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 ($Area_{ha} = 170Mass^{1.03}$; 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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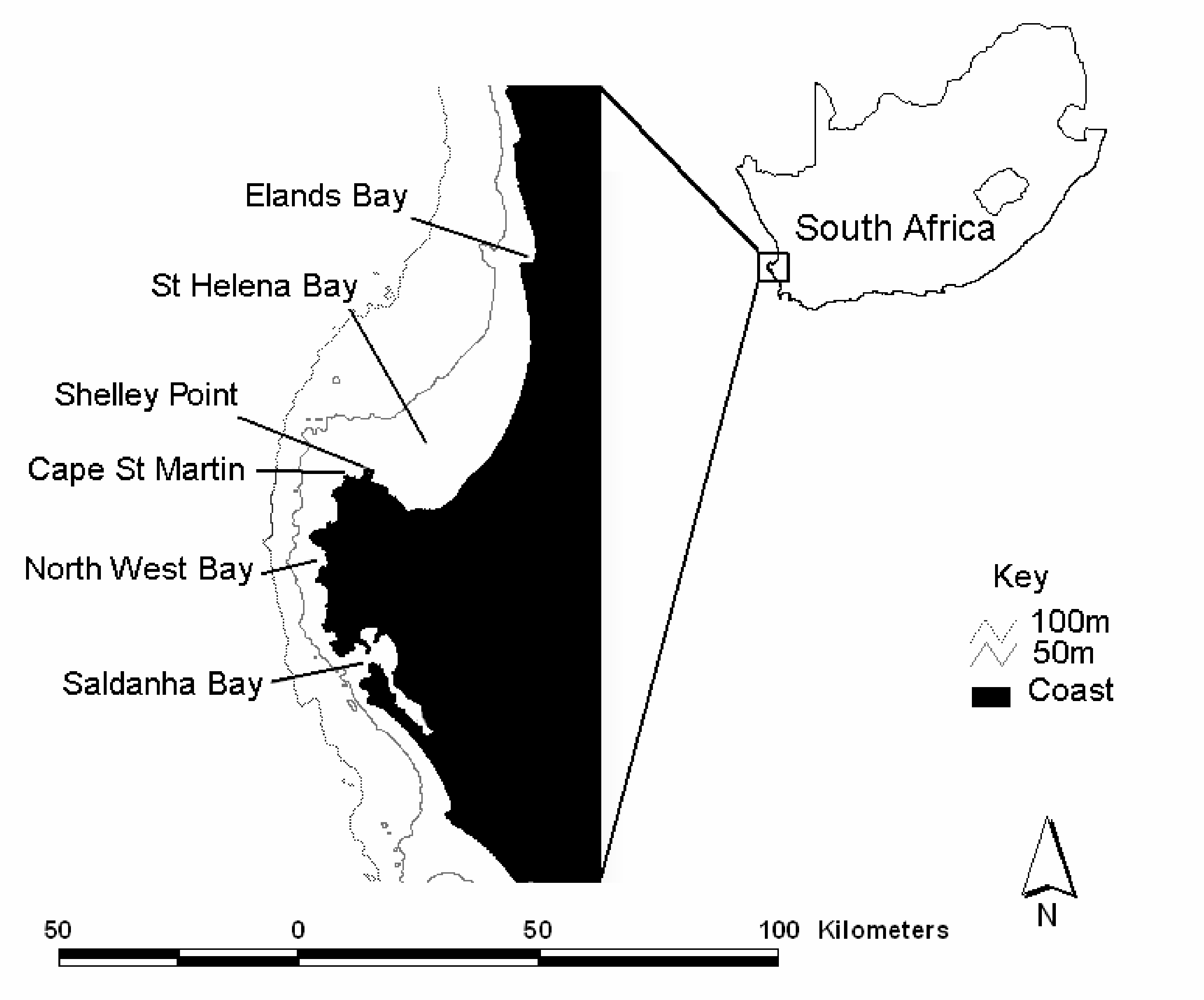

Figure 5.1. Study area and place names mentioned in the text.

