Chapter 4

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

Abstract

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

Introduction

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

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

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

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

Methods

Field techniques

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

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

Lab techniques: photographic data processing

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

Analysis: mark-recapture estimates

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

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

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

Eq 1

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

where

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

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

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

Variance for the estimate is calculated as:

Eq 2

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

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

Analysis: meeting assumptions of mark-recapture analysis.

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

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

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

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

Analysis: estimating the percentage of marked animals in the population

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

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

Analysis: estimating the total population size.

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

Total population size was then calculated by:

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

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

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

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

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

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

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

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

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

Comparison with satellite and field observations

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

Results

Petersen estimates of the number of well marked individuals

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

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

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

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

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

Investigations of theta - the mark rate of animals.

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

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

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

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

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

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

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

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

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

Interpretations of relevant satellite tag data.

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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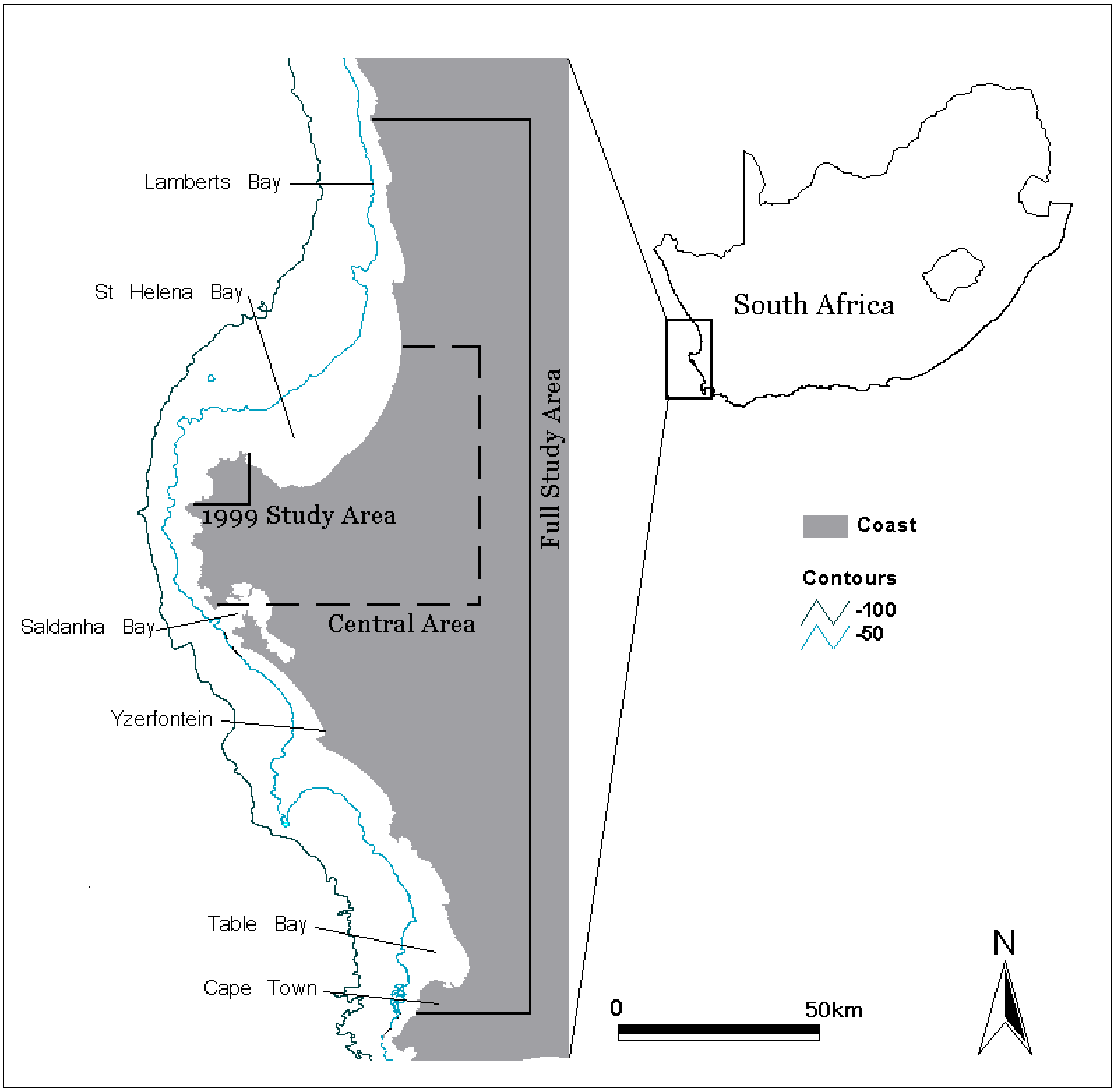


Figure 4.1. Map of study area showing three spatial scales at which abundance estimates were calculated, the full study area from 2000 to 2001, the central study area for 1999-2000-2001 and the 1999 core study area.

