Chapter 1

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

Abstract

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

Introduction

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

Two species of dolphin are commonly found nearshore along the west coast of South Africa, Heaviside’s dolphin *Cephalorhynchus heavisidii* and the similar-sized dusky dolphin *Lagenorhynchus obscurus*. Neither species has been studied in detail in the region, nor is their conservation status well known. Heaviside’s dolphin is an endemic resident that occurs from the breaker zone up to 45 nautical miles offshore, but is most abundant in water <100m deep, and the dusky dolphin is found from the coast to at least 500m depth (Findlay *et al*. 1992). Both species are subject to an unquantified level of bycatch on account of their overlap with several commercial fisheries (Sekiguchi *et al*. 1992, Best & Abernethy 1994).   They are also likely to be influenced by the growing boat-based cetacean watching industry in South Africa (Turpie *et al*. 2005), particularly the endemic Heaviside’s dolphin.

Both dolphin species are predominantly piscivorous with Heaviside's dolphins being arguably the more specialist feeder of the two taking mainly small hake (*Merluccius spp,* probably shallow water hake, *M. capensis* based on the known species distributions – F. le Clus, pers comm.) which comprises 48.9% of their diet (Sekiguchi *et al*. 1992). Heaviside's dolphins also take goby (*Sufflogobius bibarbatus*), horse mackerel (*Trachurus trachurus capensis)* and cephalopods. The stomach contents of Heaviside's dolphins caught in the morning were greater than those caught in the afternoon and it was suggested by Sekiguchi et al (1992) that they may forage nocturnally on hake as they migrate closer to the surface in the dark (Pillar & Barange 1995). Dusky dolphins are generally regarded as opportunistic feeders that alter their foraging strategies in different environments and seasons (Benoit-Bird et al. 2004). The diet of dusky dolphins in South Africa includes several of the same species, but they take a more diverse range of prey including horsemackerel, hake *(M.* spp*)* lantern (*Lampanyctodes hectoris*) and hatchet fish (*Maurolicus muelleri*) (Sekiguchi et al. 1992).

The Benguela ecosystem of the west coast of southern Africa is a cold-water, wind-driven upwelling system which is well structured at a broad scale with predictable, localised upwelling cells that affect the broad-scale distribution of the cetacean fauna (Findlay et al. 1992). The shore-based observations in this study took place near the Cape Columbine upwelling cell which creates high productivity in the St Helena Bay area, and it is feasible that the broad-scale effects on cetacean distribution by upwelling may be apparent at a finer scale if dolphins respond to upwelling conditions.

This chapter presents the results of shore-based observations of the behaviour and movements of Heaviside’s dolphins, with some appropriate data included from contemporaneous observations of dusky dolphins, and are used in an interspecies comparison to examine the way in which these sympatric predators use the nearshore environment.

Methods

Data collection

Shore-based observations of Heaviside’s dolphins were made from a temporary, gazebo structure on top of a dune approximately 5m above sea level and 100m back from the high-water mark, at Agterbaai, on the west coast of South Africa (Fig. 1). The bay was chosen because it is small enough (~1 000m wide) for dolphin movements to be followed throughout, boat traffic is minimal, and it is an area known to be well frequented by Heaviside’s dolphins. The bay is north facing, so it is largely sheltered from the southwesterly winds that are prevalent in summer. All fieldwork took place between early February and early April in 1999, 2000 and 2001 and was timed to take advantage of optimal weather conditions during the summer and occurred in conjunction with a boat-based photo-ID project. Effort was partly dependent on the number of volunteers available because boat-based work took priority and the shore-based observations were curtailed if insufficient manpower was available to staff both projects. Observations were made for all possible daylight hours, weather permitting, for a total of 420.6h (Table 1). Observations were discontinued if the wind exceeded ~15knots or if it was raining or foggy.

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

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

A team consisted of four observers, two on watch at a time for alternating 2h shifts, searching the bay by naked eye and with 7x35 binoculars. Environmental variables (cloud cover, Beaufort scale, wind strength and direction, swell height, percentage glare) were recorded hourly or if a noticeable change in conditions occurred. An index of overall sightability (from 1-5; very poor to excellent), encompassing all the above conditions, was recorded at the same time. There were some slight variations in field methods during watch handovers (when shifts overlapped) and observer training (when an extra, more experienced observer was also present) but this was not felt to bias data collection.

When dolphins were sighted, their numbers and group compositions were estimated. For Heaviside’s dolphins, their movements were visually tracked for 10min, with locations being recorded when at the surface, relative to prominent landmarks and a 100m square grid marked on a map of the bay. Although fairly widely used in similar studies on account of its generally greater precision, a theodolite was not used during this study owing to the poor accuracy it would have attained from such a low observation platform (Würsig *et al*. 1991) and the need to train new observers every two weeks. Behavioural observations were recorded for a further 10min period immediately following tracking, with one observer continuing to use binoculars to monitor the dolphins while the other acted as a data recorder. No behavioural observations were made for sightings of dusky dolphins.

The relationship between environmental factors and the variability of the sighting rate of Heaviside's dolphins was examined using a general linear model (Proc GLM in SAS ®). Dolphin presence was expressed as the sighting rate of (a) dolphins per hour, and (b) groups per hour (number of groups seen per total minutes observing; which included tracking, searching and behavioural observations). To normalise the residuals, the sighting rates of Heaviside's dolphins were rank-transformed, ties were broken by adding a small random number and then Blom transformed (Blom 1958) to decrease the inequality of the variances. *Post-hoc* testing was performed using least squares means. Time of day (i.e. daylight hours, in 1h intervals except 06:30-07:59), wind direction (N, NE, E etc. or no wind), the presence or absence of dusky dolphins and lastly the brightness of the moon (less or more than half full) were included as class variables. Wind speed was included as a co-factor in the model. Waxing and waning moon phases were combined and analysis was limited to more or less than half full. Wind direction and strength were included in the analysis as wind is the principal driver of nearshore upwelling and productivity in the Benguela ecosystem, with the strongest breezes generally coming from the southerly quarter.

Data analysis

Although observations were stopped when sighting conditions became too poor, detectability could still have been influenced by varying conditions within the search time. We therefore compared the rate of dolphin sightings between hours of ‘worse’ sightability (1-3; poor to moderate) and ‘better’ sightability (4-5; good to excellent).

We examined the relationship between environmental factors and the variability of the sighting rate of Heaviside's dolphins using a general linear model (Proc GLM in SAS ®). Dolphin presence was expressed as the sighting rate of a) dolphins per hour, and b) groups per hour (number of groups seen / minutes ‘watching’; including tracking, searching and behavioural observations). To normalise the residuals, the sighting rates of Heaviside's dolphins were rank transformed, ties were broken by adding a small random number and then Blom transformed (Blom 1958) to decrease the inequality of the variances. Post-hoc testing was performed using Least Squares Means. Time of day (daylight hours, in 1 hour intervals except 06h30-07h59), wind direction (N, NE, E, no wind, etc.), the presence or absence of the other species of dolphin seen and lastly the phase of the moon (less or more than half full) were included as class variables, while wind speed was included as a co-factor in the model. It was not moon phase *per se* that was felt to have potential influence on the dolphins, rather the effect that the amount of light in the night sky might have on their principal prey, hake (B. Rose, pers. comm.), hence waxing and waning moon phases were combined and analysis was limited to only more or less than half full. Heaviside's dolphins are hypothesised to spend more time offshore feeding (and thus less time inshore in the study area) when the moon is full and hake are deeper and harder to capture. Wind direction and strength were included in the analysis as wind is the principal driver of nearshore upwelling and productivity in the Benguela ecosystem, with the strongest breezes generally coming from the southerly quarter.

Although the total number of dusky dolphins observed was similar to that of Heaviside's dolphins, there was higher variation in group sizes and timing of sightings. Dusky dolphin sighting rates were strongly influenced by the sighting of several hundred animals in multiple groups over two consecutive days. This created a strong bias in the analysis toward the environmental factors prevalent on those two days thus potentially masking any possible relationships during the majority of days with much lower sighting rates. The analysis of variance was thus performed both with and without the data from these two days. The dusky dolphin sighting rate data were transformed as were the Heaviside's dolphins to attain normality and the same factors were included in the model with the presence of Heaviside's dolphins replacing the presence of dusky dolphins in the previous analysis.

