Chapter 3

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

Abstract:

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

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

Introduction

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

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

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

Methods

Data collection

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

Spatial data processing

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

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

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

Photographic data processing

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

Analysis

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

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

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

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

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

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

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

Results

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

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

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

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

Dispersal – Proportion at 'centre' over time

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

Observed frequency of time lags between sightings

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

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

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

Residency, using Lagged Identification rates

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

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

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

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

Association patterns

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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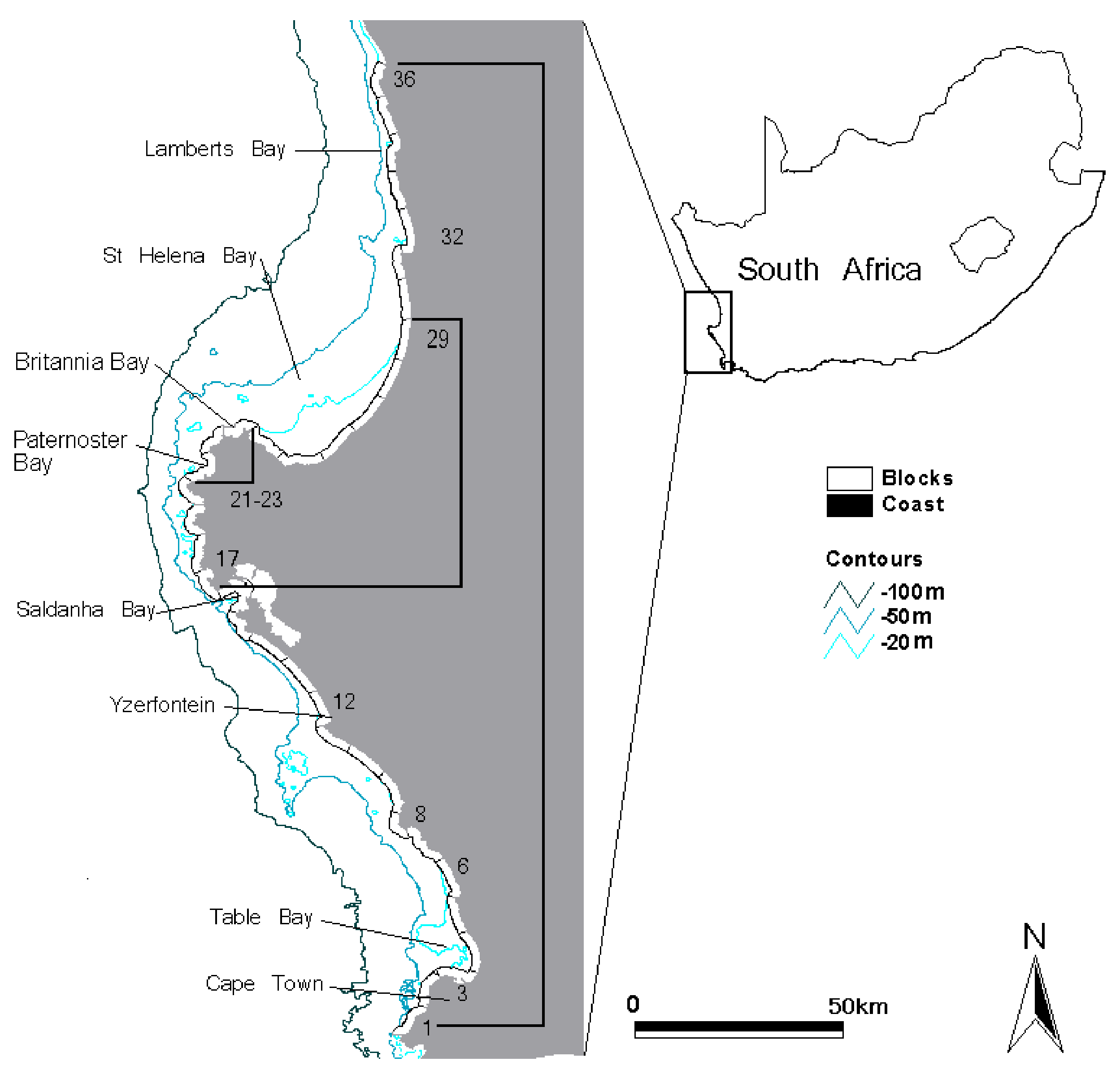


Figure 3.1. Map showing study area and place names mentioned in text. The area searched is within the blocks close to shore. The full study area includes all blocks from 1-36, the ‘central area’ blocks 17-29 and the ‘core area’ blocks 21-23.