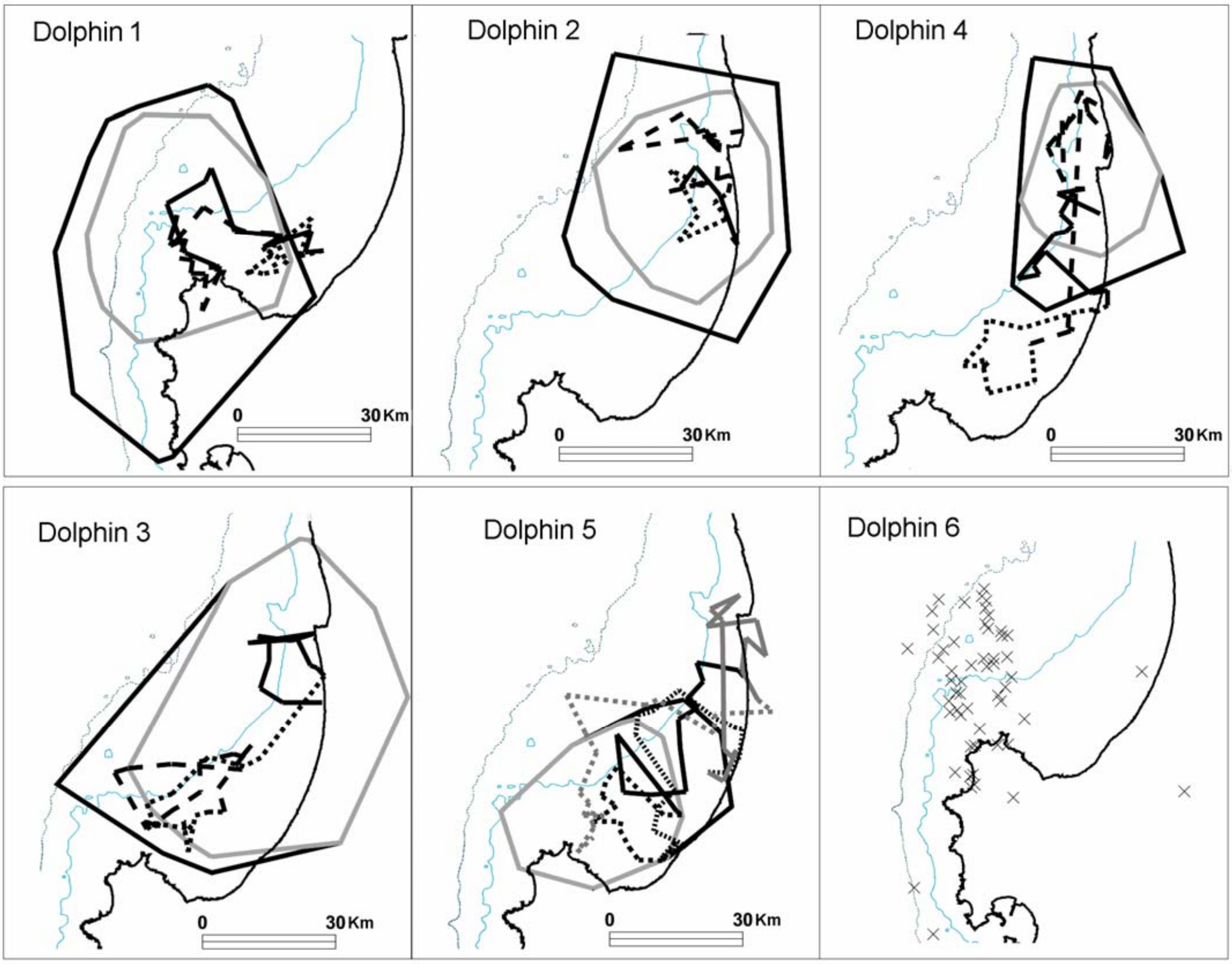

Figure 5.2. Series of maps showing home range as 100% (solid bold black line) and 95% (solid gray line) minimum convex polygons of 5 female Heaviside’s dolphins fitted with satellite-linked transmitters off the coast of South Africa. These ranges were calculated without the initial ‘‘impact period’’ (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.

