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Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the South African coast

By

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Abstract

Distributional data from 32 years of aerial surveys of southern right whales (Eubalaena australis) along the south coast of South Africa were investigated using GIS, over a variety of spatial and temporal scales to test whether their discontinuous yet predictable distribution is related to environmental characteristics. Most whales were found in areas that provided reasonable protection from open ocean swell and seasonal winds as well as having sedimentary floors with gentle slopes, despite these characteristics being less common. Correlation type analyses with whale density only showed significance at the broadest scale. Cow-calf pairs were found significantly closer to shore and in shallower water than unaccompanied whales; they also segregated longshore in nursery areas. No relationship between reproductive success and distribution was found except a higher than expected incidence of neonatal strandings in areas dominated by unaccompanied whales. Habitat choice at this time of year was concluded to be related both to energy conservation for calves and lactating females and protection of neonates.

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Note: Although maps used in this thesis are based on the digital version of the South African Naval Hydrographer's Charts (SAN 115-125) considerable changes have been made to the original Nautical Charts through both addition and subtraction of information as well as differences in projection and THEY ARE NOT TO BE USED IN ANY WAY FOR NAVIGATIONAL PURPOSES.

By order: SA Naval Hydrographers Office

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Chapter 1. Introduction

1.1 General Introduction

Along the coasts of Southern Africa, southern right whales[1] (*Eubalaena australis*) are regular annual visitors during the austral winter and spring. Although their historic distribution at this time of year included most of the South African coast as well as possible breeding areas off Mozambique and Namibia (Best & Ross, 1986), their current distribution is limited primarily to the waters adjacent to the Cape South Coast between 19^0 and 24^0degrees East (see Best, 1990).

Although 91.5% (cow-calf pairs) of the current population (Best, 1990) can be found on the Cape South Coast, distribution within this area is patchy and there appear to be distinct preferences for some areas over others (Best, 1981). By far the most populous areas are Walker Bay (mostly adults without calves) and the De Hoop/St Sebastian Bay region (mostly cow-calf pairs) which is regarded as one of the most important nursery areas of southern right whales in the world (Best & Scott, 1993). It is thought that the preference for certain areas over others could be due to various physical and environmental factors that may influence the whales (Best, 2000a). It was the goal of this study to determine what these factors might be.

Boat-based whale watching (hereafter BBWW) began in South Africa in 1999 as a high profile tourist industry. There is much debate globally over the possible (detrimental) effects that this industry may have on whales and what form that effect may take (see Findlay, 1998). It is important that the natural factors affecting right whale distribution off the South African coast are well understood if the effects of BBWW are to be properly evaluated. The current study is based on data gathered before BBWW began in this

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[1] Throughout this paper, southern right whales may be referred to as 'right whales' or as 'southern right whales', I use the term interchangeably. When northern right whales (*Eubalaena glacialis*) are mentioned they are specifically referred to as **northern** right whales.

country and thus will provide a basis for further studies that may allow the monitoring of possible effects of this industry on the distribution of right whales.

If the environmental factors influencing distribution can be determined, it may be possible to predict the likely direction that further expansion of the right whale population will take as the current habitats are filled to capacity. This could have importance for both the boat-based whale watching industry and other boat traffic on the South African coast, as well as potential shore-based whale watching sites.

1.2 Biology and behaviour of southern right whales

The southern right whale (*Eubalaena australis*) belongs to the order Cetacea, sub-order Mysticeti - the baleen whales. The family Balaenidae also includes the bowhead whale (*Balaena mysticetus*), the North Atlantic right whale (*E. glacialis*) and the North Pacific right whale (*E. japonica*). These are differentiated from other baleen whales by their lack of dorsal fin or ventral throat grooves and their extremely long baleen plates (Leatherwood & Reeves, 1983). Right whales are renowned for the wart-like callosities on their heads and lower jaws, which distinguish them from all other mysticetes and members of the Balaenidae. These callosities are dark at birth but quickly appear to become whitish due to the addition of whale lice (family Cyamidae) and barnacles (*Tubicinella* sp). The shape, pattern and number of the callosities are unique to each animal and allow for individual recognition and identification (Payne, Brazier, Dorsey, Perkins, Rowntree & Titus, 1983)

The southern right whale can reach a length of 16m as an adult (Tormosov, Mikhaliev, Best, Zemsky, Sekiguchi & Brownell, 1998) and weigh as much as 60 tons, though adult females are normally in the region of 14m (13.8m: Best & Rüther, 1992) and an estimated 40-50 tons. Calves are 4.5 – 6m at birth (Leatherwood & Reeves, 1983). The species appears to be sexually dimorphic with adult females being about 50cm larger than males (Tormosov *et al*, 1998) and can probably attain a life span in the region of at least 55 years (Hamilton, Knowlton, Marx & Kraus, 1998). Right whales generally have dark grey to black coloured skin with patches of white or light grey on the undersides (Leatherwood & Reeves, 1983). In the Southern Hemisphere calves are often born with patches of white dorsally and partially albinistic calves are known, though in all cases the latter darken with age (Leatherwood & Reeves, 1983; Schaeff, Best, Rowntree, Payne, Jarvis & Portway, 2000). On average, female southern right whales have a single calf at a three year calving interval (Payne, Rowntree, Perkins, Cooke & Lankester, 1990) and reach the age of first parturition when they are about eight to nine years old (South African population: median 7.88 years; Best, Brandao & Butterworth, 2001; Argentinian population: 9.1 years; Cooke, Rowntree & Payne, 2001).

Right whales, like most mysticetes, are not highly social animals and the only reasonably long-term social bond known to occur is that between mother and calf (Schaeff, in press). Calves only stay with the mother for 7-12 months, some cows arriving at the breeding grounds accompanied by a yearling calf which is quickly abandoned (Taber & Thomas, 1982; see also, Hamilton, Marx & Kraus, 1995). Although no other long-term social bonds occur, southern right whales do aggregate in a herd like manner in coastal waters in winter and short-term groupings for the apparent purpose of mating also occur (Saayman & Tayler, 1972; Payne, 1986). Male right whales do not defend territories; instead females vocalise to attract males who then congregate around her and vie for mating rites (Kraus & Hatch, 2000). Females avoid males by lying on their backs at the surface and only rolling over to breathe, at which point the nearest male on that side of her will attempt intromission (Kraus & Hatch, 2000; Payne, 1986); females apparently 'choose' males by rolling to one side or the other (Kraus & Hatch, 2000).

Right whales migrate seasonally between high latitude feeding grounds and low latitude breeding grounds (Payne, 1986; Winn, Price & Sorenson, 1986; Best, Payne, Rowntree, Truda Palazo, & Do Carmo Both, 1993). In particular, migration to South African waters occurs between June and November for the purpose of giving birth and suckling calves and possibly also for mating. Calving occurs between July and October with the peak in August (Best, 1994). While mating occurs throughout the year, fertilisation probably peaks between July and August (Best, 1994) and activity including apparent mating has been noted to occur in a variety of habitats along the South African coast (Best pers.

comm.). Right whales appear to have strong site fidelity to their coast of origin with at least 93.4% of female calves born off South Africa returning there to bear their first calf (Best, 2000a). They are not, however, as faithful to the particular bay or stretch of coast of their birth, with only 52.9% of females being found in the same or adjacent stretches of coast as in their natal year (Best, 2000a). However, these data were collected in October, fully 2 months after the peak calving season (Best, 2000a; Best, 1994), so many whales may well have moved some distance after calving thereby weakening the "link". Despite this, right whales are regarded as being a maternally phylopatric species. At Peninsula Valdés in Argentina, females in calf years were shown to have similar resighting rates (primarily between years, but some within years) in the three main concentration areas of the region ('moves' = 0.48 of data set).

1.3 Environmental Factors Influencing Cetacean Distribution with Special Focus on the Study Population

The distribution of cetaceans, as all animals, is normally influenced by the interaction of a few basic factors: food, shelter (from environmental factors as well as predators), mates and competitors. These factors influence each animal individually, and through a combination of their influences shape the distribution pattern, social structure and mating strategy of the species (Clutton-Brock & Harvey, 1978).

Food is probably one of the most important influences on whale distribution due to the huge amounts of it that whales must consume to survive. Kenney, Hyman, Owen, Scott & Winn (1986) estimated the basal metabolic needs of a 40 ton right whale to be 2.07 x 10^5 kcal d^{-1}, which at 2.28 x10^{-4} kcal/copepod (Mayo & Goldman, 2001) is equivalent to roughly 226kg of copepods per day at nearly 16 hours per day of feeding (Kenney *et al*, 1986). This shows how important a role food can potentially play in the life of a right whale. Indeed, there have been quite strong links shown between the distribution of right whales and the presence of their favoured food types, which include various species of zooplankton such as *Calanus* spp, *Centopages*, *Pseudocalanus* spp., *Temora*, *Nanocalanus*, euphausiids, ciprids and nauplii (Clapham, 1999).

Although the mechanism by which baleen whales find their food is still largely unknown it is obviously successful. Prey collected within metres of a feeding gray whale (*Eschrichtius robustus*) would fill the sample net within minutes (Darling, Keogh & Steeves, 1998), and a patch density of the order of millions of organisms per m^3 has been measured next to feeding right whales (see Clapham, 1999). Whale distribution has been strongly correlated with the presence of food sources in almost all whales studied including sperm whales (Jaquet & Whitehead, 1996; Griffin, 1999), gray whales (Darling *et al*, 1998), northern right whales (Clapham, 1999; Woodley & Gaskin, 1996) and fin whales (Forcada, Aguilar, Hammond, Pastor & Aguilar, 1996).

It thus appears possible that, at least on their feeding grounds, we may predict whales to be distributed at or near their food source(s). However, since the prey items are themselves animals, they too are subject to the same basic factors determining distribution; food, mates and competitors. Zooplankton (right whale prey) are much smaller than whales and as such are far more subject to the raw forces of ocean currents, fronts, temperature gradients and upwellings for both large scale movements and nutrient supply. Upwellings in particular are great sources of nutrient rich water that are moved from depth towards the surface due to various meteorological phenomena, such as wind and swell patterns (Shannon, 1989), large scale current circulation and also topographic influences such as oceanic ridges (Tynan, 1997) and continental shelves. Large scale events such as these can both be detected and monitored remotely (Clapham, 1999). This can be a very useful tool in predicting the distribution of zooplankton and thus the distribution of the whales that are so closely linked with them.

Several previous studies of whale distribution have found strong links between whale densities and abiotic factors such as water depth, sea floor relief, water temperature and distance from land. But in all these cases the physical factors themselves have been found to be of secondary importance to the distribution of prey species (which were influenced by the physical features). Tynan (1997) found higher concentrations of cetaceans (minke, humpback and sperm whales) where the effects of topography (the Kerguelen Plateau) generated the alignment of several oceanographic features leading to very nutrient-rich water and hence high primary productivity. Sperm whales (*Physeter macrocephalus*) have been associated with chlorophyll concentration at large spatial and temporal scales (Jaquet, Whitehead & Lewis, 1996), but also with areas of high sea floor relief close to land (Jaquet & Whitehead, 1996) and various hydrological phenomena (Griffin, 1999), all of which were linked closely to whale density via high primary or secondary production. Fin whales are more frequently sighted "beyond the continental slope" and closely correlate with certain water temperatures. Again, this is thought to be of secondary importance as these physical features are likely to control the distribution of prey species rather than have any direct bearing on whale distribution (Forcada *et al*, 1996). Common (*Delphinus delphis*) and white-sided dolphin (*Lagenorhynchus acutus*) distribution showed relationships with water temperature, salinity and sea floor relief, but not one of which was felt to be strictly causal by the authors, rather that these factors influenced prey abundance and thus secondarily dolphin abundance (Selzer & Payne, 1988).

The results of most previous studies therefore show that prey distribution appears to have an overwhelming effect on the distribution of cetaceans. However, most of these studies were either of mysticetes on their feeding migrations or of odontocetes, which normally have no marked seasonality in food intake. Right whales in South African waters are essentially on a breeding migration (e.g. Best, 2000a) and rarely feed while in South African waters, since they are thought to fast through the winter months (see Tormosov *et al*, 1998; Best & Schell, 1996). Therefore, prey distribution is less likely to be of significance and whale distribution in South African coastal waters may be governed by other factors. Abiotic factors may be of importance or the heterogeneity in their coastal distribution may be of purely behavioural or social origin (e.g. influences of maternal phylopatry or herding behaviours).

The distribution of (and access to) mates is also of prime importance in shaping a species distribution and social structure (Emlen & Oring, 1977). Since food distribution is unlikely to be an influence on right whale distribution within South African waters, the distribution of mates becomes a potentially large influence. The distribution of females is thought to be the major factor (after food) influencing the distribution of male whales (Clapham, 1999). Access to mates affects distribution via the social system of the animal.

Right whales are not obviously social animals like dolphins and do not form schools or herds, instead right whales apparently aggregate within various areas where mating occurs (Payne, 1986). These aggregations are very loose and whales move individually along the coast. The primary effect that "mating" is likely to have on distribution within local waters is that male whales are likely to be found near female whales and that solitary adults may be expected to aggregate to some extent to mediate access to mates. Southern right whales off Argentina are thought to form 'herds' where a single 'herd' covers as much as 30km of coast and moves in unison up and down the coast with no relation to environmental factors, leading Payne (1986) to suggest right whales are attracted to each other at this time of year. Although right whales in South African waters tend to aggregate within certain bays (Best, 1981, 1990) this type of large herd or general pattern of movement of a group has never been described off South Africa although no work has been done to look specifically at movements at this scale. It would however be difficult to distinguish between a "co-ordinated movement" and a common response to a change in some environmental parameter.

Competition in animals usually occurs for either food or mates and is often expressed as competition for land (or water) that allows access to these resources (Clutton-Brock & Harvey, 1978) and can potentially have large effects on the distribution of a species. Right whales are not generally territorial since they apparently rarely feed while in South African waters (Tormosov *et al*, 1998; Best & Schell, 1996) and male breeding competition is largely restricted to competition at the sperm level (Kraus & Hatch, 2000). However, there is some evidence that cows in Argentina may compete for favoured resting areas, but examples are few and the scale is considerably smaller than that used here (Thomas, 1987). Thus, intraspecific competition in right whales is not likely to affect distribution at any scale relevant to this study. Similarly, inter-specific competition is not likely to have any effect on right whale distribution since they are not competing with any other species for any common resources.

The distribution of 'shelter' can potentially also have a strong effect on the distribution of a species. There are two basic types of shelter, firstly shelter from the elements (heat, cold, rain, etc) and secondly shelter from predators. Sheltering from the elements is a major factor influencing the distribution of many animals (Emlen & Oring, 1977) and could occur at a variety of scales. Since whales are free swimming animals that cover large areas of ocean basins during their lifetimes they can potentially encounter all possible weather and sea conditions within that area. This makes the issue of 'shelter' one of scale. At what scale do whales seek shelter and what kind of shelter do they seek?

Whales could potentially move from regions of 'high seas' to 'calmer seas'. Antarctic winters are renowned for high winds and storms with average swells of 10 – 20 feet (3-6m) and peaks of up to 100 feet (>30m) (Deacon, 1984) compared with the ocean just south of South Africa where the average swell height is only 2m (CSIR data). Moving north in winter would thus take the whales away from potentially energy-sapping rough seas and into the calmer waters of the temperate regions. Storms may present a threat to calf survival while calm water may be easier for calves to swim (Whitehead & Moore, 1982) and suckle in, providing a potential energetic saving over rough waters (Whitehead & Moore, 1982).

A number of researchers have noted the strong preference that many species of whales have for calm water, especially for giving birth and soon after (Whitehead & Moore, 1982; Smultea, 1994). Gray whale cow-calf pairs concentrate in the areas in inlets furthest from the sea (Swartz, 1986) while humpback whale cow-calf pairs have a preference for waters in the lee of coral reefs (Whitehead & Moore, 1982). Right whale cow-calf pairs are also thought to prefer calm waters and in southwest Australia they aggregate in certain bays that provide some degree of protection from open ocean swell due to the local wind patterns (Holst, 1998). This preference for calm water has been suggested as a reason for the migration of baleen whales (Whitehead & Moore, 1982; Corkeron & Connor, 1999) and as a hypothesis is especially attractive in explaining the strong affinity of right whales for the coast as opposed to deeper waters. The proximity of right whales to the coast and their apparent preference for bays (Best, 1981) suggests that the whales may need a greater degree of shelter than that provided by the open waters of the Indian Ocean.

Previous studies where a preference for calm water has been suggested have mostly regarded 'rough conditions' to be a result of 'wind speed' or 'Beaufort Scale' effects (Smultea, 1994; Whitehead & Moore, 1982) and have not considered swell effects (other than Holst, 1998, but see final chapter). Choppy conditions were regarded as unattractive because they could potentially interfere with calf surfacing and breathing behaviours and could result in a higher energy expenditure for calves (Whitehead & Moore, 1982). Very young right whale calves have been noted to have an awkward breathing style compared to adults and struggle even more in rough seas (Thomas & Taber, 1984). Although right whales have been noted to occur right in the surf zone with waves breaking over them (Best, pers. comm.), I propose here that the presence of large swell would have a similar energy sapping effect on calves especially in conjunction with conditions of strong wind.

Shelter from predators, in the form of killer whales (*Orcinus orca*), has been cited as a possible reason that baleen whales migrate (Corkeron & Connor, 1999; but see rebuttal, Clapham, 2001). Since most (although not all) killer whales remain in the Antarctic over winter, it is possible for right whales to lessen the risk of predation, especially upon calves, by migrating away from the area of higher potential predation (Corkeron & Connor, 1999). Shelter from predation may also be shown at finer scales along the Cape South Coast. Although predation from both killer whales and sharks is believed to be a low risk to the local population, various behavioural traits (such as herding) may be shown that affect distribution of the species.

Right whales have been reported to occur very close to shore (90% <1.85km, Best, 1990), and in very shallow water, sometimes less than 5m in depth (Payne, 1986). Cow-calf pairs are found closer to shore than whales unaccompanied by calves (Best, 1981; Best 1990; Payne, 1986). It is therefore possible that the substrate of the sea-bed could be of importance in determining the distribution of right whales. Since whales are so close inshore in water little deeper than themselves, soft or sedimentary substrate with a smooth profile could be more attractive to whales (in an effort to reduce injury to calves) than rocky floors with many outcrops. Acoustic properties (reduced propagation of sound) of soft substrate might also reduce the risks of detection by predators. Similarly, the slope of the seabed may play a role in determining distribution as steeper sloped regions are often more rocky with less sediment.

Water surface temperature has been related to whale density in various species including sperm whales (Griffin, 1999) and fin whales (Forcada *et al.*, 1996) but in most cases it is thought to be a secondary link via prey distribution. Although water temperature has been mentioned as a useful tool in predicting the distribution of northern right whales (Clapham, 1999) it is not likely to be as useful a factor in the current study. Historically right whales must have occurred in sea surface temperatures ranging from 15^{0}C (Walvis Bay, Namibia) to 30^{0}C (Maputo Bay, Mozambique) in winter. This large range in temperatures, together with the very effective insulation of right whales, is felt to negate any direct effect that temperature might otherwise have on local right whale distribution. Similarly, salinity is ignored as a possible factor on the grounds that in other studies where salinity has been found to correlate with distribution it has been found to have a causal link through prey distribution and play no direct role (e.g. Selzer & Payne, 1988).

In this study, it is hypothesised that the distribution of right whales in South African waters is likely to be affected by the calmness of the water, nature of the sea bed, slope of the sea bed and the depth of water in which they are found. Also, it is hypothesised that cow-calf pairs are likely to show a different distribution pattern to unaccompanied whales and are likely to be more strongly influenced by environmental factors due to the greater sensitivity of calves and lactating cows to energy loss and potential injury, especially to calves.

1.4 The importance of scale

The issue of scale is an important one yet it is frequently ignored in studies of distribution in all animals including cetaceans. Some recent work on sperm whale distribution found the relationship between whale numbers and underwater topography, temperature and primary and secondary productivity to be scale dependent (Jaquet & Whitehead, 1996). Larger scales have been found to show a stronger correlation between sperm whale numbers and primary production (Jaquet, Whitehead & Lewis, 1996). When looking at too fine a scale minor fluctuations in variables can lead to unpredicted results. At fine scales it is easy to lose sight of the fact that whales are highly mobile animals that cover large tracts of the ocean in their lifetimes. The temperature difference between one bay and another along a coast may be totally meaningless to whales that encounter temperatures from 0^0C to 30^0C in their range. Right whales have wintering grounds where the prevailing surface temperatures vary from 10^0C at the Auckland Isles to 23^0C at the Head of the Bight, Australia (from Corkeron and Connor, 1999) and even warmer off Mozambique (close to 30^0C) where they were historically hunted.

On the other hand, fine scale distribution can also be very important and easily overlooked. Cape fur seals (*Arctocephalus pusillus*) have been found to congregate often and predictably at five specific and very small areas (only metres in size) within False Bay, South Africa, where existing topography and swell conditions result in highly localised yet predictable patches of calm water that the seals use for resting and socialising (Siegfried & Abrams, 1977). Whales may respond to similar small-scale patchiness in the environment, such as zooplankton swarms, where whales have been found feeding in areas of extreme prey density (only 10s or 100s of metres in size) within a greater area of much lower density (Mayo & Marx, 1990). Similarly, micro-scale patchiness of temperature, water calmness or wind avoidance could also occur. Unfortunately, micro-scale analysis (10s of metres) is beyond the scope of this project owing to the scale at which environmental data were generally available.

Scale also has a temporal component that can further confuse analysis. Some analyses become more accurate as time spans are increased, as small-scale (temporal) fluctuations may disguise the real pattern. In population dynamics studies for example, a short-term study may show a population to be decreasing, while a longer term study may show this decrease to be a small downswing in a general population increase. Jaquet *et al.* (1996) for example, found the coefficient of correlation between sperm whale catches and chlorophyll concentration to increase with increased temporal scales. Once-off surveys can also be misleading as they are not necessarily representative of what a population of animals may be doing and are only 'snapshots' of where the population is at the time of the survey. Potentially, the present study falls foul of this problem in that the data only reflect the positions of individual whales for a few minutes during late September or early October of each of the survey years. However, to some extent this disadvantage is offset by the length of the time series.

Data available for this project allow two scales of analysis over varying time periods (from 3 to 32 years); namely, data grouped by 20-minute wide longitudinal 'bins' along the Cape south coast (Muizenberg to Woody Cape) and data from GPS locations (±100m accuracy, Muizenberg to Natures Valley, Plettenberg Bay) which also allow fine scale analysis within bays.

Chapter 2. Description of Study Area

2.1. Meteorology and Oceanography

The South African climate is governed by two major current systems off its coastline, the warm Agulhas current on the East Coast and the cooler Benguela current on the West Coast. These currents influence the patterns of precipitation and run-off that are the underlying factors behind animal and plant distribution on the sub-continent (Heydorn & Tinley, 1980). They also form part of the greater anti-cyclonic circulation of both the Indian and Atlantic basins. Refer to Figure 1 for map of study area.

The Agulhas current carries warm tropical waters southwestwards past the East and Southeast Coasts, moving gradually further from the shore following the edge of the continental shelf as the coast line becomes more east/west in alignment. The Benguela current flows northwards along the West and Southwest Coasts and is characterised by extensive areas of upwelling that occur from the Cape Peninsula as far north as Angola that are brought about *inter alia* by the influence of southerly winds that are prevalent in summer. The upwelled water is very rich in nutrients, hence the high productivity characteristic of the Benguela system.

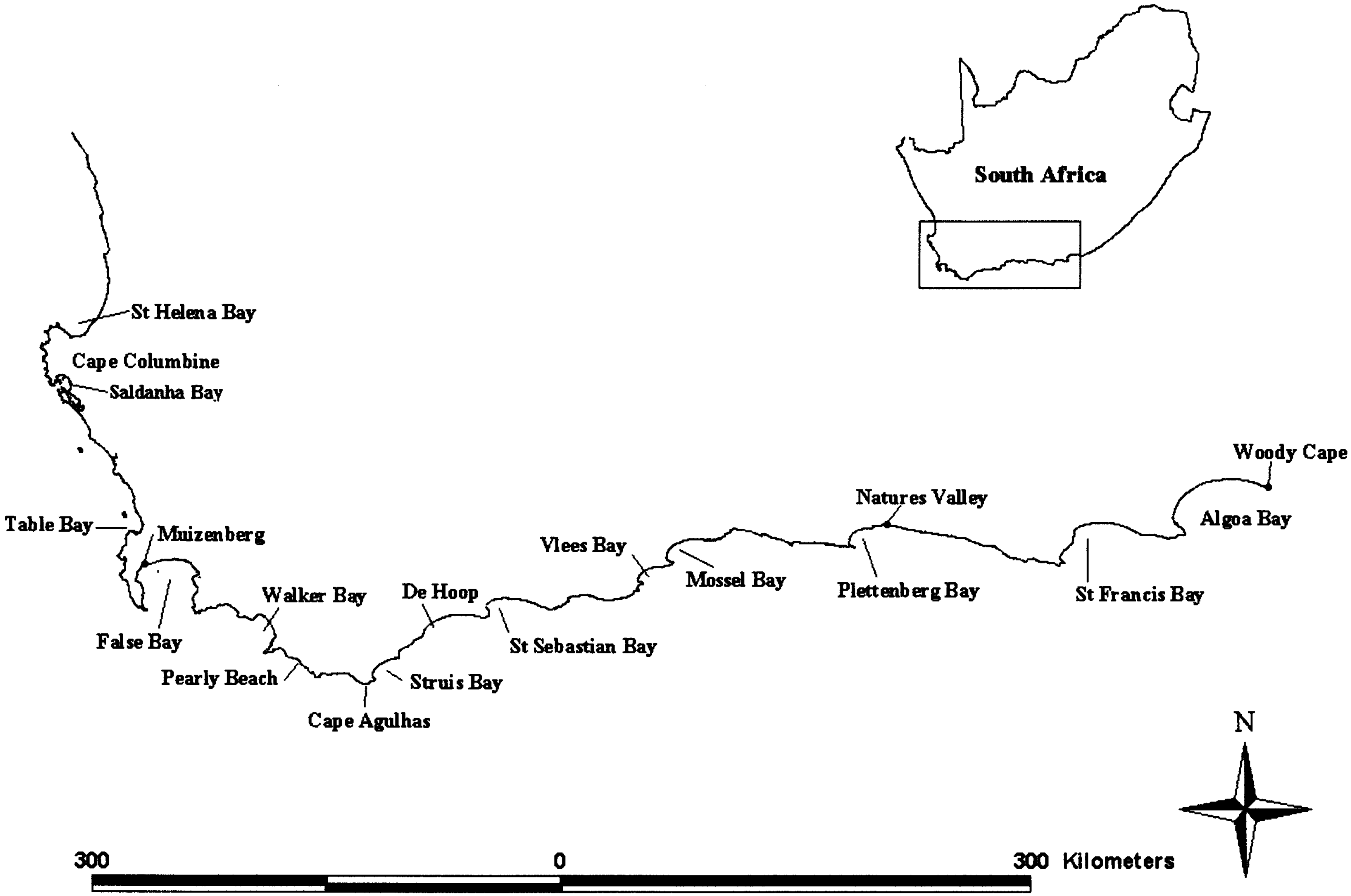

Figure 1. Western Cape coastline, showing study area and place names mentioned in the text.

The Agulhas system is substantially warmer (22^{0}C August to 27^{0}C March) than the Benguela system (surface temperatures between 10^{0}C and 14^{0}C) at all times of year (Heydorn & Tinley, 1980). The Cape South Coast lies between both current systems in temperature (17^{0}C to 22^{0}C range, CSIR data). Upwelling due to wind is the main cause of the cooler temperatures on the Cape South Coast (Shannon, 1989). The area is in a zone of transition between warm tropical and cool temperate waters. The Agulhas retroflection zone offshore periodically causes some of the Agulhas current to recurve eastwards and landwards, bringing warmer water to the coast. The Southern Cape Coast is therefore characterised by complex currents and water temperature changes (Shannon, 1995).

The climate of the Cape South Coast in winter is governed primarily by the influence of the circumpolar Ferrel Westerlies (Lenhoff, 1995). These low-pressure centres (or depressions) circle around the sub-Antarctic regions of the Southern Hemisphere and the entire system shifts north in winter and south in summer. These depressions, once formed, move from west to east and with their associated cold fronts are responsible for most of the swells that strike South Africa. The cold fronts normally pass well south of the continent in summer but frequently cross land during winter. During the passing of a cold front the wind direction tends to swing from NW through SW to SE (Lenhoff, 1995).

The Antarctic circumpolar current flows from west to east, and due to the Coriolis effect the northern parts of the current move to the left towards the Equator, bringing swells to our coast. These swells are further driven by the winds from the sub-Antarctic low-pressure systems. The combination of current and wind results in almost all swells arriving at the Cape from the southwest. The offshore swell direction off South Africa is southwest along the entire coast although waves are diffracted shorewards by the slope of the sea floor so that they end up by breaking perpendicular to the beach. The offshore swell along the East Coast tends to be more variable and wind influenced and the influence of Trade Wind generated waves can be important (Heydorn & Tinley, 1980). Swell is also affected by wind direction, so if the wind blows from one direction for an extended period the swell direction will change. In winter, most of the wind along the Cape South Coast does indeed blow from the northwest or west shifting to include occasional easterlies in spring (CSIR data). This means that there is occasional swell from these directions but it is generally much weaker than the predominant southwesterly swell.