Behavioural observations in the current study were extremely skewed toward ‘slow rolls’ supporting previous reports that aerial displays by Heaviside's dolphins are comparatively rare (Best and Abernethy 1994). On account of the very low occurrences of all the other behaviours recorded, all behaviours excluding ‘slow rolls’ were summed together and divided by group size and time monitored to give a measure of ‘active behaviours’ per dolphin per minute. The second measure of behaviour analysed, was an overall index of ‘cue production’ and included all behaviours seen; variation in both the rates of active behaviours and cue production was compared independently to wind strength, direction and moon phase as well as time of day, group size and distance from the observers (average distance of trackline from observer post, estimated to nearest 100m off tracking maps).

Variations in ‘evasive’ behaviour of dolphins (with respect to the crew’s attempt to close with the group for photography) and calf number were analysed with respect to group size.

Results

In total, 54 days were worked in the field, during which 616 Heaviside’s dolphins were seen in 203 groups, with an average group size of 3.3 (range = 1 – 10, mode = 3). In all, 660 dusky dolphins in 75 groups were seen at an average group size of 7.9 (range = 2 – 50, mode = 10). If the 2 days of very high sightings were excluded, 131 animals in 25 groups were seen. The size of tracked groups of Heaviside's dolphins did not vary with distance from shore (p = 0.899, F = 0.3209). Neither the sighting rates of Heaviside's dolphins (p = 0.51, t = -0.66) nor the observed group size (p = 0.41, t = 0.82) varied significantly between worse (152:52 hours) and better (267:41 hours) sighting conditions. This confirms that field observations were curtailed before the quality of data collection was compromised by sighting conditions, and overall sighting conditions can be considered as an essentially random variable.

The sighting rate of Heaviside's dolphins was significantly related to both time of day and brightness of the moon when measured as either groups per hour or dolphins per hour (Table 1.2). *Post hoc* analysis showed the sighting rate of dolphins to be higher when the moon was brighter and higher in the morning than in the afternoon for both groups and dolphins sighted per hour (Figure 1.2). It is noteworthy that only two groups (five individuals) of Heaviside's dolphins were ever spotted after 16:00 despite 61:16 h on watch in this period. The presence of dusky dolphins influenced the sighting rate of dolphins per hour but not groups per hour, with *post hoc* analysis showing the rate to be higher when dusky dolphins were present. This suggests that the presence of dusky dolphins in the bay may influence the group size, if not the overall number of groups of Heaviside's dolphins seen.

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

Variable	Groups (h^{-1})		Dolphins (h^{-1})	
	F	P	F	P
Overall	3.04	*<0.001*	3.13	*<0.001*
Time of Day	3.27	*0.001*	4.10	*<0.001*
Wind Direction	0.93	0.488	1.19	0.305
Dusky dolphins	2.09	0.149	5.97	*0.015*
Moon ½	16.47	*<0.001*	5.95	*0.015*
Wind Speed	0.03	0.864	3.08	0.079

To examine the pattern of movement offshore with time of day in more detail, the starting time of all tracked sightings of Heaviside's dolphins (n = 161) was correlated against each track's mean distance from shore. While there was no relationship in the overall spread between the data (r=0.005, p = 0.954), the pattern after noon appeared different to that before noon. Sightings in the morning were spread throughout the bay from close inshore (20m) to far offshore (1 100m), whereas the dolphin sightings were less spread out in the afternoon, being close to the breakers around noon then increasing in distance from shore during the afternoon, with no sightings within 200m from shore after 14:00. Correlating these data separately (Figure 1.3) shows no relationship between time and distance from shore in the morning ($r^2 = 0.018$, $p = 0.116$). However, there was a positive correlation in the afternoon ($r^2 = 0.158$, $p = 0.037$) suggesting that dolphins move farther offshore as the afternoon progresses.

The movements of dusky dolphins were markedly different from those of Heaviside's dolphins, they were seen less frequently and tended to be in larger groups. Occasionally groups of up to several hundred animals were observed (the largest group of Heaviside's dolphins observed during contemporaneous observations at sea was 40 animals and consisted of several subgroups). The principal factor influencing the sighting rate of dusky dolphins was not time of day (dolphins were seen with equal probability throughout the day, Figure 2) but the direction of the wind which showed a significant relationship with the sighting rate of dolphin groups per hour in both the full data set and the data set where the two very high sightings days were removed (Table 3, Figure 4). *Post hoc* analysis showed that the sighting rate of dusky dolphins was lower when the wind was blowing from a westerly or south-westerly direction (242:36 watch hours), than when the wind blew from a north to easterly direction (59:42 watch hours). It is noteworthy that no dusky dolphins were ever sighted from shore when the wind direction was south-westerly, despite nearly 130 watch hours during those conditions. The brightness of the moon appeared to have little effect on the sighting rate of dusky dolphins, as a significant effect was only seen on the sighting rate of groups when the two days of very high sightings were removed. *Post hoc* analyses showing the sighting rate to be lower when the moon was brighter, this is opposite to the pattern observed for Heaviside's dolphins.

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

Variable	Groups (h^{-1})		Dolphins (h^{-1})	
	F	P	F	P
Including two days of high sighting rate				
Overall	1.80	0.017	1.03	0.428
Time of Day	0.32	0.975	0.21	0.996
Wind Direction	2.03	0.042	1.65	0.108
Heaviside’s	3.45	0.064	0.66	0.417
Moon phase	0.43	0.511	1.41	0.235
Wind Speed	3.86	0.050	0.16	0.686
Excluding two days of high sighting rate				
Overall	1.78	0.018	1.20	0.243
Time of Day	1.14	0.332	0.77	0.657
Wind Direction	2.04	0.041	1.70	0.097
Heaviside’s	0.00	0.976	0.01	0.927
Moon phase	6.95	0.009	0.42	0.518
Wind Speed	0.03	0.871	1.63	0.203

Behaviour

The rate of active behaviours per dolphin per minute in Heaviside's dolphins was not significantly correlated to the brightness of the moon (Mann Whitney U test, z = - 0.266, p = 0.79) or time of day (ANOVA: p = 0.84, F = 0.448) and, although sample sizes in the afternoon were small, no active behaviours at all were seen in the nine sampling events (87min) occurring after 12:30. Further, the rate of active behaviours was not correlated with wind speed (Spearman Rank Order correlation; $r_s = 0.047$, p = >0.05) or wind direction (Kruskal Wallis: p = 0.43, H = 8.08, df = 8) although small sample sizes during certain wind directions may weaken this analysis. However, the rate of active behaviours did vary significantly with group size (Kruskal Wallis: p = 0.007, H = 15.81, df = 5) showing a general increase in such activity with group size, but with some groups of 4 being especially active

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

The overall mean rate of cue production by Heaviside's dolphins was 1.79 cues per animal per minute (range: 0.22 – 4.03, n = 70). Variation in the cue production rate was not correlated with either wind speed (Pearson: $r^2 = 0.013$, $p = 0.337$), moon brightness ($r^2 = 0.012$, $p = 0.341$) or group size (ANOVA; $F = 0.461$, df = 5, $p = 0.803$). However, cue production rate decreased significantly throughout the day (Pearson: $r^2 = 0.093$, $p = 0.007$) (although there was only one sample after 14:30) and with distance from the observer (ANOVA: $F = 5.00$, df = 5, $p < 0.001$). A post hoc comparison showed the main differences occurred between sightings farther than 500m and sightings in the 100-200m and 300-400m distance strata (Tukey HSD for unequal N; $p = 0.014$ and 0.043 respectively). The average rate of cue production in strata less than 400m from the observer was 1.961 (SD 0.134) cues per dolphin per minute and only 0.941 (SD 0.041) in strata further than this.

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

Discussion

Shore-based observations of cetaceans have been used widely and on a variety of species, from small dolphins (Würsig and Würsig 1980, Stone *et al*. 1995) to large whales (Findlay and Best 1996, Williams *et al*. 2002) to monitor the movements and behaviour of animals. The main benefit of shore-based observations is that they do not interfere with the behaviour of the subject animal. For example, boat-attraction or avoidance may take place at or beyond the visual range of observers, with profound implications for line-transect data (Dawson *et al.* 2003) and behavioural observations. Shore-based observations of dolphin movements, numbers, group composition and behaviours can provide a control for similar boat-based observations. Probably the main problem with shore-based studies is the inability to control the distance between observer and animal, so that range becomes an important factor in establishing species identity, estimating group size, and observing behaviour patterns.