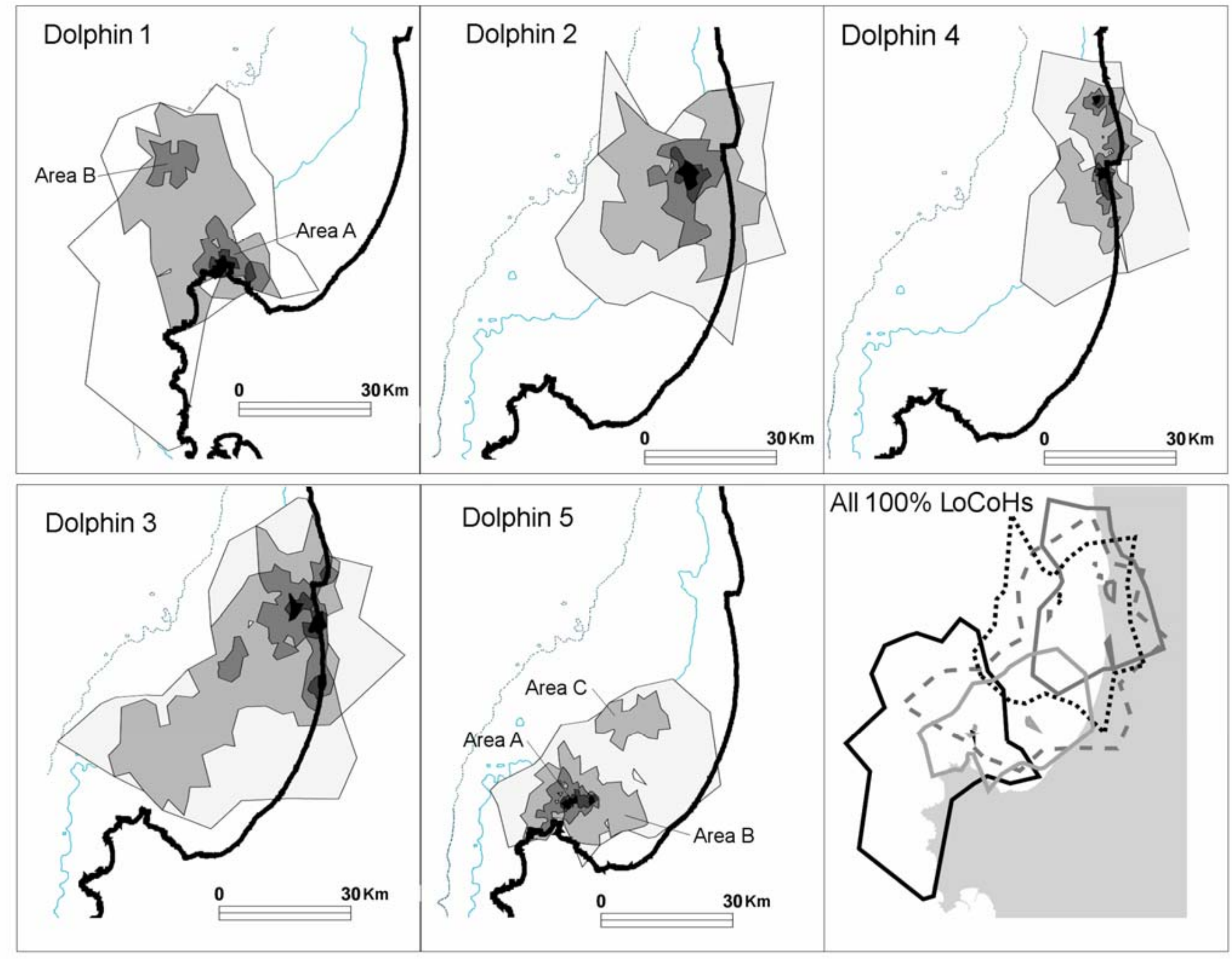

Figure 5.3. Series of maps showing home ranges as local convex hull (LoCoH) polygons with density isopleths (Getz and Wilmers 2004) for 5 female Heaviside’s dolphins fitted with satellite transmitters off the west coast of South Africa. Contours shown are the 50-m and 100-m depth. Isopleths shown are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

