

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 km² (90% isopleths) and 875.9 to 1,989.6 km² 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.

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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

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)		Sex	Body length (cm)	Method of capture
			On deck	Total			
1	17229	18 August 2004	17	23	Female	159	Tail grab
2	14066	20 November 2004	25	27	Female	165	Tail grab
3	24274	20 November 2004	25	28	Female	163	Tail grab
4	16204	21 November 2004	22	26	Female	149	Head Net
5	24276	21 November 2004	22	25	Female	143	Tail grab
6	10015	12 August 2004	24	29	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 hardwearing 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

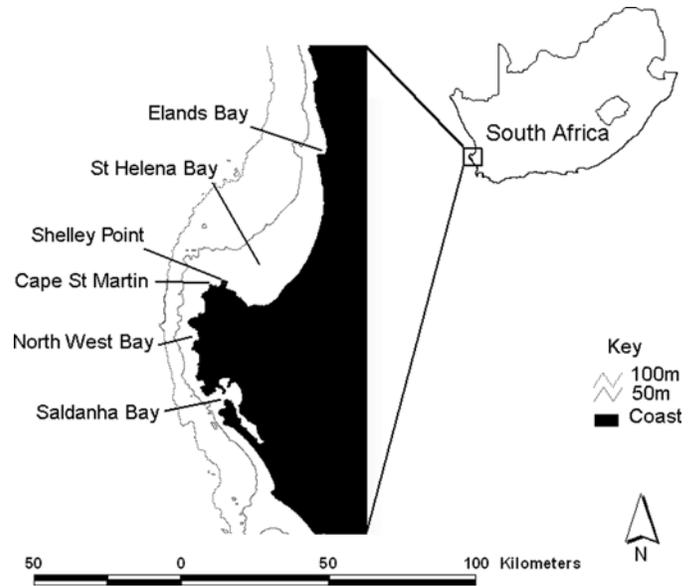


FIG. 1.—Study area and place names mentioned in the text.

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.

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

Dolphin no.	Transmission of location data		No. data points			Raw data in LCs 1–3	Points appearing to be on land	
	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 Wilmsers 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 (*Callorhynchus 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

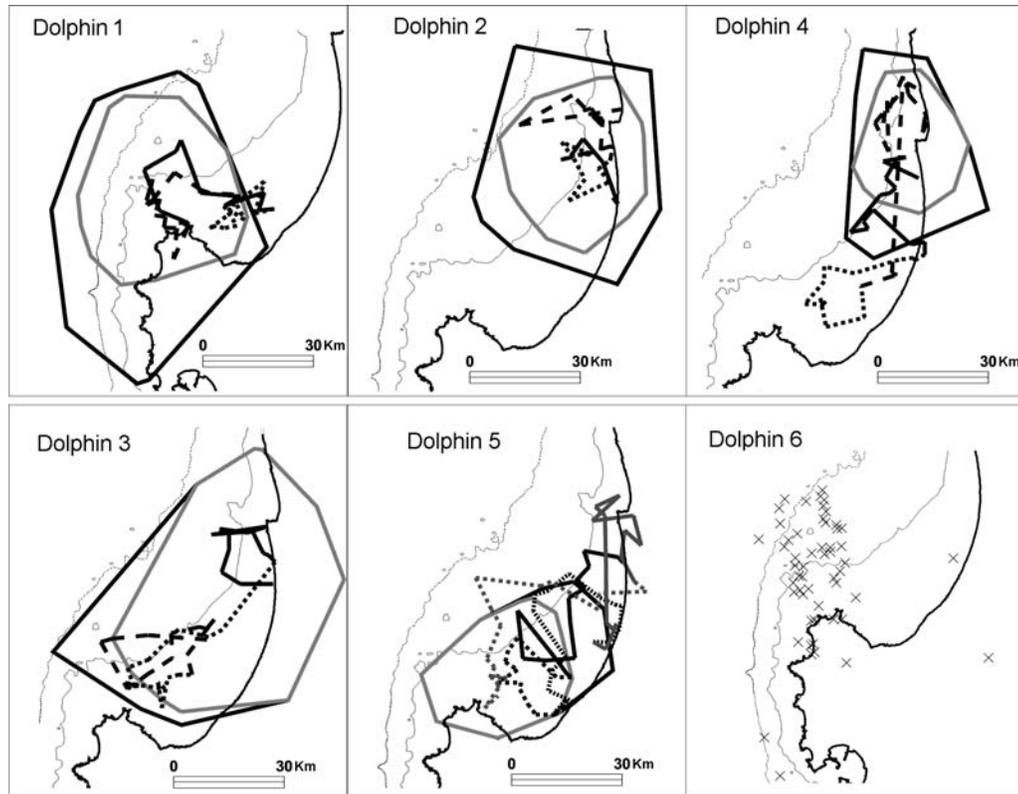


FIG. 2.—Series of maps showing home range as 100% (solid bold black line) and 95% (solid gray line) minimum convex polygons of 5 female Heaviside's dolphins fitted with satellite-linked transmitters off the coast of South Africa. These ranges were calculated without the initial "impact period" (first 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

