shore and in significantly shallower water in the morning hours (primarily 0500 h to 1300 h) and moving offshore usually just after noon and remaining in deeper waters until approximately 0300 h (Table 5; Fig. 4). Clarity of these results is slightly reduced due to the dolphins being in a large bay, because movement away from one shore may bring them closer to another. The hypothesized reduction in travel speed during feeding and resting periods was not as clear as the onshore–offshore movement; only 3 of the 5 animals showed significant variation in speed over the day (Table 5) and post hoc tests (Tukey's honestly significant difference) were not particularly informative. All dolphins exhibited 2 periods of reduced speed at similar times (see means in graphs), 1st between midnight and 0500 h then again from the late morning (1000 h or 1100 h) into the afternoon (between 1400 h and 1700 h; Fig. 4).

Along-shore range.—Along-shore range was not easy to measure in this study because 3 of the 5 dolphins (dolphins 1, 3, and 5) had ranges that extended out into St. Helena Bay and did not readily yield to the measure; these animals had generally longer along-shore ranges than the 2 dolphins on the straight coastline (Table 6).

Table 5.—Kruskal–Wallis analysis of variance results for the diurnal variation (by hour of the day) in the distance from shore, depth, and speed of travel of Heaviside's dolphins carrying satellite-linked transmitters. Data from the first 72 h after tagging (or first 120 h for dolphin 5) are omitted from analysis; *d.f.* = 23 for all analyses. Italics indicate analyses in which there was significant variation in values across the 24-h daily cycle.

Dolphin no.	Shore distance		Depth		Speed	
	H	*P*	*H*	*P*	*H*	*P*
1	67.0	*<0.0001*	68.41	*<0.0001*	31.55	0.109
2	72.55	*<0.0001*	72.50	*<0.0001*	49.25	*0.0012*
3	207.55	*<0.0001*	263.92	*<0.0001*	35.06	0.0514
4	112.02	*<0.0001*	116.7	*<0.0001*	40.06	*0.0152*
5	52.85	*0.0004*	96.25	*<0.0001*	65.28	*<0.0001*

Home-range stability.—The growth of home ranges (measured as 100% MCP) in 5-day increments (Fig. 5) showed some degree of tapering off before the end of transmissions, with dolphins 5 and 4 having the most stable ranges and dolphin 2 the least stable. The low density of locations beyond the 90% LoCoH isopleth is largely due to location inaccuracies (especially those on land) and the occasional foray by dolphins beyond their main areas of occupancy (see details of dolphin 1 in "Longer-term movements and distribution patterns" section below). The observed degree of stability in the measured home ranges indicates that they are probably representative over this timescale, at least for females of the species.

Local convex hulls.—The LoCoH method (Getz and Wilmers 2004) is analogous to calculating and combining many small MCPs for sequential (overlapping) subsets of locations, where the number of locations (k) in each subset is chosen to minimize holes or gaps in the resulting home range that can not be justified by known geography (such as those that would occur for lakes, islands, or headlands). The LoCoH home range effectively covers the minimum area needed to encompass all the location points (and thus fits inside the MCP borders; Fig. 5), and indicates density isopleths within the area used (Table 7; Fig. 3).

We believe the 90% isopleth (i.e., covering 90% of the locations) best represents the main area used by each dolphin and is the most realistic measure of area usage for comparison between individuals, since none of the 90% isopleths cover much land and are more independent of outliers from both actual movements and Argos locations. The 100% isopleth area, which takes into account all the remaining locations, is indicative of the region that may be covered by each dolphin on occasional forays. The borders of both the polygon methods used (MCP and LoCoH) end abruptly at the outermost location point, thus defining them as the farthest point a dolphin will ever move. With the apparent absence of any territorial conflict and an effectively borderless environment, we feel that the abrupt borders delineated by the methods used are not entirely representative. The area extending beyond the 90% isopleth out