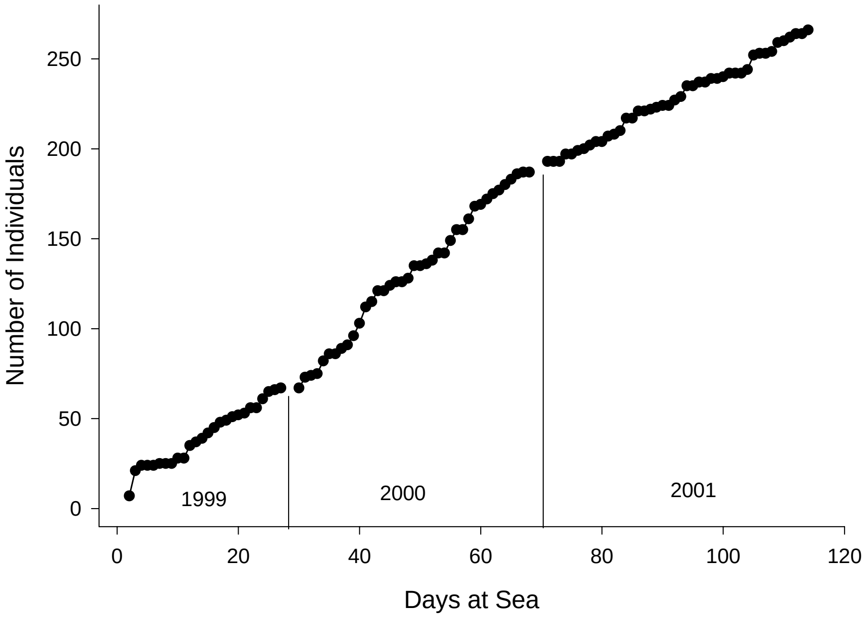


Figure 3.2. Discovery curve (number of new animals discovered per survey day) of well marked Heaviside's dolphins photographed off the west coast of South Africa in 1999, 2000 and 2001.

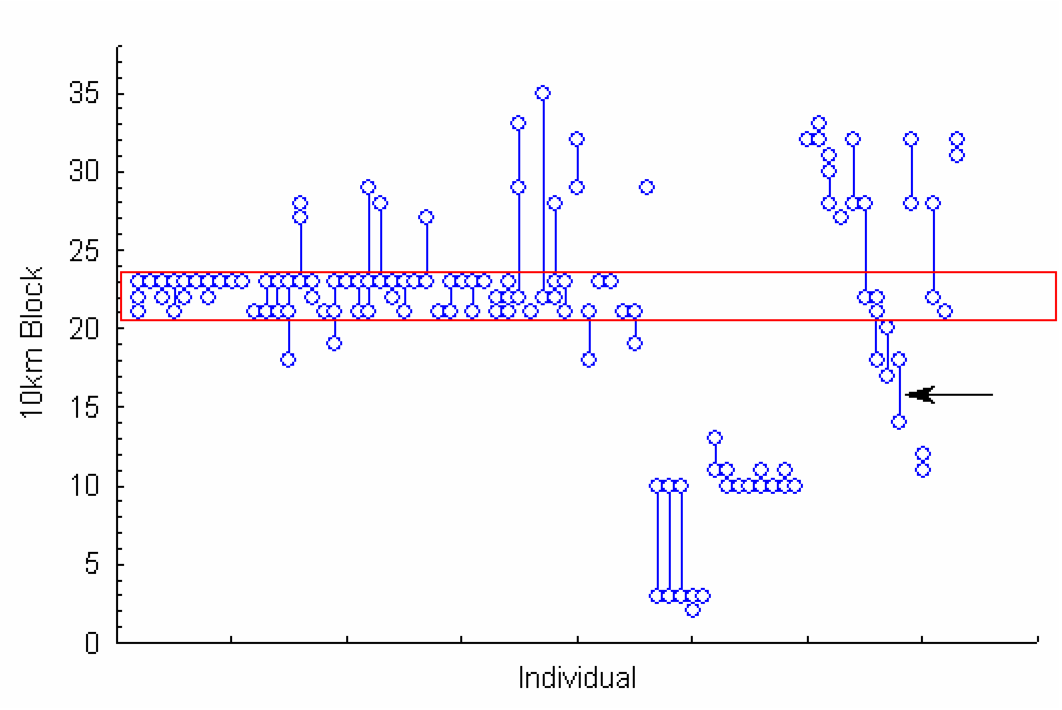


Figure 3.3. Figure showing the along shore range of Heaviside's dolphin movements (summarised by 10km block of coastline) for all individuals seen more than once. Animals first sighted in 1999 are only shown if they were seen in a later year to prevent domination of the figure by the geographically limited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