The direction of swell thus leads to regular protection behind Cape Agulhas and all the other headlands that form part of the embayments east of Agulhas. The western parts of False Bay are quite protected from swell and the northern parts are also reasonably protected from direct swell, only getting refracted swell from around Cape Point. Between Cape Hangklip and Cape Agulhas (including Walker Bay) the entire coastline is quite exposed with the direction of swell running perpendicular to the shore. In winter, the swell pattern off the South Coast is very much from the southwest. As spring progresses, the predominantly east and northeast winds of winter give way to more south easterly winds which become predominant and move the swell toward the south and southeast sectors along much of the coast.

2.2 Geology and Shape of Coastline

The Cape South and Southwest Coasts are geologically quite different to the East and West Coasts. The outstanding features of the South Coast are the major embayments and their east-jutting promontories. The shape of these bays has been described as being 'half-heart' (Silvester, 1960 in Bremner, 1991) and conforms to a log-spiral, as characterised by Mossel Bay, Plettenberg Bay, Algoa Bay and St Sebastian Bay. There is an intrinsic relationship between shore curvature and the obliquity of incoming waves (Bremner, 1991). Rock outcrops form headlands at the apex of the short part of the curve and erosion occurs behind the headland until equilibrium is reached (in an ideal state) where an incoming wave will strike all parts of the bay simultaneously (Bremner, 1991). The deepest part of the bay thus faces away from the predominant swell direction (southwest), so that a large degree of protection from swell occurs behind the headland. Although the shape of the bays is due largely to the predominant swell direction, there is also structural control by the promontories which are the eastern termination of the west-east fold ranges of Table Mountain group sandstones. These sandstones are harder than the overlying

Bokkeveld Group shales that are predominantly eroded and tend to form the valleys and main parts of the bays (Viljoen & Reimold, 1999).

The biggest indentation on the Cape Coast is False Bay which is formed between the Cape Peninsula (Table Mountain group sandstone/quartzite) and Cape Hangklip; the latter is the southern limit of the north-south fault line of the West Coast Cape fold mountains (the Hottentots Holland mountains at their southerly limit). Exceptions to the half-heart bays are the crenellated shorelines such as those that occur between Cape Point and Cape Agulhas (e.g. False Bay, Walker Bay and Sandown Bay). These bays are much more evenly shaped, having a rectangular or square shape with one side open to the ocean. Walker and Sandown Bays are both very exposed as they face directly into the predominant swell, especially during early winter.

Along the West Coast of South Africa, the southwesterly swell tends to produce embayments that face in an up-coast northerly direction, with the deepest part of the bay on the southern end next to the headland that forms it. Examples of West Coast bays are Yzerfontein Bay, Lamberts Bay and Elands Bay although these are very small bays and are only a fraction of the size of, for instance, St Sebastian Bay. Table Bay and St Helena Bays are much larger half-heart bays formed around larger hard rock outcrops of the Table Mountain area and the granite-gneiss formation of the Saldanha Bay region and are equivalent in size to Vlees Bay and Algoa Bay respectively. Saldanha Bay itself is the northern part of the Langebaan lagoon, and is a naturally deep and protected bay, roughly equivalent in size to lower reaches of Table Bay.

By contrast the East Coast of South Africa (east of Algoa Bay) has no bays other than the Bay of Natal which is now Durban harbour and no longer a bay at all. Other than this one exception, the Natal Coast is characterised by long stretches of coarse-grained sandy beaches with occasional rocky headlands. Most of the Natal Coast is formed from sedimentary rocks and lacks the extensive number of hard rocky outcrops in otherwise 'softer' rock that result in the log-spiral bays of the South and West Coasts.

2.3 Bathymetry and the Continental Shelf

The continental shelf around the tip of Africa is of roughly the same shape as the coastline and has a triangular outline. The widest point of the shelf is due south of Cape Infanta and is roughly 170km wide. To the west it narrows to 40km off Cape Point and to the east to 40km off Port Elizabeth. The bathymetry east and west of Agulhas is markedly different and is discussed briefly below.

West of Agulhas, there is an irregular, rocky inner shelf with a middle to outer shelf of subdued relief and low gradient and the outer shelf has steeper gradients with frequent narrow valleys. The rocky inner shelf is rugged with small flat patches covered by 'Recent' sediments. There is a rather larger region of sediment just north of the Danger Point ridge, a nearshore sand wedge (Rogers, 1985). This sandy patch extends into most of Walker Bay nearshore (from Lenhoff, 1995). Between Danger Point and Agulhas there is rather less sedimentation than elsewhere in the rocky belt and the topography is more rugged. The outer boundary of the rocky inner shelf is limited by about the 120-140m isobath, deeper than which the sedimentation is younger (Gentle, 1987).

East of Agulhas, between Agulhas and Cape Infanta, the inner rocky shelf is roughly 20km wide and more indented than the rocky belt west of Agulhas. The indentations are due to structures running roughly parallel to the overlay of later beds (Tertiary and Cretaceous), while west of Agulhas they run normal to the overlay of beds (Gentle, 1987). Hence the anticlines and synclines tend to form headlands and embayments to the east of Agulhas (the 'half-heart' bays e.g. St Sebastian and Mossel Bay) but not to the west of Agulhas. Further east than Cape Infanta the rocky inner bank rarely exceeds 2km in width, only widening again at Cape St Francis (Gentle, 1987). This stretch of coastline tends to have a fairly rocky shoreline with sandy beaches only in the protected bays.

Of considerable interest along the entire continental shelf is the existence of submarine valleys that are the former courses of rivers from when a greater part of the continental shelf was exposed during the last ice age 20 000 years ago. The shelf was probably exposed down to between 100m and 140m below the current sea level (Birch, 1980).

These valleys can be seen in the contour map of the shelf; most notable are the river courses from the Breede, Gouritz, Keurbooms and Gamtoos rivers. This is important at a fine scale because around the mouths of rivers there is considerable sedimentation along the former tracks of the rivers, resulting in a muddy or sandy bottom around most river mouths. These sedimentary areas run considerably further out from shore than might be expected from sediments pushed out to sea by the force of the river and tides only. The Breede river channel runs to at least 20km offshore, substantially further out than Cape Infanta (Birch, 1980).

2.4 The Beaches and Shore types

The Kwazulu-Natal Coast (Ponta do Oura to Port Edward) consists mainly of coarse grained sandy beaches with occasional rocky outcrops. The Eastern Cape Coast (formerly Transkei and Ciskei) from East London (28^0 E) to the Natal Coast (30^0 15' E) consists largely of wave-cut rocky platforms (flat beds of rock, usually underlain by shales and sedimentary rocks) and occasional exposed rocky headlands (harder rocks resulting in rough, lumpy surfaces slow to erode) interspersed with coarse grained beaches. Both these sections of the coastline are very straight and exposed with no protected areas.

The Cape South Coast is a lot more variable and needs to be described in parts. Cape Point to Agulhas is predominantly rocky along areas where headlands and mountains result in steep slopes near the sea (Cape Point, Cape Hangklip, Onrus, Danger Point etc). The flat areas between the mountains generally have fine grained sandy beaches (Walker and Sandown Bays, Pearly Beach etc). The coastline between Cape Agulhas and Cape Infanta consists almost totally of fine grained sandy beaches with very few rocky outcrops before the Cape Infanta headland. East of St Sebastian Bay the coast is predominantly rocky with only small sandy beaches occurring mostly in the bays (Vlees Bay and Plettenberg Bay); sandy beaches only predominate again from St Francis Bay until as far as East London. Along most of the study area, the underlying geology of the near shore region has a strong effect on the shore type in the region. The harder sandstones of the Table Mountain group erode slowly and tend to end abruptly in the sea as cliffs or steep shores (e.g. Cape Infanta headland) while the flatter Bokkeveld shales tend to be shallow sloping and often underlie sandy beaches and flat rocky platforms (e.g. central beach of Walker Bay).

The entire Cape Peninsula is very rocky from Simon's Town all the way around to Cape Town with only small sandy beaches. From Table Bay (33^0 53'S) the West Coast as far north as the Olifants river (31^0 40'S) is predominated by long stretches of sandy beaches with sparse rocky outcrops. North of the Olifants river the coast becomes predominantly rocky (and with no more bays of any significant size) as far north as the Orange River.

Chapter 3: Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa: Broad scale patterns

3.1 Introduction

Southern right whales (*Eubalaena australis*) are regular annual visitors to the coasts of South Africa and other continents and islands during the austral winter and spring. Mating and calving are the apparent purposes of this migration and whales, especially cows with calves, may stay at the coast for several weeks to months (Best, 2000a). While at the coast right whales seem to preferentially occupy certain areas each year (Best, 2000a). This predictability in distribution was one of the features that made right whales so popular with the early bay whalers, who could simply wait for the whales to arrive in the same places each year (Richards & Du Pasquier, 1989). Although the population was highly depleted by both boat-based and shore-based whalers and was last estimated to be at 10% of its original numbers (Butterworth & Best, 1990), right whales are still behaving in a predictable fashion (Best, 2000a) albeit in a much smaller range. Right whale cows exhibit a high degree of maternal phylopatry to the coast of their birth as well as a lesser degree of faithfulness to a particular nursery area between calves, although Best (2000a) thought this tendency to return to some areas preferentially could be a result of environmental characteristics associated with the areas.

Most previous studies of the influence of environmental factors on the distribution of cetaceans have been performed in the summering grounds of the animals where the distribution of the animals is highly influenced by the presence of food. Studies on sperm whales (*Physeter macrocephalus*) (Griffin, 1999), fin whales (*Balaenoptera physalus*) (Forcada, Aguilar, Hammond, Pastor & Aguilar, 1996), northern right whales (*Eubalaena glacialis*) (Clapham, 1999), common (*Delphinus delphis*) and white sided (*Lagenorhynchus acutus*) dolphins (Selzer & Payne, 1986) have found relationships with water depth, temperature, sea floor relief, distance from land and various hydrological phenomena. In all cases however, the influence of these environmental factors has been of secondary importance to the distribution of prey species. Since right whales apparently rarely feed while on a breeding migration and while in coastal waters, other factors are likely to be influencing their distribution. No large scale studies of environmental factors influencing southern right whale distribution on wintering grounds have occurred, although several common patterns regarding habitat use have been reported, including Thomas (1987) and Holst (1998).

Female humpback whales (Whitehead & Moore, 1982; Smultea, 1994), southern right whales (Best, 2000a; Holst, 1998; Thomas, 1987) and gray whales (Swartz, 1986) have all been reported to show some form of preference for calmer waters, either in bays, lagoons or behind headlands or coral reefs. Choppy sea conditions were regarded as unattractive for humpback whales because they could potentially interfere with calf surfacing and breathing behaviours and so result in a higher energy expenditure (Whitehead & Moore, 1982). Very young right whale calves have been noted to have an awkward breathing style compared to adults and to struggle even more in rough seas (Thomas & Taber, 1984). Although right whales have been seen right in the surf zone with waves breaking over them (Best, pers. comm.), I propose here that the presence of large swell would have a similar energy-sapping effect on calves, especially in conjunction with high wind conditions.

The energetic and safety benefits of calm water for calves have been proposed as possible reasons for whale migration from higher latitudes by both Whitehead and Moore (1982) and Corkeron and Connor (1999). However, Corkeron and Connor (1999) propose the principal reason for migration of large baleen whales to be avoidance of intense killer whale predation levels at high latitudes. Although predation from both killer whales and sharks is believed to be a low risk to the population off South Africa, various behavioural responses (such as aggregating) could affect distribution of the species. This is more likely to be shown by cow-calf pairs than unaccompanied whales as calves are at a greater risk from predation, such risk diminishing as body size increases (Corkeron & Connor, 1999).

Although water temperature and salinity have been related to cetacean density in other species (Selzer & Payne, 1986), neither was thought likely to have much influence in the current situation. Southern right whales are found during winter in surface temperatures ranging from ~15^{0}C in Walvis Bay to ~30^{0}C in Maputo Bay, and salinity has always been found to relate to whale presence via prey density. Further, the current study covers a long time series and precise temperature or salinity data for the days of survey were not available for the entire study area.

Since right whales are often found very close to shore in water little deeper than themselves (~5m; Payne, 1986), the nature of the substrate could be important. Acoustic properties (reduced propagation of sound) of soft substrate might also reduce the risks of detection by predators. Similarly, the slope of the sea bed may play a role in determining distribution. Cow-calf pairs especially may avoid areas with steeper slopes, which are characteristically rocky with little sediment.

Baleen whale migration is often regarded as being a female-mediated event in which cows migrate for some apparent benefit to their calves, while there are no apparent benefits associated with migration for unaccompanied whales (Corkeron & Connor, 1999). If this is correct it implies that any environmental factors influencing right whale distribution along the South African coast are likely to have a stronger influence on the distribution of cow-calf pairs than unaccompanied whales. In this study, it is hypothesised that the distribution of right whales in South African waters is likely to be affected by the calmness of the water, nature of the sea bed, slope of the sea bed and the depth of water in which they are found. It is also hypothesised that cow-calf pairs are likely to show a different distribution pattern to unaccompanied whales and are likely to be more strongly affected by environmental factors.

3.2 Methods

3.2.1 Distributional Data

Since 1969 annual aerial surveys for the specific purpose of counting and/or photographing right whales have been undertaken along the southern Cape coast. Sightings were classed as cows with calves, ("cow-calf pairs", photographed) or as juveniles or adults unaccompanied by calves ("unaccompanied whales", not photographed). Between 1969 and 1987 the aerial survey was performed with a fixed wing aircraft starting at 18^0 30'E (Muizenberg, the northwest corner of False Bay) and finishing at 26^0 30'E (Woody Cape, eastern end of Algoa Bay). Since 1979 a second survey was performed by helicopter but was only run from Muizenberg as far as Natures Valley (Plettenberg Bay, 22^0 50'E), roughly two thirds of the original survey length. This resulted in two sets of data, 19 years of surveys (1969-1987, fixed wing only) covering the larger area and 32 years (1969-2000, fixed wing and helicopter) of the smaller area. Both data sets are used since they have the respective benefits of a larger area and a longer time series, and are referred to as the 19-year and 32-year data sets.

The entire coastline was searched within these standard survey areas, in a flight pattern parallel to but about 1km offshore. All sightings were circled to establish species, group size and composition. In some years the fixed wing survey extended up either the East or West Coasts, but the standard survey area (Muizenberg to Natures Valley) has been surveyed regularly each year since 1969, between late September and mid October (see Best, 1990 for full survey procedures).

Since this aerial survey programme was started well before the advent of GPS positioning, the position of most whale sightings was given relative to adjacent landmarks like headlands and river mouths. Since the coastline runs in a largely east to west direction, the surveyed area was subdivided into bins 20 minutes of longitude in width (Figure 2), following Best (1981). Within each bin the length of the coastline varied from 30.6km to 68.5km (average = 41.4km) and to compensate for these differences whale density in each bin was used (number seen per kilometre of coastline) as well as actual whale numbers per bin. These data have been used previously to monitor various attributes of the local right whale population (Best, 1981, 1990, 2000). In order to correspond with these other studies, the data have been grouped in a similar manner, both temporally and spatially. Since 1969, the data set is divided into three 'periods', 1969-1979, 1980-1987 and 1988-2000.

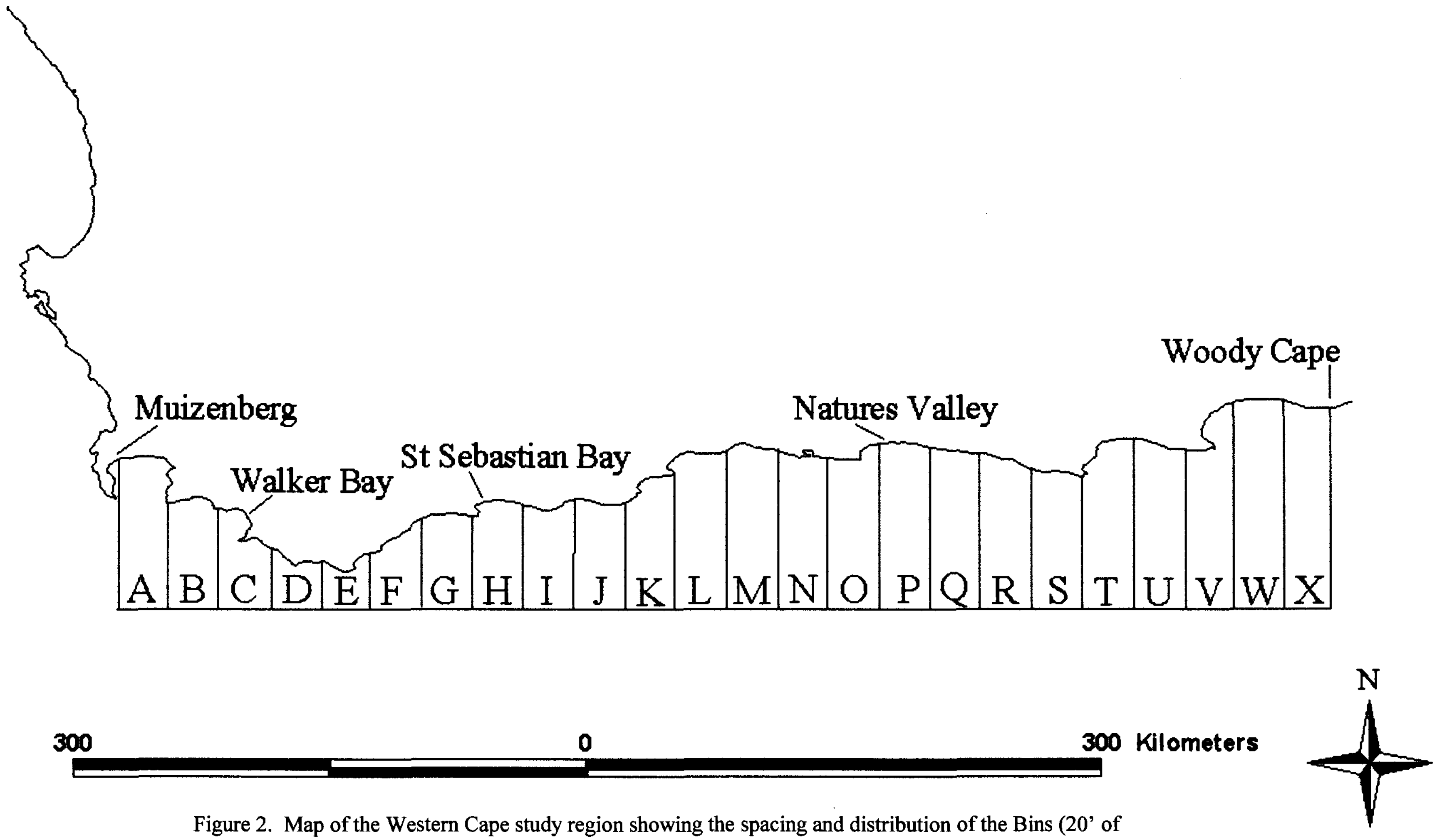

Figure 2. Map of the Western Cape study region showing the spacing and distribution of the Bins (20' of Longitude wide) used to define whale distribution within the surveyed region by Best (1980, 1990, 2000)

Accurate whale positions in the form of GPS locations are available from three helicopter surveys (1997, 1999, 2000). These GPS data are substantially more accurate than the 'binned' whale positions and allow for analysis of whale distribution at a much finer scale using more environmentally uniform areas. These smaller stretches of coastline were called 'zones' to differentiate them from the 'bins' of the longer-term data sets (Figure 3). Due to the bays along the coast being of different sizes no attempt was made to equalise zone size, instead they were defined to be as environmentally uniform as possible. Protected bays for example were separated from exposed stretches of coastline, and a bay was usually split into a protected 'head' and an exposed 'tail'.

By using the 20-minute wide bins of the long-term data sets, accuracy is considerably reduced compared to those surveys for which GPS data are available. However, these bins are still suitable for looking at large-scale coastal distribution and are fine enough to resolve the patterns of patchiness in distribution at this scale. The length of time that these surveys have been run makes them especially useful for describing long term trends in distribution patterns. For details of the full survey methods, see Best (1981, 1990).

3.2.2 Environmental Data

In order to describe the range of characteristics to which whales within the surveyed area are exposed, it was necessary to define the width of the surveyed area within each segment or bay as well as along the entire coastline. Inspection of the precise GPS positions available for whales from aerial surveys (1997, 1999, 2000) on the GIS system (see below) shows that all sightings were contained within 3000 metres of the coast, although most were substantially closer inshore. Since it was impossible (in retrospective analysis) to define the exact area and distance from shore surveyed or the intensity of survey effort at any point, 3km was assumed to represent the extreme limit of the surveyed area from the coast. Environmental factors used in the analyses include water depth, slope, degree of protection from swell and wind as well as shore type, related to this 3km wide strip.

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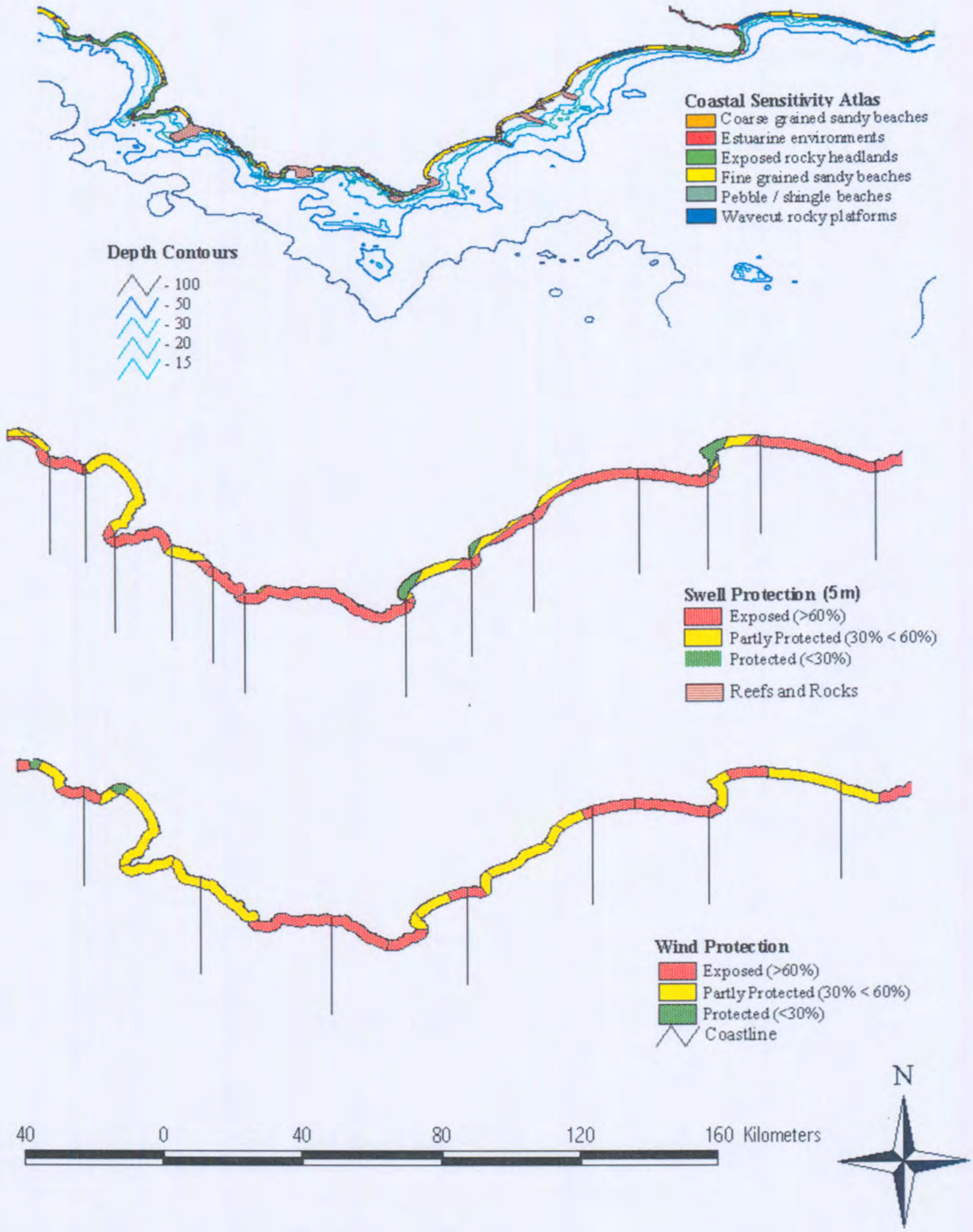

Figure 3. Series of maps to illustrate hoe Zones – middle coastline (used on GPS scale data) were placed specifically to maximise environmental uniformity (compare three coastlines) within each Zone, whereas Bins – bottom coastline (used on long term data sets) were simply placed 20' of Longitude apart.

An accurate digital coastline (as well as soundings and depth contours) of the southern Cape Coast was obtained from the S.A. Naval Hydrographer's office from the marine navigation charts that are drawn, and regarded to be accurate, at 1:150 000 scale. The coastline, soundings and depth contours were used in a GIS package (Arcview 3.2) to create an artificial 'surface' that mimicked the sea floor (Figure 4). This is not the 'true' sea floor but is the best representation attainable with the available data. "Ground truthing" in the form of comparisons to maps with finer bathymetry contours that were available for some sections of the coast, produced favourable results. From this artificial surface, it was possible to measure the depth and slope at any given point as well as average depth and slope for any defined area within the surface.

In lieu of good data on sea floor substrate the only information available at a useful scale that is related to the sea floor, is data on the shore type adjacent to the seabed. It was felt that although the shore type is not always the same as the near-shore substrate, it is similar enough, often enough that the information could be useful. The Coastal Sensitivity Atlas (1982) defines the shore line along the entire South African coast as being one of six basic types, exposed rocky headlands (in the study region: hard rocks, usually granites and quartzites of the the Table Mountain group characteristically rough, lumpy surfaces slow to erode, forms most cliffs in the region), wave-cut rocky platforms (flat beds of rock, usually underlain by shales and sedimentary rocks of the Bokkeveld group, forms the body of most bays in the region), estuarine environments, fine sandy beaches, coarse sandy beaches (East Coast only) and pebble/shingle beaches. A digital version of this atlas was available for use on the GIS system.

Protection from swell and wind was less easy to quantify than the factors above, because the strength, direction and frequency of oceanic swell and wind patterns vary greatly. As this study encompasses such a large area of coast, it was not possible to get precise measurements of swell or wind characteristics at all points along the surveyed region for the last 30 years. However, because the distribution of whales along the coast is reasonably predictable (Best, 1981, 1990, 2000), it is possible to describe long-term average conditions in these high density areas and compare and contrast them to those in areas where whales tend to occur in much lower densities. Averaged long-term data

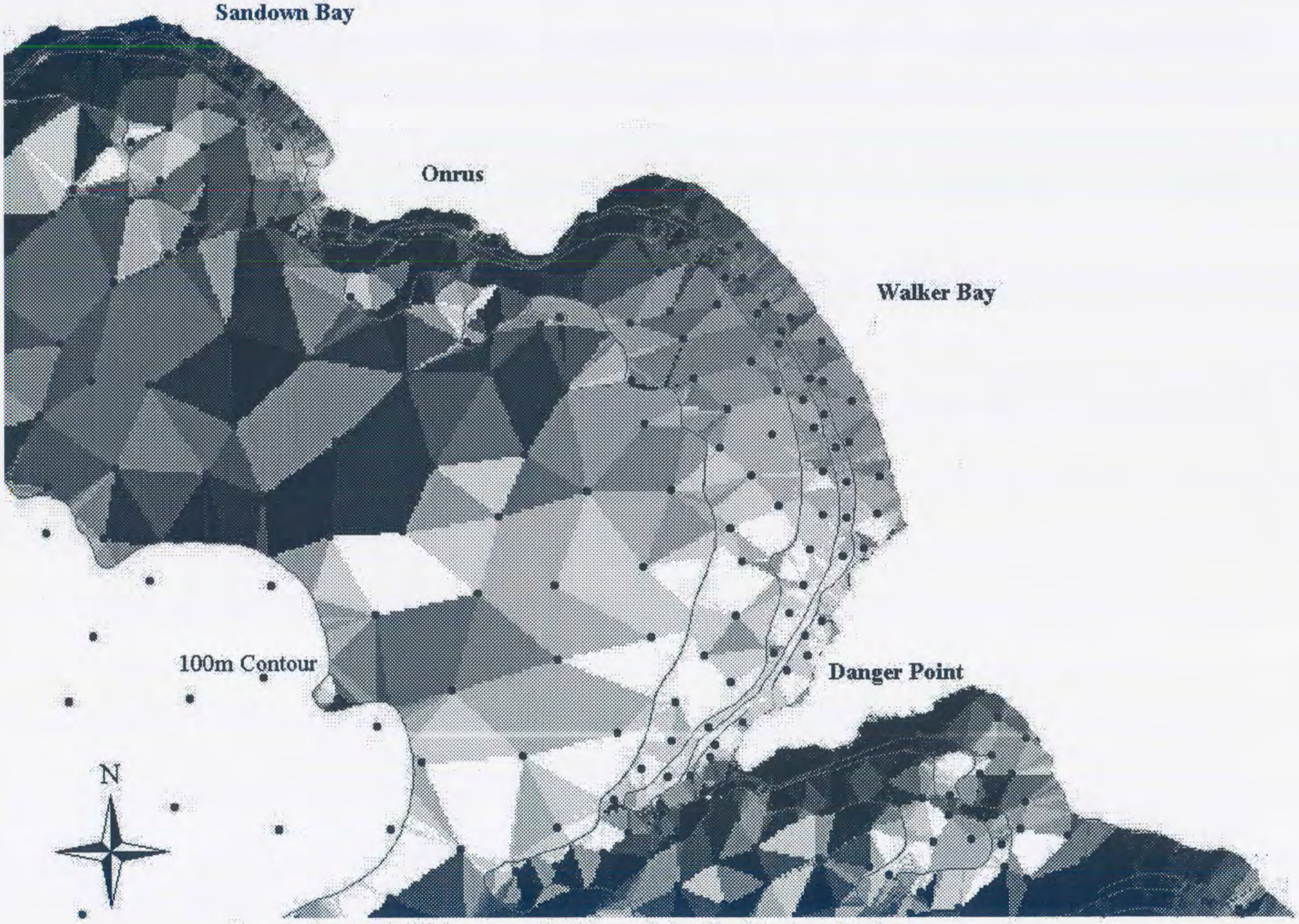

Figure 4. Example of artificial sea floor surface (TIN) as calculated from SAN chart's depth and soundings..Walker Bay shown. Shading is a graphic lighting effect to highlight the planar nature of the surface and does not represent any particular feature of the sea floor.