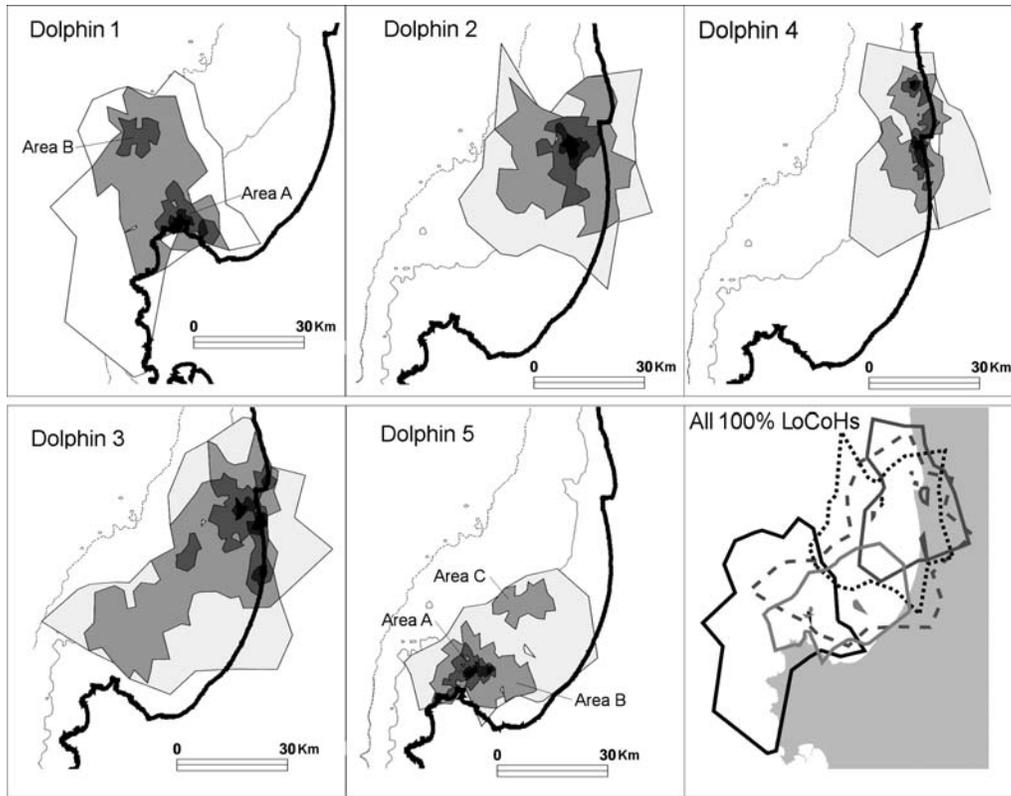


FIG. 3.—Series of maps showing home ranges as local convex hull (LoCoH) polygons with density isopleths (Getz and Wilmers 2004) for 5 female Heaviside’s dolphins fitted with satellite transmitters off the west coast of South Africa. Contours shown are the 50-m and 100-m depth. Isopleths shown are 100% (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	
	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\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	
	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\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

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	
	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>
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

generally longer along-shore ranges than the 2 dolphins on the straight coastline (Table 6).

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 Wilmsers 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

