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ENVIRONMENTAL FACTORS INFLUENCING THE DISTRIBUTION OF SOUTHERN RIGHT WHALES (*EUBALAENA AUSTRALIS*) ON THE SOUTH COAST OF SOUTH AFRICA I: BROAD SCALE PATTERNS

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ABSTRACT

Aerial surveys over the last 32 yr have shown that the distribution of southern right whales *Eubalaena australis* along the south coast of South Africa is markedly discontinuous, but highly predictable. A GIS was used at a variety of scales to investigate whether this pattern was related to environmental characteristics. Whale distribution was analyzed as density per 20-min bin of longitude over two temporal and spatial scales, namely 15 bins for 32 yr, and a wider scale but shorter time period, 23 bins for 19 yr, as well as using three years of GPS accuracy data (15 bins) for finer scale analysis. Environmental factors tested were depth, distance from shore, sea floor slope, protection from swell, protection from wind, and shore type. The majority of whales were concentrated in areas that provided reasonable protection from open ocean swell and seasonal winds, and had sedimentary floors with gentle slopes. They generally avoided exposed rocky shorelines. Cow-calf pairs were found significantly closer to shore and in shallower water than unaccompanied whales, particularly off sandy beaches. Habitat choice at this time of year may be related both to energy conservation for calves and lactating females (calm sea conditions) and to protection of the new-born.

Key words: *Eubalaena australis*, right whale, distribution, spatial scale, environmental factors, GIS, sexual segregation, South Africa.

Southern right whales (*Eubalaena australis*) are annual visitors to the coasts of South Africa and other southern 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 2000). While at the coast, right whales seem to preferentially occupy

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certain areas each year with a high degree of predictability (Best 2000). This predictability in distribution was well utilized by the early bay whalers, who could simply wait in the same places for the whales to arrive each year (Richards and Du Pasquier 1989). Although the population was highly depleted by both ship-based and shore-based whalers and was last estimated to be at only 10% of its original numbers (Butterworth and Best 1990), right whales are still behaving in a predictable fashion (Best 2000) albeit in a much smaller range. Right whale cows exhibit a high degree of phylopatry to the coast of their birth as well as a lesser degree of fidelity to a particular nursery area on that coast. Best (2000) thought this tendency to return to some areas preferentially could be a result of environmental characteristics associated with the areas. It was the goal of the current study to investigate relationships between environmental conditions and right whale distribution.

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 is highly influenced by the presence of food. Studies on sperm whales (*Physeter macrocephalus*) (Griffin 1999), fin whales (*Balaenoptera physalus*) (Forcada *et al.* 1996), northern right whales (*Eubalaena glacialis*) (Clapham 1999),[2] common (*Delphinus delphis*), and whitesided (*Lagenorhynchus acutus*) dolphins (Selzer and Payne 1988) 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. Because right whales apparently rarely feed while in coastal waters in winter and are thought to fast while on a breeding migration (Tormosov *et al.* 1998, Best and Schell 1996), other factors are likely to influence 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 (Payne 1995, Thomas 1987).

Environmental factors that have been considered important in determining baleen whale distribution in coastal waters include, (1) calm water for female humpback whales (Whitehead and Moore 1982, Smultea 1994), southern right whales (Payne 1995, Thomas 1987) and gray whales (Swartz 1986), (2) water depth and slope for southern right whales (Payne 1986), and (3) the softness (non-rocky) of the substrate for southern right whales (Payne 1995, Thomas 1987).

Although water temperature and salinity have been related to cetacean sighting rates in other species (Selzer and Payne 1988), and sea surface temperature is potentially useful in predicting northern right whale (*Eubalaena glacialis*) distribution (see Clapham 1999),[2] neither were considered likely to have much influence in the current study. During winter, right whales are found in surface temperatures ranging from ~15°C in Walvis Bay to ~30°C in Maputo Bay, and salinity has always been found to relate to whale presence through effects on prey density. Furthermore, the current study covers a long time series and precise, fine scale, temperature and salinity data for each survey day were not available for the entire study area or period.