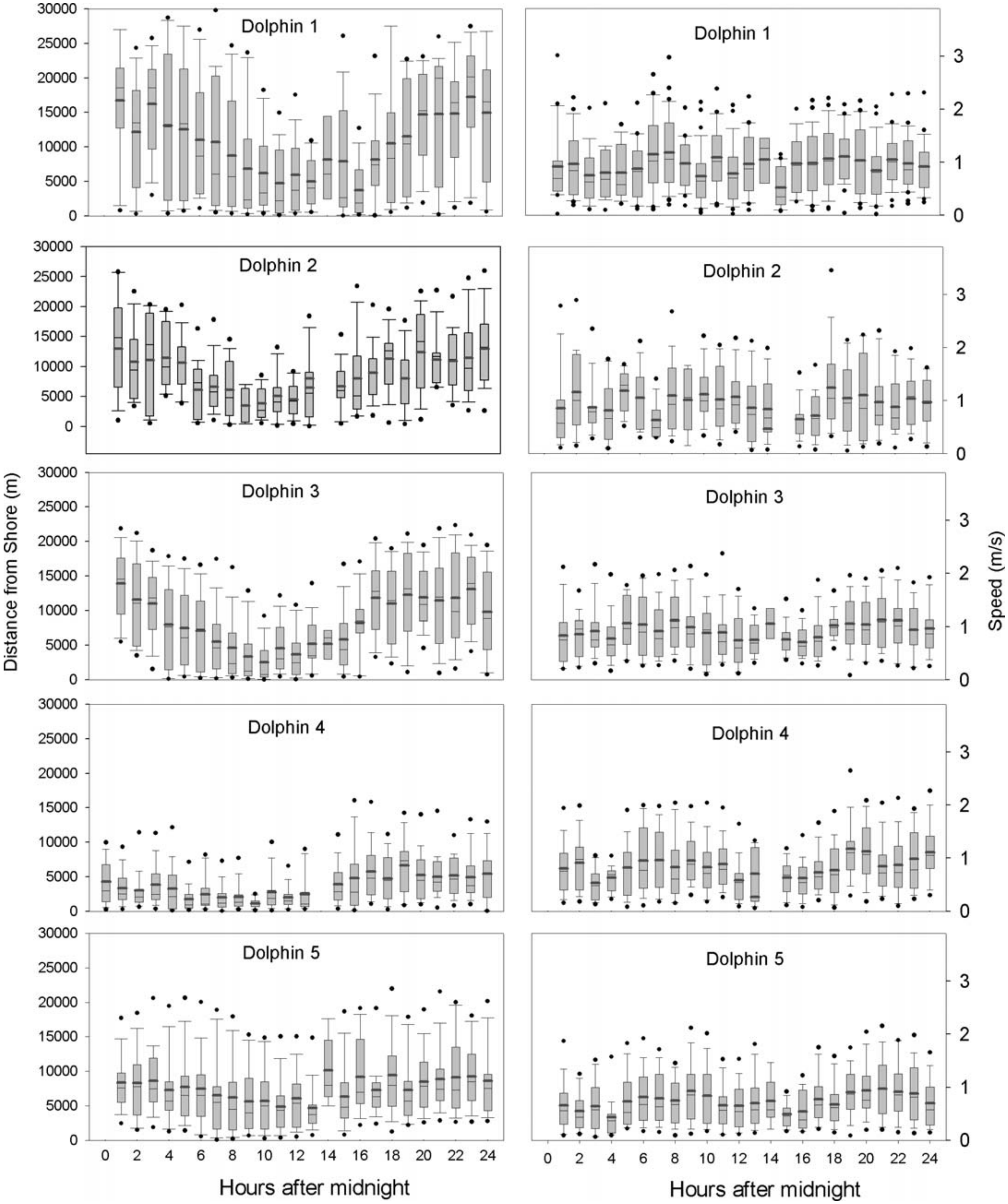

FIG. 4.—Distance from shore (m) on left and speed (m/s) on right of Heaviside's dolphins fitted with satellite transmitters off west South Africa. Means are shown as thick lines, medians as thin lines within boxes. Points, whiskers, and boxes represent the 5th, 10th, 25th, 75th, 90th, and 95th quartiles, respectively.

TABLE 6.—Along-shore distances (km) of the 90% and 100% local convex hull (LoCoH) home ranges of Heaviside's dolphins studied off the west coast of South Africa.