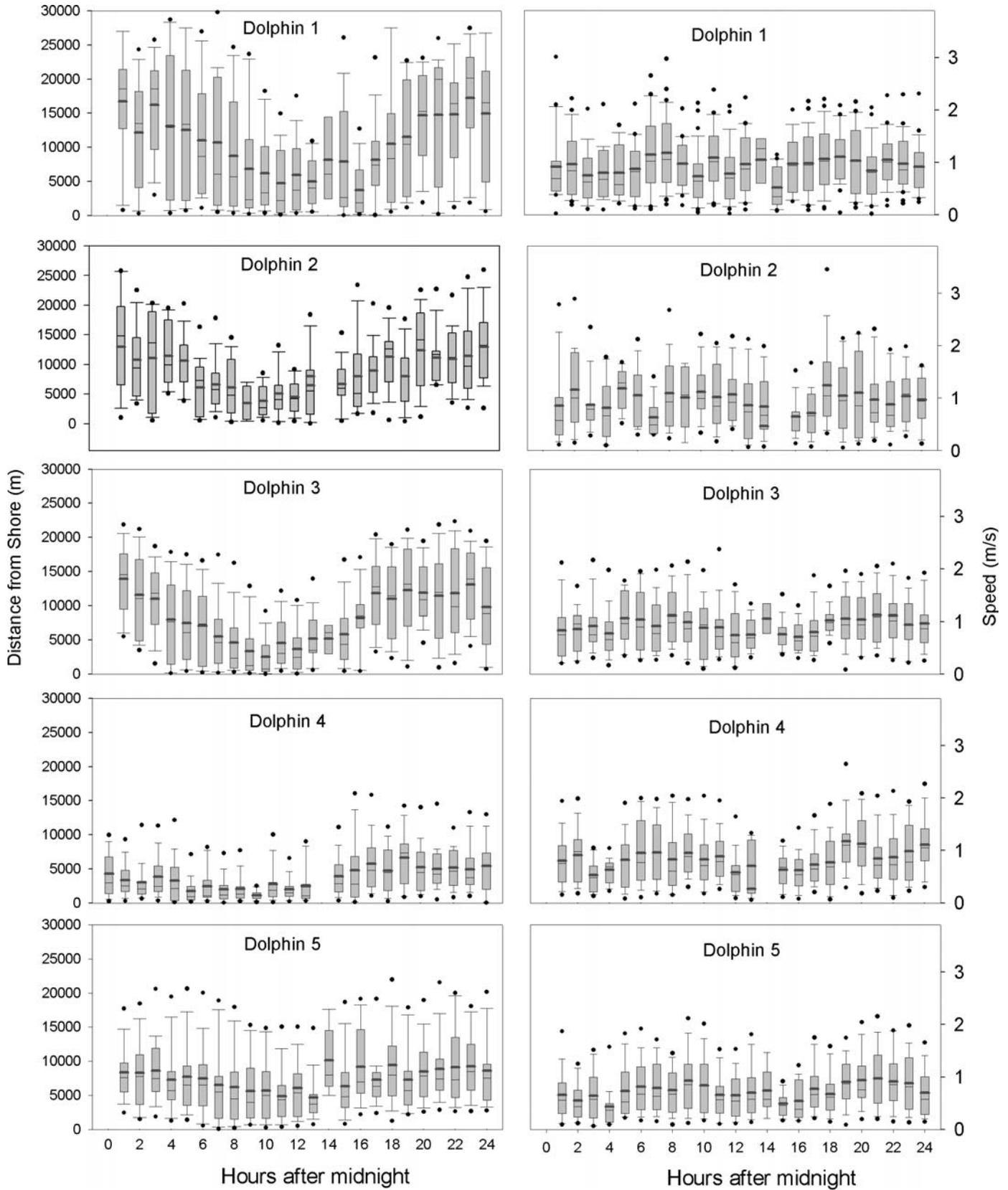


FIG. 4.—Distance from shore (m) on left and speed (m/s) on right of Heaviside’s dolphins fitted with satellite transmitters off west South Africa. Means are shown as thick lines, medians as thin lines within boxes. Points, whiskers, and boxes represent the 5th, 10th, 25th, 75th, 90th, and 95th quartiles, 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 km² (90% LoCoH isopleths) and 875.9 to 1,989.6 km² 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 (weight = 17.59 × length^{2.66}—Best and Abernethy 1994) and correlated against the home-range size (km²) 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 (area_{ha} = 170 × mass^{1.03}—Lindstedt et al. 1986). The exact relationship varied with the measure of home range used: 100% MCP = 20,297 × mass^{2.2167}; 95% MCP = 26,127 × mass^{2.0435}; 100% LoCoH = 94,619 × mass^{1.7884}; 90% LoCoH = 0.5428 × 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