(1979-1999) on offshore swell and wind direction, strength and frequency were available from the CSIR Marclim database. The data were divided into prescribed areas (usually one degree or half a degree square of latitude and longitude) that correspond to particular stretches of coast (Figure 5). Data from spring (September, October, November) were used as the aerial survey always took place between late September and early October (Best, 1990). The offshore swell climate is representative of what the swell patterns are in the absence of any effects from the land.

Swell data took the form of "roses" which described the proportions of swell coming from each direction in a 16 point compass, as well as the frequency of the various swell heights from that direction (Figure 5). Wind data were in a similar format of "roses" showing proportion and strengths of winds from each direction (Figure 6). The swell roses for each stretch of coast were used to estimate the percent of swell that would be striking the adjacent section of coast and conversely the amount of swell from which a section of coast was protected. This was done by adding the frequencies of all swell or wind (all heights/strengths) from each direction to which a piece of coast was exposed, and then inverting this value to calculate 'protection'.

By using long-term swell data it was possible to decipher which areas of the coast are likely to provide regular, predictable protection from the predominant swell directions. After discussion with oceanographers and in an effort to retain simplicity, it was decided to use a three-tier system of description, "protected", "partly protected" and "exposed". Because it split the three tiers into roughly equal parts it was decided that any area protected from more than 60% of swell would be defined as "protected", any area protected from more than 30% of incoming swell as "partly protected", and any area protected from less than 30% of swell as "exposed". Refraction of waves around headlands was ignored as it was not possible to accurately model every bay along the coast for every conceivable swell direction and at the scale used (3-tier system and 16 point compass) it would not have been useful to attempt to include refraction. The effect of reefs in breaking up swell was ignored because of incomplete mapping of nearshore reefs.

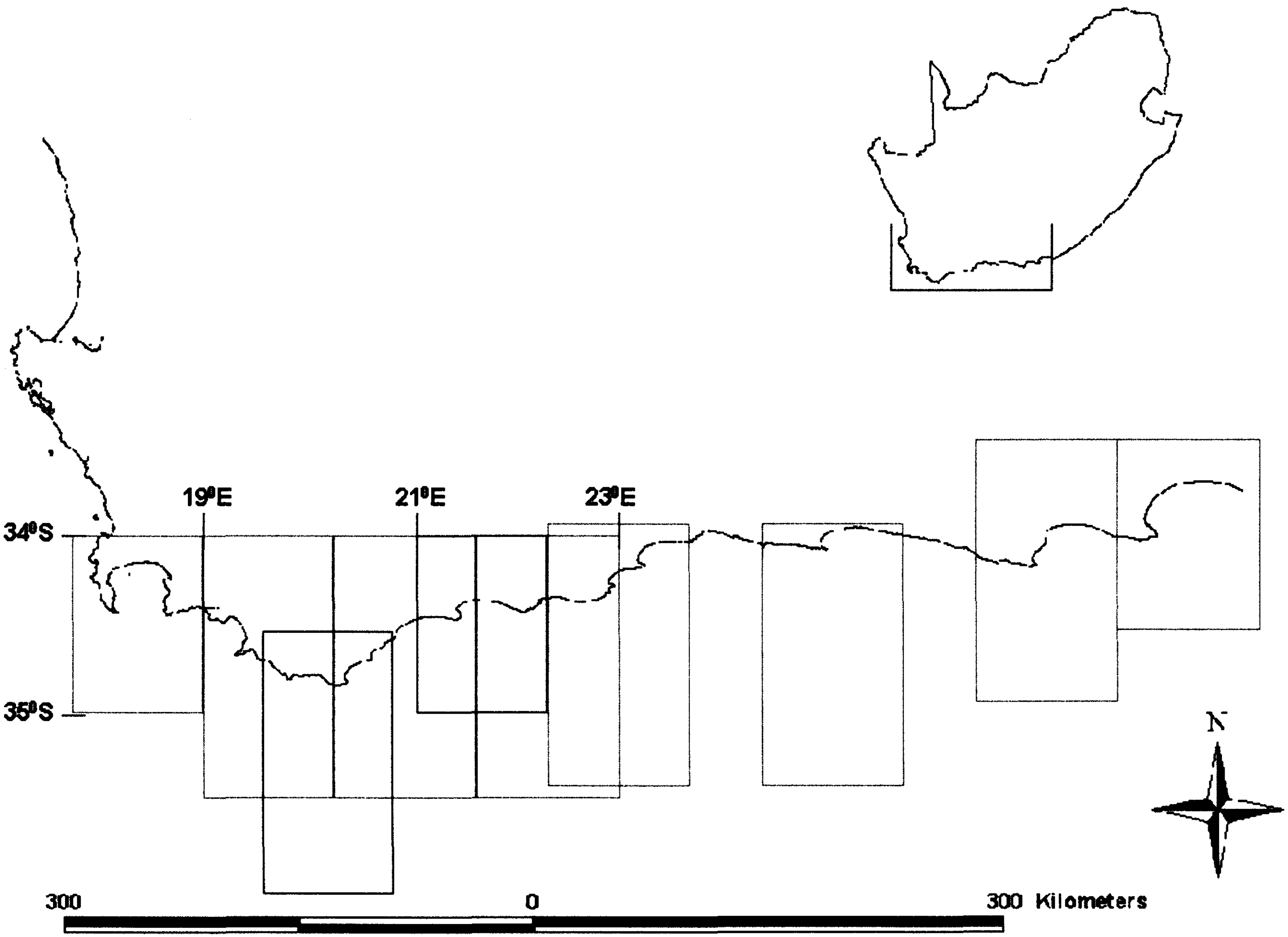

Figure 5. Map shows the areas from which the CSIR took ship based data from the Marclim database for use in generating the wind and swell "roses" used here. Roses used were from the most geographically appropriate area

It is worth noting that during winter (June-August) the swell along the entire surveyed coastline is almost totally from the southwest quadrant, but during spring (when the survey is run) more of the swell comes from the southeast quadrant due to the shift in wind patterns towards the south-east. These southeasterly swells are more predominant in the western section of survey area (west of Cape Agulhas) than in the eastern section where swell is still distinctly southwesterly during spring. Due to the greater 'spread' of swell directions in the western end of the survey region, protection levels are higher than might be expected considering that the predominant annual swell direction off this coast is regarded as southwesterly. Thus, the coastlines of False Bay as well as Walker and Sandown Bays are each classified as at least 'partly protected'.

The effects of wind on nearshore water are complicated by the influences of the height and shape of near shore land masses. However, some shelter is provided by land of any shape, resulting in a certain degree of protected water close to shore. Due to the broad scale of the study and the lack of fine scale data, a three-tier system of description was used to describe protection from wind on the same basis as protection from swell. Because the size of this protected area is highly variable it is not possible to determine the exact areas that are sheltered at each point along the coastline. Therefore, an area of water was regarded as protected from all offshore breezes but not longshore breezes (those parallel to the coast) or onshore breezes (Figure 6).

Due to the complications of variable wind speeds, near shore topography and the reasonably calm weather of survey days it was not possible to calculate how far from shore the sheltering effect applied under all conditions and at all times, although it was almost certainly less than the 3000m buffer used to define the 'surveyed area'. Thus in an effort to retain simplicity and generality (applicable to long-term data) a stretch of coast was defined with its level of protection from the shore to as far as the 3km buffer. Any whales along that stretch of coast whether 200 or 2000m from shore were described as being within that level of protection (on the basis that a right whale could easily and rapidly move the few hundred metres inshore necessary to gain any added protection closer to shore).

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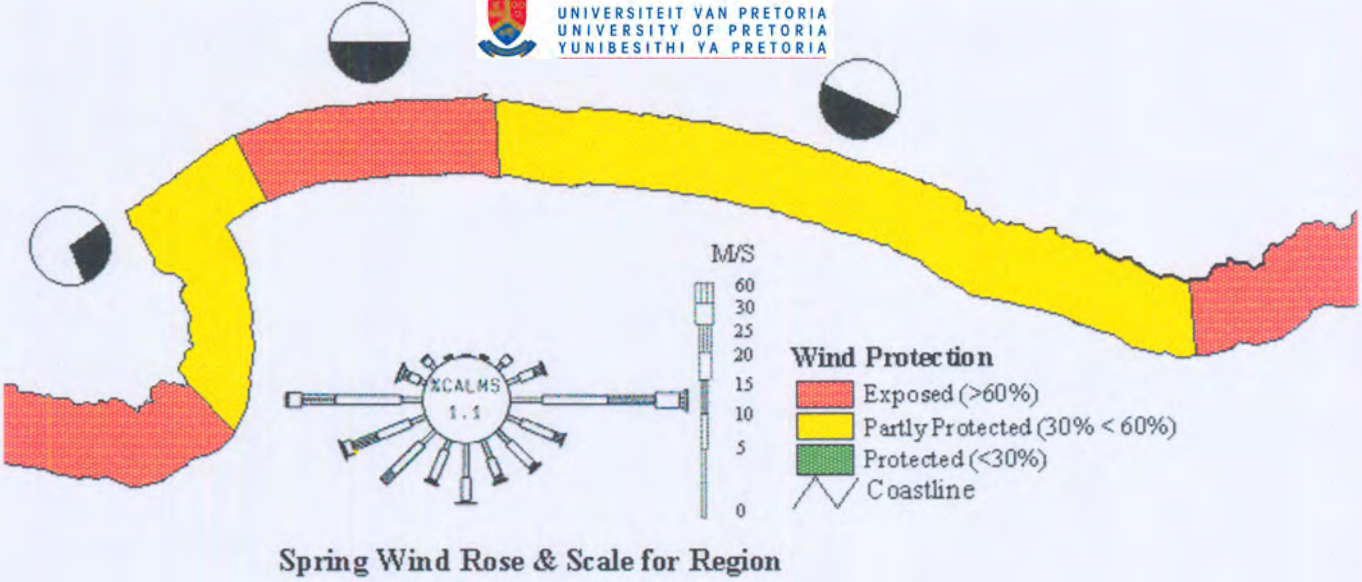

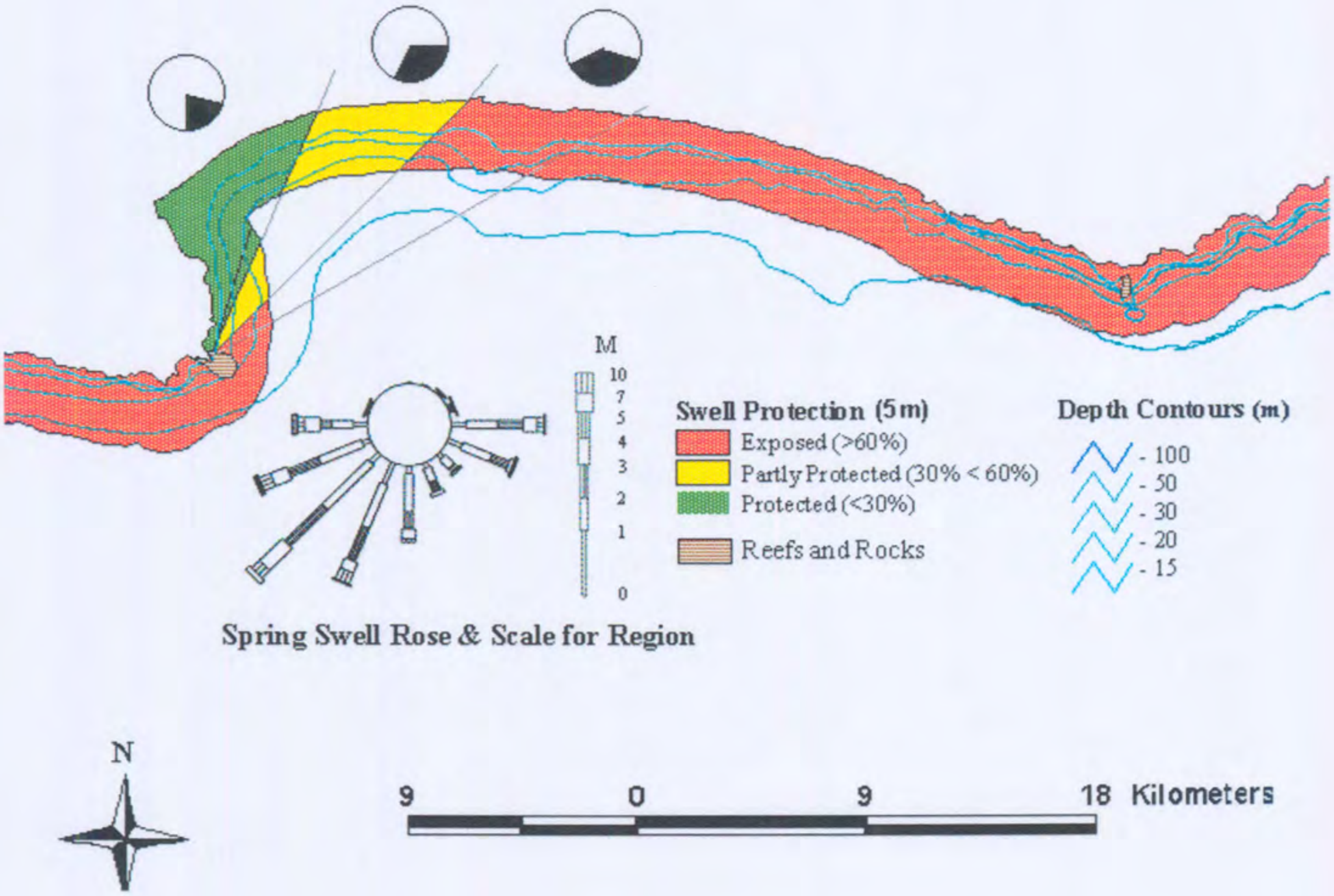

Figure 6. Wind (top) and swell (bottom) protection for St Sebastian Bay, shown with respective 'roses' and pie charts showing directions from which wind and swell were regarded to be striking the coastline (shown in black)

3.2.3 Analyses

The distributions of cow-calf pairs and unaccompanied whales were compared in both a longshore and offshore direction. Longshore comparison was performed on the numbers of animals seen per bin for the long-term (32 year) and widest area (19 year) data sets using a Chi-squared analysis. Specific GPS positions for each whale sighting made it possible to assign values of environmental conditions to specific whales. The depths, slopes and distances from shore at which cow-calf pairs and unaccompanied whales occurred were compared. The distributions of primiparous and multiparous cows were similarly compared for depth, slope and distance from shore. Longshore comparison of these classes of whale was not possible due to the low numbers in many of the areas but distribution patterns evident are discussed.

The stability of the pattern of whale distribution over time (between periods) was tested using a Wilcoxon signed rank test, where periods 1 and 2 were compared directly and ›eriod 3 was compared to the equivalent areas from the first two periods. Since the right whale population is increasing (Best *et al*, 2001), the absolute density of whales per bin will increase as time passes, biasing any time dependent tests. To overcome this problem, between-period tests were performed on the number of whales in each bin relative to the total (proportion) instead of the density.

In order to test the usefulness and accuracy of shore type as an indicator of near shore substrate type, analysis was performed on the distance from shore and sea floor depth over which whales were sighted in relation to the main shore types to ascertain whether whales showed any response to shore type.

To test whether whale distribution was related to the environmental variables in particular areas, the densities of cow-calf pairs and unaccompanied whales per bin (19 year and 32 year data sets) and per zone (3 year averages) were correlated against each of the environmental factors per bin or zone. Environmental factors correlated were the average ᵈᵉᵖth and slope of the areas, the proportion of each area exposed to either swell or wind the proportion of each area that consisted of attractive shore type (regarded as sandy beaches + estuarine environment + pebble/shingle beaches). Whales were expected to occur at higher densities in shallower areas with flatter slopes and in areas where there was relatively little 'exposed' water as well as in areas with attractive shore types representing sedimentary bottoms.

Using the GPS data it was possible to calculate the number of whales per category for each environmental factor and compare the distribution of whales per category with the numbers expected if they were distributed uniformly with regard to the categories of each environmental factor. In order to show how whales distribute with respect to the slope and depth 'available' within the surveyed area it was necessary to categorise the continuous depth and slope measurements. Depth was split into 2m intervals, while slope was split into 0.2^0 intervals. Since there was very little of the surveyed area (and very few whales) beyond 30m in depth or 3^0 in slope, categories beyond these measurements were summed. For analyses of protection from swell and wind, the proportion of each protection level of the total area along the surveyed coast was used to define an expected distribution of whales. Similarly, the proportion of each shore type of the total shore was used to define an expected 'random' pattern of distribution that whales would have if they distributed with no relationship to environmental factors. These expected patterns of distribution were compared with the actual distribution of whales in each category of each tested factor using a Chi-squared test or a log-likelihood test if numbers were too low.

3.3 Results

The longshore distribution patterns of cow-calf pairs and unaccompanied whales along the Cape Coast are significantly different over both the widest ($Chi^2 = 328.1$, $p = <0.0001$, df = 47) and most long-term ($Chi^2 = 842.5$. $p = <0.0001$, df = 29) data sets available. The overall pattern and the differences are stable over time since no significant differences were found for the proportion of whales in each bin between any of the periods tested (Table 1). Definite peaks are obvious in the bins that include bays (Walker Bay, St Sebastian Bay, Mossel Bay and Plettenberg Bay), the obvious exception being False Bay, which is the largest bay in the surveyed area but has relatively few whales (Figure 7 and 8), although only two-thirds of this bay's shoreline was surveyed.

Table 1: Comparison by 'period' of proportion of animals in each bin using a Wilcoxon signed Rank test. The proportion of animals in each bin remained statistically constant through time.

Class	Dates	W =	N =	P value
Cow-calf	1969-'79 vs 1980-'87	-75.0	24	0.1984
	1969-'79 vs 1988-'00	4.0	15	0.9341
	1988-'00 vs 1980-'87	2.0	15	0.9780
Unaccompanied whales	1969-'79 vs 1980-'87	-28.0	24	0.6997
	1969-'79 vs 1988-'00	24.0	15	0.5245
	1988-'00 vs 1980-'87	-22.0	15	0.5614

Due to the small sample sizes involved, a statistical comparison of the longshore distribution of primiparous and multiparous cows is difficult without extensive pooling of bins (so reducing the power of discrimination). In 1997, the highest concentrations of primiparous cows occurred in Walker Bay and De Hoop with low numbers in all other zones including St Sebastian Bay. Multiparous cows in this year were primarily concentrated in De Hoop and St Sebastian Bay with further concentrations in Struis Bay and Pearly Beach and relatively few in Walker Bay. In 1999, almost all the primiparous cows were found in or near the nursery region (De Hoop/St Sebastian Bay). Multiparous cows were primarily found in the nursery with Walker Bay and Struis Bay following as smaller areas of concentration. No pattern was obviously stable between years for either class of cow. No significant difference between primiparous and multiparous females was found for distance from shore, depth or slope (Mann-Whitney U test) (Table 2).

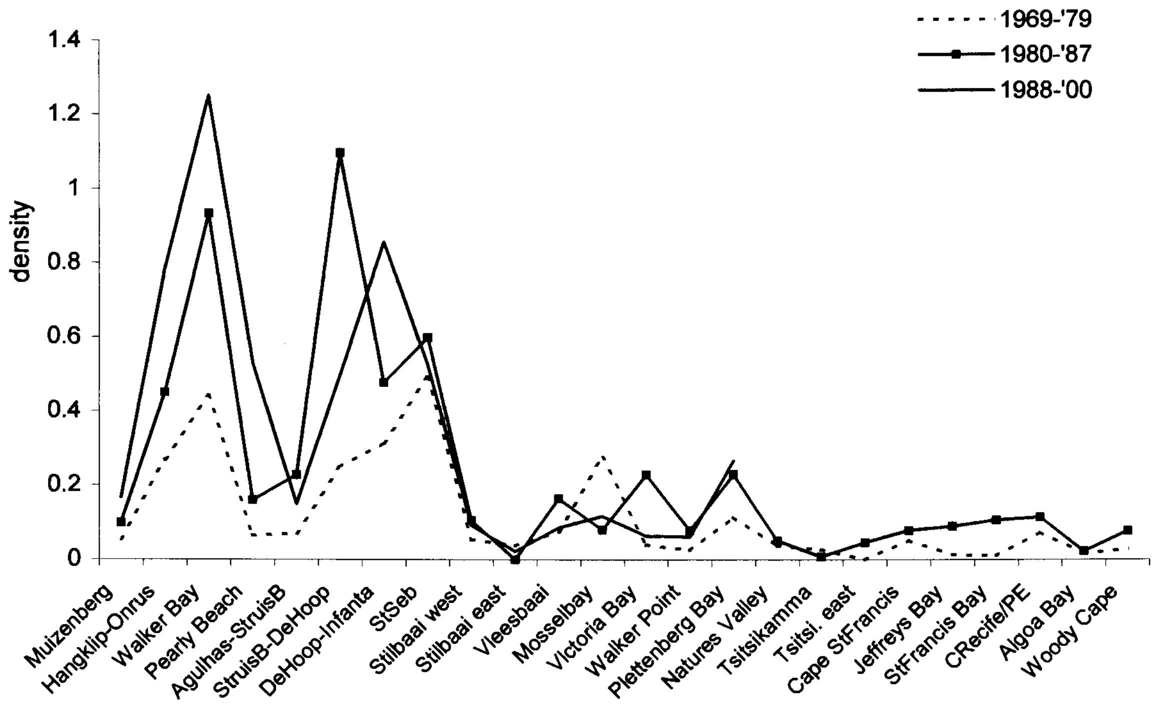

Figure 7. Density of whales per bin (#/km) for full surveyed length for Unaccompanied adults

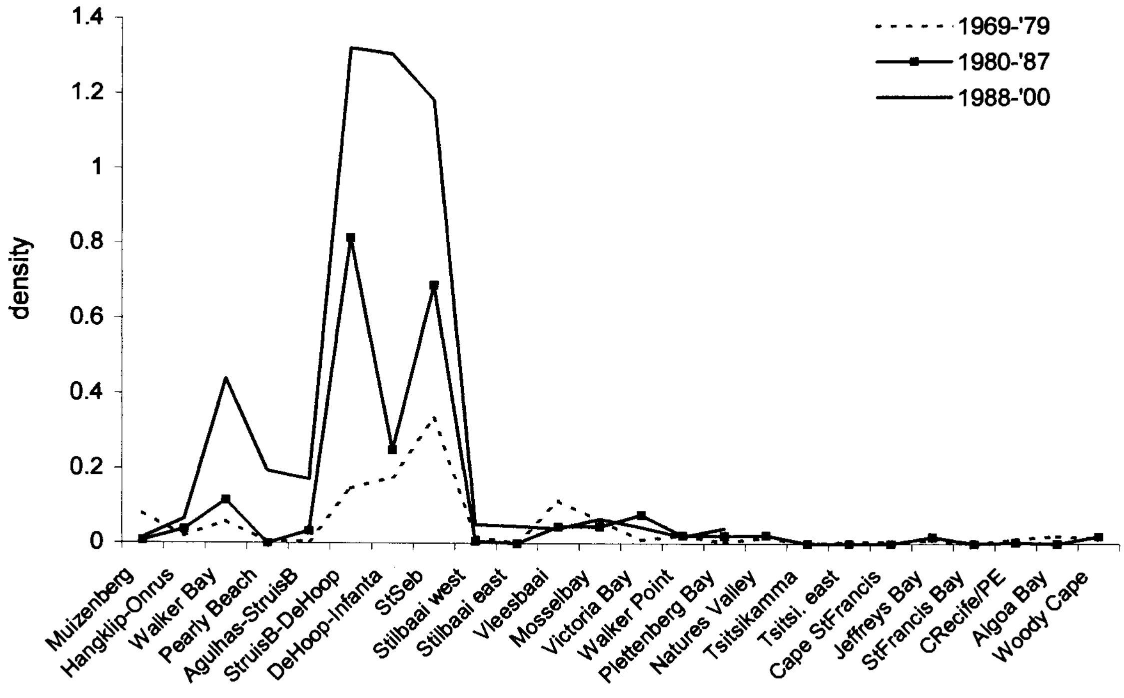

Figure 8. Density of whales per bin (#/km) for full surveyed length for Cow-calf pairs

Table 2. Mean distance from shore, depth and slope values for primiparous and multiparous cow-calf pairs from the 1997 and 1999 helicopter survey years.

Survey Year	Primiparous			Multiparous			T	P
	N	Mean	Se	N	Mean	se		
	Distance from Shore (m)							
1997	40	**729.828**	456.311	80	**725.759**	461.032	2465.0	**0.8043**
1999	48	**572.372**	300.474	123	**585.584**	252.24	18051.0	**0.5635**
	Depth (m)							
1997	40	**8.012**	4.5118	80	**9.4463**	16055	7420.0	**0.0706**
1999	48	**6.5313**	3.5967	123	**8.4141**	5.0354	4042.0	**0.9361**
	Slope (degrees)							
1997	40	**0.654**	0.282	80	**0.635**	0.378	2654.0	**0.1936**
1999	48	**0.718**	0.347	123	**0.678**	0.366	7420.0	**0.4630**

The offshore distributions of cows with calves and unaccompanied whales were found to be significantly different for both depth and distance from shore. For each class, data from the entire surveyed coast length were compared as one set for each factor tested (depth, slope and shore distance) with a Mann-Whitney U test. In all three years cow-calf pairs were found to be significantly closer to shore as well as in significantly shallower water than unaccompanied whales along the entire surveyed length of coast (Table 3). The pattern is not totally clear-cut with regard to slope, but it generally supports the predicted hypothesis of cow-calf pairs preferring shallower slopes.

Table 3: Mean distance from shore, depth and slope values for cow-calf pairs and unaccompanied whales from the helicopter surveys of 1997, 1999 and 2000.