In this study, the recorded rate of cue production by Heaviside's dolphins dropped off significantly with increased distance from the observer indicating that 400m was the farthest distance at which dolphin surfacings could be detected without a significant bias, at least from the low observation platform used here. However, the size of observed groups did not vary significantly with distance from the observer, suggesting that although the ability to see surfacing cues lessened with distance, the proportion of animals seen did not differ within and beyond 400m in the study site.

The sympatric Heaviside's and dusky dolphins in this study appeared to respond to different environmental cues. The most obvious behavioural pattern exhibited by Heaviside's dolphins was the diurnal variation in their numbers inshore. The total number of observed dolphins reduced greatly after noon, and those groups that were tracked were seen farther from shore as the afternoon progressed. Observations of Heaviside’s dolphins made at sea during the concurrent boat-based photo ID work over 390km of coast (SHE pers. obs.) confirm this reduction in inshore dolphin numbers in the afternoon throughout the surveyed area. Data from satellite tagging of five female dolphins in the St Helena Bay area, Elwen *et al.* (2006) showed that, although there was variation between the animals in the distance moved from shore, and sometime several days could be spent either inshore or offshore, all five animals showed a clear diurnal inshore-offshore movement pattern throughout the transmission period of their tags (up to 54 days). These dolphins were closest to shore between about 05:00 and 13:00. It is therefore reasonable to assume that there is a general offshore movement throughout the species' range rather than a specific movement away from the shore-based station.

The principal prey of Heaviside's dolphins is juvenile hake which was shown by Sekiguchi *et al*. (1992) to comprise nearly half (48.9%) of their diet by volume, with goby *Sufflogobius bibarbatus* the next main prey type at 13.6% of volume. Dolphins caught early in the day (07:00-10:00) had fuller stomachs than those caught in the afternoon and Sekiguchi (1994) proposed that Heaviside's dolphins feed at night and in the early mornings when hake migrate vertically into midwater (Barange *et al*. 1994, Pillar and Barange 1995). Goby also tend to be more prevalent near the surface at night (O'Toole 1977, this may also increase the motivation to move offshore to feed nocturnally. The movements of Heaviside's dolphins observed in this study are consistent with the hypothesis of a nocturnal feeding excursion to exploit the vertical migration from deeper water of their dominant prey species. A general pattern of resting inshore and feeding offshore has been observed in several other delphinids including dusky dolphins in Argentina (Würsig and Würsig 1980, Markowitz 2004) and Hawaiian spinner dolphins *Stenella longirostris* (Würsig *et al*. 1994). Both of these species nocturnally exploit prey species associated with a vertically migrating scattering layer and are though to move inshore when not feeding due to a reduced predation risk in shallower water where sharks and killer whales (O*rcinus orca*) are less prevalent. Although killer whales are rarely sighted along the west coast of southern Africa (Findlay et al. 1992), several Heaviside's dolphins have been seen bearing scars consistent with shark bites (Best & Abernethy, 1994). Predator avoidance may therefore also play a role in the movements of Heaviside's dolphins, in particular the choice to move inshore when not feeding rather than remain offshore.

Although hake and vertically migrating mesopelagic fish such as lantern and hatchet fish (Prosch *et al*. 1989) form a large part of the dusky dolphin diet (33% by modified volume combined, Sekiguchi *et al.* 1992), the sighting rate of dusky dolphins showed no predictable variation with time of day. However, their presence inshore appeared to be related to wind direction; the absence of dusky dolphins inshore when the wind was south-westerly is particularly noteworthy given that this was the predominant direction from which the wind blew during the study. The larger area in which the study site was located (St Helena Bay) has a regular, predictable, wind-driven upwelling plume off Cape Columbine (Shannon 1989). Upwelling in this region occurs when the wind is south-easterly, southerly or south-westerly (generally an offshore direction at the study site but an alongshore direction to the majority of the coast) but not when the wind is from the opposite directions, i.e. north-westerly to easterly. Our data show a potential link between the absence of dusky dolphins inshore and strong upwelling offshore that merits further investigation. It is possible that in the study area, dusky dolphins may use wind strength as a cue to move offshore, since during watch hours when the wind blew >10kn, only 1% of those occurred from a ‘non-upwelling’ direction.

It is not known if dusky dolphins exhibit a similar relationship with wind direction or upwelling in other parts of their range in south-western Africa or only in areas of localised upwelling, as observations in this study are limited to St Helena Bay and summer months only. However, dusky dolphins are adaptable predators that use different foraging strategies throughout their range. In the deep canyon habitat of Kaikoura, New Zealand, they exhibit a strong diurnal migration pattern of resting inshore during daylight hours and moving offshore in the late afternoon to feed on vertically migrating organisms associated with the deep scattering layer (Cipriano 1992). In shallow water bays in both New Zealand (Markowitz *et al*. 2004) and Argentina (Würsig and Würsig 1980) scattered groups of dolphins feed diurnally on schooling fish near the surface. There is some evidence to suggest that dusky dolphins in South African waters use different feeding strategies. Two animals caught in a beach-seine net early in the morning in Hout Bay (~200km south of St Helena Bay) had eaten mesopelagic lantern fish and were thus thought to have been feeding on the continental shelf over night and subsequently moved inshore to rest (Sekiguchi 1994). Thus, although the observed relationship between dusky dolphins and upwelling conditions is reasonably clear from the data collected in this study, these observations must be placed in the broader context of the environment as a whole and the flexible foraging habits of the species, as the observed relationship may be both area and season specific.

Variation in dolphin numbers and behaviours with regard to the brightness of the moon was examined on the grounds that the vertical migration behaviour of many fish species is affected by the light intensity in the sky, including moonlight (Woodhead 1966) with fish not migrating as close to the surface under brighter light conditions. Heaviside's dolphins were hypothesised to spend more time offshore feeding (and thus less time inshore in the study area) when the moon is brighter and hake are deeper and theoretically harder to capture, however the opposite pattern was observed and Heaviside's dolphins were seen in higher numbers inshore during the brighter full moon. Two alternate hypotheses exist although neither can be tested in this context: either the dolphins do not move offshore to hunt when foraging is sub-optimal, or they may shift prey type.

Behaviour and Group size observations

The Heaviside’s dolphins in the bay generally exhibited slow movement, sometimes milling and in specific directions, but high activity and speed were rare. During the more than 400 h of shore-based observations and the 110 days of concurrent boat-based operations, there was only a single observation of obvious feeding behaviour by Heaviside's dolphins. On 13th February 2001, a group of five Heaviside's dolphins was seen harassing a single cormorant (probably white breasted *Phalacrocorax carbo*) until the cormorant released the fish that it had just caught. Although it is not known if the dolphins then ate the fish, this same group of dolphins was described as ‘feeding with the cormorants’ by the observers on watch at the time. Our observations of the timing, behaviours and movements of the dolphins, combined with the general lack of feeding observed, all add support to the theory that Heaviside's dolphins rest inshore between offshore nocturnal foraging bouts.

Resting or non-feeding behaviour is difficult to interpret because it is inherently undirected. Würsig *et al.* (1994) describe Hawaiian spinner dolphins (*Stenella longirostris*) as bunching more closely and becoming much less active when resting inshore during the day. Aerial behaviour observed in Hector's dolphins was associated with sexual and aggressive behaviours and not feeding behaviour, but in that particular population feeding appears to occur throughout the day (Slooten and Dawson 1994). In this study, no predictable variations in the active behaviours of Heaviside's dolphins were noted with wind direction, speed or brightness of the moon and although not statistically significant, the lack of any active behaviours observed after 12h30 may be associated with a motivation to disperse at that time and move offshore to begin feeding.