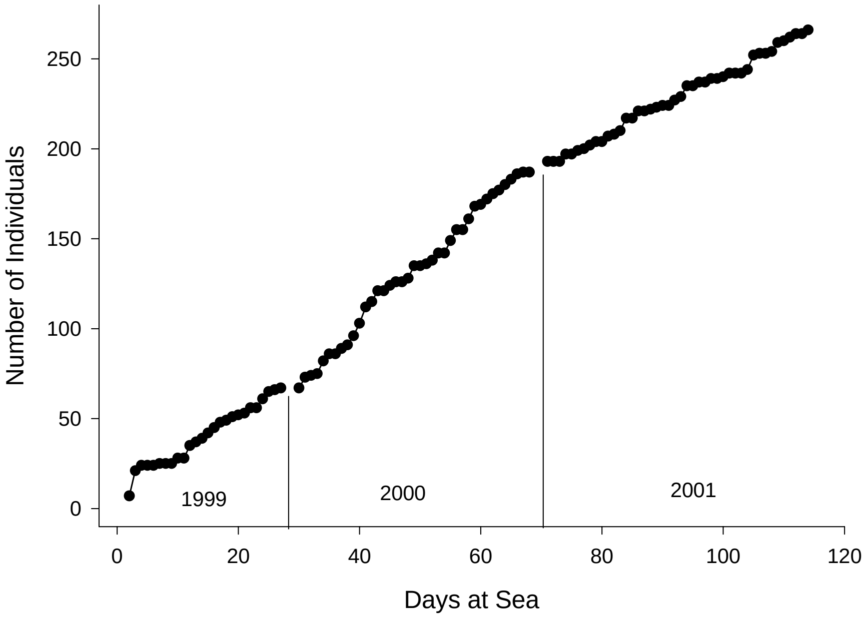


Figure 4.2. Discovery curve (number of new animals discovered per survey day) of well marked Heaviside's dolphins photographed off the west coast of South Africa in 1999, 2000 and 2001.