Survey Year	Cow-calves			Unaccompanied whales			T	P
	N	Mean	Se	N	Mean	Se		
	Distance from Shore (m)							
1997	120	**728.298**	728.29	181	**1094.64**	742.94	14815.0	*<0.0001*
1999	172	**584.297**	690.99	162	**737.632**	527.37	29436.0	*0.0122*
2000	164	**621.274**	404.02	237	**899.206**	635.92	28295.0	*<0.0001*
	Depth (m)							
1997	120	**8.17165**	5.26	181	**13.7985**	9.68	22010.5	*<0.0001*
1999	172	**6.88854**	5.35	162	**11.5358**	6.47	20411.5	*<0.0001*
2000	164	**6.6984**	3.63	237	**12.4173**	6.98	43340.0	*<0.0001*
	Slope (degrees)							
1997	120	**0.66711**	0.662	181	**0.6797**	0.389	16700.0	**0.3605**
1999	172	**0.70802**	0.477	162	**0.95047**	0.954	311100.	*<0.0001*
2000	164	**0.69951**	0.338	237	**0.86675**	0.654	30127.0	*0.0246*

Shore type significantly influenced the depth and distance from shore at which unaccompanied whales (Kruskal-Wallis, one-way ANOVA on ranks, for mean of all 3 years: distance from shore: $H = 13.8118$, $p = 0.001$; depth: $H = 13.6966$, $p = 0.0011$) and cow-calf pairs (for mean of all 3 years: distance from shore: $H = 26.8335$, $p = <0.0001$; depth: $H = 37.9891$, $p = <0.0001$) (Figure 9-12) were found. The significance values of the post hoc pair-wise test (Dunn's method) are shown on the graphs (Figures 9-12). Cow-calf pairs are found in deeper water off wave-cut rocky platforms than off either sandy shores or exposed rocky headlands. However, they are found closer to shore off exposed rocky headlands than off either sandy shores or wave-cut rocky platforms. Unaccompanied whales did not exhibit a stable pattern between years for depth but were on average shallowest off wave-cut platforms and deepest off exposed headlands. Similarly, although there was no significant difference for distance from shore between

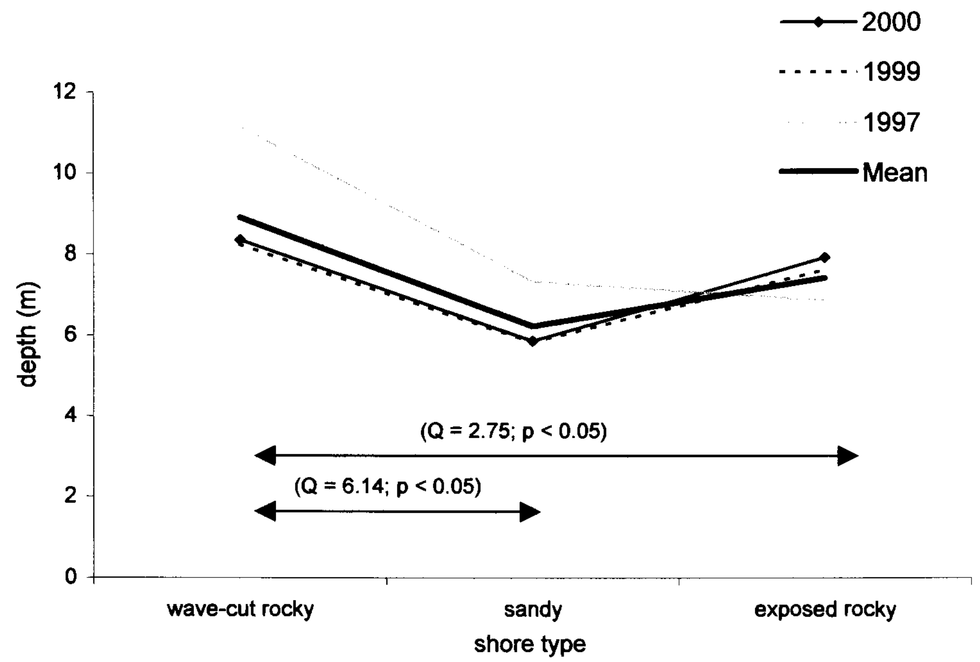

Figure 9. Depth of cow-calf pairs off three main shore types, shown with mean for all three years Pairwise significance indicated by arrows (Dunn's Method)

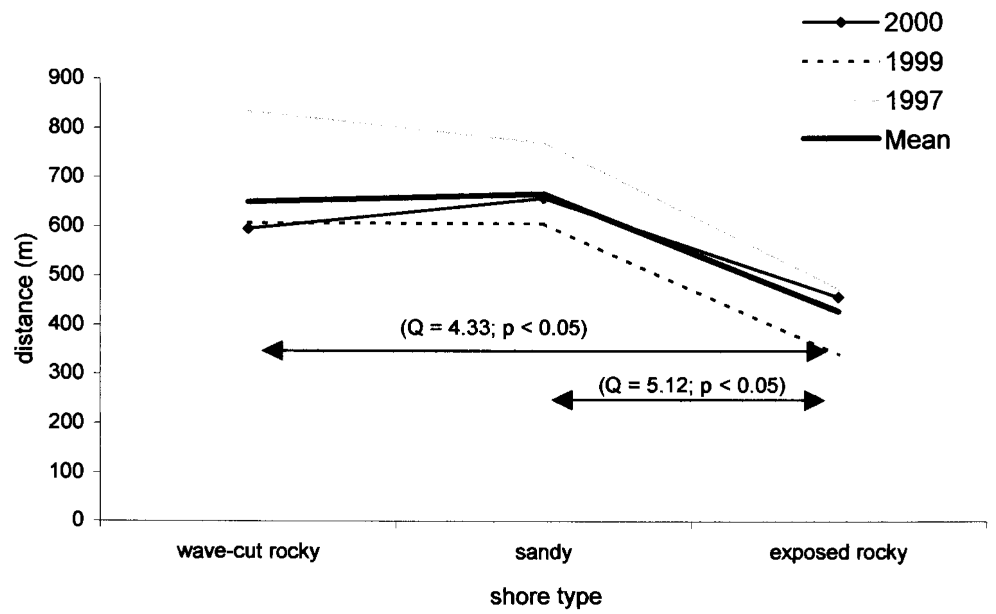

Figure 10. Distance from shore for cow-calf pairs off three main shore types, shown with the mean for all three years. Pairwise significance shown with arrows (Dunn's Method)

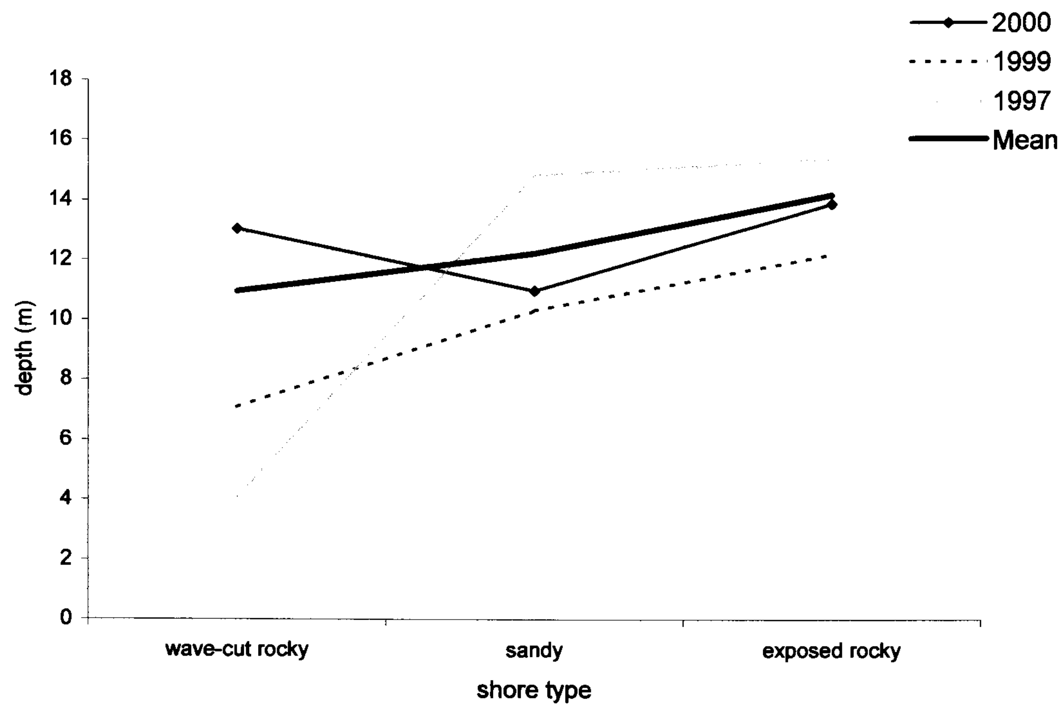

Figure 11. Depth of unaccompanied adults off the three main shore types shown with the mean for all three years. No pairwise significance was found (Dunn's Method)

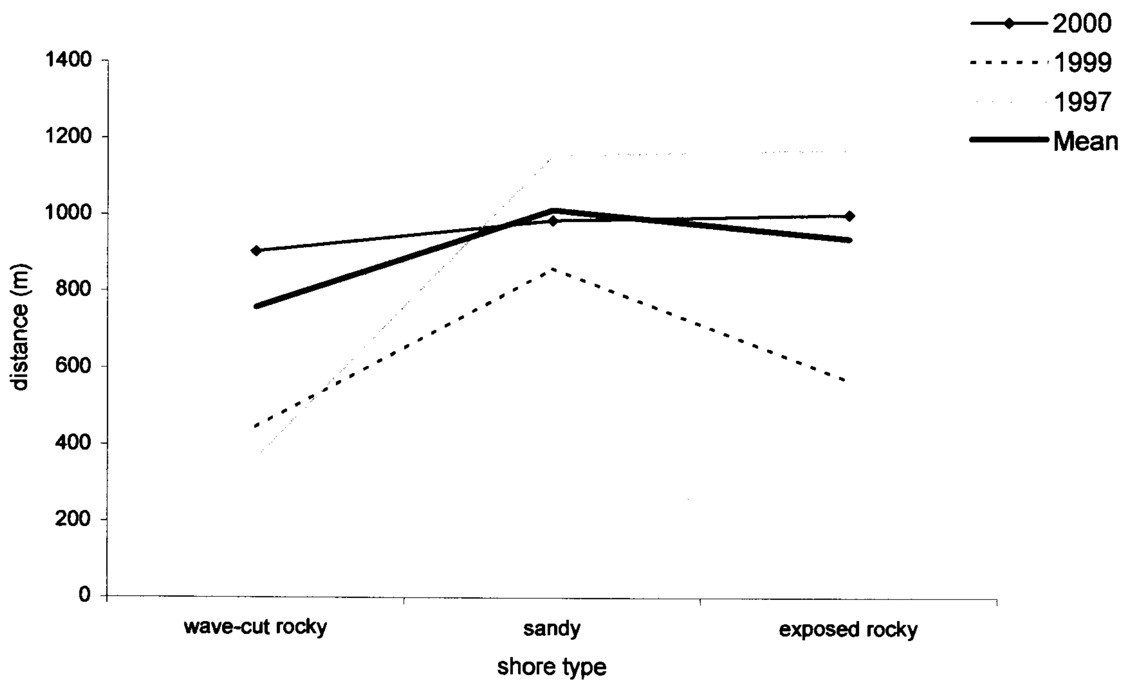

Figure 12. Distance from shore of unaccompanied adults off the three main shore types shown with mean for all three years. No pairwise significance was found (Dunn's Method)

shore types, in general unaccompanied whales were furthest from shore off sandy beaches and closest off wave-cut platforms.

The density of whales per 20-minute longitudinal bin was correlated with the average values for each of the environmental factors at each of the scales used (Table 4). The 19 year data set and the 32 year data set both use the same bins and all the data from the 19 year data set are included in the spatially relevant parts of the 32 year data set. For swell and wind protection, the percent of 'exposed' (unattractive) water per longitudinal bin was used while for shore type the proportion of attractive shore type was used (defined as sandy beaches + estuarine environment + pebble beaches).

Table 4: Shows the results of all correlations between whale density and environmental factors per area, at all scales. Significant p-values are italicised.

	19 year Unaccomp.		19 year Cow-calf		32 year Unaccomp.		32 year Cow-calf		GPS (zone) Unaccomp.		GPS (zone) Cow-calf	
	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p
Depth	-0.425	***0.043***	-0.452	***0.031***	-0.296	**0.275**	-0.614	***0.014***	-0.375	**0.163**	-0.618	***0.014***
Slope	-0.289	**0.177**	-0.357	**0.093**	-0.007	**0.974**	-0.468	**0.076**	-0.125	**0.648**	-0.471	**0.073**
Swell Protection	-0.512	***0.013***	-0.539	***0.008***	-0.459	**0.081**	-0.395	**0.138**	-0.298	**0.275**	-0.319	**0.241**
Wind Protection	-0.570	***0.005***	-0.478	***0.021***	-0.343	**0.204**	-0.450	**0.089**	-0.336	**0.214**	-0.375	**0.163**
Attractive Shore	0.161	**0.458**	0156	**0.472**	0.175	**0.523**	0.314	**0.246**	0.250	**0.359**	0.361	**0.180**

There was a significant negative correlation between cow-calf density and depths at all scales tested, suggesting a preference for bins that are shallower on average. The strongest relationships were found in the largest spatial scale data set (19 year data set) where both cow-calf density and unaccompanied adult density were significantly related to depth, as well as protection from swell and protection from wind. Thus more whales were found in areas of increased protection from swell and wind. Despite being closely correlated to depth (for zones: r = 0.9470, $p = <0.001$), slope was not significantly related to whale density at any scale, however it was very close to significance for all cow-calf tests (significant at 10% level). Whale density was poorly related to the proportion of attractive shore type at all scales and for both classes of animal.

The observed distributions of cows with calves taken from the GPS data were compared to the distributions that would be expected if the animals distributed uniformly with respect to the tested variable. The distribution of unaccompanied whales as well as cow-calf pairs was significantly different from the expected distribution within the various levels of "protection from swell" when tested individually or summed for 3 years (Cow-calf summed for 3 years: $Chi^2 = 180.4$, $p = <0.0001$, df = 2; Unaccompanied whales summed for 3 years: $Chi^2 = 243.7$, $p = <0.0001$, df = 2) (Figure 13). Both cow-calf pairs and unaccompanied whales are found less often than expected in 'exposed' areas of the coast but more often than expected in 'partly protected' areas. In 'protected' areas cow-calf pairs are found more often than expected but unaccompanied whales occur slightly less often than expected.

Similarly, both cow-calf pairs and unaccompanied whales distribute significantly differently from expected for the various levels of protection from wind whether tested by years or summed for three years (Cow-calves summed for 3 years: $Chi^2 = 96.58$, $p = <0.0001$, df = 2; Unaccompanied whales summed for 3 years: $Chi^2 = 126.52$, $p = <0.0001$, df = 2) (Figure 14). Unaccompanied whales occur more often than expected in partly protected areas and less often in exposed areas; distribution is similar to expected for protected areas. Cow-calf pairs are also found more often than expected in partly protected areas, less often than expected in exposed areas and slightly less often than expected in protected areas.

Both cow-calf pairs and unaccompanied whales distribute with respect to shore type at significantly different ratios to expected if tested singly or summed for three years (cow-calf: $Chi^2 = 176.95$, $p = <0.0001$, df = 3; unaccompanied whales: $Chi^2 = 119.79$, $p =$

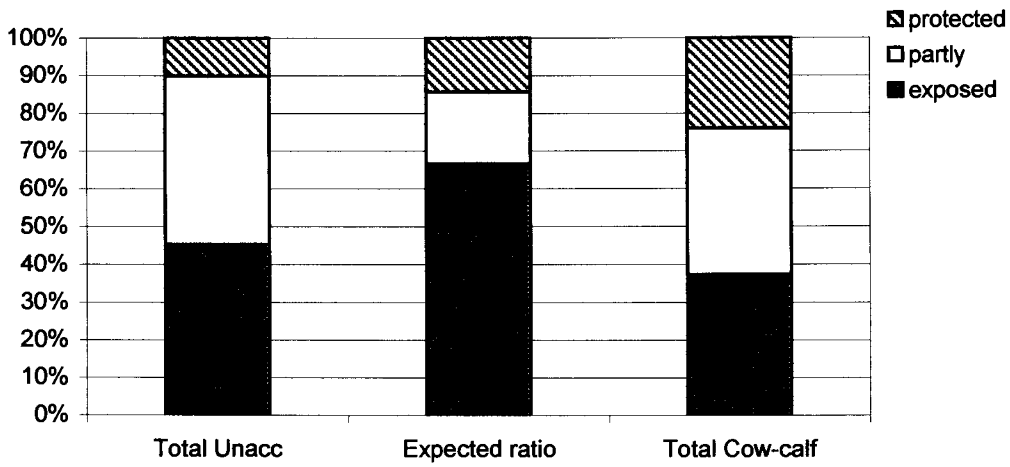

Figure 13. Proportion of unaccompanied adults and cow-calf pairs in each level of swell protection shown with the expected ratio

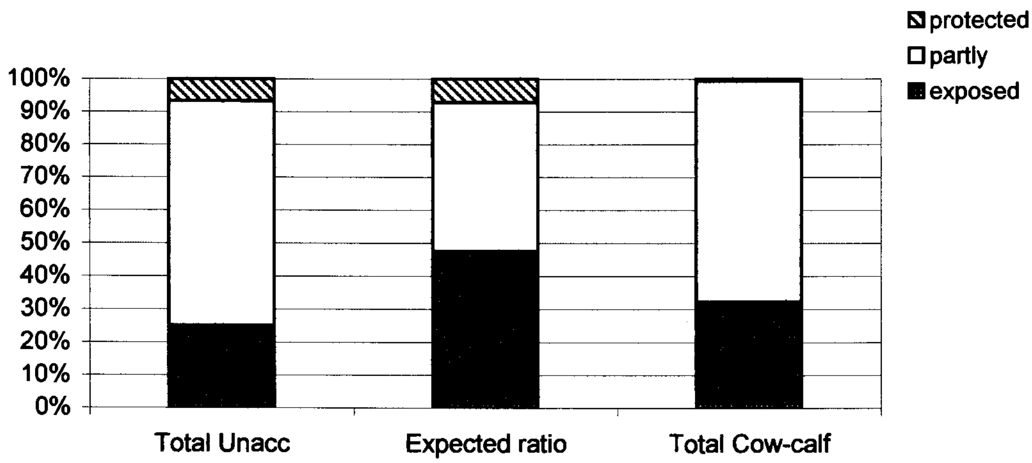

Figure 14. Proportion of unaccompanied adults and cow-calf pairs in each level of wind protection shown with the expected ratio

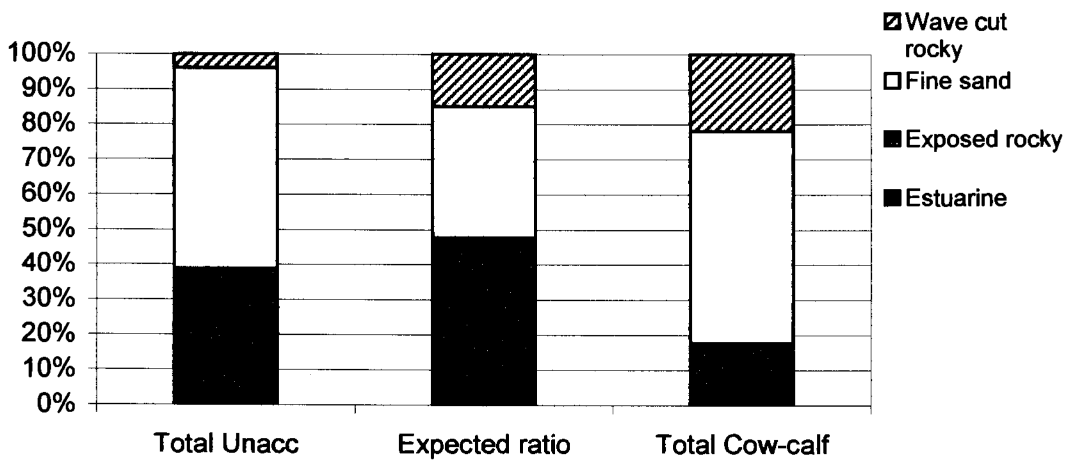

Figure 15. Proportion of unaccompanied adults and cow-calf pairs in each shore type shown with the expected ratio

<0.0001, df = 3) (Figure 15) All whales occur more often off sandy beaches and less often off exposed rocky headlands than expected. Unaccompanied whales occur less often than expected off wave-cut rocky platform shore types while cow-calf pairs occur slightly more often than expected.

When compared to a uniform depth distribution both cow-calf pairs and unaccompanied whales occur in significantly different proportions to expected (Cow-calf: $Chi^2 = 952.6$, $p = <0.0001$, df = 17; unaccompanied whales: $Chi^2 = 352.7$, $p = <0.0001$, df = 17) (Figure 16). Both cow-calves and unaccompanied whales are clustered toward the shallower waters of the surveyed area and few are found in the deeper water offshore.

Both classes of right whales showed a significant difference from a uniform distribution with respect to slope (Cow-calf: $Chi^2 = 54.93$, $p = <0.0001$, df = 10; unaccompanied whales: $Chi^2 = 180.14$, $p = <0.0001$, df = 10) (Figure 17). The majority of both whale classes were found less often in the very shallowest slope categories than expected from a random distribution.

3.4 Discussion

Right whale distribution patterns are non-uniform but predictable along the South Coast of South Africa and have shown the same general distribution for 32 years with only minor changes, supporting previous work on this population (Best, 1981, 1990, 2000). Most notable of these minor changes is the increase in relative and actual cow-calf density in Walker Bay, which was formerly almost exclusively a breeding area. It is unlikely that they return to these areas because it is the only attractive habitat available, as many of the low density bins in the study have apparently attractive habitat (e.g. False Bay, Mossel Bay). This suggests some form of behavioural influence in habitat selection, such as maternal phylopatry as suggested by Best (2000). Although males, females and juveniles visit the coast along with the pregnant females, these "unaccompanied whales" have a different main congregation area (bin C - Walker Bay) to the cow-calf pairs (bins F-H, De

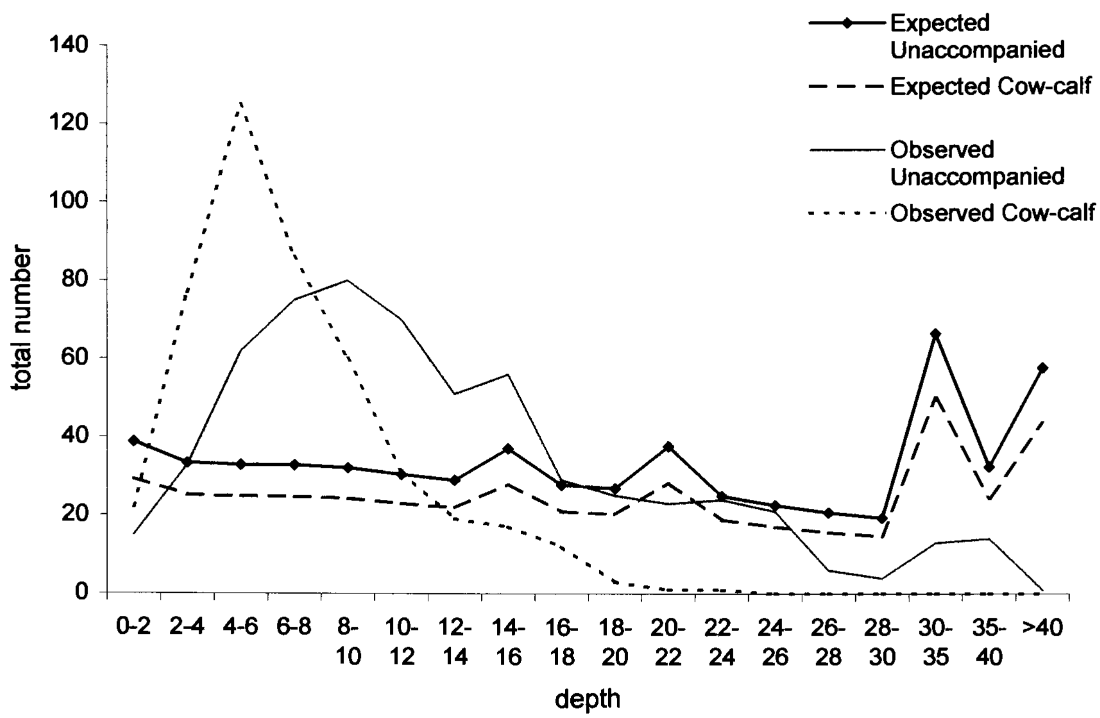

Figure 16. Distribution of unaccompanied whales and cow-calf pairs across depth classes for the full survey area. Shown with numbers expected from an "uniform" distribution.

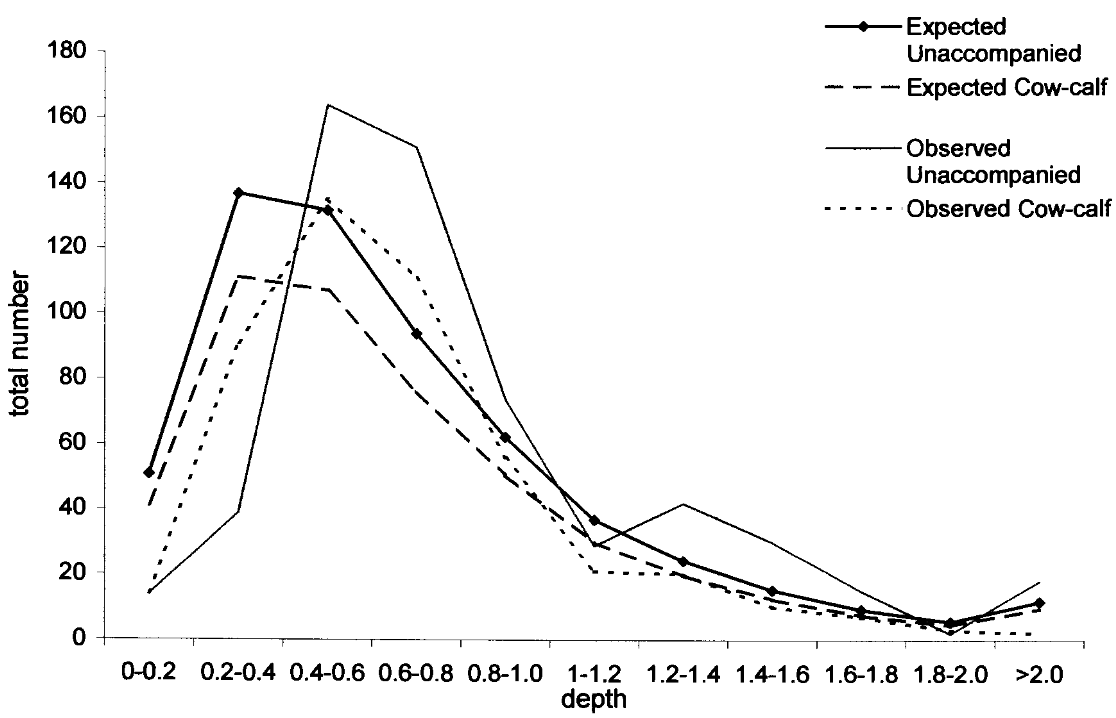

Figure 17. Distribution of unaccompanied whales and cow-calf pairs across slope classes for the full survey area. Shown with numbers expected from an "uniform" distribution.

Hoop and St Sebastian Bay), and although increasing numbers of both classes of whale are found in all regions of the coast, this segregation is consistent over time. It is possible that cow-calf pairs purposely segregate themselves into a 'nursery area' at this scale to avoid harassment by courting males or herd together to provide some form of protection from predation for their calves through the dilution effect, selfish herd effect or simply increased predator detection that occurs in groups (see Connor, 2000 for discussion of group living in cetaceans).

The distribution of primiparous and multiparous cows are fairly different between years but the two classes of cow did not exhibit predictable differences in distribution. The lack of any significant differences between primiparous and multiparous cows with respect to depth, slope or distance from shore can be interpreted to mean that both classes of animal choose similarly with respect to these factors, regardless of which part of the coast they are currently occupying. Thus, primiparous and multiparous females do not have a predictably segregated distribution at this scale and primiparous cows appear to have as large a range as multiparous cows. The distribution of primiparous cows may therefore be determined by social rather than environmental factors. Increases in sample size (by analysing more years of data) might result in patterns becoming obvious. Direct observation of known animals may also be productive in this regard to monitor and compare directly the interactions of 'experienced' mothers and primiparous mothers.

Cow-calf pairs are found closer to shore, in shallower water and in general above gentler sloping sea-beds than unaccompanied whales. The apparent segregation of cow-calf pairs into a slightly different habitat/niche to unaccompanied whales is supportive of previous work on both right whales (Best, 1990, 1981; Payne, 1986; Thomas, 1987) and other species such as humpback whales (Smultea, 1994) and grey whales (Swartz, 1986). It is not made clear in any of these studies if the whales are segregating themselves based on some environmental factor (e.g. calmer waters or decreased predation or harassment) or due to some behavioural influence (e.g. benefits of aggregation or a tendency to be social) but usually it is thought to be a combination of the two. Behavioural and social influences on distribution are not directly part of this study and although they are ignored in analysis and are difficult to account for, they can have strong influences. The distinction between the influences of various environmental factors is further confounded because (based on the data available for this study) it is impossible to separate the potential benefits of proximity to shore from the benefits of shallowness of water. However, the potential benefits are closely linked and the two factors can probably be treated as one with a reasonable degree of confidence. The tendency for cow-calf pairs to be closer to shore (and thus shallower) than unaccompanied whales is probably the result of a number of influences.

Firstly, the only real predation threat to right whales (both adults and calves) is the killer whale (which hunts by aural cues), although they are currently rarely seen in South African near-shore waters. The noises and sand thrown up in the surf zone have a potentially camouflaging effect, thus providing an area of reduced threat in close proximity to shore. Proximity to shore has also been suggested as an effective defence against killer whale predation in both right whales (Thomas, 1987) and bottlenose and dusky dolphins (Würsig & Würsig, 1979), especially in conjunction with continuous longshore movement (Würsig & Würsig, 1979). Secondly, proximity to shore serves as a functional means to segregate themselves from the rest of the population (see Thomas, 1986), any member of which could potentially injure the calf or generally interrupt feeding behaviour; this is especially applicable to curious juveniles and courting males. Thirdly, the shallowness of the water probably does not allow males to attempt intromission since in this species, intromission generally occurs with the female lying at the surface and the male swimming upside-down underneath her (Kraus & Hatch, 2000). In water that is barely deeper than the adult whales, this manoeuvre would be impossible for males to perform and would most likely discourage any courting attempts. Lastly, the proximity to shore potentially reduces the number of directions from which either predators or conspecific harassers can approach, a "backs to the wall" approach to defence.

Right whale distribution is clearly related to the adjacent shore type. The patterns evident are expressed more clearly by cow-calf pairs than by unaccompanied whales, which probably reflects the decreasing importance of the substrate with the latter's greater depth and distance from shore. Although cow-calves were furthest from shore off sandy beaches, this probably only reflects the generally shallower slope of sandy beaches making a wider surf zone than off steeper rocky slopes, since they were found in shallower water here than off either type of rocky shores. These results support the hypothesis of sandy substrates being a preferred environment for cow-calf pairs, either because of its acoustic dampening properties, or because of a lowered likelihood of injury from rocky projections. Further, this analysis supports the use of shore type as a substitute for near-shore sea bed type as whales are responding to the different shore types in the predicted patterns.

At broader scales (19 year data set), the densities of both classes of whales are significantly negatively correlated with the mean depth of bins as well as positively correlated with the proportion of protection provided from both wind and swell per bin. This is congruent with the hypothesised patterns of distribution in that whales seem to prefer shallower water and areas with greater protection from wind and swell. However, these patterns are more weakly expressed in the 32 year data set (which covers a smaller area) and in the GPS data set for zones, where only depth is significantly correlated to cow-calf density. Although the trends for all tested factors are in the predicted directions, significance is not reached. This is most surprising for the correlations using zones, since these coast segments were specifically chosen to be environmentally uniform and a stronger relationship was expected.