The behaviour of Heaviside's dolphins varied with group size, with larger groups being more active, boat friendly and containing proportionally. It is likely that protection of individual cetaceans is greatly increased in schools at least partly due to greater levels of awareness (Norris and Dohl 1980, Markowitz 2004). Activity levels of Atlantic white-sided dolphins (*Lagenorhynchus obliquidens*) have been observed to increase with group size (Weinrich *et al.* 2001). Slooten (1994) found much higher rates of sexual behaviour and associated active behaviours (such as jumps) in groups of 11-15 animals than in either larger or smaller groups, and for the level of sexual behaviours to increase when two groups fused. Increased school size presumably creates greater opportunities for social interactions and hence is likely to lead to a higher incidence of behaviours other than ‘slow rolls’.

In conclusion, these first shore-based observations of Heaviside's dolphins in South Africa have provided some support for previous hypotheses on the diurnal movement and feeding pattern of this species (Best and Abernethy 1994, Sekiguchi 1994), as well as providing some baseline data on their inshore behaviours and how they may vary with environmental and social influences. Concurrent observations of dusky dolphins show that, at least in St Helena Bay, they respond to different environmental cues, which may be indicative of the two species employing different foraging strategies as a result of niche differentiation between similar-sized competitors.

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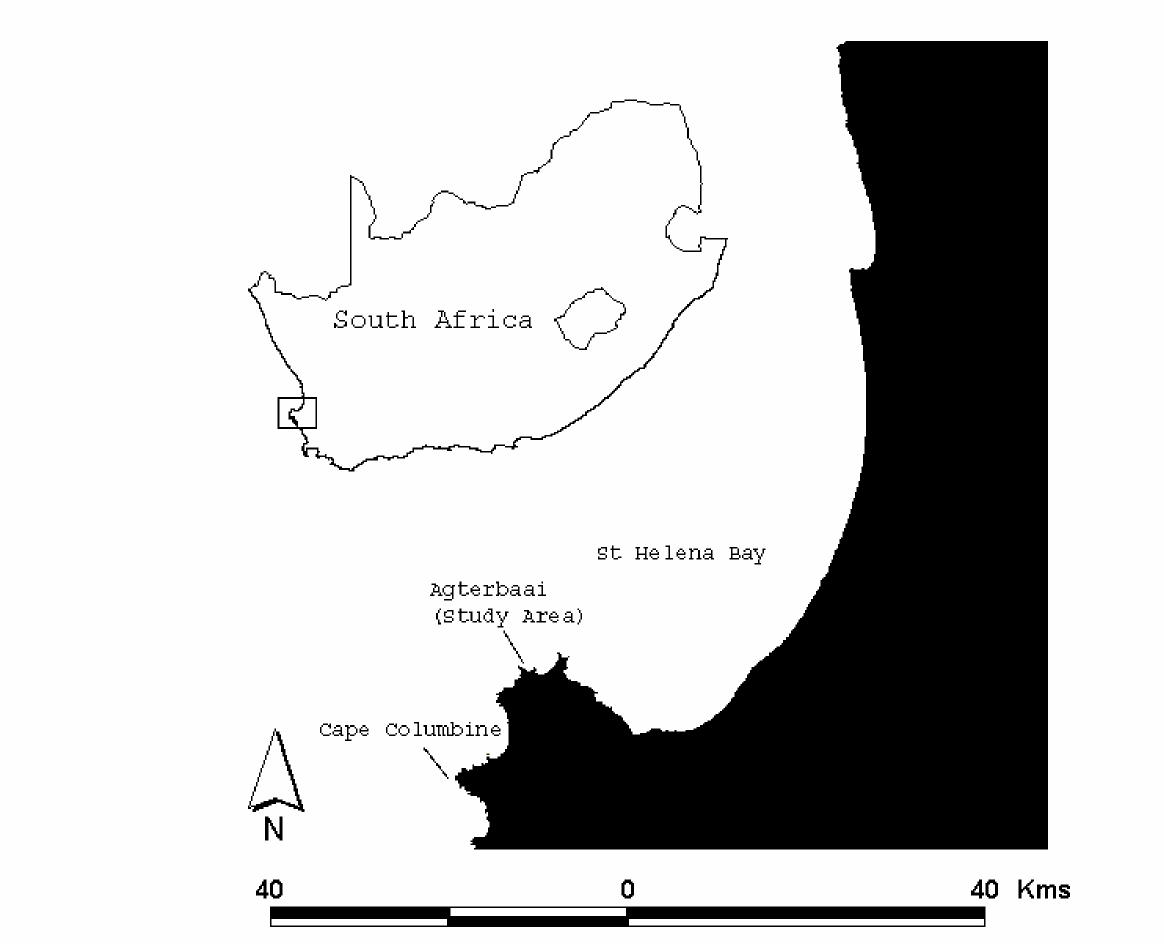

Figure 1.1. Study Area at the tip of St Helena Bay, South Africa.

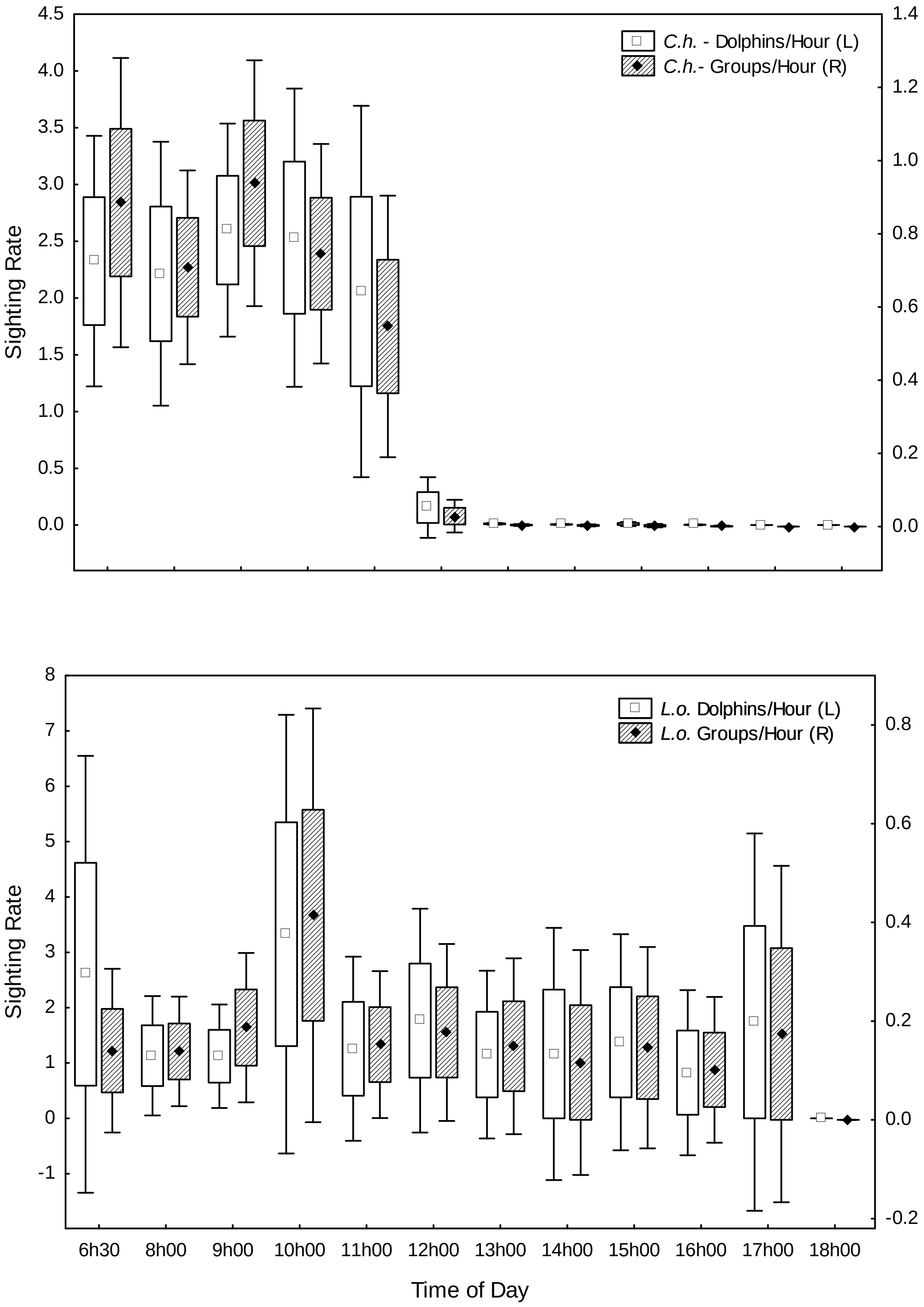

Figure 1.2. Variation in the sighting rate of individuals per hour (left axis) and groups per hour (right axis) of Heaviside's dolphins (top) and dusky dolphins (bottom) with Time of Day. Whiskers, boxes and points represent 1.96SE, SE and Means for each hourly category.