Dolphin no.	90% LoCoH	100% LoCoH
1	43.7	83.1
2	37.3	46.8
3	43.4	62.5
4	33.3	38.8
5	25.4	68.0
$\bar{X} \pm SD$	36.6 ± 7.6	59.8 ± 17.5

to the 100% isopleth border (and probably the 100% MCP border and possibly a little way beyond) should instead be regarded as an area in which the probability of occupation by the animal is gradually reduced, but not zero. In general, we are satisfied with the LoCoH method to describe home-range usage by Heaviside's dolphins. The only real drawback of the LoCoH method is that there is no temporal component in the description of home range and this needs to be analyzed separately and is done below in the "Longer-term movements and distribution patterns" section. We conclude that the home ranges used by these 5 animals ranged from 301.9 to 1,027.6 km^2 (90% LoCoH isopleths) and 875.9 to 1,989.6 km^2 using the 100% LoCoH isopleths (Table 7).

Home range and body size.—Not all dolphins could be weighed but their body mass in kilograms was estimated from their total body length in meters ($\text{weight} = 17.59 \times \text{length}^{2.66}$—Best and Abernethy 1994) and correlated against the home-range size (km^2) of each animal (Fig. 6). The measured home ranges generally increased with body size, as predicted (Fig. 6) but are 2.5–20 times larger than those predicted for a terrestrial carnivore of the same mass ($\text{area}_{\text{ha}} = 170 \times \text{mass}^{1.03}$—Lindstedt et al. 1986). The exact relationship varied with the measure of home range used: $100\%\ \text{MCP} = 20.297 \times \text{mass}^{2.2167}$; $95\%\ \text{MCP} = 26.127 \times \text{mass}^{2.0435}$; $100\%\ \text{LoCoH} = 94.619 \times \text{mass}^{1.7884}$; $90\%\ \text{LoCoH} = 0.5428 \times \text{mass}^{2.8495}$.

Longer-term movements and distribution patterns.—No measure of home range currently takes into account the temporal aspect of an animal's area usage. We have given some idea of the movements of individual dolphins on a daily timescale, but longer-term movements in the order of several days are not conducive to any form of statistical analysis and we are therefore reduced to describing any interesting anomalies from the raw data itself and contrasting the behaviors of individuals. The instrument on animal 2 had the oldest battery and consequently was the least precise and least informative of the animals, whereas dolphin 6 (12 days transmission) is discussed in the "Tag effects" section. Here we briefly discuss the movements of dolphins 3 and 4 and then contrast the movements of dolphins 1 and 5 in slightly more detail to better highlight some individual differences that may impact on any future surveys or population estimates.

The highest density area used by dolphin 3 was inshore along the coast south of Elands Bay; it also had a slightly higher-usage area in the south of its range with a "corridor" between (Fig. 3). This animal used both areas throughout the tagging period and exhibited the general onshore–offshore diurnal movement fairly predictably.

Dolphin 4 had the most nearshore distribution of all the tagged dolphins, hardly ever even crossing the 50-m depth contour (Fig. 3). Although it did exhibit onshore–offshore diurnal movement, this was not as pronounced as in the other