Part of the reason for the poor overall relationship between whale density and the various correlated factors at these scales is the very high density of whales in some areas and the very low numbers in other areas of apparently attractive habitat. This may in part reflect the fact that the South African population of right whales is still substantially depleted (previously estimated to be at 10% of its original projected numbers, Butterworth & Best, 1990) so that a considerable amount of recolonisation still has to take place. Between Walker Bay and St Sebastian Bay whale density is markedly higher than elsewhere in the survey range outside the main concentration areas, and whales are occupying most of the attractive areas and avoiding the less attractive regions within this stretch of coast in close to an ideal free distribution. This higher density either side of Cape Agulhas may be an artefact induced by whales in transit between the main concentration areas or perhaps reflects a contracted range of some kind, bounded principally by Walker Bay (west) and

St Sebastian Bay (east). Outside this concentration area, whales also exhibit some degree of preference for the more attractive areas (e.g. Plettenberg Bay) but at considerably lower densities and in a far less predictable fashion. There are several apparently attractive areas that are currently under-occupied, which were historically known to be important whaling areas (Best & Ross, 1986) for instance False Bay, Plettenberg Bay and Algoa Bay. These environmental outliers are likely to negatively affect the strength of a correlation.

Despite the generally poor relationship between whale density and the correlated environmental factors in the bins and zones, the majority of right whales are found in more "attractive" habitat areas along the coast, if not necessarily in all the attractive habitats. This pattern holds for all tested factors except slope, but since no analyses involving slope showed any strong patterns or relationships it is likely that any relationship between whale density and slope of the sea floor is secondary in nature. Shallower slopes probably occur when large amounts of sediment are deposited on the seabed. The contracted range of the population makes overall analysis difficult to interpret, but the patterns exhibited by the majority of the population within the higher density areas as well as the remainder of the population along the rest of the coast suggest that the presence of calm water is a very important factor for right whales in coastal waters. The areas that are protected from open ocean swell also tend to be protected from the majority of seasonal winds, thus making them doubly attractive.

Similarly, although extensive areas of the coast that have long stretches of sandy beaches or known sedimentary substrates are under-utilised by whales (e.g. False Bay, Algoa Bay), the majority of whales still follow the predicted distribution with respect to shore type. More whales are found off sandy shores and fewer off exposed rocky headlands than expected. The fact that cow-calf pairs occur more often than expected off "wave-cut rocky platforms" is primarily because of the large numbers of cow-calf pairs found at the head of St Sebastian Bay which although having rocky shores has a predominantly sedimentary floor (Birch, 1980). This is due to both the flat nature of the shale rock, which is easily covered in sediment, as well as the Breede River having buried river channels and also currently depositing sediment in the bay (Birch, 1980). The shore types in this study were assumed to reflect the near shore substrate. The tendency for cows with calves to be in significantly shallower water off sandy beaches, as well as the pattern of the majority of whales preferentially occupying areas with sandy shores is strongly supportive of the hypothesis of whales preferring sedimentary substrates. The comparatively high number of unaccompanied whales found off exposed rocky headlands is probably indicative of the lesser importance of substrate for these animals since they are generally deeper and further from shore than cows with calves. Also, unaccompanied whales are apparently more mobile (Burnell & Bryden, 1997) and are potentially more likely to be detected in transit between preferred areas.

No other published studies have looked directly at the environmental factors affecting right whale distribution on their wintering grounds. However Thomas (1987) did consider abiotic factors to be a likely influence in the distribution patterns of southern right whales in the area of Golfo San Jose, Argentina, covered by his study, while Payne (1983) discussed the effects of prevailing wind, sea state and bay shape on the distribution and behaviour of right whales in the same area.. Other authors have mentioned various factors that could be influencing distribution, including calm water (Thomas, 1987; Holst, 1998; Rowntree, Payne & Schell, 2001), shallowness (Payne, 1986; Patenaude & Baker, 2001) and distance from shore (Payne, 1986; Thomas, 1987; Holst, 1998; Patenaude & Baker, 2001; Rowntree, Payne & Schell, 2001). However, none of these studies attempted to directly and quantitatively link these environmental factors to whale density and none took scale into account. Patterns described by the authors generally agree with the findings of this study, although no author covers all the factors investigated here.

Rowntree, Payne & Schell (2001) suggest extensive changes in bottom topography following powerful storms in 1975 to be one of the possible causes for the abandonment of the Outer Coast nursery ground at Peninsula Valdés, Argentina. They specifically mention the erosion of a large sedimentary 'bulge' that created a calm eddy that whales preferentially occupied. In Golfo San Jose, Rowntree *et al.* (2001) report the area of maximum whale numbers (not specified by sex) during the 1970s to be a broad, gradually sloping, sandy bottomed beach but that in subsequent years whales have moved away from this area possibly due to gull harassment, an environmental factor that does not play a significant role in South African coastal waters.

In the wintering ground off the Auckland Islands, Patenaude & Baker (2001) report a high concentration of right whales each year in a small area on the northeast side of the main island (Port Ross). Although substantially further south (~50^0S) than South Africa (~32^0S) and with a much colder climate and water temperature, the predominant weather conditions in the Auckland Islands are still controlled by frontal systems from the Antarctic, so that most of the swell will come from the southwest. Thus, right whales here are apparently sheltering in both the lee of the island and further in a sheltered bay, in a similar pattern to those evident in this study. It would be interesting to look at substrate type in this area.

Holst (1998) came closest to describing environmental influences in the southwest Australian population that mirror those tested in this thesis, although a lack of rigorous testing did not allow for the forming of firm conclusions. He postulated that the NE/SW orientation of the high density whale areas allowed "prevailing westerly winds (to) reduce the southern ocean swells, creating calm areas close inshore with added protection from headlands". He also reports other behaviours that were both predicted and supported by this study. Whales were reported to "skirt underwater reefs" (highly unattractive environment) as well as move further offshore in storm conditions (large swell, therefore increased surf zone).

Thomas (1987) found mother-calf pairs in Golfo San Jose, Argentina to cluster close to the shore in shallow water more often than expected from chance. He suggested this behaviour could be due to increase safety from predators, especially killer whales, warmer water in the shallows, decreased wave action (although wave height throughout the Gulf is small) as well as weaker currents (up to 35km/h in some parts of Golfo San Jose). He also describes preferred resting areas for mother-calf pairs to be wide, gently sloping beaches where cows could drift in and out with the tidal change (a distance of 0.25 to 1km in the region) and suggests the lack of underwater obstructions to be the reason for the attractiveness of the area.

Payne (1983) describes the region Peninsula Valdés frequented by right whales to be generally very well sheltered from open ocean storms due to a combination of strong, frequent easterly winds, the shape of the coastline (two Gulfs) and the presence of offshore reefs off the stretch of coast exposed to the open ocean. He further agrees with Best (1981) that the areas occupied by right whales usually have sandy bottoms (or pebbles in the case of the Eastern Outer Coast, Peninsula Valdés) although no analysis was performed in either study. Payne (1983) postulates the preference for bays could also be due to increased efficiency of acoustic communication in areas with concave coastlines. Payne reflects on right whale distribution in South African waters and suggests a strong correlation between whale numbers and protection from wind with absence from apparently attractive (and formerly well occupied) areas being due to the increase in anthropogenic activities associated with harbours (a factor not included in this study) but again there is a lack of statistical testing.

Studies of North Atlantic right whales on their wintering grounds seem to have found similar patterns of distribution to those in southern right whales. Whales (mostly cow-calf pairs) off Georgia and Florida were found to occupy areas with flat bottom topography and a surface temperature of 10^0 to 14^0C (Clapham, 1999). This part of the coast is described as having the lowest sea state anywhere in the western North Atlantic (Clapham, 1999), thus calm water was also considered to play a role in northern right whale distribution. This study apparently only considered wind effects and including swell size and substrate type in analysis could have clarified wintering distribution for this population. Conversely, it is necessary to mention the North Pacific right whales (*E. japonica*) which are a conundrum since no definite coastal wintering grounds have even been identified (see Scarff, 1986). Clearly it is not only the South African population that exhibits preferences for sheltered water and although general references have been made to right whales preferring this type of habitat, more detailed analysis in each of these areas is likely to show very similar patterns of distribution.

The benefits of each of the attractive factors is linked but can be broken down into two important areas, energetic savings for the calf and mother and direct survival and injury reduction of calves (and to a lesser extent cows). The presence of calm water is obviously of an energetic benefit, especially for neonatal stage one calves that are weak swimmers and struggle in rougher waters (see Thomas & Taber, 1984). Energetic savings *post-partum* can allow calves to invest more heavily in growth and for a more efficient transfer of energy from cow blubber to calf mass. Since calves apparently need to attain a minimum size before leaving coastal waters (Best & Rüther, 1992), faster growth would potentially allow for a quicker departure to polar waters where feeding can begin for the cow.

Injury reduction benefits for calves are primarily gained from the preference for sandy floors and the proximity to shore helps both mother and calf avoid and hide from predators and segregate themselves from unaccompanied whales. Considering the low threat of killer whales in at least South African waters, combined with the obvious, stable, longshore segregation of cow-calves from unaccompanied whales that occurs in South Africa, Argentina (Payne, 1986; Thomas, 1987) and possibly off Brazil (Groch & de Freitas, in press) there may be some long-term (evolutionary) benefit in population segregation. The differential distribution of cow-calves may be more for segregation from unaccompanied whales than predation avoidance, suggesting that perhaps harassment of mother-calf pairs by males or juveniles may be more important than previously thought.

This study has shown quantitatively what at least some of the environmental features are that make for an attractive coastal environment for right whales. At all scales studied, cow-calf pairs are apparently segregating themselves from unaccompanied whales although there is a significant amount of overlap. Both classes of whale are found predominantly in the areas of postulated attractive habitat but they are not occupying all such areas. Animals with abundant habitat can either spread out in an ideal free distribution across it, or they may cluster for the benefits associated with sociality or aggregating. Whales along the South African coast are clearly clustering for more than just environmental reasons and the social interaction of the population is an important factor to consider in distribution. These social interactions may be for the benefits of aggregation that would be gained by cow-calf pairs as well as the obvious benefits of being in contact with conspecifics during the apparent mating season. These social and behavioural influences are having a large effect on the distribution and are likely to have important implications for the range expansion of the species into its old environmental areas. This has ramifications for industries like boat-based whale watching and also shipping, considering the large amounts of money that are being spent in the north Atlantic to divert ships from potential right whale collisions[1]. Social and behavioural influences on distribution and population expansion are clearly important and would benefit from further study.

[1] see "Right Whale News", Feb 2001. Newsletter of the Southeastern United States Implementation team for the Recovery of the North Atlantic Right Whale and the Northeast Implementation Team. US Dept of Commerce, NOAA. Gray's Reef National Marine Sanctuary, 10 Ocean Science Circle, Savannah, GA 31411

Chapter 4: Environmental factors influencing the distribution of southern right whales (*E. australis*) on the south coast of South Africa: Within bay distribution

4.1 Introduction

Southern right whales (*E. australis*) were extremely depleted along the coasts of southern Africa due to whaling between about 1770 and 1940, although some illegal catches did occur after this (Best & Ross, 1986). Termed 'right' whales because of the tendency of this whale to be slow moving, rich in oil and floating when dead, another of the traits that made them so attractive to hunt was their predictable distribution in coastal waters (Best, 2000a; Richards & Du Pasquier, 1989). Although considerably fewer right whales are now found along the coasts of South Africa their distribution is still predictable and they return to the same areas in great numbers each year (Best, 2000a). Although a certain degree of maternal phylopatry seems to be involved in habitat choice in this species, environmental conditions were felt to be an important factor determining coastal distribution (Best, 2000a). Analyses in the previous chapter showed that despite low whale numbers influencing overall distribution patterns, the majority of right whales along the southern coast of South Africa are found in areas that are characteristically protected from open ocean swell and prevalent seasonal winds as well as having generally shallow sloping sandy or muddy sea floors.

Studies on distribution are well known to be influenced by the scale at which the study is performed and marine mammals have been shown to have stronger relationships with environmental factors at both larger scales (Jaquet & Whitehead, 1996) as well as at very small scales (Siegfried & Abrams, 1977). In chapter 3 analysis was performed at a variety of spatial and temporal scales with stronger relationships between whale density and environmental factors generally being found at larger scales. Along the South African coast right whale distribution is highly biased toward two main areas either side of Cape Agulhas, a nursery area (two bays, De Hoop and St Sebastian Bay) and an apparent breeding area (Walker Bay). In this chapter, analysis is performed on whale distribution within these three bays to ascertain whether the factors influencing large scale distribution are also important at a fine-scale.

4.2 Methods

Since 1979 annual aerial surveys for the specific purpose of counting and photographing right whales have been undertaken, during early to mid October, by helicopter along the southern Cape coast between Muizenberg (18^0 30'E) and Natures Valley (Plettenberg Bay, 22^0 50'E). Whales were classed as cows with calves ("cow-calf pairs", photographed) or as juveniles or adults unaccompanied by calves ("unaccompanied whales", not photographed). GPS positions of whale sightings within the three analysed bays were available for the 1997, 1999 and 2000 surveys. The distribution of the predominant whale classes (summed for three years' surveys) within each bay was analysed separately and for every available environmental variable. The method of analysis was the same for each bay and is thus given only once. The within-bay relationships between whale distribution and swell and wind protection, depth, slope and shore type were analysed. Whale distribution with respect to river mouths was analysed within Walker Bay only, due to various confounding factors in De Hoop and St Sebastian Bay. Data were all analysed using a GIS (Arcview 3.2); see previous chapter for details of analysis techniques.

In order to describe the range of characteristics to which whales within the surveyed area are exposed, it was necessary to define the width of the surveyed area within each bay. Inspection of the precise GPS positions of whales from the aerial surveys shows that all sightings were contained within 3000 metres of the coast, although most were substantially closer inshore. Since it was impossible (in retrospective analysis) to define the exact area and distance from shore surveyed or the intensity of survey effort at any point, 3km was assumed to represent the extreme limit of the surveyed area from the coast.

Protection from swell and wind was defined in the same way as in the previous chapter (see for details) and a three-tier level of protection was used. Any stretch of coast protected from less than 30% of wind or swell was defined as exposed, more than 30% as partly protected and more than 60% as protected. Refraction around headlands was not included in swell analysis and swell protection was calculated from the 5m contour on the GIS system (as opposed to the 0m contour of the previous chapter). The use of the 5m contour only made a noticeable difference in the De Hoop analysis due to the presence of a large reef off the southern headland (Martha's Point) potentially providing substantially more protection than that estimated from land alone.

4.3 Study Sites

4.3.1 St Sebastian Bay

St Sebastian Bay is typical of the log-spiral bays that occur along the Cape South Coast (Figure 18). It is recognised as one of the premier right whale nursery areas in South Africa and along with De Hoop is one of the most important right whale nursery areas in the world. Right whale cows have been sighted with calves here since the aerial survey was first run in 1969 (Best, unpubl. data). Due to its orientation, the bay provides considerable protection from the predominant southwesterly swell of the south coast and in fact its log-spiral shape is a consequence of the predominant swell direction (Bremner, 1991). Side-scan sonar work in the bay, shows the substrate to be predominantly muddy and sandy due to fluvial deposits from the Breede River (Birch, 1980) as well as multiple, sediment filled buried river channels of the Breede River. Thus, the sea floor at the head of the bay can be regarded as sedimentary in nature despite the rocky shores of the adjacent coast.

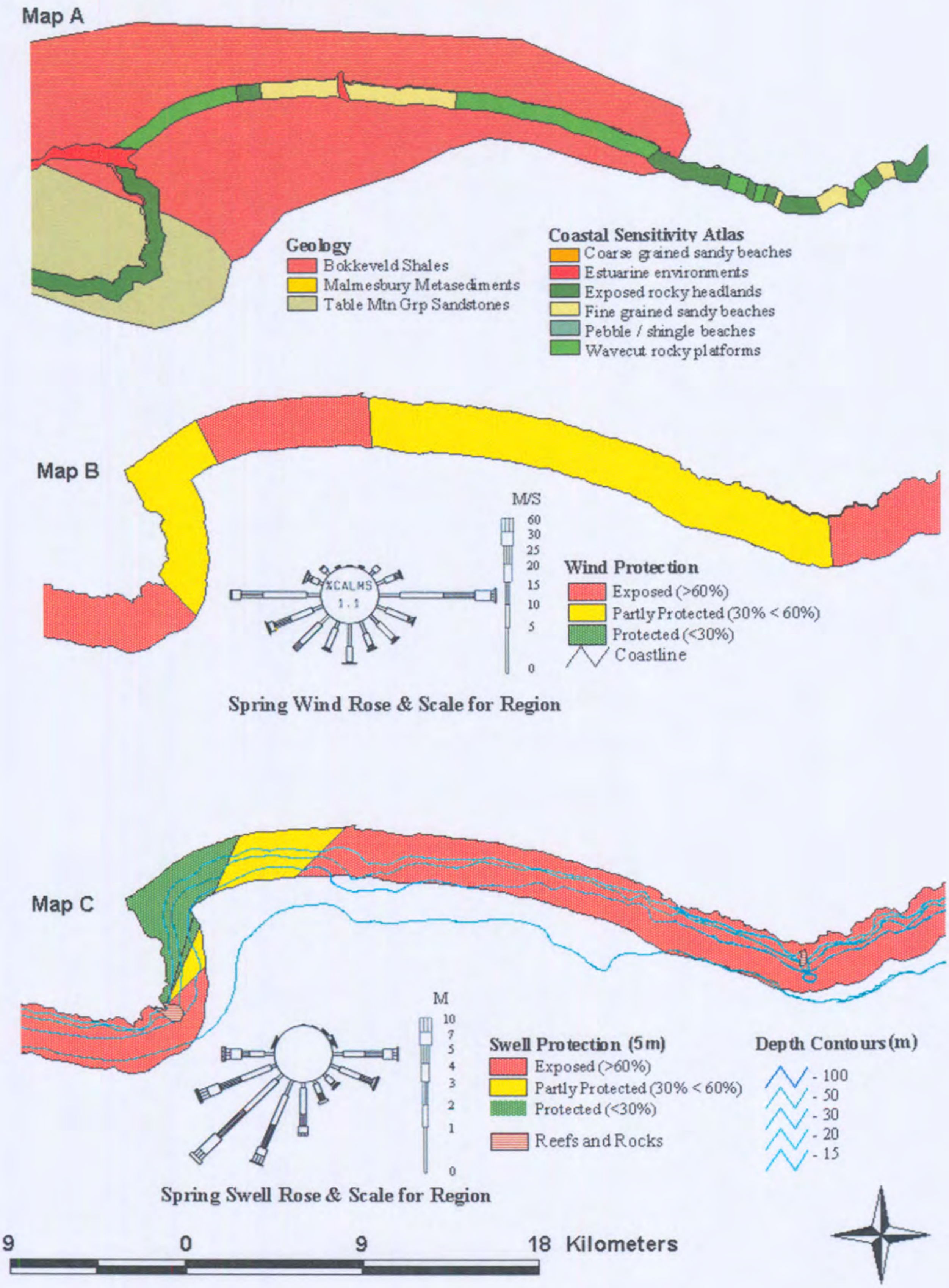

Figure 18: Environmental data within the St Sebastian Bay study area. Map A – geology and shore type. Map B – wind protection. Map C – Swell protection, depth contours and rocks and reefs.

4.3.2 De Hoop

The De Hoop region conforms to the logarithmic spiral shape typical of bays along the Cape South Coast (Bremner, 1991), although it is a rather open spiral shape due to its alignment (southwest/northeast) with the predominant swell direction (Figure 19). Although cow-calf numbers are now often higher in the lower De Hoop region than elsewhere in the range, it is a newer nursery area and whales only started to occupy this southern area of De Hoop with regularity after St Sebastian Bay was established as a nursery area (Best, 1990; compare Best, 1981). No side-scan sonar work is available for this area so the substrate type is not well known but near-shore substrate is thought to conform more closely to the shore type than in St Sebastian Bay, since there are no rivers currently depositing sediment in the bay. The southern tip of the De Hoop region is dominated by Martha's Reef which lies directly off Martha's Point, runs at least 6km out to sea and is quite shallow (±15m at 3000m from shore) thus potentially providing a reasonable amount of protection from swell in its lee, especially close to shore.

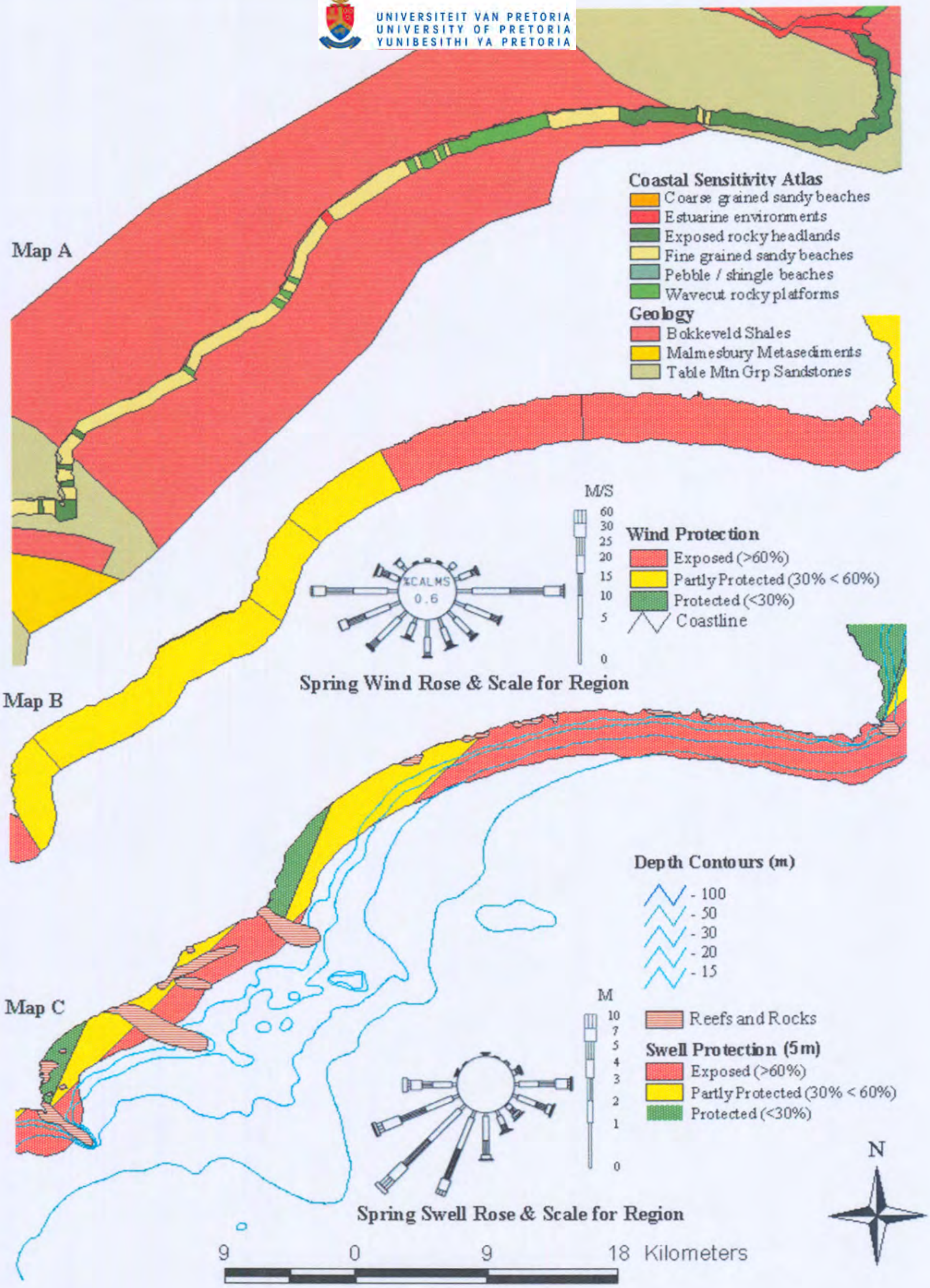

Figure 19: Environmental data within the DeHoop study area. MapA – geology and shore type, Map B – wind protection, Map C – Swell protection, depth contours and rocks and reefs

4.3.3 Walker Bay

Walker Bay is the only one of the three bays in this study that is not regarded as a nursery region. Due to the high numbers (and proportion) of unaccompanied whales that occupy this bay throughout the whale season, Walker Bay is generally regarded as a "breeding" area (Best, 2000a). Walker Bay is shaped like an open rectangle with the two short ends being defined by harder rock outcrops forming cliffs falling into the sea while the central flatter section of the bay forms a long, wide sandy beach with a gentle slope (Figure 20). The Klein River flows into the northern end of the sandy beach and ends in a large lagoon estuary which undergoes severe siltation (Birch, 1980) and frequently does not reach the open ocean. The near shore sea floor is primarily sedimentary in nature with some rocky outcrops in the bay but these are largely limited to the central offshore section and the southern area off Gansbaai and Danger Point (Lenhoff, 1995). In general, Walker Bay is a smooth, flat-bottomed sandy bay with few rocky outcrops. The whole of Walker Bay provides a fair degree of protection from both swell and wind during spring (September to November) when the survey is run, but much less during winter when frontal systems result in most winds and swells coming from the southwest. These southeasterly swells and winds are more predominant in the western section of the survey area (west of Cape Agulhas, including Walker Bay and False Bay) than in the eastern section where swell is still distinctly southwesterly during spring.

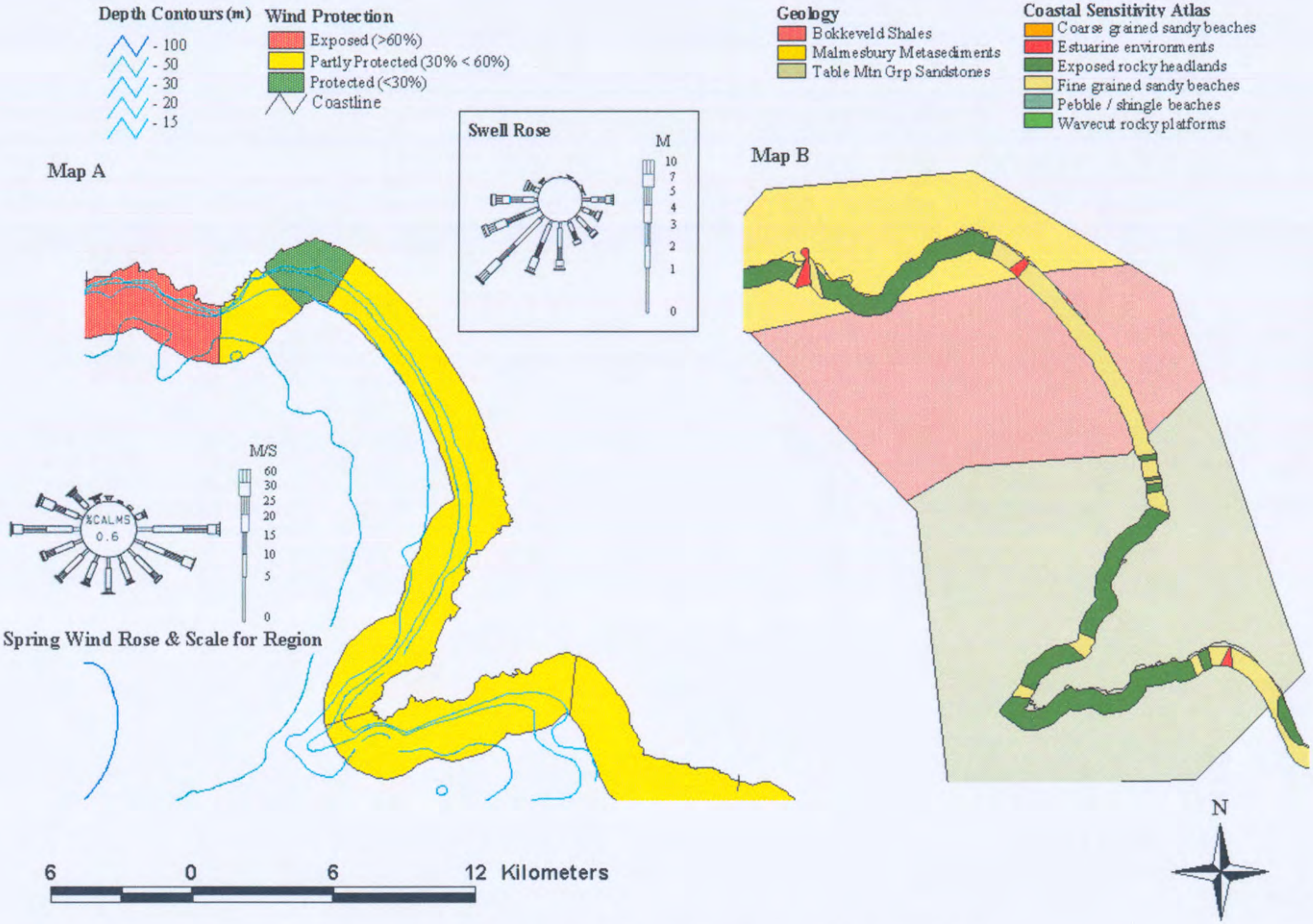

Figure 20: Environmental data within the Walker Bay study area. Map A – wind protection (and rose) and depth contours; Swell rose shown in separate block. Map B – geology and shore type.

4.4 Analyses

Within each of the three bays tested, the same analyses were performed on each of the variables, except in Walker Bay, where swell and wind protection are virtually constant throughout the bay so distribution with respect to these factors was not tested. A Chi-squared analysis was used to compare the proportion of whales in each level of each factor within the bays to the proportion that would be expected from a random distribution. Only cows with calves were tested in De Hoop and St Sebastian Bay because there were too few unaccompanied animals for a Chi-squared analysis.