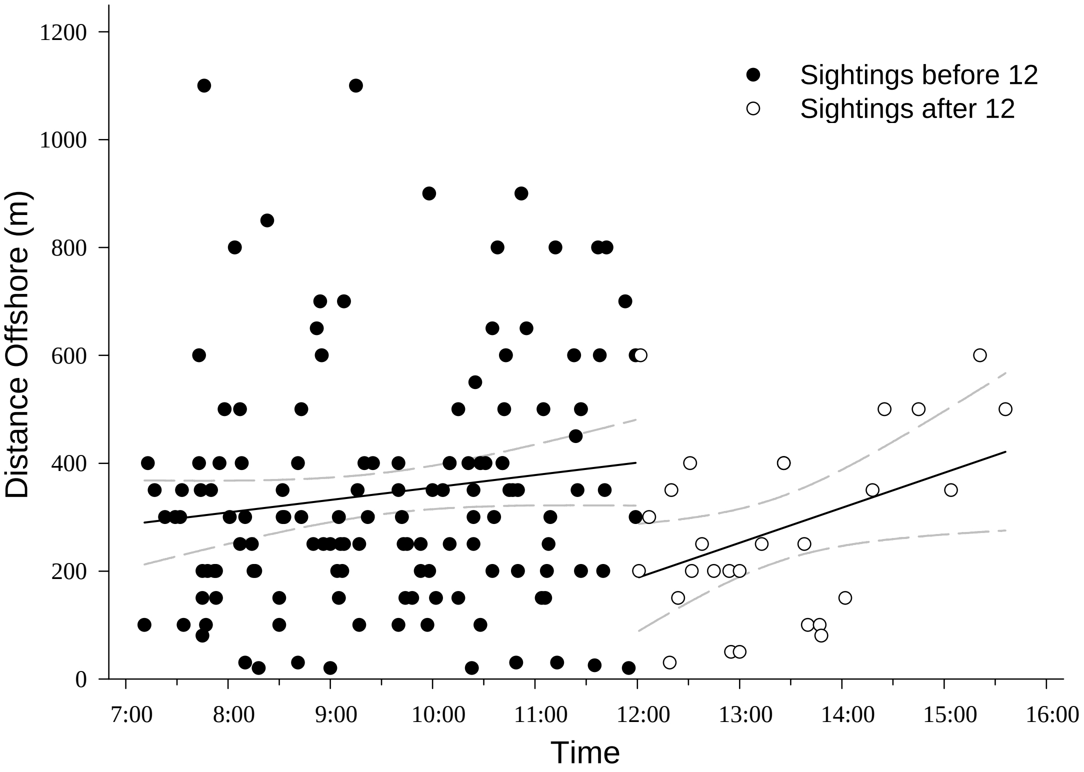

Figure 1.3. Correlation of distance offshore of tracked groups of Heaviside’s dolphins with time of day. Data and correlations split at 12h00 to show movements of animals offshore after noon.

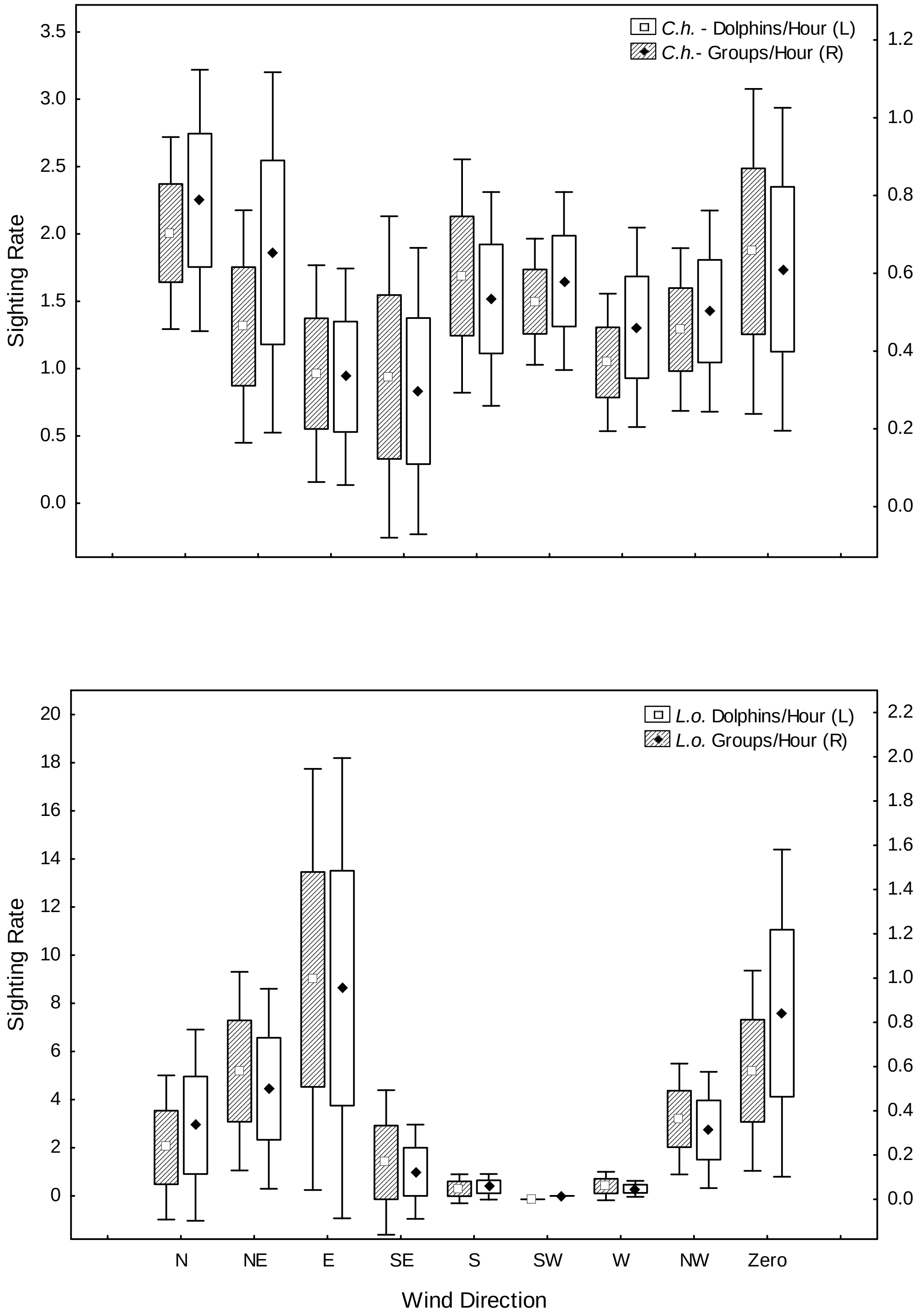

Figure 1.4. Variation in the sighting rate of individuals per hour (left axis) and groups per hour (right axis) of Heaviside's dolphins (top) and dusky dolphins (bottom) with wind direction (2 days of high dusky sightings included in this figure). Whiskers, boxes and points represent 1.96SE, SE and Means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