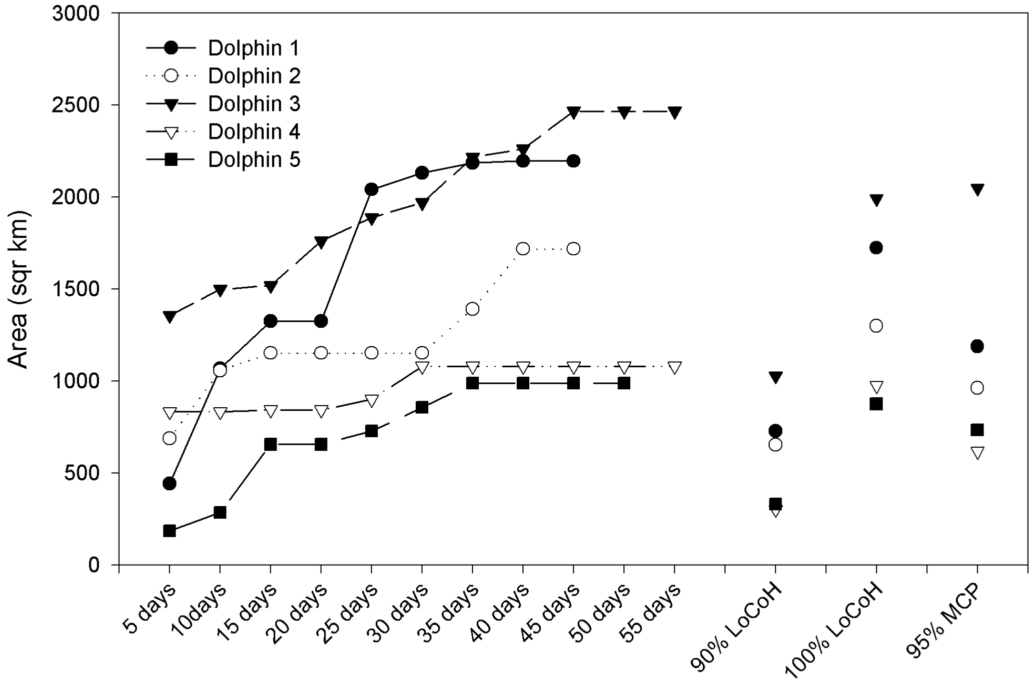

FIG. 5.—Minimum convex polygon (MCP) home-range growth in 5-day increments (area as km^2) of Heaviside's dolphins starting after impact period (72 or 120 h postrelease). Full 90% and 100% LoCoHs and 95% MCPs shown on right of graph for comparison.

TABLE 7.—Size of the area covered (km^2) by the each of the 10%, 20%, 50%, 90%, and 100% isopleths (indicating decreasing density and increasing coverage of received, filtered locations) of the local convex hull home ranges of Heaviside's dolphins fitted with satellite-linked transmitters off the west coast of South Africa, as well as the value of k (number of nearest neighbor locations) used to calculate local convex hull home ranges.

Dolphin no.	k	Area covered by isopleths (km^2) 10%	20%	50%	90%	100%
1	15	8.53	22.96	149.31	728.41	1,723.15
2	13	11.82	32.14	148.08	653.52	1,299.73
3	14	18.58	45.43	239.49	1,027.62	1,989.61
4	15	5.83	16.69	72.49	301.97	973.82
5	15	5.02	14.35	61.65	301.97	875.96

animals (see "Diurnal movements" section). This animal had 2 high-density usage areas, in the north and center of the LoCoH range. Other than tending toward the northern part of its range during the early part of the tagging period and toward the south in the 2nd part, the dolphin used its whole range throughout the tagging period.

The LoCoH range of dolphin 1 shows 2 areas of higher use, an area very close to shore in and around Britannia Bay (area A) and an offshore area roughly 22 km north–northwest of the inshore area (area B; Fig. 3). For the first 5 days of the data set, the dolphin moved between this inshore resting area and the offshore feeding area on the diurnal cycle shown previously. It then moved south along the coast and spent 4 days (26–30 August) in the westernmost section of its home range (showing normal onshore–offshore diurnal movements) in the area due west of area A. The dolphin then moved back to the Britannia Bay area where it then spent 5 days very close (<5 km) to shore, not moving offshore at all. It resumed the normal onshore–offshore movement between areas A and B for 9 days, after which it made a 1-day (12 September) foray around the coast to the most southerly point it reached, near Saldanha Bay. The dolphin then moved north to area B and spent 11 days in a scattered region centered on area B staying at least 5 km offshore all this time. During the last 8 days of transmission it returned to diurnal movement between areas A and B.

Dolphin 5, despite a high degree of range overlap, shows quite different movements compared to animal 1. Where the main center of distribution of animal 1 was actually within Britannia Bay, the center of distribution of animal 5 was roughly 5 km offshore off the bay (Fig. 3) and in general this animal had far fewer received locations close to shore, and did not generally range as far offshore as dolphin 1. It must be noted that although dolphin 1 was captured within the area regarded as the postimpact home range, dolphin 5 was captured well outside its postimpact range (~10 km from LoCoH border and ~40 km from the highest-density LoCoH region), and it was the only animal that was believed to be impacted for more than 72 h by the tagging procedure. When in the main area of distribution, area A, this animal stayed within about 12 km of the coast all the time, although it still had a clear onshore–