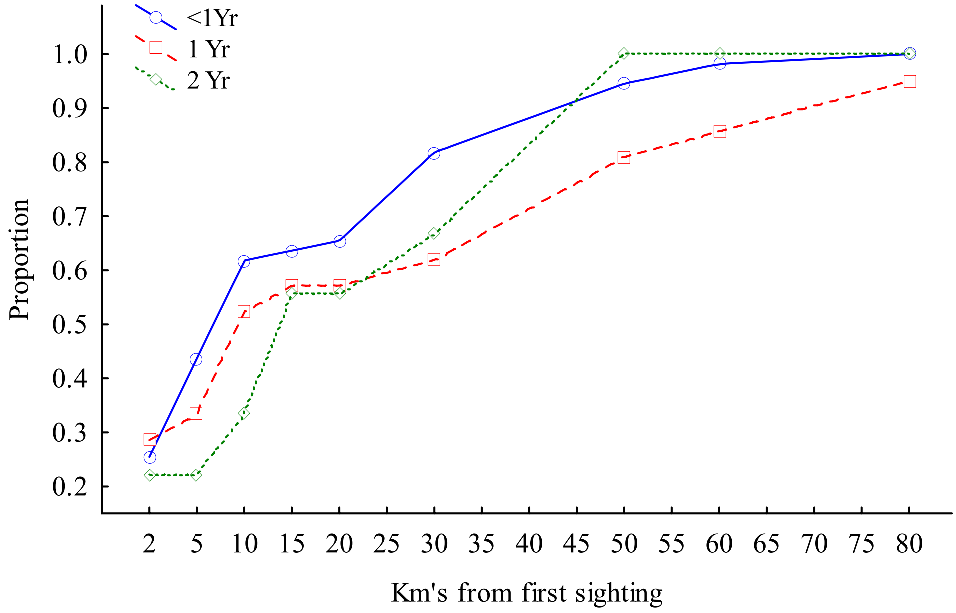


Figure 3.4. Cumulative proportion of Heaviside's dolphin movements (Y axis) occurring within a given distance (X axis) from the 1st sighting of the animal, shown separately for movements observed within one year (2000 and 2001 only), after one year and after two years at large. Observed movements were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

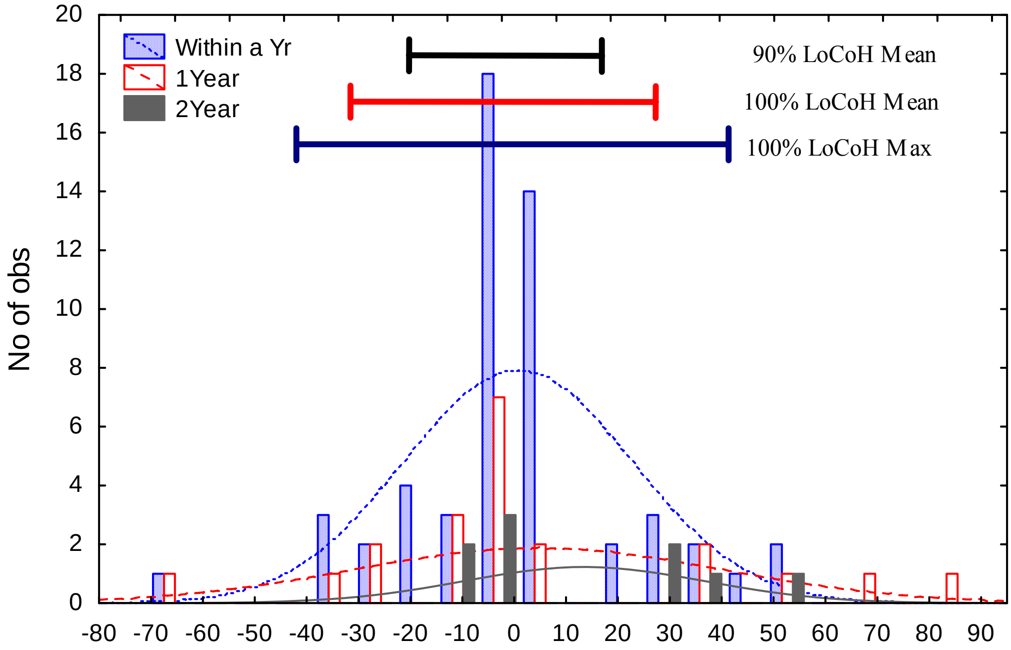


Figure 3.5. Histogram of coastwise movement vectors of all resighted individual Heaviside's dolphins from their first sighting, north as positive and south as negative. Bars across the centre line represent the alongshore ranges calculated from the 90% (mean) and 100% (mean and maximum) isopleths of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