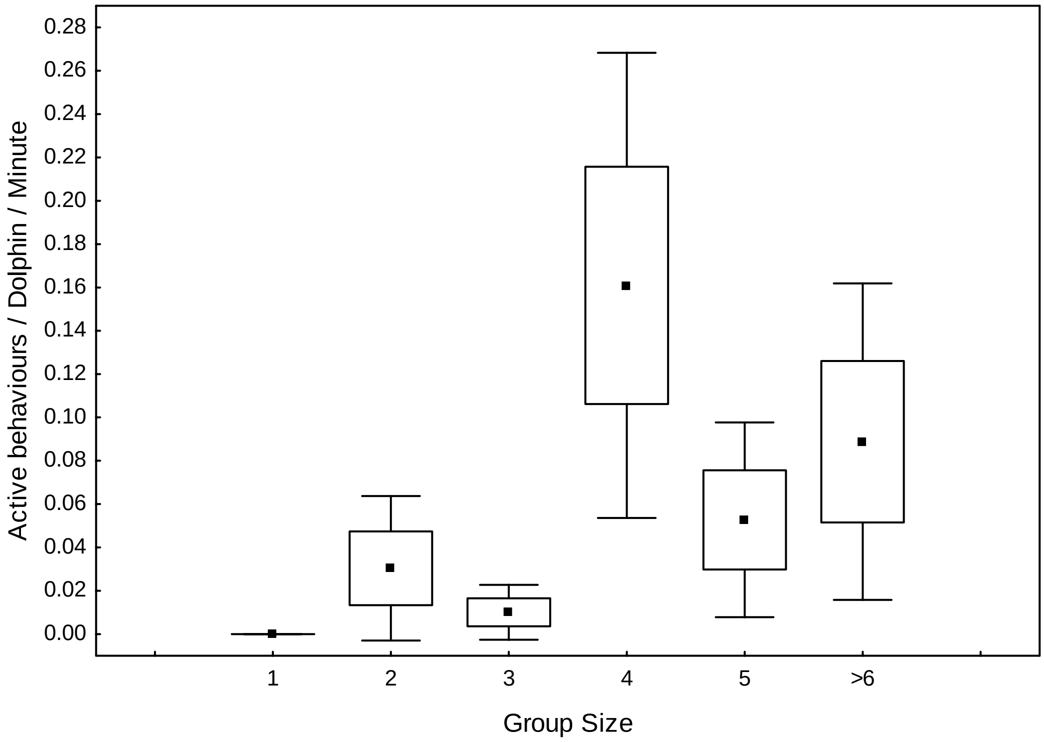

Figure 1.5. Variation in mean “Active behaviours” (per dolphin per minute) of Heaviside's dolphins with group size (the last category includes groups larger than 6). Whiskers, boxes and points represent 1.96SE, SE and Means for each direction category.

Chapter 2

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

Abstract

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

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

Introduction

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

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

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

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

Methods

Field data

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

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

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

Environmental Data

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

Prey availability data

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

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

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

Potential Fishery Interactions

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

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

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

Analysis

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

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

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

Results

Heaviside’s dolphins

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

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

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

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

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

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

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

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

Dusky dolphins

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

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

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

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

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

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

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

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

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

Interspecies comparisons

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

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

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

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

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

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

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

Potential cetacean- fisheries conflicts.

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

Interspecies interactions

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

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

Fisheries Conflicts

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

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

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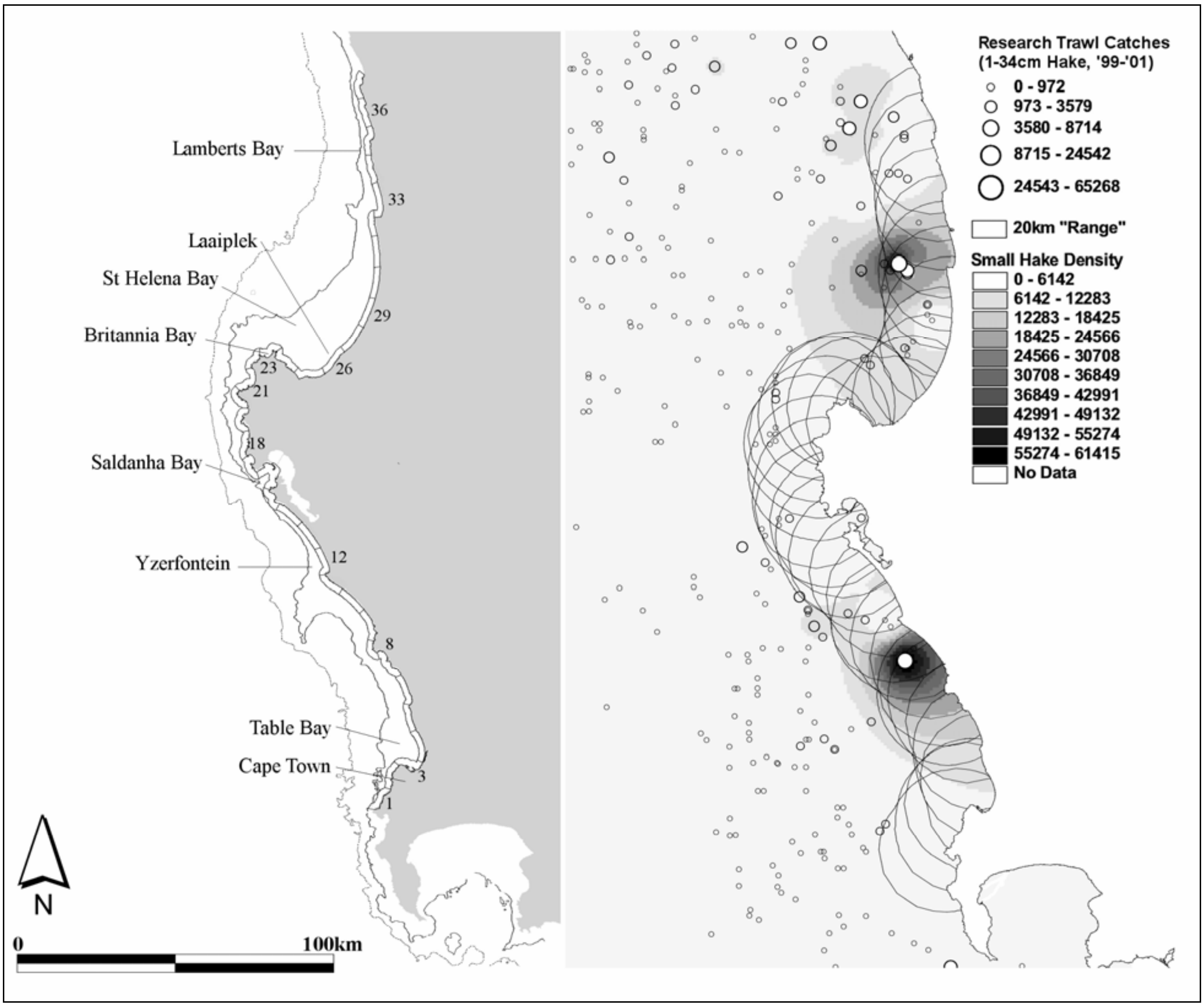

Figure 2.1. a) Study area on the southern west coast of South Africa, showing bathymetry and places mentioned in the text as well the 10km long bins used to defined search effort along the coast (numbered from south to north 1-36) and b) interpolated research trawl data of number of small (1-34cm) shallow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