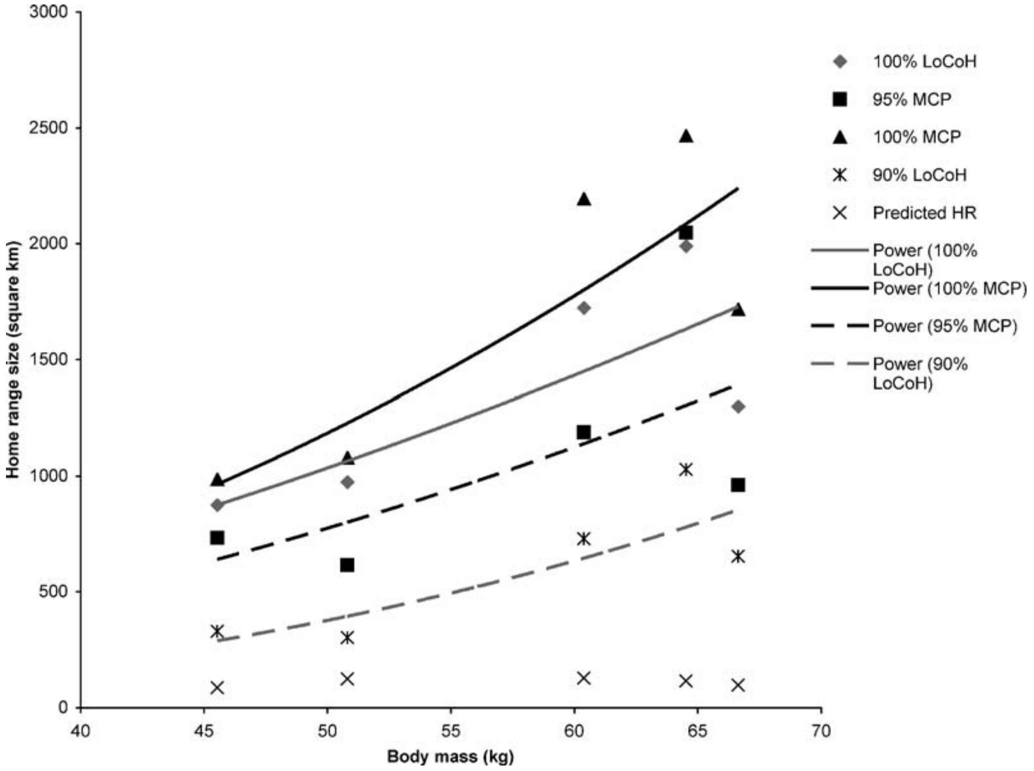

FIG. 6.—Relationships between body size (using mass estimated from total length) and home-range size (km^2) for 4 measures of home range; local convex hulls (LoCoHs) and minimum convex polygons (MCPs). Compare with Table 1, which gives body length. Power curves were fitted for each measure of home range. Predicted home-range sizes are from Lindstedt et al (1986) based on terrestrial carnivores.

offshore diurnal movement. After spending 2 days in area A it moved to the more offshore area B for 2 days, almost in the center of the bay, before returning to area A, where it spent almost a month with an occasional foray into the 100% isopleth region. In late December, animal 5 spent 5 days out in area C, an area it had barely touched upon before this, 15–20 km from area A and 15 km from the nearest coast. After this period the dolphin again returned to a distribution centered on area A (although slightly on the west side of the highest-density area) with occasional forays into the 100% isopleth region, including a trip to the northernmost edge of its range.

DISCUSSION

Satellite telemetry provides a very powerful tool for studying the movements of individual cetaceans and is the only available method for studying an animal's movement 24 h a day for long periods, and as such can sometimes produce surprising results. Read and Westgate (1997) found that satellite-tracked harbor porpoises (*Phocoena phocoena*) in the Bay of Fundy-Gulf of Maine area moved much greater distances than previously thought, and occupied previously unrecognized feeding areas with implications for the population's management regime. Suydam et al. (2001) found belugas (*Delphinapterus leucas*) in the eastern Chukchi Sea to be using a previously unrecognized offshore deepwater habitat. In contrast, the telemetry results from this study did not show any unpredicted movements or behaviors but gave very good support of our 2 main hypotheses, that Heaviside's dolphins exhibit some degree of site fidelity (or have a limited home range), at least over the 2 months of the study period, and that the onshore–offshore diurnal movement observed by us was shown by all the tagged dolphins. However, the fine scale of our results do highlight the high degree of variability between individuals in both behavior and home-range sizes, a pattern frequently observed in studies focusing on single animals, both those using telemetry (Read and Westgate 1997; Suydam et al. 2001) and photo identification (e.g., Odell and Asper 1990).