The distribution of right whales with respect to depth and slope was compared to the actual distribution of the two factors within the surveyed area of the bay by categorising them into 2m and 0.2^0 intervals respectively and working out the distribution pattern of the categories within each of the bays. Due to low sample sizes, the categories were sometimes further summed to allow for valid testing, and log-likelihood tests were used where Chi-squared tests were deemed invalid.

Each bay was subdivided into areas that related roughly to environmental factors, but primarily to shore type (St Sebastian Bay, n=7; De Hoop, n=6; Walker Bay, n=6). To test whether whale distribution within the bays was related to the environmental variables in each sub-area the number of whales (summed for three years) was correlated against each of the environmental factors per sub-area. The mean depth and slope of each sub-area was used as well as the proportion of exposed water (swell and wind) and the proportion of unattractive shore type (rocky shores) per sub-area. Analysis was performed for both cow-calf pairs and unaccompanied whales in all three bays.

Since this study is a retrospective analysis of previously collected data it is not possible to directly test for individual strength of preference nor for the relative attractiveness within or between the various tested factors. The finer scale used in this chapter does however allow for a certain degree of ruling out or 'controlling for' environmental factors. This makes it possible to compare whale numbers between two areas differing in only one factor, thereby mimicking a two-choice test. Although this is not as ideal as performing direct testing (which is all but impossible on whales in the wild) it does allow an analogy thereof and as such is worth investigating. The results are presented separately in section 4.6 and 4.7.

The relative influence of swell protection was interpreted from a Chi-squared comparison of the cow-calf numbers off two sandy beaches in De Hoop with differing levels of exposure to swell, but an otherwise reasonably uniform environment. Relative preferences for the three main shore types were interpreted by comparing cow-calf numbers, off an area of the De Hoop coast where roughly equal areas of the three shore types lie next to each other within the same level of wind and swell protection, using a Chi-squared test. In both comparisons, the expected number of whales in each sub-category was calculated from the mean density/km (total whales/total length of relevant coastline) multiplied by the length (km) of the segment. De Hoop was also compared (not statistically) to the adjacent Marcus Bay to compare whale numbers in an area of reefs and a non-reef area.

The attractiveness of river mouths for whales was tested within a part of Walker Bay where all environmental factors are relatively constant except the presence of a river mouth (Klein River). The sandy beached area was broken up into six 3 kilometre segments, all of which were predominantly sandy shored with a similar gentle slope (sub-areas 2 – 4; mean slope: 0.60^0, 0.59^0, 0.47^0; mean depth: 23.2m, 13.2m, 11.4m; proportion sandy shore type: 0.97, 1.0, 0.71 respectively). Whale numbers of both classes (summed for three years) within each 3 kilometre segment were compared to an expected 'uniform' distribution using a Chi-squared test. The Klein River mouth tends to silt up and it is bulldozed open by the Hermanus Municipality at varying times during late winter/early spring. This was taken into account during analysis.

4.5 Results

4.5.1 St Sebastian Bay

In each of the three surveys analysed, cow-calf pairs in St Sebastian Bay were predominantly clustered at the head of the bay, in the lee of the headland (Figure 21). In 1997, all whales in the bay were in fact in the "protected" area with none out to the tail of the bay. In 1999 and 2000, whales were more spread out with some (1999, n = 5; 2000, n = 3) apparently clustered around the Duiwenhoks river mouth, but with the majority of whales again at the head of the bay (1997:100%; 1999: >80%, 2000: >70%).

Numbers of both cow-calf pairs and unaccompanied whales were strongly correlated with the proportion of protection from swell in each sub-area but no significant relationship was shown with any of the other tested factors (see Table 5). Chi-squared analysis could not be performed on unaccompanied whales but analysis of cow-calf numbers showed cow-calf distribution to be significantly different to expected for slope, depth, swell and shore type (see Table 6).

Table 5. Results of Spearman-Rank correlations within St Sebastian Bay of environmental factors and both cow-calf pairs and unaccompanied whales for sub-areas

	Unaccompanied (n = 24)		Cow-calves (n = 104)	
	R_s	P	R_s	P
Slope	0.1441	0.72	-0.357	0.3884
Depth	-0.09	0.78	-0.5357	0.182
Shore type	0.7091	0.055	0.4685	0.255
Wind protection	0.00	0.968	0.00	0.968
Swell protection	-0.8685	*0.0061*	-0.9543	*<0.0001*

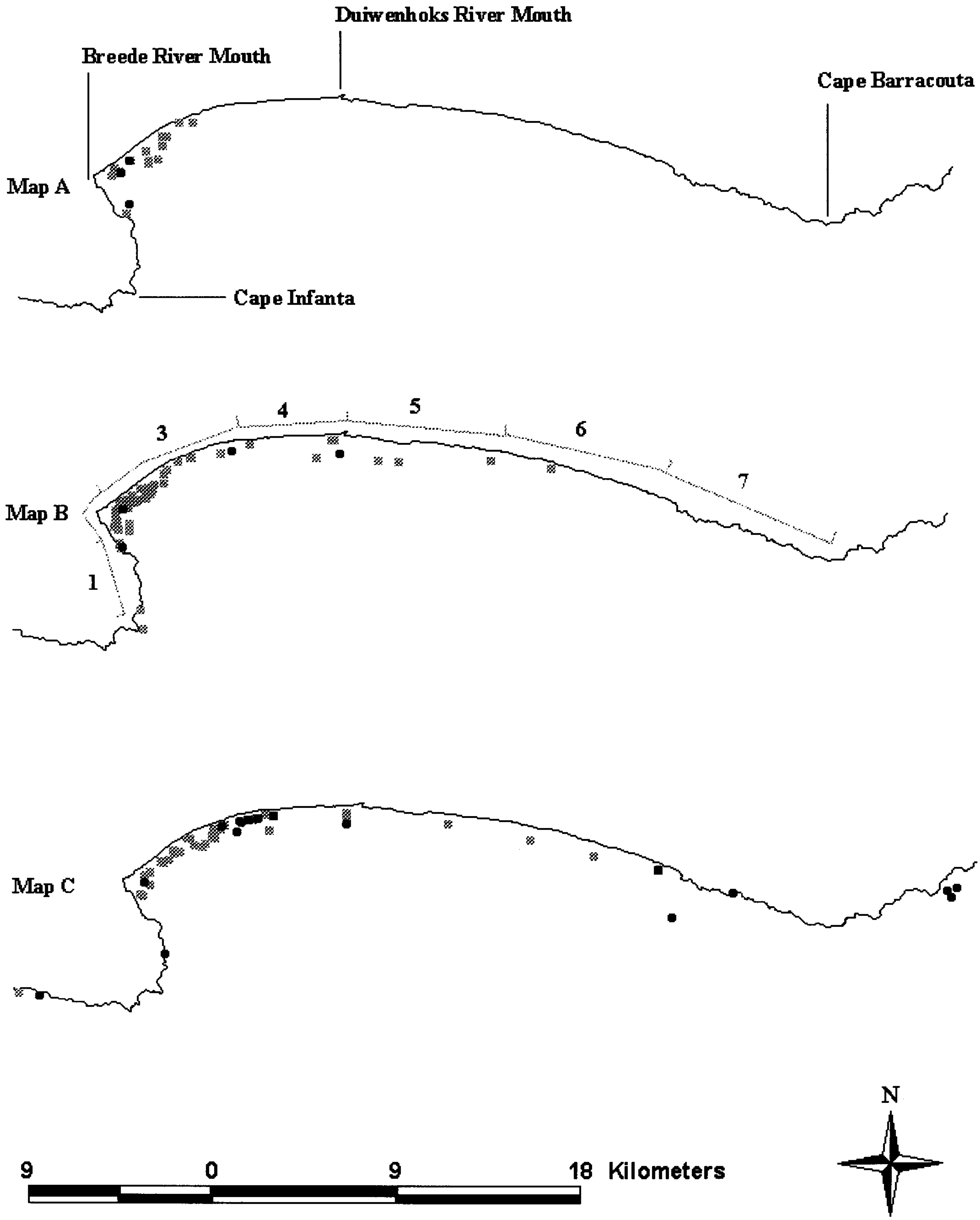

Figure 21: GPS positional data of cow-calf pairs (grey squares) and unaccompanied whales (black circles) within St Sebastian Bay. Map A –1997; Map B – 1999; Map C – 2000. Map A shows place names; Map B shows approximate size and placing of "sub-areas". Compare with Figure 18.

Table 6. Results of Chi^2 analysis for St Sebastian Bay, cow-calf pairs only were tested due to small numbers of unaccompanied whales

	Cow-calves (n = 104)		
	Chi^2	P	Df
Slope	29.02	*<0.0001*	6
Depth	316.59	*<0.0001*	8
Swell protection	278.03	*<0.0001*	2
Wind protection	0.918	0.1700	2
Shore type	61.86	*<0.0001*	3

Cow-calf distribution in Sebastian Bay was significantly different from expected for swell protection and the majority of whales were strongly clustered in the protected water, but they did not distribute differently from the expected pattern with respect to protection from wind. Most animals were clustered in the region partly protected from wind at the head of the bay as opposed to the partly protected region of the tail of the bay. Although both sections were 'partly protected' the head of the bay provides more protection than the tail of the bay (protected from 56% versus 34% of winds).

Cow-calf distribution was significantly different from the actual distribution of the various shore types within the bays. Whales occurred more frequently off the "estuarine environments" and "wave-cut rocky platforms" at the head of the bay than off sandy beaches (middle section of bay) and "exposed rocky headlands" (Infanta headland and the foot of the bay).

Cow-calf pairs were found significantly more often than expected in the shallower waters within the observed portions of the bay (depth intervals were summed to 4m due to small sample size). This is largely a result of their proximity to shore (see previous chapter). Although the distribution of cow-calf pairs in St Sebastian Bay relative to the slope of the sea floor, is significantly different from the expected distribution (slope categories larger than 1.2^0 summed due to small sample size), it is difficult to interpret. The shape of the observed distribution is similar to that of the expected distribution but shifted towards slightly steeper slopes. This is possibly a result of an extensive patch of shallower slope around the

Duiwenhoks River, which is slightly flatter than the head of the bay and thus skews the expected values slightly. Whales do however appear to avoid the steepest parts of the bay (just north of the headland) although they are not preferentially occupying only the flattest parts.

4.5.2 De Hoop

Certain patterns of distribution are obvious and apparently consistent within the De Hoop region for the three surveyed years (Figure 22). Starting at Skipskop (the western edge of the analysed region) there is a northerly stretch of coast on which few whales, in any of the survey years, were seen. This stretches to mid-way along the dune field almost in line with the De Hoop vlei (Die Mond) whereupon whale density increases dramatically to potentially its highest along the entire coast. At the end of the dune field/beginning of the wave-cut rocky platform area (near Koppie Alleen) whale density begins to taper off but maintains a fairly high, although patchy density as far as Vaalkrans. Whale density appears to maintain a regularly higher density for the ~5km between Vaalkrans and Hamerkop, the area with a sandy beach. Once east of Hamerkop, in the exposed rocky shore of the Infanta headland, whale density drops off rapidly.

The western-most sub-area was left out of correlation analysis because it is an anomaly in the distribution within De Hoop, whale density being extremely low here despite 'attractive' environmental characters (refer to Figures 19 and 22). The only apparent reason for the almost total avoidance of this region is its extreme shallowness (the mean depth is 6.6m from the coast to 3km offshore) and although reefs may be present as an extension of Martha's Reef, no data are available for this area.

The pattern of unaccompanied adult distribution was not significantly correlated to any of the environmental factors in the sub-areas (see Table 7); further Chi-squared analysis could not be performed due to a low sample size. Cow-calf numbers were greater in the sub-areas with gentler slopes and shallower sea floors and with a higher proportion of protection from swell (significant at the 10% level only). There was no significant

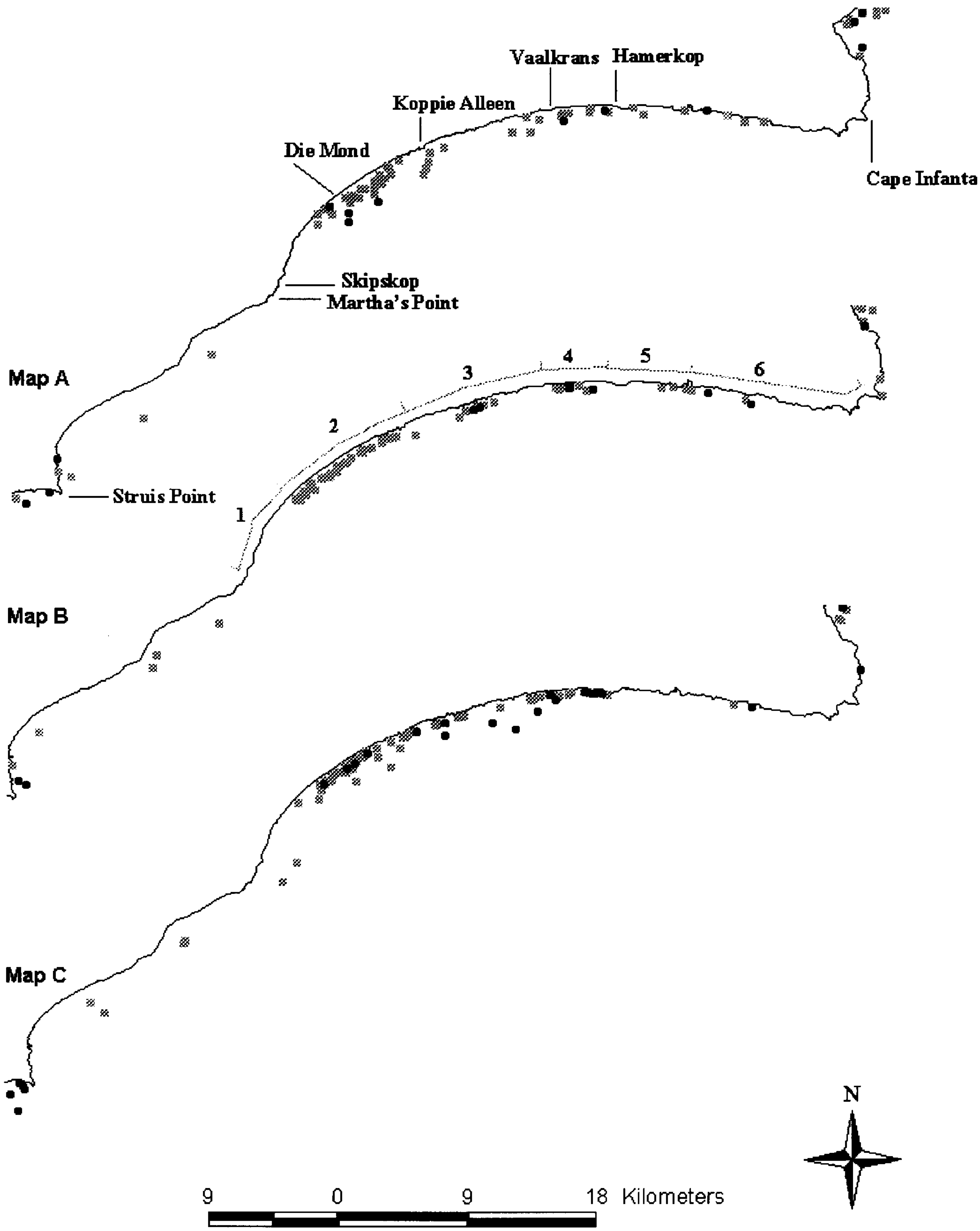

Figure 22: GPS positional data of cow-calf pairs (grey squares) and unaccompanied whales (black circles) within the DeHoop region. Map A –1997; Map B – 1999; Map C – 2000. Map A shows place names; Map B shows approximate size and placing of "sub-areas". Compare with Figure 19.

increase in whale numbers in the sub-areas with more attractive shores or greater protection from wind (see Table 7 and 8).

Chi-squared analysis of cow-calf pair distribution supports the distribution by sub-area analysis in that significantly more whales were found in shallower water than deeper water as well as in the areas of gentler slope. There was also a clear tendency for most cow-calf pairs to be found in the more swell-protected western end of the bay but there was no apparent distributional bias shown toward the areas with greater protection from wind only.

Table 7. Results of Spearman-Rank correlations within the De Hoop area of environmental factors and both cow-calf pairs and unaccompanied whales for sub-areas (* = significant at the 10% level)

	Unaccompanied (n = 50)		Cow-calves (n = 183)	
	R_s	P	R_s	P
Slope	-0.700	0.233	-0.900	0.0833*
Depth	-0.700	0.233	-0.900	0.0833*
Swell protection	-0.3354	0.5164	-0.894	0.0833*
Wind protection	-0.1118	0.783	-0.224	0.6833
Shore type	-0.600	0.350	-0.700	0.2333

Table 8. Results of Chi^2 analysis for the De Hoop region, cow-calf pairs only were tested due to small numbers of unaccompanied whales

	Cow-calves (n = 183)		
	Chi^2	P	Df
Slope	34.69	*<0.0001*	7
Depth	44.37	*<0.0001*	7
Swell protection	134.91	*<0.0001*	2
Wind protection	128.15	0.170	1
Shore type	81.97	*<0.0001*	3

Significantly more cow-calf pairs were found off sandy beaches and fewer off rocky shores than expected from a random distribution. The only sandy-beach area with very low whale density is the section within sub-area 1, which was excluded from analysis.

The overall pattern of whale distribution was biased toward the western end of the bay which is the most swell-protected part of the bay; it also has sandy beaches (and most likely a nearshore sedimentary substrate) as well as a gentle bottom slope and a degree of protection from wind. Whales were also frequently found along the sandy section of beach just west of Hamerkop, despite a lower amount of protection from either swell or wind here. Wave-cut rocky platforms were occupied at an intermediate density but less predictably by whales of both classes; the steep rocky Infanta headland was almost totally avoided by whales in all three years.

4.5.3 Walker Bay

The highest densities of whales occur off the central sandy beaches of Walker Bay (Die Plaat) and this density tapers off gradually towards the headlands on either side of the bay (Figure 23). In 1997, there was a clustering of unaccompanied whales around the Klein River mouth but this is not discernibly different to any other cluster of whales within the bay. Cow-calf pairs are predominantly found off the sandy beaches of Die Plaat while unaccompanied whales appear to have a more diffuse distribution within the bay.

The distribution of neither class of whale was significantly correlated to the mean slope or depth of the sub-areas (see Table 9). However, Chi-squared analysis showed neither unaccompanied whales nor cow-calf pairs distributed uniformly with respect to depth and both showed a significant preference for the shallower waters within the bay (depth categories summed into 6m intervals to satisfy Chi-squared demands) (see Table 10). Both unaccompanied whales and cow-calf pairs show a significantly different distribution pattern to the expected one for "slope" within Walker Bay (slope categories $>1.4^0$ summed in both tests to satisfy Chi-squared demands) and appear to be clustered toward the medium slopes rather than the extreme slopes (gentle and steep) within the bay.

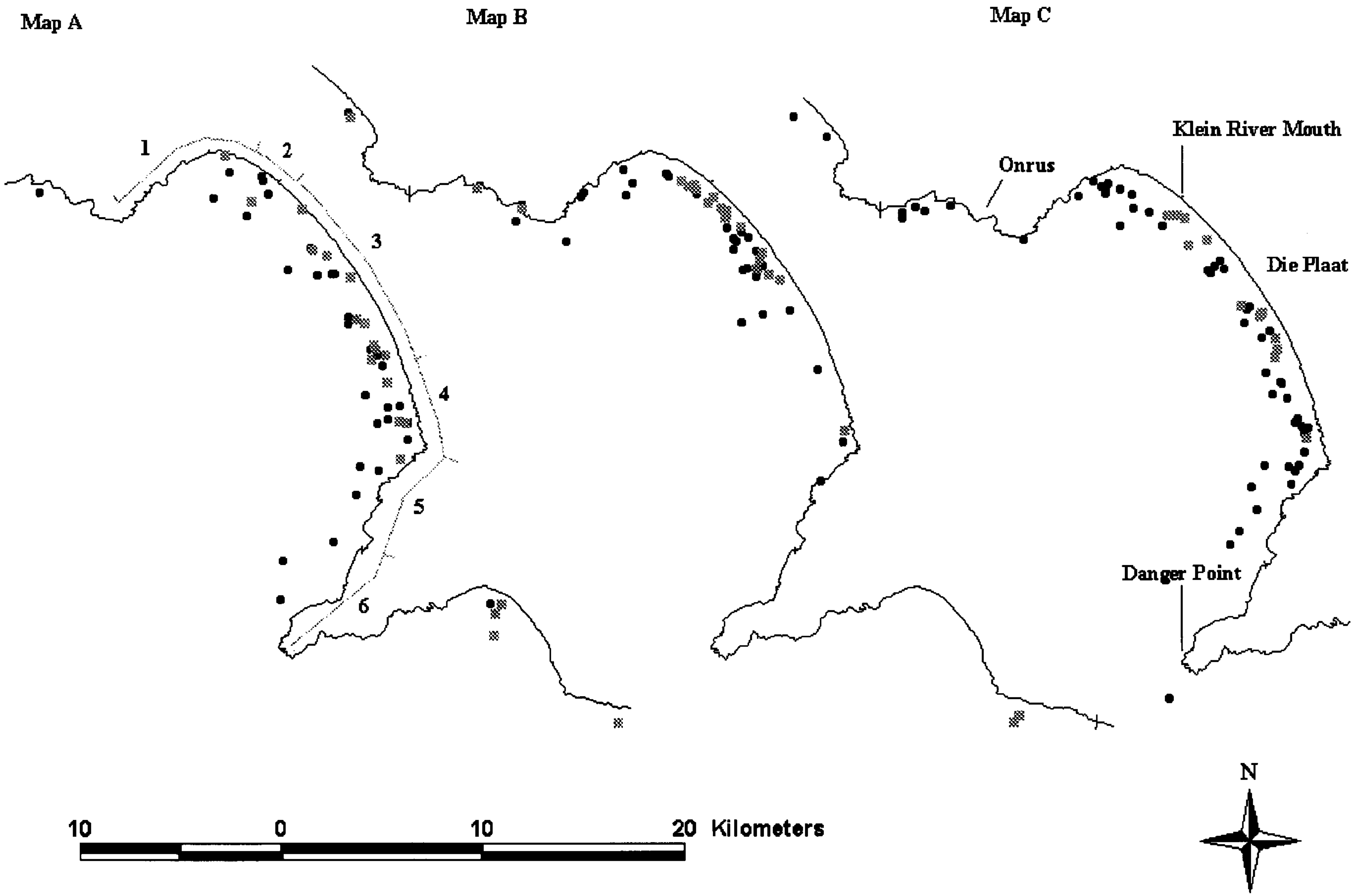

Figure 23: GPS positional data of cow-calf pairs (grey squares) and unaccompanied whales (black circles) within Walker Bay. Map A –1997; Map B – 1999; Map C – 2000.; Map A shows approximate size and placing of "sub-areas"; Map C shows place names. Compare with Figure 20.

Table 9. Results of Spearman-Rank correlations within Walker Bay of environmental factors and both cow-calf pairs and unaccompanied whales for sub-areas (* = significant at the 10% level)

	Unaccompanied (n = 212)		Cow-calves (n = 45)	
	R_s	P	R_s	P
Slope	-0.3143	0.5639	-0.6667	0.1361
Depth	-0.1429	0.8028	-0.5798	0.2417
Shore type	0.05798	0.9194	-0.8235	0.0583*

Table 10. Results of Chi^2 analysis for Walker Bay

	Cow-calves (n = 45)			Unaccompanied whales (n = 212)		
	Chi^2	P	Df	Chi^2	P	Df
Slope	34.36	*<0.0001*	3	49.83	*<0.0001*	8
Depth	167.24	*<0.0001*	17	80.81	*<0.0001*	5
Wind protection	G = 2.099	>0.05	1	G = 6.22	*0.025 >p > 0.01*	1
Shore type	G = 35.20	*<0.001*	*2*	G = 19.08	*<0.001*	2

Cow-calf numbers were higher in the sub-areas with more attractive shore type (significant at the 10% level) but no relationship was found for unaccompanied whales. The majority of cow-calf pairs were found off the sandy beaches and estuarine environments and less off the exposed rocky headlands than expected from a random distribution. Unaccompanied whales distributed more closely to the expected pattern, but still occurred more often off sandy beaches than rocky shores and occurred very close to expected ratios in the estuarine environment.

No analysis was made of distribution with respect to swell type as the whole of Walker Bay was classified as "partly protected" by the three tier system used. Wind protection within the bay was similarly high with no exposed areas. Chi-squared analysis of distribution did not show significant differences for cow-calf pairs with respect to wind protection and they distributed very closely to the expected random pattern. However, unaccompanied whales did distribute significantly differently to expected and were found more often in the partly protected areas and less often in the protected areas of the bay.

4.6 Direct Comparisons under "controlled" conditions

4.6.1 "Protected sedimentary bottom" versus "Exposed sedimentary bottom"

The lower section of De Hoop (sub-area 2) as well as the middle section (sub-area 4) both have sandy beaches and are presumed to have a near shore sedimentary substrate. Although sub-area 1 also has sandy beaches, the extremely shallow nature of this region is presumed to be the underlying reason behind the very low whale numbers here and this does not weaken the current comparison. Sub-area 2 is ~7km long, 85% of which is 'partly protected' and 15% 'protected' from swell, 97% is 'partly protected' from wind and it contained 100 cow-calf pairs during the three surveyed years. Sub-area 4 is a comparable length (5.2km) but is entirely exposed to swell and wind and only contained 27 cow-calf pairs during the survey years. This is a considerable difference in whale numbers even considering the steeper slope in sub-area 4 (0.740 ± 0.240se) than in sub-area 2 (0.360 ± 0.120se). Balancing for area of each region, sub-area 2 has a total density of 14.2 whales/km (4.7 whales/km/year) while sub-area 4 has a total density of 5.2 whales/km (1.7 whales/km/year). When the observed number of cow-calf pairs in each sub-area was compared to the number expected if there was no preference shown between the areas (balanced for area, expected 67.9 and 50.44 cow-calves respectively), the result was significantly different ($Chi^2 = 26.068$; $p < 0.001$, df = 1). Unaccompanied whales have a different pattern and less (n=13) were found in sub-area 2 than in sub-area 4 (n=16); Chi-squared analysis was not possible due to low sample sizes. Swell and wind protection may be a less important factor for unaccompanied whales, but the presence of calm water appears to be a strong attractant for cows with calves even within the nursery area itself.

4.6.2 "Rocky headland" versus "Wave-cut platforms" versus "Sandy Beach" in an Exposed Environment

The De Hoop region provides a method for comparing the relative attractiveness of the three main shore types within one level of swell protection and on a fairly constant slope.

The area between Koppie Alleen and just past Hamerkop is all classified as exposed, has a relatively constant slope (roughly 0.61^0, 0.74^0 and 0.93^0; mean slope of sub-areas 3-5 respectively) but has three different shore types lying adjacent to each other. Between Lekkerwater and Hamerkop there is a 5.2km fine sandy beach, either side of which there is a 7.0km area of wave-cut platforms (west) and a 5.3km area of exposed rocky headlands (east). This area of the coastline is unique in its high numbers of whales and the three shore types adjacent to each other within the same swell classification level. Analysis was performed using the same procedure as in section 4.6.1.

Markedly more cow-calf pairs are found off the sandy beach (5.2 whales/km, n = 27, summed for three years surveys) than off either the exposed rocky headlands (2.1 whales/km, n = 11) or rocky platform (2.6 whales/km, n = 18) stretches of coastline. This is significantly different to the numbers expected if no preferences were shown (Chi^2 = 66.31, $p < 0.001$, df = 2). These observations support the hypothesis that sandy substrates are substantially more attractive to cow-calf pairs than either type of rocky shore. The density of whales off the two rocky shore types is fairly similar suggesting no preference by whales in this regard.

The apparent preference of whales for sandy bottomed areas is further supported by the distribution patterns in the Marcus Bay (ca. 12 km Struis Point to Rys Point) and the lower De Hoop areas (ca. 14km Martha's Point to Koppie Alleen) (refer to Figures 19 and 22). The lower De Hoop area has been described as shallow sloped with a very sandy bottom, Marcus Bay however, is dominated by a number of reefs (including Saxon, Miles Barton and Atlas Reefs). The two areas lie 20km apart on the coast but right whales in this region are strongly biased toward the De Hoop side (n = 102, summed for three years), while very few whales have been sighted in the Marcus Bay area (n = 8 in three years).

4.7 Effects of River mouths

Within St Sebastian Bay whale density is high near the Breede River mouth in all three surveyed years but this pattern is not as clear around the Duiwenhoks river where, although there does appear to be a small degree of clustering, it is not obviously different from the small groupings of whales that occur elsewhere in the bay (see Figure 21). It is not possible within St Sebastian Bay to remove the effects of protection from swell, protection from wind or the presence of a sedimentary substrate at the head of the bay. All these factors have been shown to strongly and positively influence whale density, so the strong clustering of whales around the Breede River mouth is more likely to be a result of these factors than any apparent benefits that derive from the river itself.

No rivers presently flow into the sea in the De Hoop region and the only river there (Potberg River) ends in a vlei a few kilometres from the sea. Whales do however seem to cluster in the area where the river formerly flowed into the sea, which suggests a preference for the sandy bottom caused by the sediment filled, buried river channel (see maps of whale distribution, Figures 19 and 22). This area is similar to the mouth of the Breede River in that several factors interact to make it an overall attractive area. The sedimentary bottom as well as the protection from both swell and wind strongly bias distribution in favour of this area.