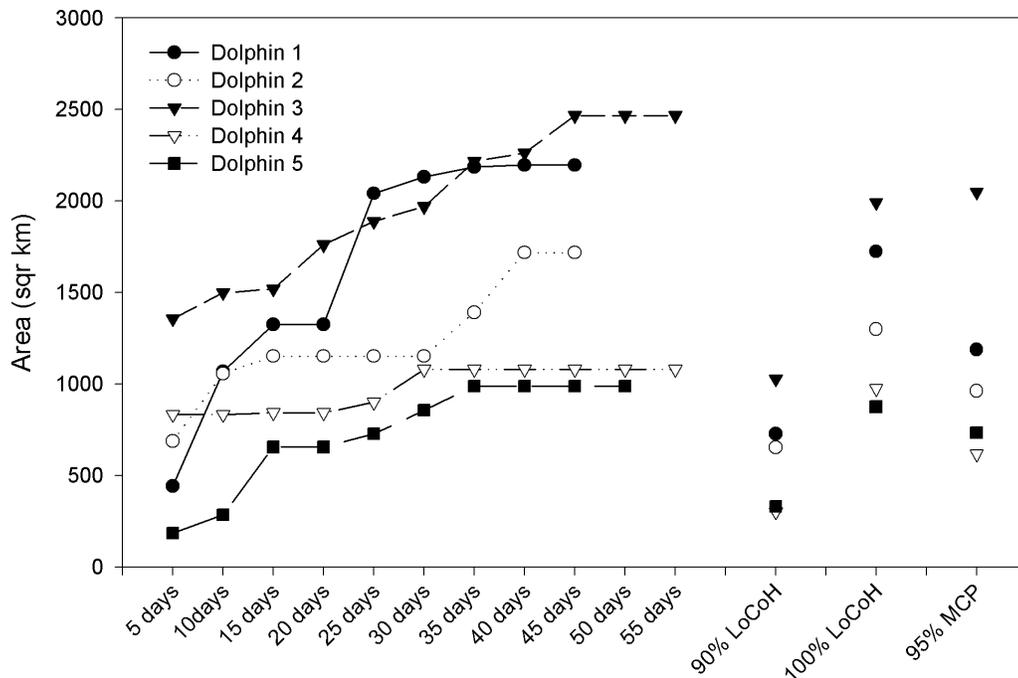


FIG. 5.—Minimum convex polygon (MCP) home-range growth in 5-day increments (area as km²) of Heaviside’s dolphins starting after impact period (72 or 120 h postrelease). Full 90% and 100% LoCoHs and 95% MCPs shown on right of graph for comparison.

TABLE 7.—Size of the area covered (km²) 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–

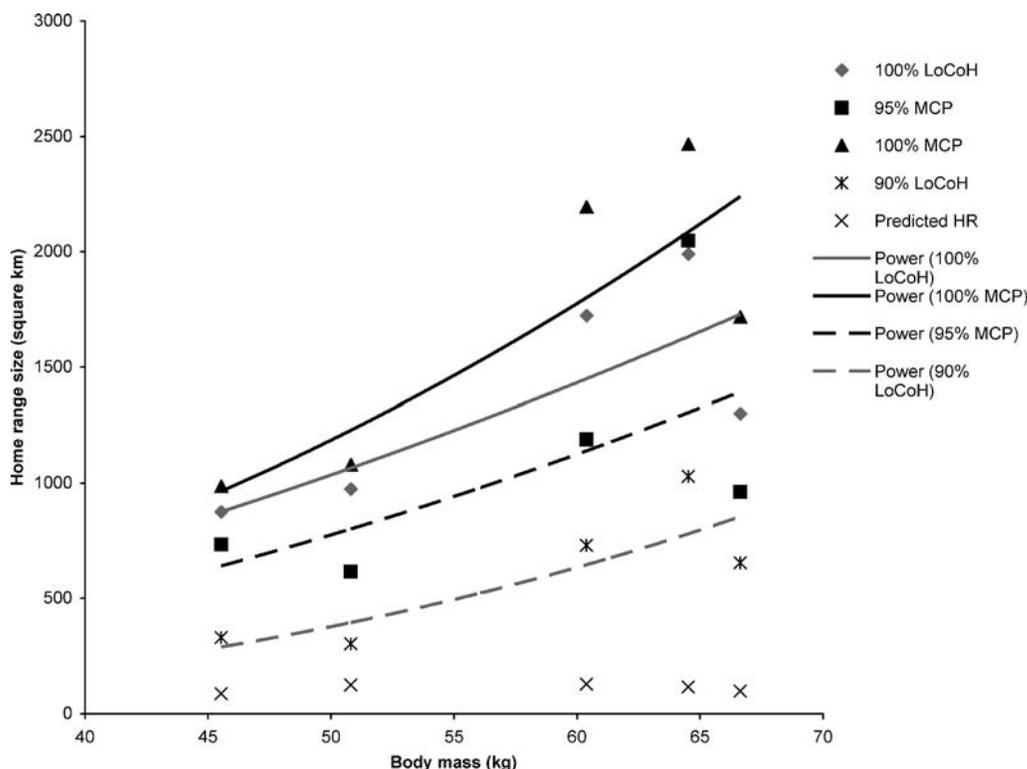


FIG. 6.—Relationships between body size (using mass estimated from total length) and home-range size (km²) for 4 measures of home range; local convex hulls (LoCoHs) and minimum convex polygons (MCPs). Compare with Table 1, which gives body length. Power curves were fitted for each measure of home range. 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 than those measured for the closely related and slightly smaller Hector's dolphins (average $31.0 \text{ km} \pm 2.43 \text{ SD}$ 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 ($7,738$ – $11,289 \text{ km}^2$) 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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