Diurnal movement patterns.—The pattern of diurnal onshore–offshore movement was common to all the tagged dolphins and was the overriding behavioral pattern observed, although significant individual variation was observed. Dolphin 4 stayed closest to shore of all the tagged dolphins (within 6 km from shore) and rarely crossed the 50-m depth contour, dolphin 5 also stayed largely within the 50-m depth contour but farther offshore, whereas dolphin 1 with an overlapping distribution moved large daily distances up to 22 km from within Britannia Bay to offshore waters 100 m deep; yet despite these large variations in range, depth, and general distance from shore, all the dolphins tended to exhibit the inshore–offshore diurnal movement, suggesting that it is very closely tied to the ecology of the species.

The offshore movement of Heaviside's dolphins at night is believed to be strongly linked to the vertical migration of one of their main prey species, juvenile hake (probably shallow water hake [*Merluccius capensis*]—Sekiguchi et al. 1992), which are known to migrate vertically in the water column on a diurnal scale (Pillar and Barange 1995), coming closer to the surface to forage at night. A similar pattern of offshore movement to feed on fish associated with the vertical migration of the deep scattering layer was observed by Würsig et al. (1991) for dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand, and by Norris and Dohl (1980) and Lammers 2004 for Hawaiian spinner dolphins (*Stenella longirostris*). The associated period of inshore movement of Heaviside's dolphins is thought to be for rest, socializing, and a potentially reduced level of predation near shore, as in spinner dolphins (Lammers 2004).

The variation in speed of movement throughout the day is not as clear as the daily variation of depth and distance from shore. In general, all the tagged dolphins exhibited 2 minima in speed of movement, in the early afternoon (roughly 1100–1500 h) and from midnight to early morning (0000–0500 h). This pattern suggests that after a high-speed active morning inshore, the dolphins move offshore slowly then seem to speed up, possibly while searching for prey and feeding, then slow down again after midnight, either while feeding in a fairly localized area or moving slowly back inshore. With the current data set it is not possible to say exactly when the dolphins were feeding, and future studies should include time–depth recorders and temperature sensors to investigate this aspect of their ecology in greater detail.

Home range, along-shore range, and movements.—Few published examples of a full home range exist for small cetaceans; most work on individual distribution and site fidelity has been done with photo identification or similar inshore boat-based work (Bräger et al. 2002; Odell and Asper 1990; Würsig and Harris 1990) limited to working in daylight hours, usually close to shore. Because of the relatively low number of known individual locations (at least compared to satellite telemetry studies) authors tend to define along-shore ranges (e.g., Ballance 1992; Bräger et al. 2002) rather than home ranges per se. Our measure of along-shore range as well as a full home range in this study allows for comparisons with other and future studies using primarily photo-identification techniques.