To test the effects that river mouths may have on whale distribution it is necessary to observe a river mouth that is effectively isolated from any other influence by being in a large area where all other factors are uniform. The only place where a reasonably large river occurs within a fairly high whale density area that does not lie in conjunction with several other attractive factors is Walker Bay. The entire bay is classified as partly protected from swell and wind and the river mouth opens onto the northern end of a long sandy beach, thus it does not open into the only attractive part of the bay (see Figure 20). The river mouth was opened 13 weeks before the survey in 1997; about 2 weeks before the 1999 survey, but in 2000 the river was opened only after the survey was completed.

When all three survey years are considered, both unaccompanied whales and cow-calf pairs are found more often off the northern end of the sandy beach area (closer to the river) and less often off the southern end of the beach (see Figure 23). The distribution of unaccompanied whales is significantly different from uniformity (df = 5, $Chi^2 = 26.86$, $p = <0.001$), their lowest numbers occur in the 3km segment overlaying the river mouth itself (n=12), while the highest numbers (n=38) occur in the adjacent 3km segment (Figure 24). Cow-calf pair distribution is slightly different from uniformity (only significantly different at the 10% level: df = 5, $Chi^2 = 10.45$, $0.1 > p > 0.05$), the lowest numbers of whales occurring in the two segments furthest from the river mouth (n = 4 and n = 1) (Figure 25). This overall pattern is largely influenced by the 1999 survey year when most whales of both classes were clustered toward the northern side of the bay. Unfortunately, analysis could not be performed on each year individually due to small sample sizes invalidating Chi-squared analysis. Since the river mouth was not opened during the 2000 survey, analysis was re-done on the 1997 and 1999 years only. Unaccompanied adults again showed a significant preference for the river side of the beach area (df = 5, $Chi^2 = 28.5$, $p = <0.001$), but cow-calf pairs showed no significant preference for either side of the beach (df = 5, G = 7.5, $p > 0.05$; log-likelihood test due to small sample sizes).

4.8 Discussion

The three bays analysed individually were chosen because between them they contain 73.1% of cow-calf pairs and 49.4% of unaccompanied whales within the entire survey area and represent by far the largest congregations of whales along the South African coast. All three bays have several characteristics in common; they provide a fair degree of protection from swell and wind, they have sandy or sedimentary bottoms and gentle slopes. These are all characteristics that were predicted to be 'attractive' to whales, especially cow-calf pairs. In all three bays, whales distributed in the predicted patterns, clustering predominantly in the swell and wind protected ends of the bays as well as avoiding steeper rocky slopes in preference to shallow sloping sandy floors and flat rock platforms. Whales were most likely to be found where several attractive factors coincided

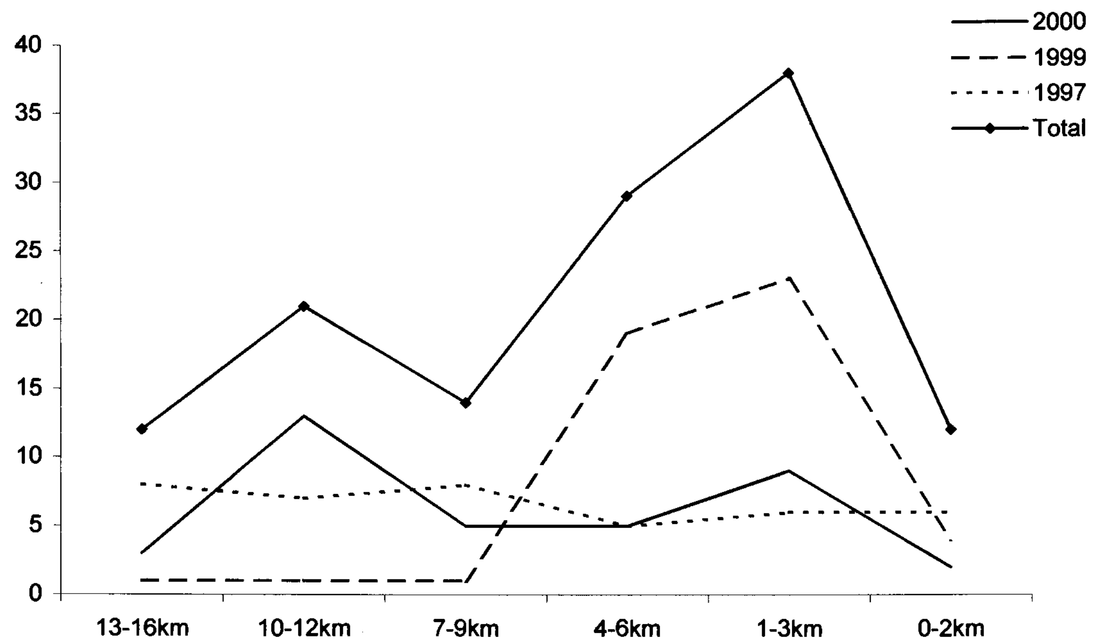

Figure 24. Distribution of unaccompanied whales per 3km segment relative to the Klein River mouth, Walker Bay. Each survey year as well as total number of whales shown.

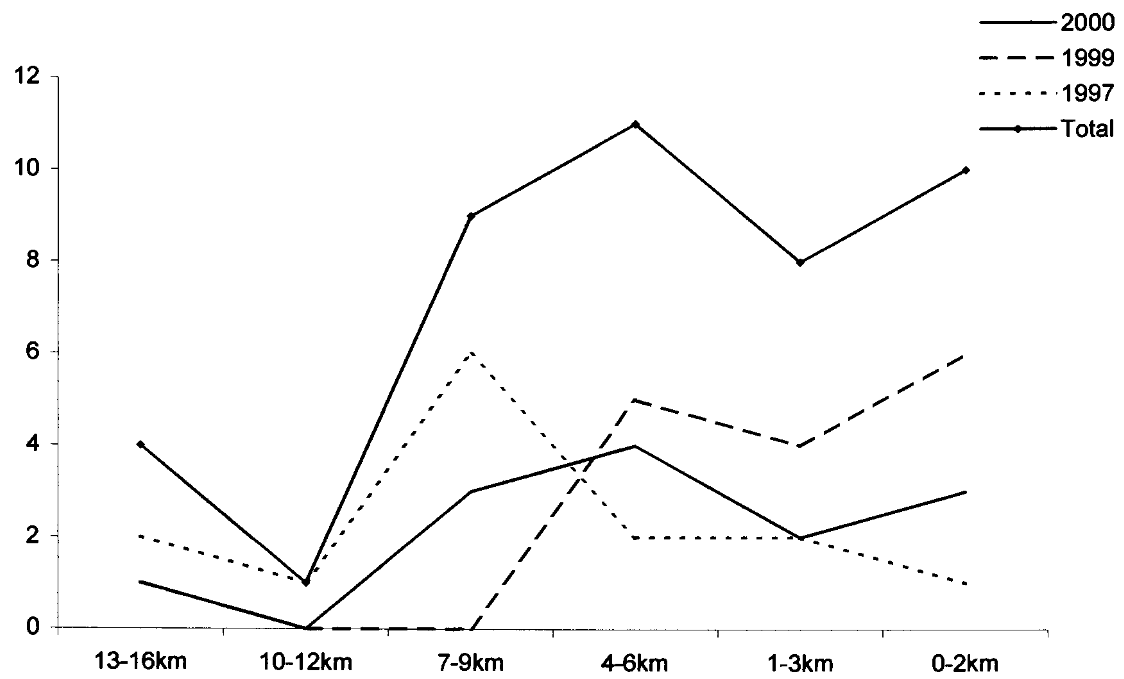

Figure 25. Distribution of cow-calf pairs per 3km segment relative to the Klein River mouth, Walker Bay. Each survey year as well as total number of whales shown.

and in general exhibited very similar patterns of distribution to those found at the larger scales of study in the previous chapter.

The results pertaining to slope are difficult to interpret, as in De Hoop whales cluster above the gentle slopes, in Walker Bay in the medium slopes and on the medium and slightly steeper slopes in St Sebastian Bay. This suggests that at this scale any benefits of slope are overridden by other more important factors (notably substrate type and swell protection). There is no biological reason for whales to show a distinct preference for shallow slopes since no direct benefit is likely to be derived from them, the apparent (though not very clear) preference for shallow slopes is probably secondary in nature. Shallow slopes arise when sediment is deposited, usually in calmer water, so it is likely to be this rather than any direct benefit that results in any relationship with whale numbers

The influence of river mouths on whale distribution is not clear since the analysed river mouth in Walker Bay was not in a similar state of flow between years, but there seems to be some degree of attraction. When all survey years are considered together, both classes of whale appear to show some preference for the side of the beach nearer to the river mouth. However, at this scale small changes in distribution in response to wind or swell patterns on the day or social interactions could have strongly influenced the observed patterns. Due to the small sample sizes involved and the varying nature of the river mouth, summing between years may not be the best approach for this analysis and the distribution during each survey should be considered; unfortunately sample sizes do not allow useful statistical analysis. Although both cow-calf pairs and unaccompanied whales appeared to cluster nearer the river in the year in which it was most recently opened (1999), they showed a very similar, if slightly more spread out pattern in 2000 when the river mouth was closed! In 1997 (when the river had been opened for over 3 months, and had possibly silted up to some degree) whales were spread almost evenly along the sandy beach. Thus, there is some evidence that right whales may be attracted to river mouths but a larger sample size and a more direct analysis technique are needed before firm conclusions can be drawn.

The benefits of river mouths for whales are unknown but could potentially include assisted exfoliation of skin or loss of external parasites as has been observed in beluga whales (*Delphinapterus leucas*) (Watts, Draper & Henrico, 1991). Although higher numbers of whales were found on the end of the beach closer to the river mouth in Walker Bay, some of those whales are up to seven kilometres from the actual mouth. However, the river's water flow can extend out to sea for several kilometres (pers. obs.) and if assisted exfoliation and loss of parasites is the reason for the attraction, then the increased freshness of the water may still play a role at these considerable distances. One would expect that if assisted exfoliation was the goal of proximity to river mouths, then more whales would concentrate more closely and more often to all river mouths and not just those in otherwise already (presumed) attractive habitats. I feel this link is tenuous and that the principal benefit of river mouths for right whales is most likely to be a sedimentary bottom in the vicinity due to fluvial transport and subsequent deposition of sediment. This is supported by the distribution of whales both during the 2000 survey in Walker Bay and off De Hoop where the river mouth similarly does not reach the open sea.

Although long term and wide scale distribution is not likely to be affected by short-term weather changes (e.g. previous chapter), fine scale distribution within bays might well be. Thus, on calm days it might only be necessary for whales to be in the proximity of protected areas but not actually be in those areas since whales could easily move from the one part of the bay to another. This is not likely to apply to depth, substrate type or distance from shore as these factors are more likely to be related to segregation of the population than to energy conservation. Despite these considerations of movement, whales, especially cow-calf pairs, are showing a clear preference for the swell protected parts of the bays rather than the exposed parts.

The preferential occupation of at least partly protected areas even under apparently calm conditions can be interpreted in two ways. Either the preference for calm waters is strong enough to keep them in very close proximity most of the time, or alternatively, the 'protected' waters are more attractive than the 'exposed' waters even during the apparent calm of the survey days. Since the decision to fly on any given survey day was influenced primarily by wind strength (which influenced sightability), and swell height was not specifically considered, it is thus possible that there was still an active benefit to be gained from the calmer waters on the survey day. If this is so, then protection from swell only is clearly important enough to strongly influence the distribution patterns of whales at this scale, and suggests that swell protection may well be more important for whales than wind protection. But protection from both together will most likely be more attractive to whales than either factor alone.

The patterns of distribution observed in this study are not unique to this population or species, as an apparent preference for calmer waters has been observed in southern right whales off Australia (Holst, 1999), the Auckland Islands (Patenaude & Baker, 2001) and Argentina (Payne, 1983; Thomas, 1987) as well as in humpback whales off Hawaii (Whitehead & Moore, 1982; Smultea, 1994) and gray whales off Mexico (see Swartz, 1986). The preference for calmer water is further supported when one considers the variety of scales at which whales exhibit these behaviour patterns. In the previous chapter whales were shown to prefer 'bins' (20-minutes of longitude wide, mean = 41.4km of coast) that contained greater amounts of protection from swell and wind. This is a considerably larger scale than the sub-areas within bays (~5-7km) used in this chapter. At an even larger scale, whales along the South African coast are more prevalent along the southern and western coasts (Best, 2000b) where bays exist that provide shelter from open ocean swell, than along the exposed East Coast. The benefits of calm water have been suggested as a reason for baleen whale migration (Whitehead & Moore, 1982) although this is not an entirely accepted theory (see Corkeron & Connor, 1999; Clapham, 2001). Migration across ocean basins to get to calmer water could be argued to be the largest scale at which this behaviour is exhibited since whales are leaving the rougher winter seas of the Antarctic for the (relative) calm of the temperate oceans.

Multi-scale evidence of whale preference for calm water is not exclusive to South Africa as similar patterns are evident off Argentina. The majority of right whales off Argentina occupy the Peninsula Valdés (Payne, 1986) which is dominated by two large gulfs that presumably provide some degree of protection from open ocean wind and swell, though being the east coast of the continent, prevailing swell conditions are considerably different to those off South Africa. Rowntree, Payne & Schell (2001) show whale numbers (mostly cow-calf pairs) to peak sharply in one part of their distribution within Golfo Nuevo, Argentina (almost twice anywhere else in the study site). This particular 5 kilometre segment appears to align closely to a small area of coast that is behind a smaller headland (Piramides) within the greater bay (see Fig.1 and 6 in Rowntree *et al.*, 2001) suggesting greater protection than elsewhere in the region. Elsewhere on the Peninsula Valdés, in a small part of Golfo San Jose, Thomas (1987) described the small scale distribution of mother-calf pairs relative to various environmental factors in the area. He found the bulk of cow-calf pairs to rest (the hypothesised 'preferred' activity) close to shore off shallow sloping sandy beaches in preference to cliff areas or areas exposed to strong currents. In Western Australia, Holst (1998) reports whale numbers to be higher in bays where some degree of protection from swell is provided due to the local wind patterns, and (at a smaller scale than the one used here) he reported right whales to "skirt underwater reefs" as well as move further offshore in storm conditions.

The potential benefits of 'calm water' are two fold. Firstly, conservation of energy is most likely the principal benefit for both lactating cows and calves, which can potentially invest any saved energy in lactation and growth respectively . Secondly, increased survival and decreased injury, especially of calves, may occur since calves have been reported to have difficulty surfacing to breathe in extremely rough waters (Thomas & Taber, 1984) so there is a small chance of actual drowning as well as the greater risk of being pushed ashore or injured by strong currents and waves. The strength of the patterns evident from the South African right whale population suggests that calm water is a primary factor in habitat choice in wintering grounds. Further, these results potentially support the theory that movement to calm water may act as one of the reasons underlying migration, at least for this species.

Although calm water is clearly a very important factor in habitat choice, the number of cow-calf pairs that can be found far from any protection (for example those whales in Stilbaai and around Cape Agulhas) suggest that, although important, it is not critical to survival, at least not throughout the lactation period of a calf's life. The interaction of several factors influencing distribution makes this a very dynamic situation and the distribution of right whales cannot be reliably predicted from any one factor. Further, the factors influencing distribution of calves may change as the calves grow and become less vulnerable.

Further work based on direct measures of whale responses to different environmental conditions would be beneficial to gain a fuller understanding of how important each of these factors is to individual whale movement and survival and how the relationships change through a whale's life.

Chapter 5: Reproductive success and coastal distribution of right whales (*E. australis*) off South Africa

5.1 Introduction

Southern right whales exhibit phylopatry to both their coast of birth and (to a lesser degree), at the smaller scale of to particular bays (Best, 2000a). This phylopatry may be at least partly responsible for the highly predictable distribution pattern that both cow-calf pairs and unaccompanied whales have shown along the South African coast since 1969 (Best, 1981, 1990, 2000). The distribution is segregated generally into a cow-calf region (De Hoop and St Sebastian Bay) and an unaccompanied adult area (Walker Bay), although numbers of both classes of whale can be found in either area and many whales fall outside these two main concentration sites. As well as phylopatry, it was suggested that the greater preference exhibited by whales for certain areas may be related to particular environmental features (Best, 2000a).

It has been shown earlier that the majority of right whales along the South African coast occupy areas of the coast that are environmentally similar. The three main areas of right whale concentration are all reasonably protected from open ocean swell as well as the predominant winds of the season and have predominantly sandy shores and substrates. Cows with calves occur significantly closer to shore and in shallower water than unaccompanied whales. The benefits of calm water are believed to be predominantly for conservation of energy by the calves (Corkeron & Connor, 1999) which are weak swimmers during their early stages of life (Thomas & Taber, 1984). Sandy bottoms are thought to serve primarily for reduction of injury compared to rocky bottoms, especially for calves in shallow water. The sandy bottoms and proximity to shore could possibly have acoustic benefits by reducing and/or masking any noises by the cow or calf from potential killer whale predators, as well as serving to physically segregate cows from both potential predators (Würsig & Würsig, 1979; Thomas, 1987) and the rest of the population.

Since the majority of whales occupy environmentally similar areas, and are mostly within a comparatively small range it was felt that there could be some measurable reproductive or survival benefit associated with using these areas. Since 1979, photography of cows with calves for individual identification has taken place annually (Best, 1981, 1990, 2000). The ability to individually identify right whales has allowed for the collection of data on return rates of individual cows to particular areas, individual movements of animals, inter-calf intervals and age at first parturition for those animals identified both as calves and mothers (Best, 2000a; Best *et al*, 2001). In this chapter, the observed calving intervals of individual females have been used as an index of reproductive success. In addition, the incidence of stranded neonates has been used as an index of neonatal survival. Both indices have been examined in relation to features of the coastal environment.

5.2 Methods

Since 1979, the aerial survey for photography has been performed in early to mid October of each year and covered the area between Muizenberg (False Bay) and Natures Valley (Plettenberg Bay). Details of the survey procedures are given in Best (1990). Since the survey pre-dated the adoption of global positioning systems, the positions of animals were described relative to adjacent landmarks. For analysis, the coastline was divided up into "bins" 20-minutes of longitude wide labelled from east to west as A – P (Best, 2000a). For the purpose of this study whale positions and movements along the coast have been described using these bins.

Totals of 1397 calving events, 1012 inter-calf intervals, and 34 stranded dead calves were available for analysis. The normal inter-calf interval of right whales is believed to be 3 years (Best, Brandao & Butterworth, 2001; Burnell, 2001) but observed calving intervals between 2 years and 12 years are known. The occurrence of a 2-year calving interval is thought to represent the loss of a neonate, followed by ovulation of the cow after one year rather than two (Burnell, 2001). Burnell (2001) suggests that a proportion of the population may calve normally at a 4-year interval due to the high proportion of such intervals (14%) in the Australian population.

However, the occurrence of 4-year calving intervals is much lower in the South African population (6% - unpubl data) and in this chapter 4-year calving intervals are regarded to be the result of the loss of two successive calves with the second calf being missed in (or dying before) the survey.

For spatial analysis, successful and unsuccessful calving intervals were defined as 3 years for a successful interval and 2 and 4 years as unsuccessful intervals (summed and treated as one); calving intervals longer than 4 years were ignored due to difficulties with interpretation (thereby reducing the sample to 808 inter-calf intervals). On the assumption that some areas may be more suitable as calving grounds than others and result in more successful calvings, the occurrence of successful and unsuccessful calving intervals was compared for different areas along the coast. Furthermore, since it was possible for cows to move to certain areas rather than others after having a successful or unsuccessful calving interval, the bin occupied after successful and unsuccessful calving intervals was also analysed. Since the distribution of these animals is highly concentrated in some areas but not others, data outside of the four main concentration bins (C, F, G, H) were summed to increase sample size. These low density bins were split into two categories, bins containing potentially attractive calving areas that currently have low density (A, B, D, E, K, L, O) and those bins that have very low apparent attractiveness for cows (I, J, M, N), based on conclusions of previous chapters. These grouped areas are referred to as "GLD" (good bin, low density) and the unattractive areas (Unatt.) respectively.

As well as calving intervals, the tendency to 'stay' or 'move' between bins for subsequent calves and the spatial distribution of these factors were examined. All the above factors were compared to each other where possible to look for possible influences and interactions. Site fidelity was analysed under two definitions, the strict definition being a resighting of a cow with its next calf in the same bin, and the broad definition a resighting in the same or an adjacent bin (as used by Best, 2000a). Calf number was used as a measure of the experience of cows; to simplify analysis, animals were classified as 'inexperienced' (1^{st} or 2^{nd} calves) and 'experienced' mothers (3^{rd} to 7^{th} calves). The distribution of experienced and inexperienced cows per bin as well as the tendency for cows to 'move' or 'stay' at each level of experience were analysed. In the beginning of the survey series, all cows were by definition 'inexperienced' since they had never been seen before. To compensate for this, only the data from 1988 onwards were analysed, as by this date (nine years after the start of the survey series, or 3 potential calving intervals) any female seen for the first time with a calf would most likely be an inexperienced individual. All comparisons in this analysis were done using a Chi-squared test to compare the actual distributions with those expected on a basis of equality, working with the null hypothesis of no difference between any of the tested factors.

A data set of all stranded cetaceans in the Western Cape since 1963 was available for study. The positions of all right whale calves (animals < 8.0m in length) stranded (live or dead) during this time period were noted and assigned to equivalent survey bins where relevant. Animals stranded on the West Coast were grouped together since population numbers here are very low and any further spatial breakdown would reduce samples to an unusable size (see Best, 2000a). The West Coast in this analysis is regarded as that area west of the standard survey range from Muizenberg, around the Cape Peninsula as far north as St Helena Bay (refer to Figure 1). Data generated from all the aerial surveys (of the standard survey area) were used to create an expected number of stranded calves based on the average proportion of cow-calf pairs present in each bin. The number of expected strandings on the West Coast was based on the proportion of cow-calves found in this area (6.6%) as described by Best (1998). The actual and expected distributions of the 34 stranded calves were compared using a log-likelihood test (Chi-squared assumptions were violated due to small sample sizes in most areas). Distributional bins were similarly summed into "Good, Low Density" (GLD) and "Unattractive bins" as for calving interval analyses.

5.3 Results

No pattern was found for there to be a higher proportion of more successful calvings in some bins rather than others ($Chi^2 = 4.63$, $p = 0.46$, $df = 11$) (Figure 26). Nor were cows more likely to occupy certain areas rather than others after having either a successful or unsuccessful calving interval ($Chi^2 = 0.88$, $p = 0.97$, $df = 11$) (Figure 27). Cows were more likely to be resighted with their subsequent calves ('stay') within the same bin in the four main bins than in the rest of their range ($Chi^2 = 36.1$, $p = <0.001$, $df = 11$) (Figure 28). This pattern is further exaggerated when a 'stay' is broadened to include an adjacent bin ($Chi^2 = 156.0$, $p = <0.001$, $df = 11$) (Figure 29) and the ratio changes more noticeably in the nursery areas (bins F-H) than any other bins: these results are similar to those of Best (1990, 2000).

There is a clear trend for the proportion of cows experiencing shorter calving intervals to decline from first calf onwards (tested for 1^{st} to 4^{th} calves: $Chi^2 = 10.29$, $p = 0.018$, $df = 7$) (Figure 30). If 'new' mothers are less successful than experienced mothers, they might be expected to occupy substandard habitat or different bins to experienced mothers. Clear differences between the ratios of experienced and inexperienced cows were found in different bins when all years were analysed ($Chi^2 = 16.9$, $p = 0.005$, $df = 11$) (Figure 31) but this difference fell away when only the current distribution (post 1988) was tested ($Chi^2 = 4.62$, $p = 0.464$, $df = 11$) (Figure 32). Bin F had the highest proportion of experienced cows in both the long-term and recent analysis (Figures 31 and 32). The tendency to move or stay after having a calf did not change with the number of calves that a cow had had, when using either the strict or broad definition of 'stay', nor was any pattern of a change in these behaviours with 'experience' evident (strict: $Chi^2 = 0.75$, $p = 0.944$, $df = 9$; broad: $Chi^2 = 3.54$, $p = 0.472$, $df = 9$) (Figure 33).

Cows were not found to move or stay more after either a successful or unsuccessful calving interval when using the broad definition of 'stay' ($Chi^2 = 2.38$, $p = 0.123$, $df = 3$) (Figure 34). However, they are more likely to move after a successful calving interval when using the strict definition of stay ($Chi^2 = 311.5$, $p = <0.001$, $df = 3$) (Figure 35). This result seems contrary to expectation but is probably influenced by cows moving between the three main nursery bins, which have been shown to be treated as one

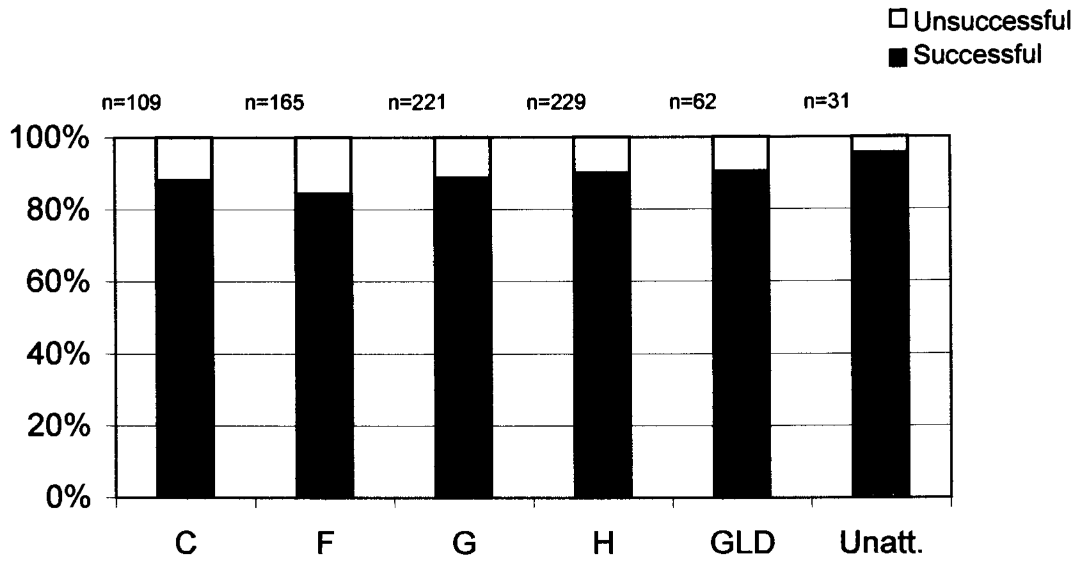

Figure 26. The proportion of successful and unsuccessful calving intervals occurring following a sightir particular bin or group of bins

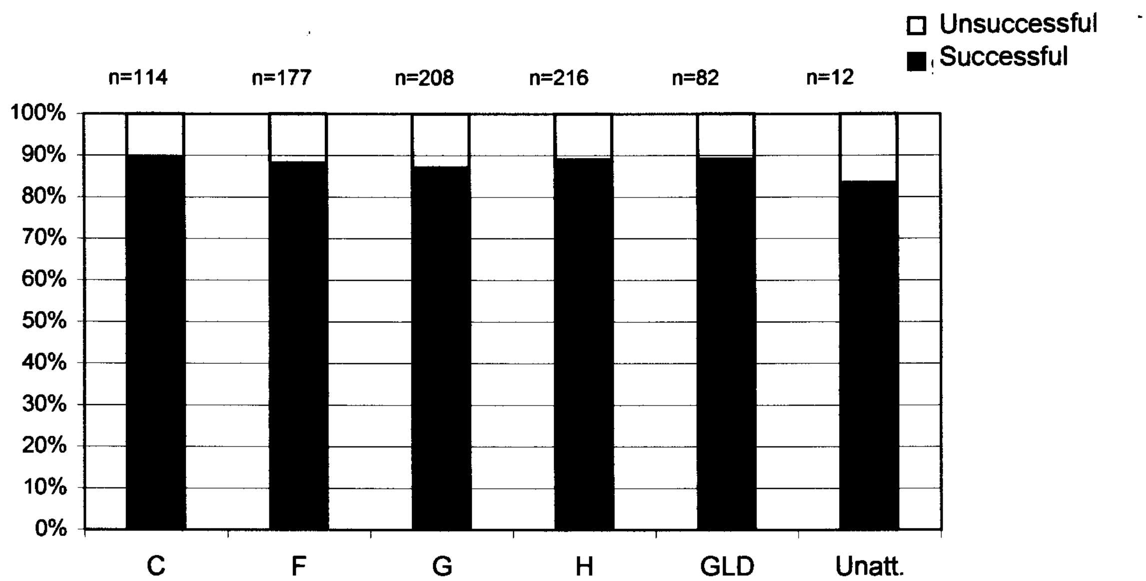

Figure 27. The proportion of successful and unsuccessful calving intervals occurring previous to sightii particular bin or group of bins