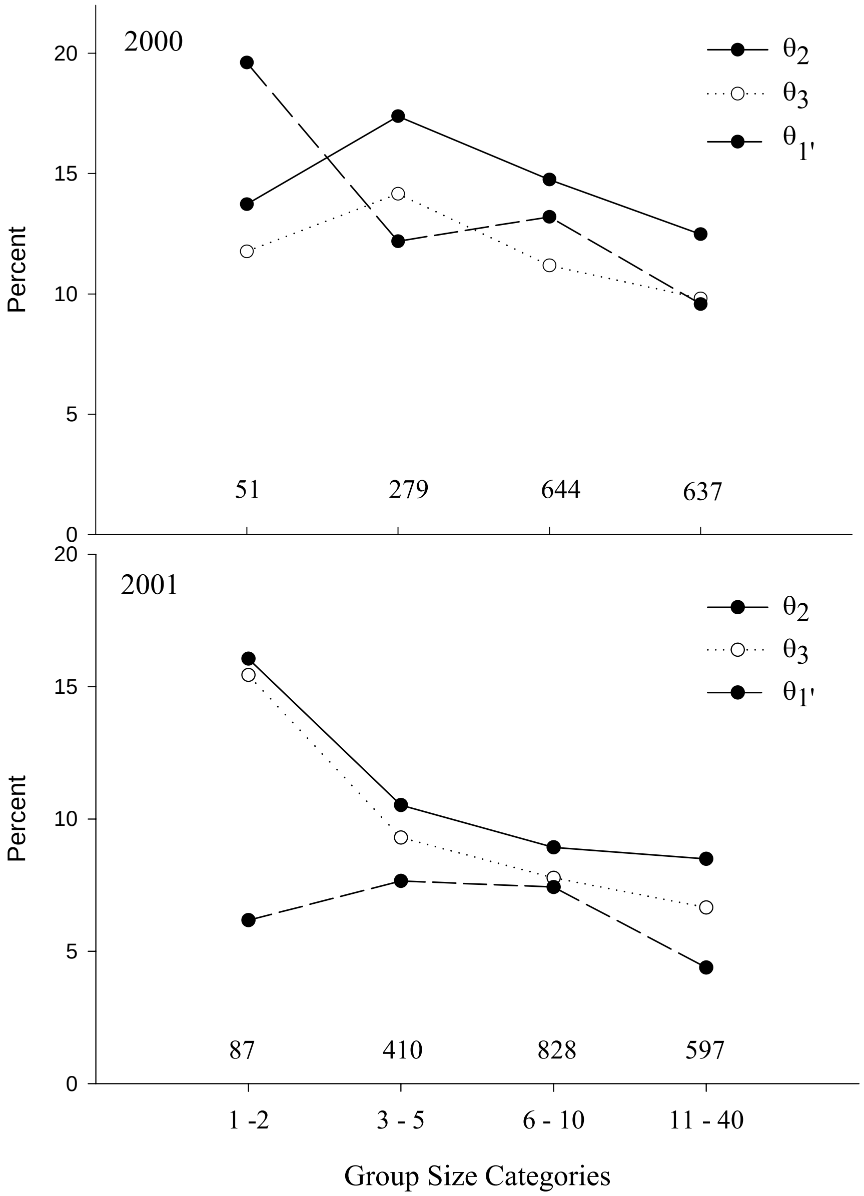


Figure 4.3. Figure showing the variation with observed group size of the three different measures of the mark rate of Heaviside's dolphins calculated for the 2000 and 2001 field seasons. The percent of marked animals seen (θ_2) and photographed (θ_3) in the field, and the percent of catalogued animals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