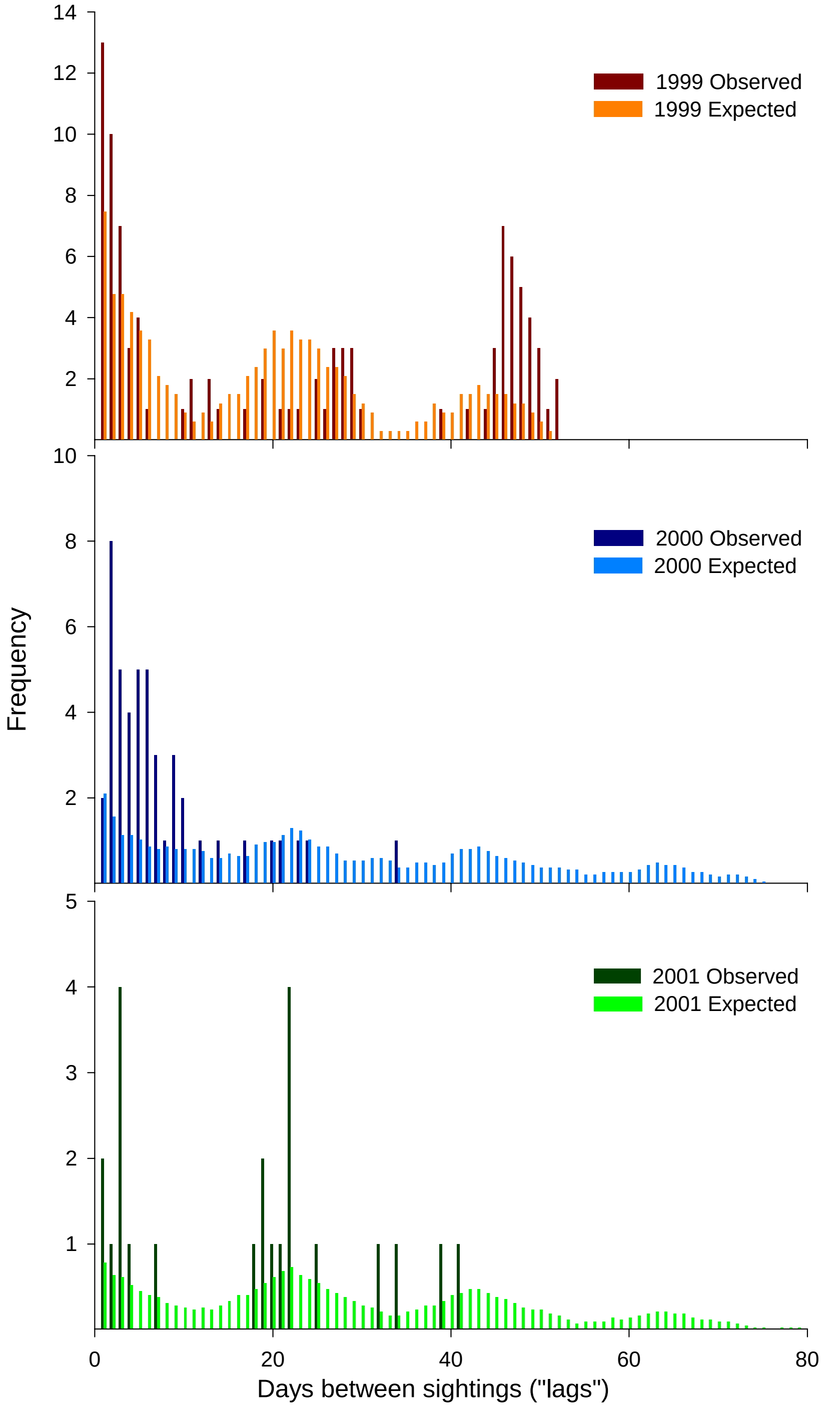
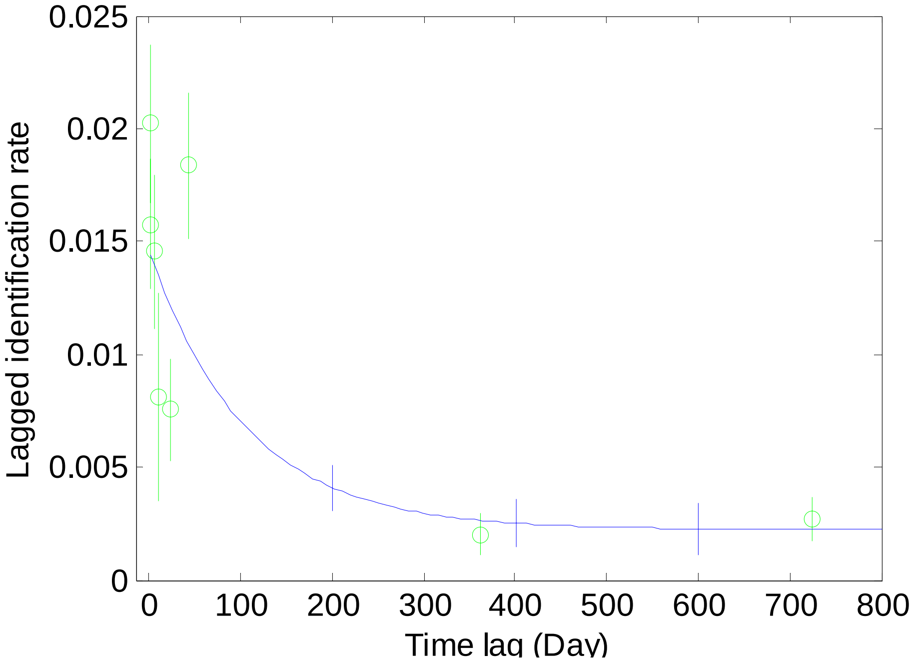