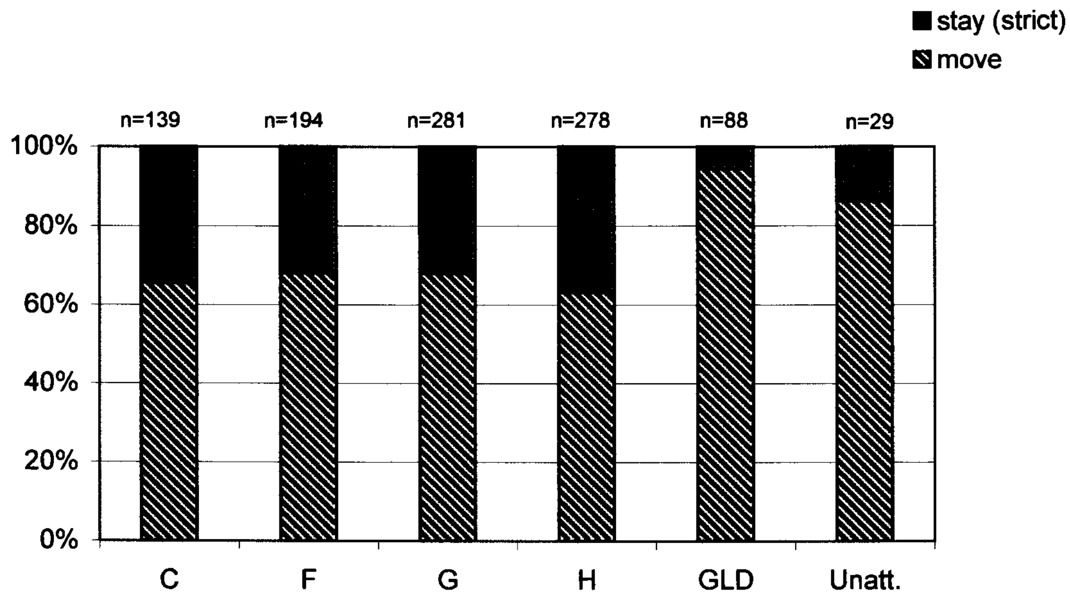

Figure 28. The proportion of "stays" or "moves" subsequent to sighting with a calf in a particular bin or group of bins (strict definition of "stay")

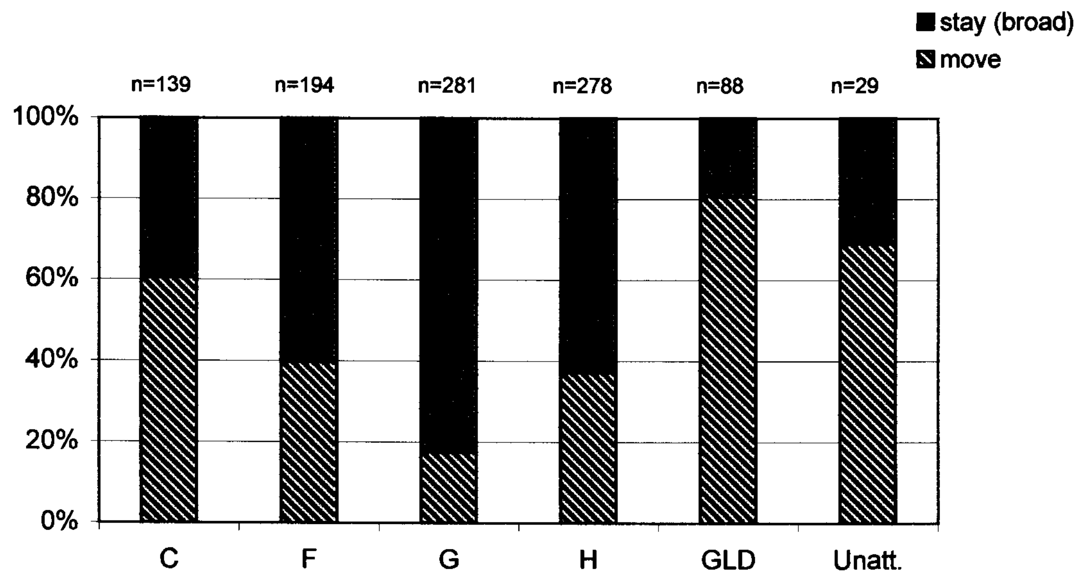

Figure 29. The proportion of "stays" or "moves" subsequent to sighting with a calf in a particular bin or group of bins (broad definition of "stay")

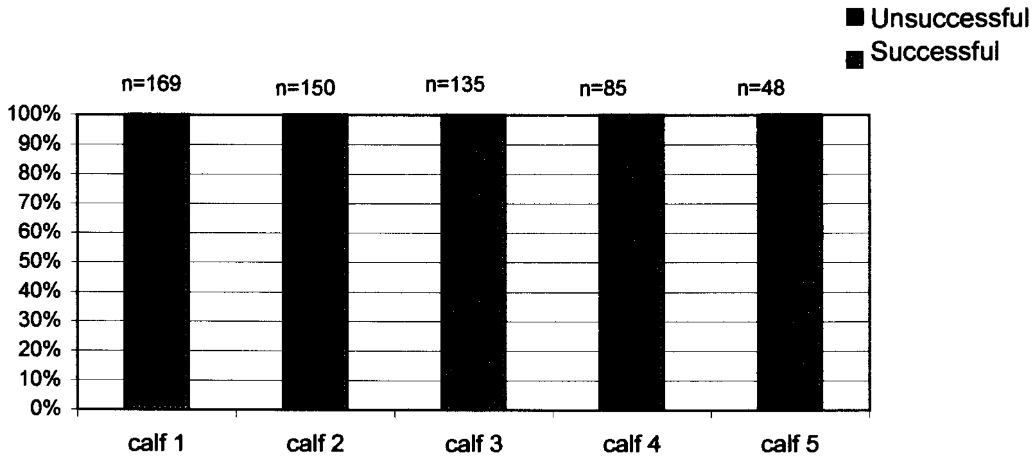

Figure 30. The proportion of successful and unsuccessful calving intervals following subsequent calves

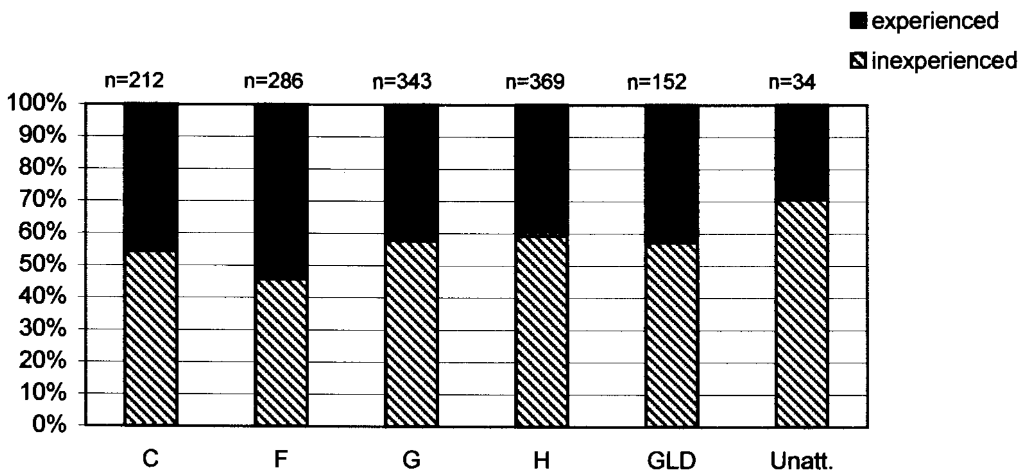

Figure 31. The distribution of experienced and inexperienced cows, shown as proportion per bin or group of bins (all data shown from 1979-1999)

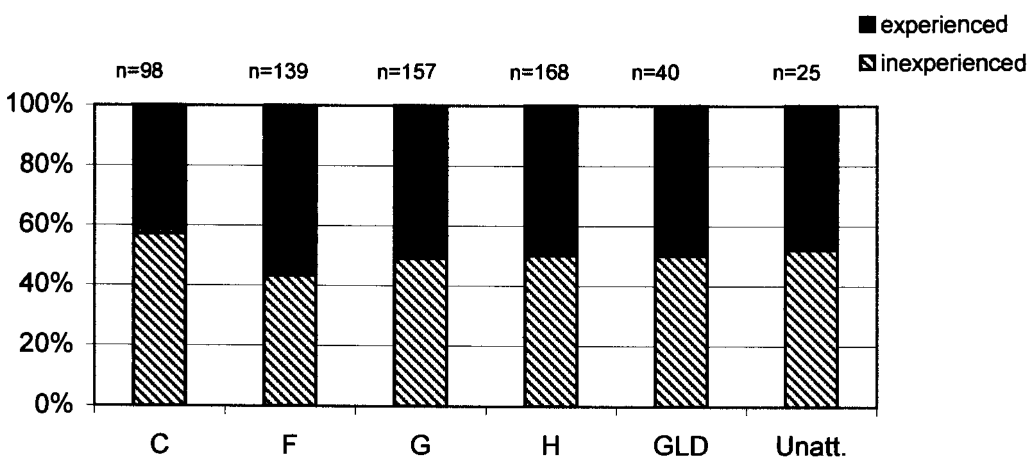

Figure 32. The distribution of experienced and inexperienced cows, shown as proportion per bin (or group of bins) but only data from 1988 shown to compensate for the pattern of range expansion

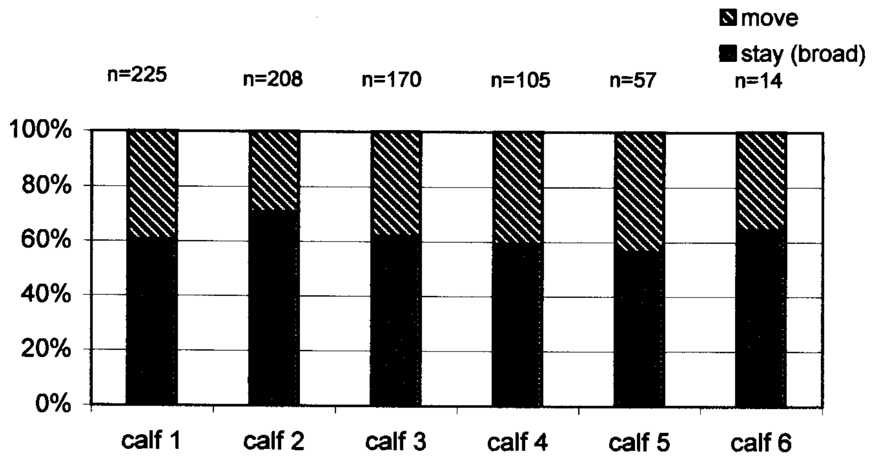

Figure 33. The proportions of cows that stay or move subsequent to each calf

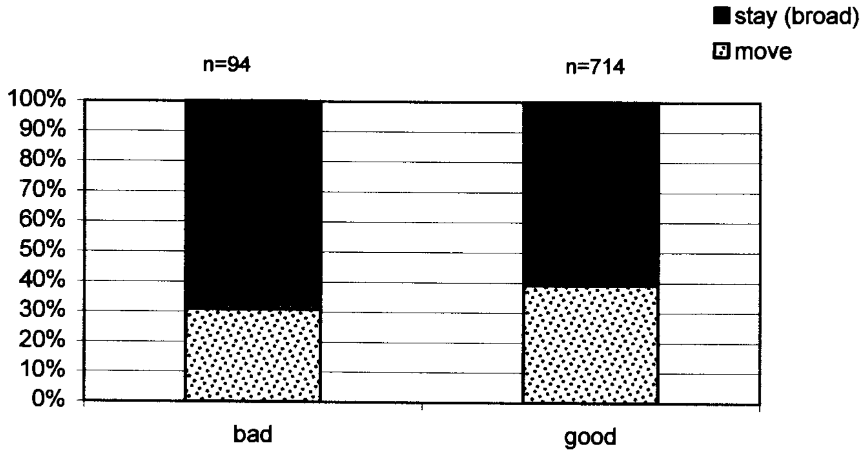

Figure 34. The proportions of animals that move or stay after having either a successful or unsuccessful calving interval (shown for broad definition of 'stay')

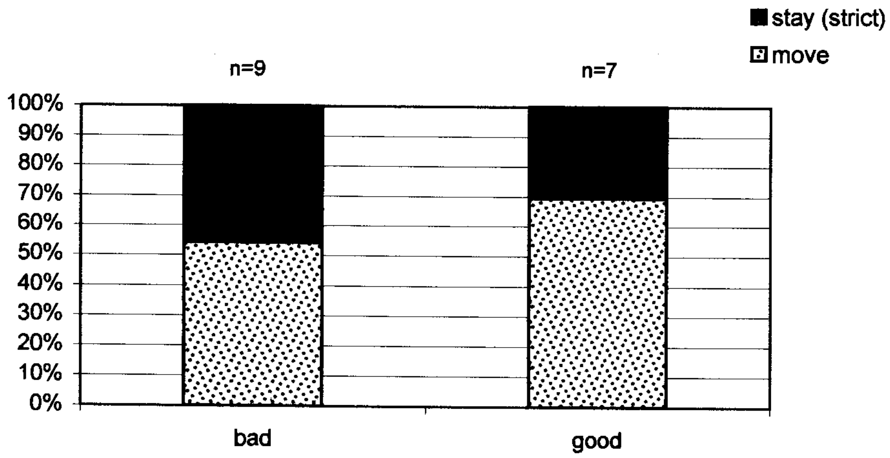

Figure 35. The proportions of animals that move or stay after having either a successful or unsuccessful calving interval (shown for strict definition of 'stay')

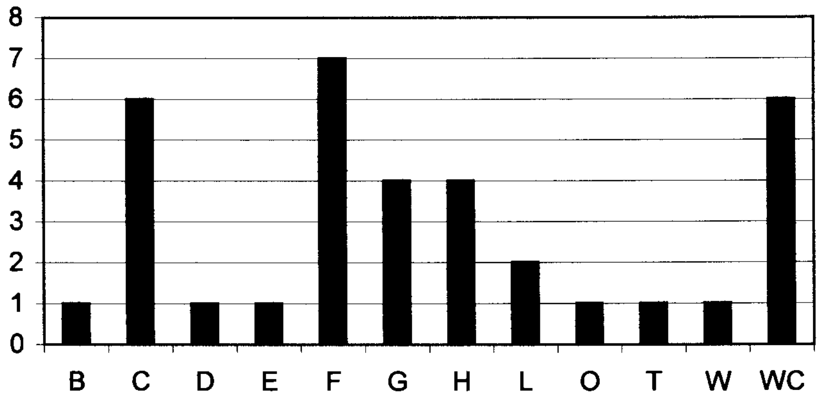

Figure 36. Numbers of dead calves that have stranded since 1963 along the Cape coast shown as number per bin, the West Coast (WC) shown as one area

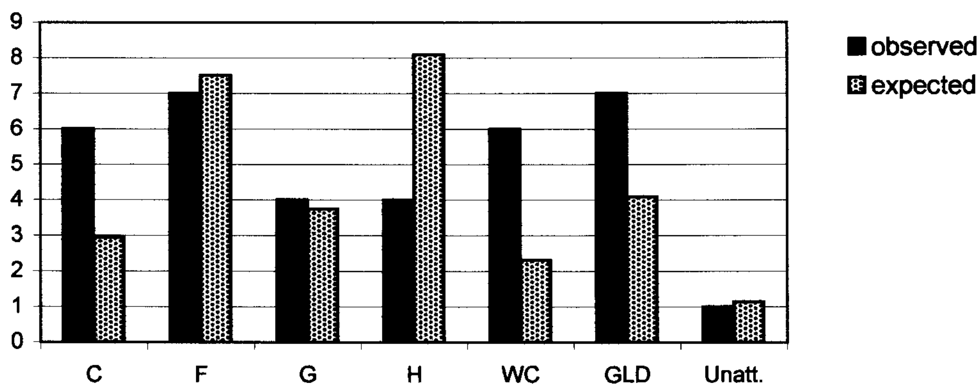

Figure 37. The expected and observed distributions of calf strandings along the Cape Coast shown for the four main bins and groups of bins, as well as the West Coast. Expected distribution based on the distribution of cow-calf pairs around the coast.

interchangeable area, with cows moving frequently in both directions within the region (Best, 2000a).

The distribution of all stranded calves in the Western Cape is shown per bin in Figure 36. The actual distribution of stranded calves is significantly different to that predicted from the distribution of cow-calf pairs along the coast (G = 21.453, p = <0.05, df = 11) (Figure 37). The expected and observed distributions were very 26-27 similar in bins F and G while fewer animals than expected strand in St Sebastian Bay. In all other areas more calves strand than would be expected from the number of cows present, this is most noticeable in Walker Bay and along the West Coast but is also evident for low density, potentially attractive calving areas. It is important to note that several of the animals stranded in bins F and G (3 from each) were found very close to the common border of the two bins and could potentially have stranded in either bin depending on prevailing currents of the day. The very similar environment either side of this arbitrary border and the influence of currents make the difference between the highly occupied parts of bins F and G potentially arbitrary.

Other factors that can potentially influence the validity of this data set, are the effects of currents and the probability of reporting a stranded calf being different in different areas. Also, almost all the stranded calves in the data set are smaller on average than their contemporaries, so they probably died very soon after birth or were still born and may be first-born young of inexperienced mothers (Best & Rüther, 1992). Potentially, their deaths could be the result of factors other than the environment, for instance their mothers' lack of care, poor nutrition of the cow or a lack of biological capability in young cows.

n= n=

5.4 Discussion

The distribution of cow-calf pairs along the South African coast is clearly biased toward certain areas (Best, 1990; this thesis). Best (1981, 1990) reports a nursery area (Bins F, G, H) and a breeding area dominated by unaccompanied whales (Bin C). Whale density is much higher in these areas than along the rest of the coast and this high degree of clumping has a considerable influence on any study of distribution. Most southern right whales calve at a 3-year interval (Best *et al*, 2001; Burnell, 2001) and the interpretation of at least a 2-year interval as representing the loss of a calf has some observational support (Payne *et al*, 1990; Burnell, 2001). This is thus a fairly acceptable method for measuring calving success. The use of successful or unsuccessful calving intervals in this paper as an indication of reproductive success is supported by the higher proportion of unsuccessful calving intervals occurring in inexperienced mothers. The tendency for new mothers to lose more offspring than experienced mothers is a pattern that has been shown in multibrood animals of several phyla and has been previously suggested as the reason for the small size of most stranded right whale calves in local waters (Best & Rüther, 1992).

The lack of any spatial pattern associated with successful or unsuccessful calving intervals is indicative that there is no difference in calving success between the different areas. However, the data set used for this analysis does have certain limitations that may also influence results. The aerial surveys took place fairly late into the season in order to maximise calf numbers: since peak calving occurs in August (Best, 1994) most calves along the coast would have been born by October. Cows with calves have been shown to move long distances along the coast within a season (Best, 2000a; Burnell & Bryden, 1997). Thus it is possible that the bin in which a whale is photographed with a calf is neither the bin in which the calf was born nor the bin in which it spent its early post-natal period (when calves are at their most susceptible). The late timing of the survey as well as the instantaneous nature thereof could thus have considerable influence on all the data used here.

Cows are not preferentially moving to any areas after having an unsuccessful calving interval (i.e. losing a calf or two) which can be interpreted two ways. Either they do not learn from experience and avoid returning to an area that resulted in a lost calf (assuming the reality of better and worse calving areas), or there are no reproductive benefits associated with moving to any particular area rather than any other. This result is also subject to the constraints of the previous analysis. Although there is no clear pattern in the distribution of cows either before or after a successful or unsuccessful calving interval, it seems likely that there must be some benefit associated with specific areas along the coast. Since the distribution of these animals has been predictable and stable for as long as the survey has been run, and the majority of cows have been found to occur in areas that are environmentally similar, there must be some benefit for cows to return to these areas each year. This suggests that the lack of any obvious patterns could be the result of a lack of resolution in the data collection technique resulting from the timing of the survey relative to movements away from the true birth areas, or that the benefit is not reproductive in nature.

Best (1990) showed a net immigration of cow-calf pairs into the Cape Infanta nursery region (bins E-I), resulting in a low or zero increase rate of cow-calf pairs throughout the rest of the survey region. This pattern of movement is largely responsible for the higher rates of resightings found in the nursery area by Best (2000) as well as in this analysis, since cows were more likely to move to this area than away from it. Cows appear to be treating the entire nursery region as one area and have been noted to move between the two main sub-areas both within and between years (Best, 2000a). Best (1990) only attained a 26.9% (1979-1987) resight rate for cows in the Walker Bay region (regarded as bins A-D in this paper) which is considerably lower, despite a broader scale, than the rate attained either in Best (2000; 1979-1998: 32.3% strict; 38.5% broad) or in this paper (1979-1999: 35.5% strict; 39.6% broad). The considerable increase in resight rates between the two periods reflects the strong increase in importance of the Walker Bay area for cows with calves since the early 1990's (see earlier chapters in thesis).

Best (2000) suggested that the higher fidelity to the nursery region could be related to environmental characteristics making this area more attractive for cow-calf pairs. Work in this thesis has shown that although environmental features are important and the majority of animals occur in 'attractive' areas, other environmentally attractive areas occur throughout the survey range that have very low whale density. So although environmental characteristics are important in a calving area, the higher resighting rates in the four main bins are strongly affected by immigration into these areas and are not likely to reflect directed movement here due to increased calving success *per se*. Because cows return to these areas of high cow-calf density each year, it is possible that there are stronger benefits associated with the presence of other cow-calf pairs than an environmentally attractive area alone.

Differences in the distribution of the proportions of experienced and inexperienced cows between bins seem intuitively correct, as the highest proportion of experienced mothers is found in the nursery area (especially bin F) and the lowest proportion of experienced mothers occurs in the low density 'Unattractive' bins. This suggests that experienced mothers are more frequently selecting premier calving grounds than inexperienced mothers. However, the distribution pattern generated by animals since 1988 is very close to parity which suggests that the differences shown when all the data is considered are possibly an artefact of the pattern of range expansion of the population rather than a real pattern of distribution. It is worth noting at this point that in Golfo San Jose, Argentina several right whale cows have been reported to show agonistic behaviours toward one another suggesting some degree of territoriality for a small sandy beached area (Thomas, 1987). Such agonistic behaviour between cows has never been observed in South African waters (Best, pers comm.), although behavioural observations have been limited.

The lowest proportional occurrence of stranded calves occurs in St Sebastian Bay which is probably the most attractive calving area within the nursery region (based on findings of earlier chapters), while strandings in the remainder of the nursery area are close to parity with expected. The higher number than expected of calf strandings in the rest of the range, particularly along the West Coast, possibly reflects an inferior quality in these areas. The 'quality' of these areas is unlikely to be due to the environmental factors tested earlier in this thesis since Walker Bay, False Bay and several other regions are of a similar level of environmental attractiveness to the De Hoop area. There are also several areas along the West Coast (e.g. St Helena Bay) where cows with calves were historically found (Richards & DuPasquier, 1989) and appear to be environmentally similar to the attractive areas along the South Coast.

The areas that are found to have a higher than expected number of calf strandings are all characterised by having a higher number of unaccompanied whales than cow-calf pairs. Harassment either of the calf or the mother by other animals could play a crucial role in the survival of neonatal calves. Records exist of calves being separated from their mothers by other animals and cows are thought to purposely avoid the very active socialising behaviours of unaccompanied animals by moving closer to shore (Thomas, 1986). Cow-calf pairs have also been noted to segregate at larger scales both in South Africa (Best, 1990) and Argentina (Payne, 1986). It is thus possible that the presence of a high number or proportion of unaccompanied whales is detrimental to the survival of neonatal calves, especially those of inexperienced mothers that may lack the skill to avoid harassment: the diminutive size of most of the stranded neonates suggests that they are likely to be the offspring of first time mothers (Best & Rüther, 1992).

The segregated distribution of cow-calf pairs and unaccompanied whales in both a longshore and an offshore direction (Best, 2000a; earlier this thesis) suggest there may be a benefit for cows with calves in avoiding contact with unaccompanied whales. The significantly higher losses of neonatal calves in areas with higher ratios of unaccompanied whales support this theory. The higher losses of calves incurred by new mothers suggest that as well as body condition and cow size, experience in avoiding or controlling contact with non-mothers could play a crucial role in the survival of neonatal calves. This is probably at its most important in the small stage one calves where if separated, the calf requires the approach of the mother to re-establish contact (Taber & Thomas, 1982). The greater vulnerability at this stage is indicated by the small size of most stranded calves. This possibly explains why very little relationship was found with any of the aerial survey results, since most calves have grown beyond stage one by the time the surveys were performed. These findings indicate that the presence of a 'nursery area' where the number of unaccompanied whales is low could be at least as important to cows as being in an environmentally suitable area. Population structure within the nursery area could therefore potentially be of greater importance than previously thought.

Chapter 6: General Conclusions and Synthesis

Previous observations of right whales have resulted in a described preference or preferential occurrence in 'bays' (Best, 2000a; Richards & Du Pasquier, 1989) or 'calm water' (Thomas, 1987; Holst, 1998; Clapham, 1999; Payne, 1983), as well as for sandy-bottomed or shallow, beached areas (Thomas, 1987; Clapham, 1999; Rowntree *et al.*, 2001). Work in this thesis has shown quantitatively that these patterns occur within the South Africa population of right whales, and that whales were most likely to be found in areas where several factors coincided. These animals showed a clear preference for areas of calm water, with avoidance of large swell possibly being the most important factor involved and protection from wind apparently being secondary to this. A clear preference was also shown for areas with sandy substrate and also shallower parts of the coast, but no clear preferences for shallower slopes were exhibited (which were felt to be a secondary factor, conducive to or a result of sediment deposition, although possibly having an effect on near shore wave action). The weak attraction shown by whales for river mouths was felt to be secondary in nature (due to sediment deposition, although other potential benefits exist, e.g. accelerated exfoliation) but larger sample sizes are needed for before firm conclusions can be drawn. Shore type was found to be a useful indicator of near-shore substrate type as whale distribution was clearly related to different shore types in the predicted patterns.

The benefits for whales of the environmental factors deemed 'attractive' were felt to be extended in two areas, energy conservation (primarily calm water, although slope and shore type may play a role in wave action) and physical protection due to proximity to shore (reduced threat from predation and harassment, and sedimentary substrate reducing the risk of injury). The range of spatial and temporal scales at which the same patterns were observed, especially the smaller scales where weather could have a potentially large effect on results, reinforced the significance of the preferred areas to these animals. However, the large number of animals found outside of apparently attractive areas, as well as the amount of longshore movement that occurs (thereby exposing animals to harsh conditions for extended periods) indicate that although important, the preferred environmental characteristics are not critical to the animals' survival.

The distribution of right whales differed between classes of animals. Cows with calves were found closer to shore and in shallower water than unaccompanied whales and in general off more gently sloping sea floors. This segregation was also reflected at larger scales in a longshore direction with the population generally separated into nursery and breeding areas along this coast. Longshore separation of these classes was not so apparent at small scales within the three main bays studied in detail, but offshore separation possibly suffices at this scale. Segregation of cow-calf pairs from other whales is thought to serve primarily to reduce harassment of cows and calves by juveniles and sexually interested males, which can potentially separate a calf from its mother for extended periods, thereby leading to injury or death of the calf. The increased proximity to shore of cows with calves could also reduce the likelihood of their being detected by any predators (especially killer whales). The long-term nature of the segregation between cow-calves and unaccompanied whales is indicative that this separation is important on an evolutionary time scale (several generations) and may be as important a factor in habitat selection by cows as abiotic environmental factors. No differences in distribution were found between primiparous and multiparous cows either longshore or offshore, although a longer time series is needed before firm conclusions can be drawn. A similar lack of pattern was evident from the analysis of experienced and inexperienced cows (interpreted from calving intervals), despite a reasonably long time series, suggesting all cows choose similarly with respect to environmental conditions regardless of experience.

Since cow-calf pairs have such a biased distribution toward the nursery region and there is apparently immigration into this area (Best, 2000a), possible differences in calving success between different areas of the coast were investigated. Calving intervals for known cows were compared between bins along the coast. Three-year calving intervals were regarded as successful (i.e. the calf survived) while two- and four-year intervals were regarded as unsuccessful intervals (i.e. one and possibly two successive calves died, respectively). The proportion of successful calving intervals was not significantly greater in one bin than in another, whether the intervals were measured after calving in a particular bin or preceding calving in a particular bin. This was interpreted to mean that there are no differences in reproductive success between bins as well as that cows do not apparently learn from experience by choosing "better" areas after having lost a calf. This analysis suffered from low temporal resolution because the data were based upon single aerial surveys per year and considerable dispersal of cow-calf pairs could have occurred between birth and the survey.

Proportionally higher strandings of neonatal calves than expected from the number of cow-calf pairs present were found outside the nursery area, in regions where unaccompanied whales generally outnumber cow-calf pairs. More calves were lost (as inferred from calving intervals) by younger mothers (<3 calves) than more experienced cows (3 or more calves). This greater loss by inexperienced cows is most likely due to a combination of physical immaturity as well as social inexperience. It was concluded that the ability to control or avoid contact with unaccompanied whales and juveniles may thus be very important for cows with calves, especially during stage one of calf development (as most stranded calves were, judging from size).

Initial predictions of right whales preferring calmer water and sedimentary substrates as well as of the preferences being stronger in cow-calf pairs than unaccompanied whales were supported. The patterns exhibited by this population provide some support for the theory that movement to calm water may be a factor in baleen whale migration, as well as migration being a predominantly female-mediated activity. Although certain environmental factors clearly play a very important role in determining the distribution of right whales off the South African coast, they are not the only factors involved and are not critical for the presence of whales. Social factors, possibly including the benefits of aggregations for cows with calves, increased sociality during the mating season and most importantly the ratio of unaccompanied whales to cow-calf pairs may play an equally important role in determining the distribution and reproductive success of right whales at the coast.

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