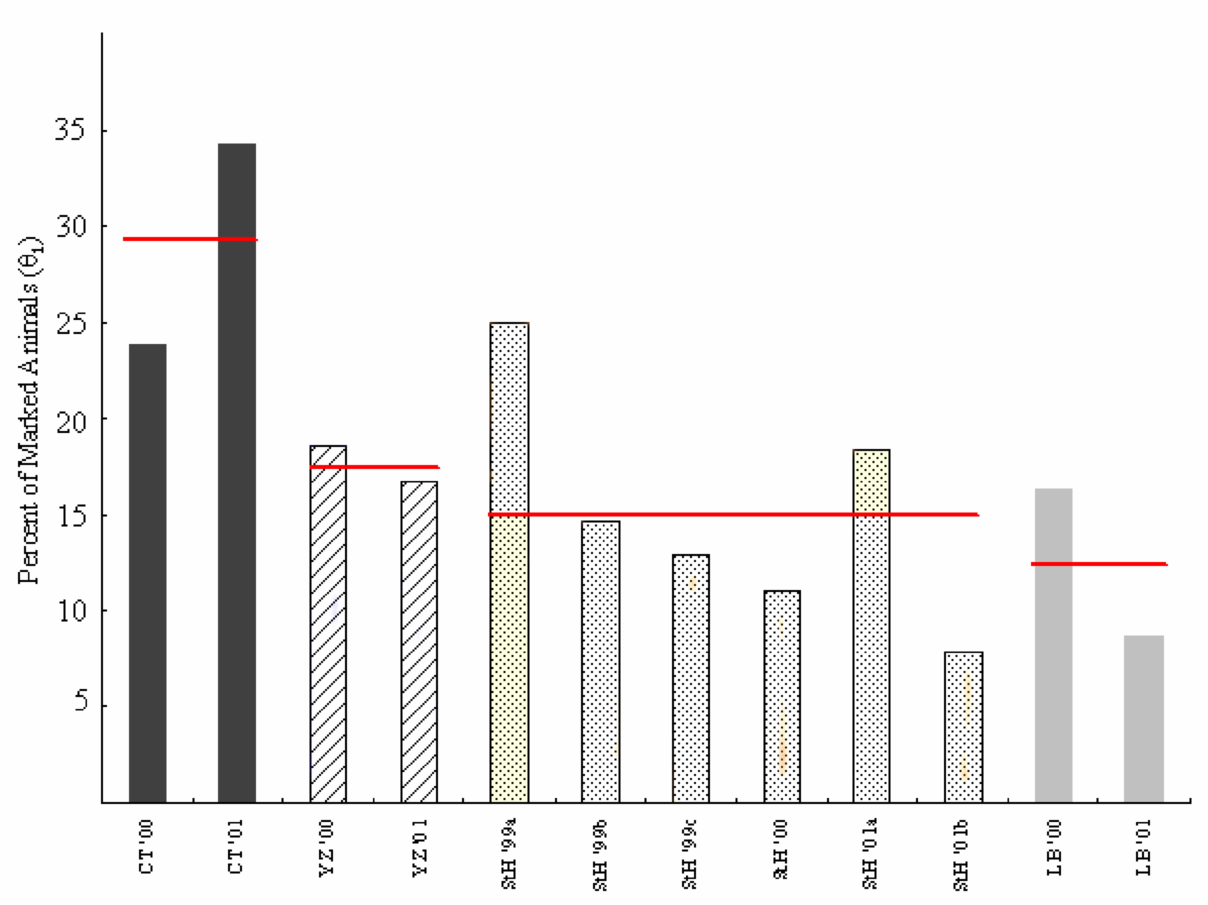


Figure 4.4. Variation in θ_1 (the percent of good quality images containing distinctive individuals) with area (CT – Cape Town, YZ – Yzerfontein, StH – St Helena Bay, LB – Lamberts Bay) and field trip (a/b/c) for all three study years ('99-'01). The 4 regions of the study area are represented geographically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

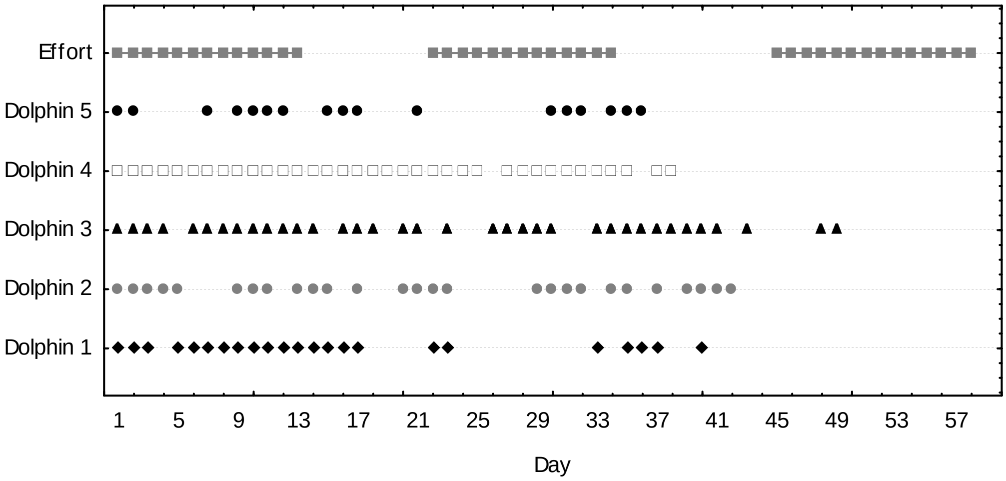
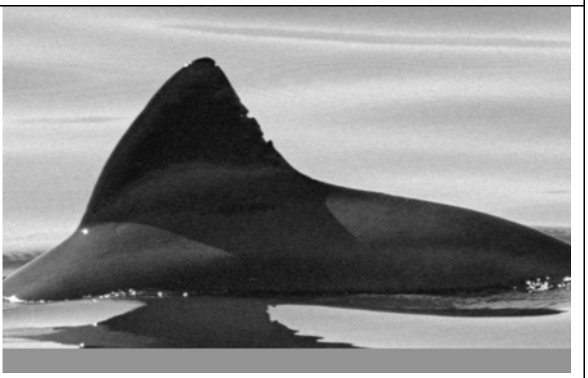
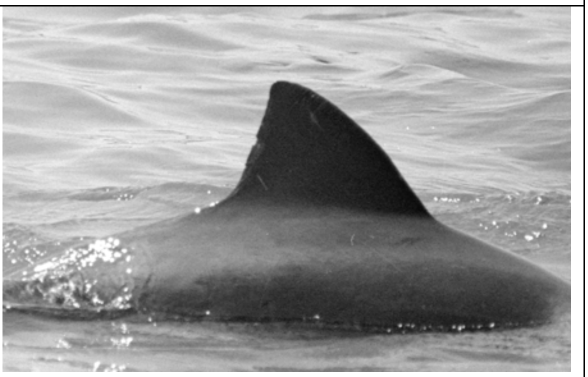


Figure 4.5. Figure showing the days from the first usable day of data transmission on which satellite tagged dolphins were inshore (<2km) during daylight hours (07h00-16h00) and theoretically available to be found and captured photographically by the methods employed in this study. The effort (top) represents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

Appendix 1

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

 D5	 D4
 D4	 D3
 D3	 D3
 D3	 D3