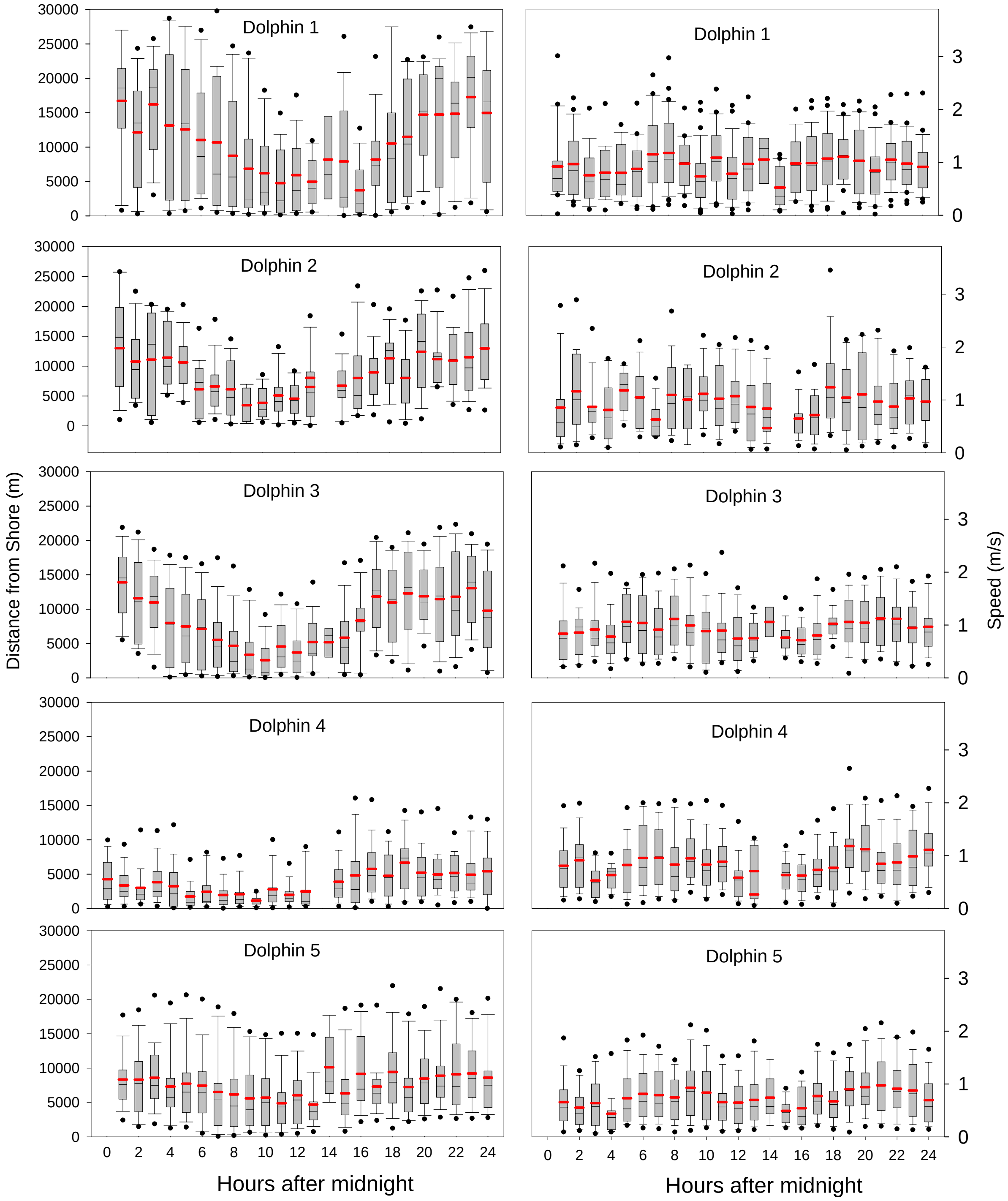

Figure 5.4. Distance from shore (m) on left and speed (m/s) on right of Heaviside's dolphins fitted with satellite transmitters off west South Africa. Means are shown as thick lines, medians as thin lines within boxes. Points, whiskers, and boxes represent the 5th, 10th, 25th, 75th, 90th, and 95th quartiles,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