Ecological theory predicts that in general home-range size should increase with body size (Buskirk 2004; Lindstedt et al. 1986) and, because of the reduced cost of locomotion for swimming animals, dolphins should have larger home ranges than terrestrial animals of the same body size (Connor 2000). As predicted, Heaviside's dolphins have a much larger home range than that predicted by the model of Lindstedt et al. (1986) for terrestrial carnivores; however, for all measures of home range used the relationship between the 2 is well above the three-fourths power expected from metabolic requirements or the linearity more commonly observed (Lindstedt et al. 1986). Larger territorial mammals require a home range that is larger than predicted from metabolic needs alone because they share resources with their neighbors more than smaller animals do (Buskirk 2004; Jetz et al. 2004); Heaviside's dolphins do not hold territories so it is perhaps this large degree of home-range overlap and the associated sharing with the neighbors that causes range size to increase so rapidly with body size; however, sample sizes are small and we only have good data from female dolphins. The relationship linking body size to home-range size in odontocetes seems to break down in interspecies comparisons. Although the along-shore ranges measured in this study were of the same order and tended to be slightly larger that those measured for the closely related and slightly smaller Hector's dolphins (average 31.0 km ± 2.43 *SD* long—Bräger et al. 2002), satellite-monitored harbor porpoises in the North Sea (Teilmann et al. 2004) and in the northeastern United States (Johnston et al. 2005) have far larger ranges (7,738–11,289 km^2) and are far more transitory (although over more than 3–4 times the monitoring period) than the slightly larger Heaviside's dolphins in this study. Evidence from different populations of bottlenose dolphins (*Tursiops truncatus*) and dusky dolphins suggests that ecology and habitat type (particularly openness) may override body size as the determining factor in home-range or along-shore range size. The minimum linear home ranges of bottlenose dolphins in a protected, inshore, closed habitat in the Indian and Banana river systems in Florida vary from as little as 1.8 km to as much as 100 km (Odell and Asper 1990), whereas on the west coast of the United States bottlenose dolphins in a very open habitat are thought to be essentially transient along the California coast with very low site fidelity (Defran and Weller 1999). Dusky dolphins living in a shallow bay and feeding on schooling fish in Argentina differed in their ranging behavior and degree of site fidelity to dusky dolphins living in deeper, open water in New Zealand and feeding on vertically migrating prey (Würsig et al. 1991). The small sample sizes in this study and the large amount of variation within and between species somewhat limit comparisons made at this level but the evidence suggests that as for group size (Gygax 2002), home-range size in delphinids may be influenced by both phylogeny and habitat openness. However, none of these populations are reported to exhibit any territoriality, and despite varying degrees of site fidelity, ranges appear to overlap freely.

With respect to range and movements, the most important results from this study are that all tagged Heaviside's dolphins showed a clear onshore–offshore movement pattern on a daily scale, had a spatially limited range and exhibited some degree of site fidelity. Home ranges showed considerable variation between individuals where they varied in their size, shape, and proximity to shore, and even at the individual level the movements varied considerably and single animals both ranged widely, presumably in search of food, and remained in a fairly localized region for several days. Both these latter traits may influence attempts to count the dolphins.

These conclusions are limited to the 5 female dolphins for the period of monitoring in this study. Male dolphins might be expected to range more widely, and, over much longer monitoring periods even the home ranges of females might expand to some extent. Nevertheless, we believe that the ranges presented here are probably representative and certainly of the correct magnitude, unless the species exhibit some kind of as yet unsuspected seasonal movement.

Tagging and effects thereof.—The frequency of the locations received allowed us to examine in reasonable detail the movements of the animals posttagging. We interpreted the large movements away from the tagging site by some of the animals to be an initial avoidance of the tagging site as observed in harbor porpoises (Geertsen 2004; Teilmann 2000), which returned after "several days." Only 1 animal (dolphin 5) did not return to the tagging site in this study, suggesting it was more disturbed or more sensitive than the other dolphins. Nothing abnormal occurred during the capture or tagging of this animal and we must assume that the apparently greater reaction to tagging was due to higher individual sensitivity of this dolphin. Interpretation of this "reaction" in terms of home-range estimation is difficult; avoidance of the tagging site could mean underestimation of the existing range (e.g., dolphin 5) or extension of the normal range. Animal 6 was the only dolphin resighted postcapture and was swimming normally with 3 other animals (normal group size for Heaviside's dolphins) 8 days after capture and did not avoid the boat at all when approached; in fact this animal had actually attempted to bow ride the capture boat directly after release back into the water.

A dramatic increase in logging behavior (lying still at the surface) of a captive harbor porpoise on the day of tagging as well as the longer surfacing rolls observed (Geertsen et al. 2004) and a sinking backward behavior (after breathing, rather than a normal forward dive) observed in both harbor porpoises (Teilmann 2000) and bottlenose dolphins (Irvine et al. 1982) was thought to be a behavioral adaptation to the discomfort of the tagged fin striking the air–water interface. We could not observe such fine-scale behaviors with the data set used in this study, but the periods of localized movements of some of the animals (particularly dolphins 1 and 4) could represent a period when the dolphin was moving slowly and spending extended periods at the surface while adjusting to the feel of the tag.

In conclusion, our results suggest that researchers should be wary of the impact period of the tagging process on cetacean behavior and movements. We agree with Geertsen et al. (2004) that more focused study is needed on all the potential impacts of tagging on cetaceans over both the short and longer term.

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