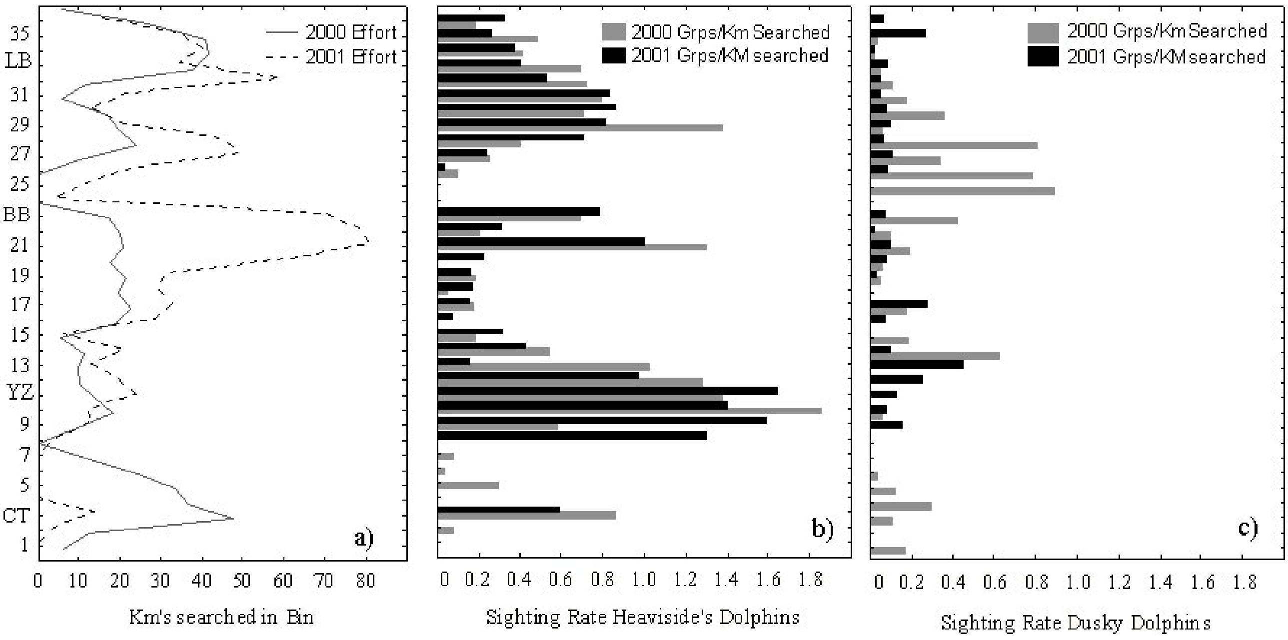

Figure 2.2. Figure oriented with north at the top and south at the bottom, with the bins containing Cape Town (CT), Yzerfontein (YZ), Britannia Bay (BB) and Lamberts Bay (LB) shown by letters. a) Number of km's searched in each ~10km long bin along the southern west coast of southern Africa in 2000 and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

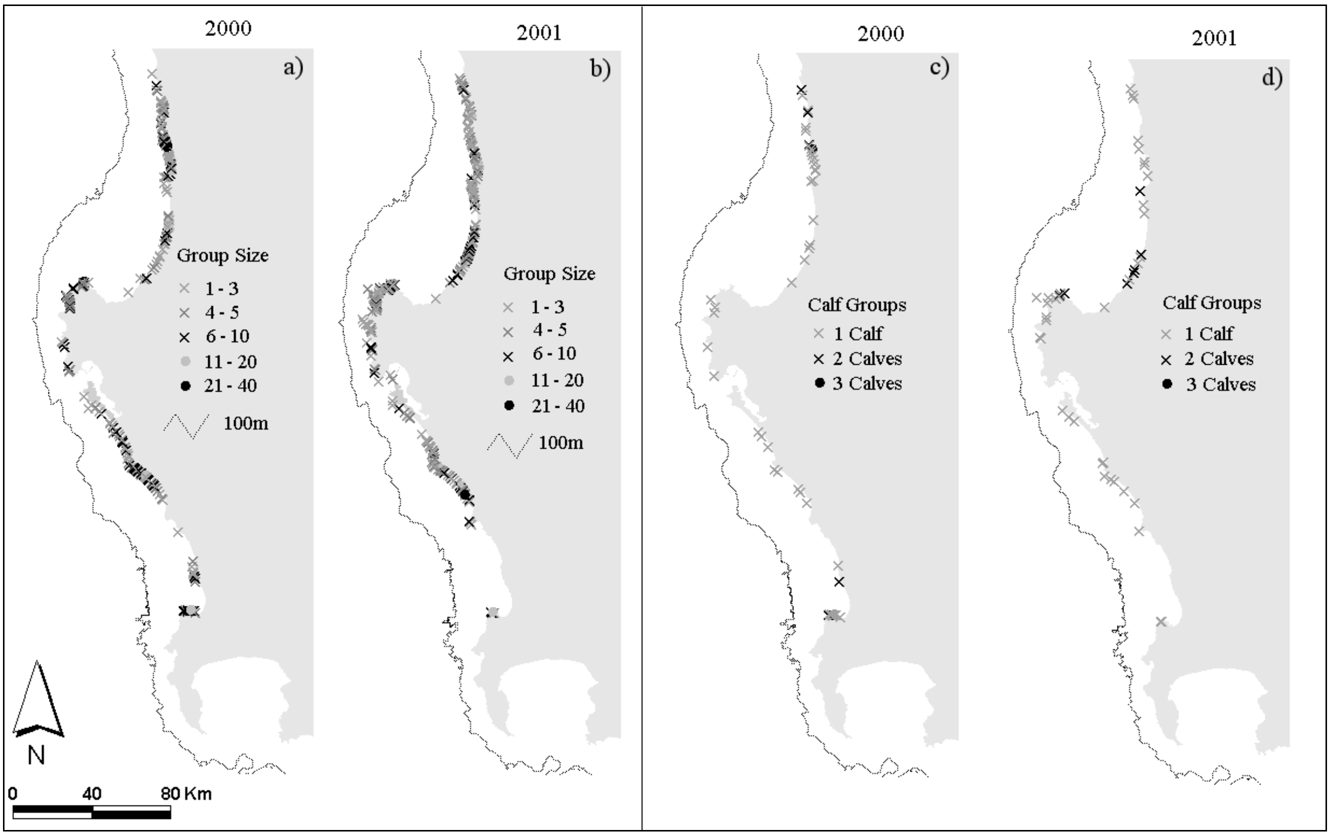

Figure 2.3. a) and b) Distribution of all Heaviside's dolphins sightings in 2000 and 2001 respectively, colours show variation in group sizes; c) and d) show the distribution of groups of Heaviside's dolphins containing calves in 2000 and 2001 respectively. All maps shown with the 100m contour as a dotted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

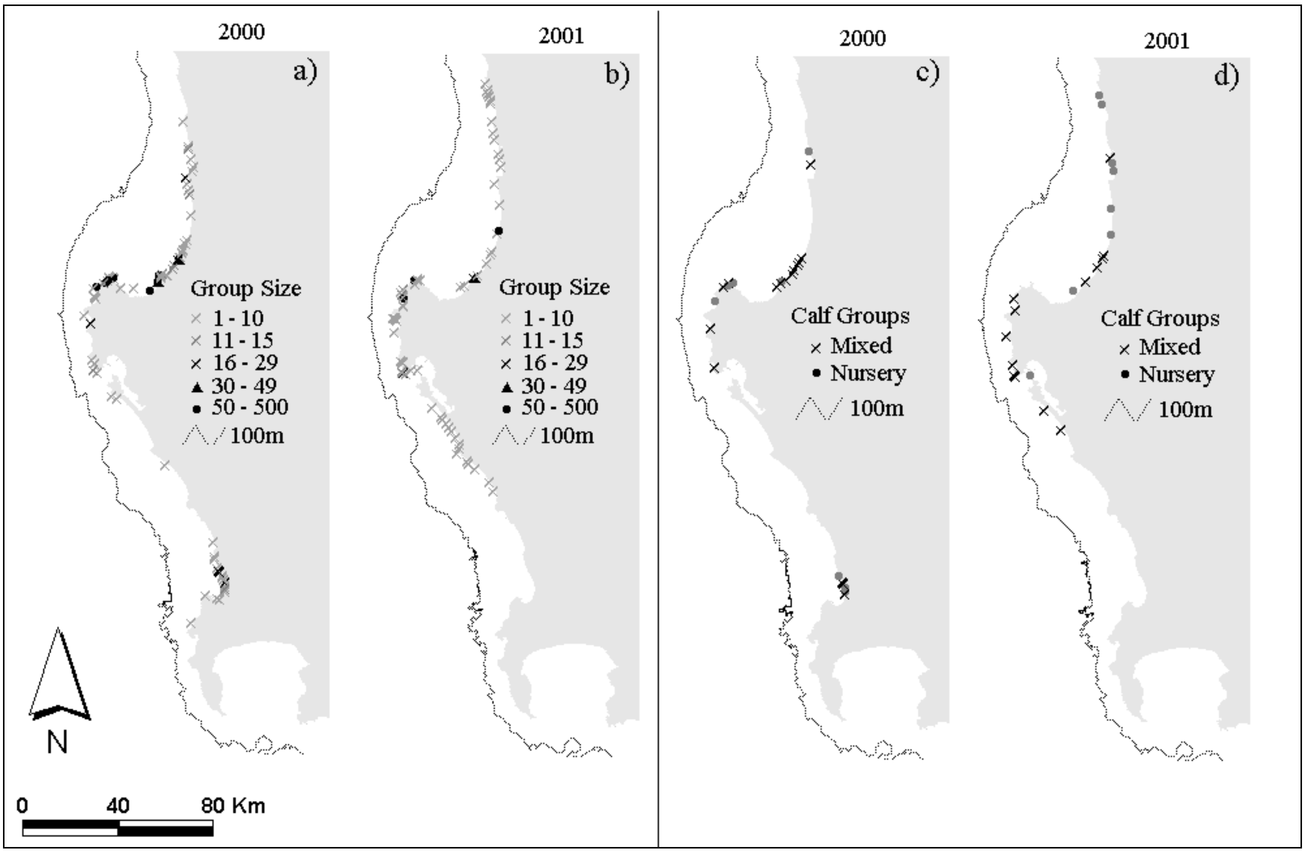

Figure 2.4. a) and b) Distribution of all dusky dolphin sightings in 2000 and 2001 respectively, colours show variation in group size; c) and d) the distribution of the two types of groups containing dusky dolphin calves 2000 and 2001 respectively (mixed groups containing adults, juveniles and calves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