Baleen whale migration is generally regarded as being a female-mediated event in which cows migrate for some apparent benefit to their calves, while there are no

[2] Clapham, P. J., ed. 1999. Predicting right whale distribution. Report of the workshop held on 1 and 2 October 1998, in Woods Hole, MA. Northeast Fisheries Science Center, Woods Hole, MA.

apparent benefits associated with migration for unaccompanied whales (Corkeron and 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.

Observations of environmental factors influencing right whale distribution in South African waters were made as long ago as 170 yr, Owen (1833) stated "The cow whales generally come into all the bays on the coast for still-water and sand, both of which are said to be necessary to the black whale in parturition." In this study we hypothesized that the distribution of right whales in South African waters was associated with 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. We also hypothesized that cow-calf pairs would exhibit a different distribution pattern than unaccompanied whales and would be more strongly associated with particular environmental factors.

METHODS

Distributional Data

Since 1969 annual aerial surveys have been used to count and photograph right whales 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, aerial surveys were flown with a fixed wing aircraft between 18°30′E (Muizenberg, the northwest corner of False Bay) and 26°30′E (Woody Cape, eastern end of Algoa Bay) (Fig. 1). From 1979, a second survey was flown by helicopter, but only from Muizenberg as far as Natures Valley (Plettenberg Bay, 23°50′E), roughly two thirds of the fixed-wing survey length. This resulted in two sets of data, 19 yr of surveys (1969–1987, fixed wing only) covering the larger area (bins A–X) and 32 yr (1969–2000, fixed wing and helicopter) of the smaller area (bins A–O). The data sets will be referred to as the 19-yr and 32-yr data sets, respectively. For the overlapping period, the fixed wing results were used as they covered the larger area and counts from the two surveys have been shown to be equivalent (Best *et al.* 2001). For full details of the survey methods, see Best (1981).

The entire coastline was searched once per annum within these standard survey areas, in a flight pattern parallel to but about 1 km offshore. All sightings were circled to establish species, group size and compositions. All surveys took place between late September and mid-October (see Best 1990 for full survey procedures).

As this aerial survey program was started before GPS positioning, the location of most whale sightings was given relative to adjacent landmarks such as headlands and river mouths. At this level of accuracy, we thought it appropriate to bin the data. Since the coastline runs in a largely east to west direction, the surveyed area was subdivided into bins 20 min of longitude wide, following Best (1981) (Fig. 1). Within each bin the length of the coastline varied from 30.6 km to 68.5 km (average = 41.4 km). Because each section of coast was only searched once per survey, no further controlling for search effort was felt necessary. Despite their relative imprecision 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.