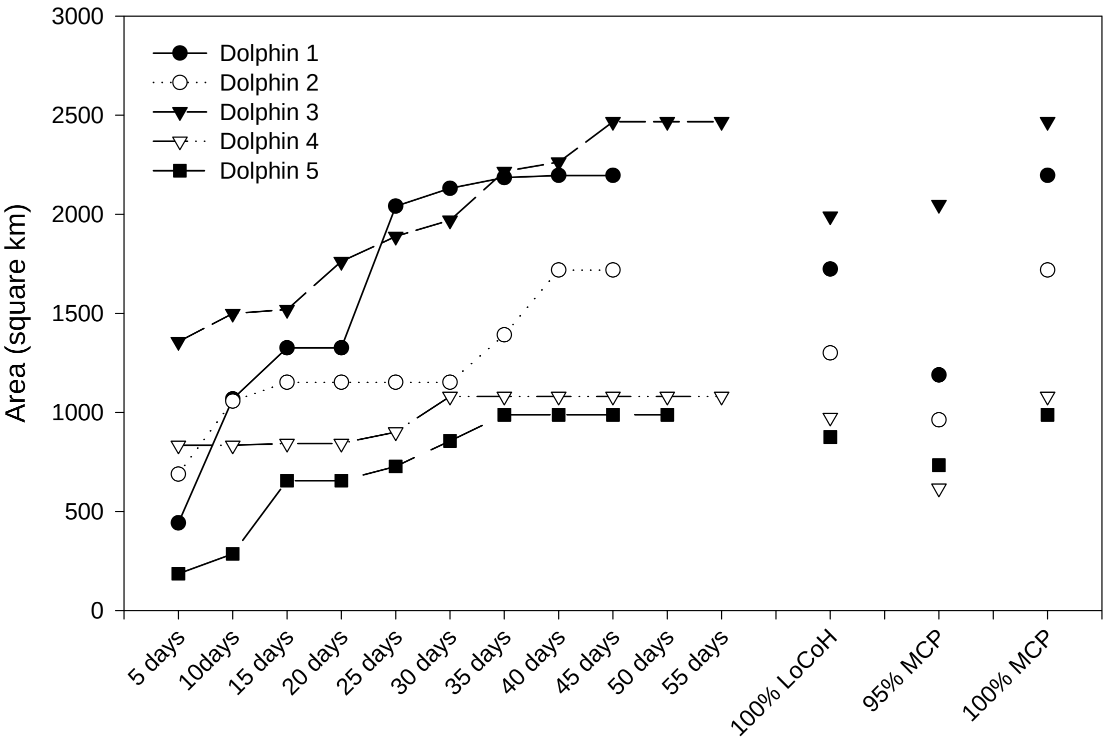

Figure 5.5. Minimum convex polygon (MCP) home-range growth in 5-day increments (area as km2) of Heaviside's dolphins starting afterimpact period (72 or 120 h postrelease). Full 90% and 100% LoCoHs and 95% MCPs shown on right of graph for comparison.

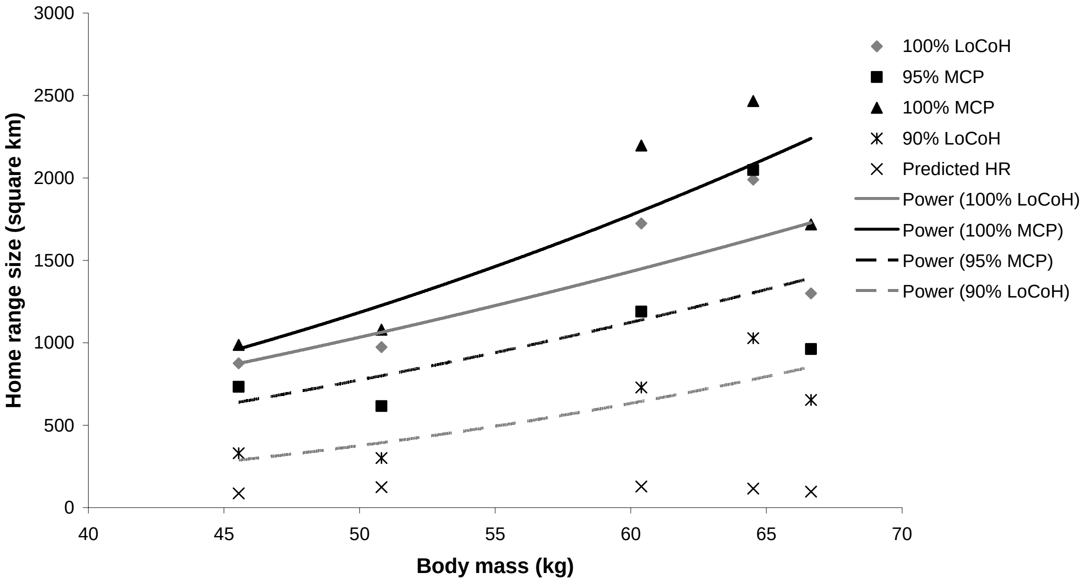

Figure 5.6.—Relationships between body size (using mass estimated from total length) and home-range size (km2) for 4 measures of home range; local convex hulls (LoCoHs) and minimum convex polygons (MCPs). Compare with Table 5.1, which gives body length. Power curves were fitted for each measure of home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