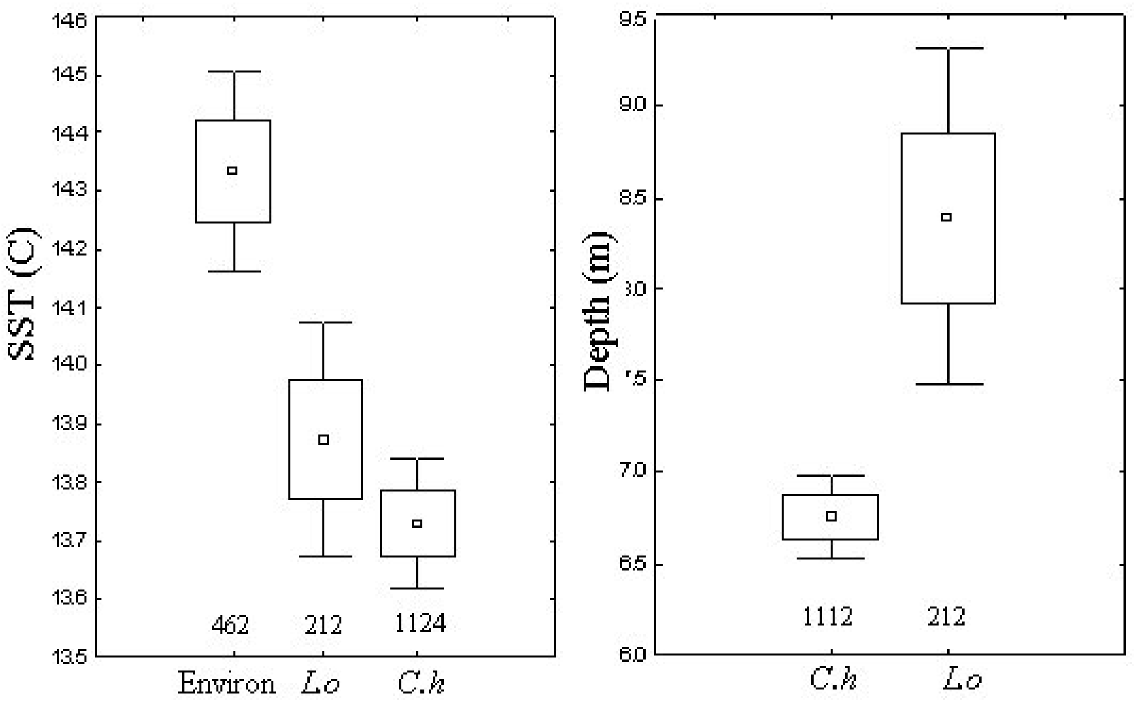

Figure 2.5. Box plots (point: mean, box: SE, whiskers: 1.96SE) showing (left) the mean sea surface temperature at sightings of Heaviside's (*C.h*) and dusky dolphins (*L.o*) and in the environment generally and (right) the mean depth measured at the beginning of each dolphin sighting.

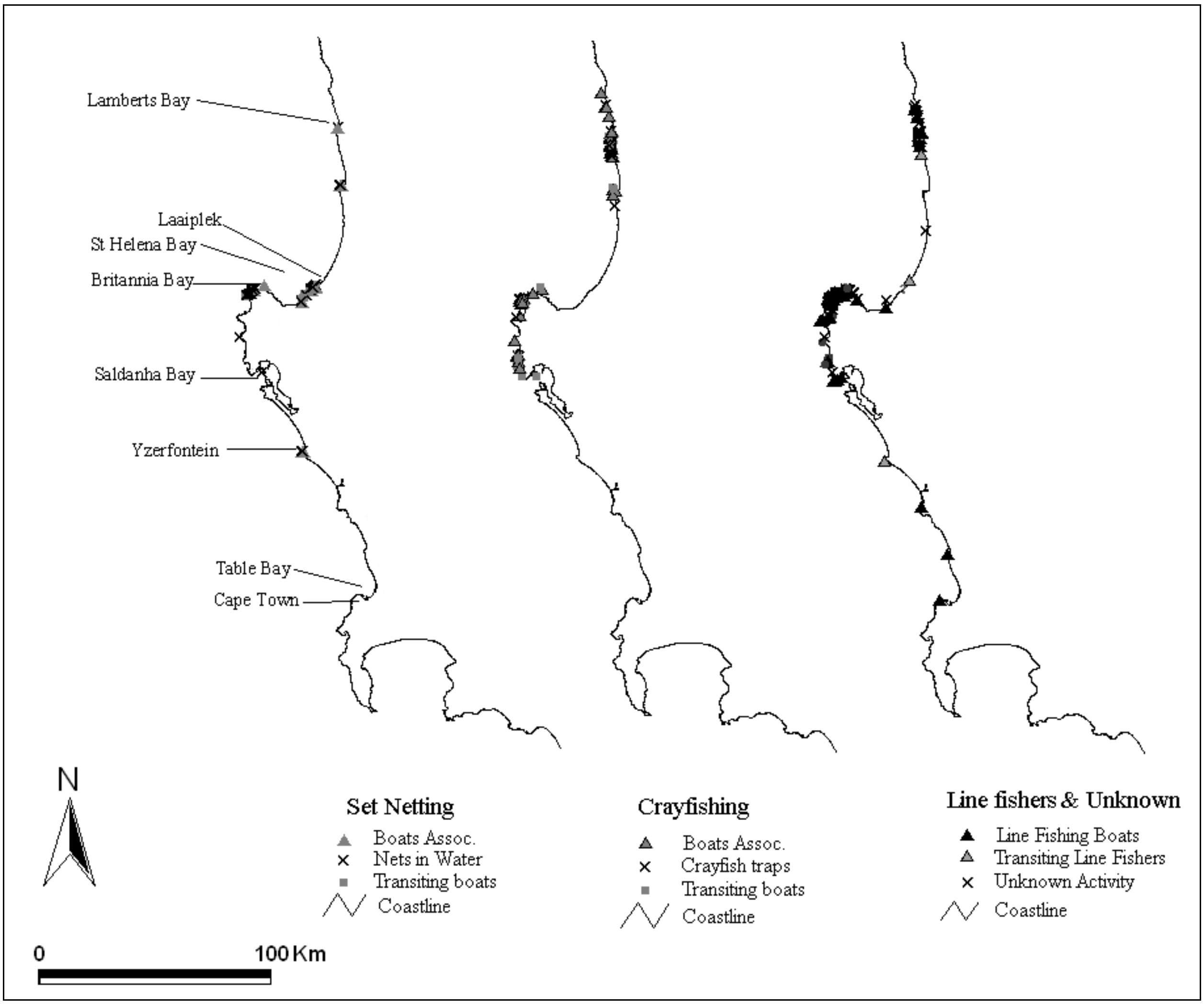

Figure 2.6. Maps showing the distribution of fishing effort observed during field work, split into the set netting (left), crayfishing (centre) and line fishing and unknown vessel (right) operations, showing the positions of traps/nets and boats associating therewith.