Figure 3.6. Time lags in days between resightings of individual Heaviside's dolphins seen more than once in the study period. Peaks and troughs in the expected values are caused by the 2 weeks on – 1 week off structure of the field work. Observed time lags between sightings were calculated between all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



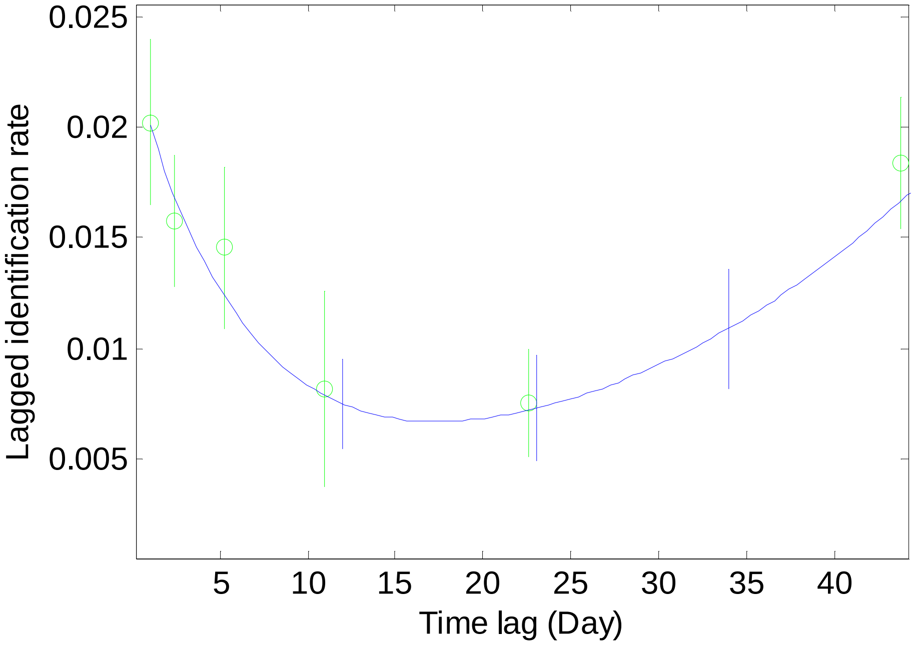


Figure 3.7. Calculated lagged identification rates (the probability of resighting an individual over time) with bootstrap errors of Heaviside's dolphins for the Central Area of the study site with best fit models (Socprog 2.3). Top: results for the full time period (~800 days) with fitted model of emigration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