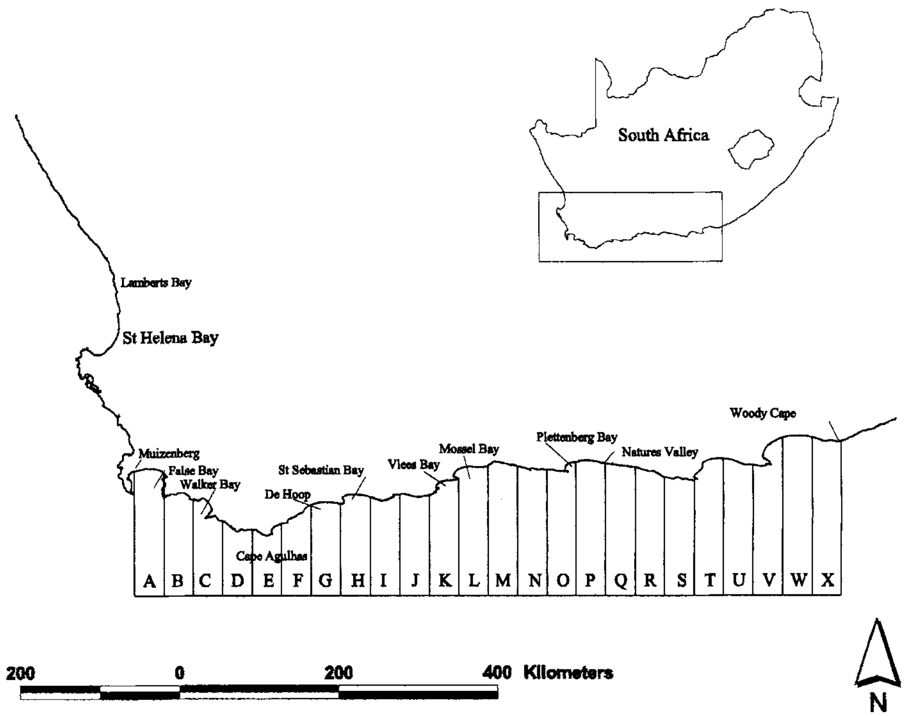

Figure 1. Southern and south-western coast of South Africa showing place names and the surveyed region of the coast with an indication of the longitudinal bins used in analysis. Fixed wing surveys (1969–1987) covered bins A–X, helicopter surveys (1979–2000) covered bins A–O.

Accurate whale positions in the form of GPS locations were available from three helicopter surveys (1997, 1999, 2000). Each whale sighting within this area could thus be associated with a class of each environmental factor analyzed.

Environmental Data

To describe the range of characteristics to which whales within the surveyed area were exposed, we defined the seaward extent of the surveyed area within each segment or bay as well as along the entire coastline. Inspection of the raw GPS positions showed that all sightings were contained within 3,000 m 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, 3-km was assumed to represent the extreme limit of the surveyed area from the coast. Environmental factors used in analyses were thus limited to this "searched" area for testing.

An accurate digital version (coastline, soundings and depth contours) of the marine navigation charts SAN 117-125 (scale 1:150 000) for the southern Cape Coast was obtained from the S.A. Naval Hydrographer's office. The coastline, soundings and depth contours were used in a GIS software package (Arcview 3.2, ESRI, Redlands, CA) to create a computer-generated "surface" (TIN) that mimicked the sea floor. "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 of the sea floor at any given point as well as to calculate the average depth and slope for any defined area within the surface.

In lieu of good data on sea floor substrate, the only related information available at a useful scale was for the adjacent shore type. Jackson and Lipschitz (1984) defined 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 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 these data was available for use in the GIS system.

It was not possible to get precise measurements of swell or wind characteristics at all points along the surveyed region for the last 30 yr. However, averaged long-term data for the almost the entire study period (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-degree squares of latitude and longitude) that correspond to particular stretches of coast. Data from spring (September–November) were used as the aerial survey always took place between late September and mid-October (Best 1990).

Swell data were directional roses and described the proportions of swell coming from each direction of a 16 point compass, as well as the frequency of the various swell heights from that direction (Fig. 2). Because the data were collected from voluntary observer ships offshore, they represent the offshore swell conditions in the absence of any land. Sections of the coast that are behind headlands or in bays are thus protected from a certain amount of the swell. We calculated the amount of swell (of all heights) striking each section of the coast and, after consultation with oceanographers, used a 3-tier level of "protection" from open ocean swell to describe the coast. Any area protected from more than 60% of seasonal swell was defined as "protected," any area protected from 30%–60% of incoming swell as "partly protected," and any area protected from less than 30% of swell as "exposed." Refraction of waves around headlands or the effects of reefs were ignored as it was not possible to accurately model every bay along the coast for every conceivable swell direction and the reefs were incompletely mapped.

The majority of swell on the South African coast comes from a south-westerly direction (Fig. 2). However, 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 southeast. These southeasterly swells are more predominant in the western section of the survey area (west of Cape Agulhas) than in the eastern section, where the swell is still distinctly southwesterly during spring. Due to the greater "spread" of swell directions in the western end of the survey, 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."

Wind data were in a similar format to swell data showing proportion and strengths of winds from each direction (Fig. 2). The 3-tier system of description was used to describe protection from wind on the same basis as protection from swell.

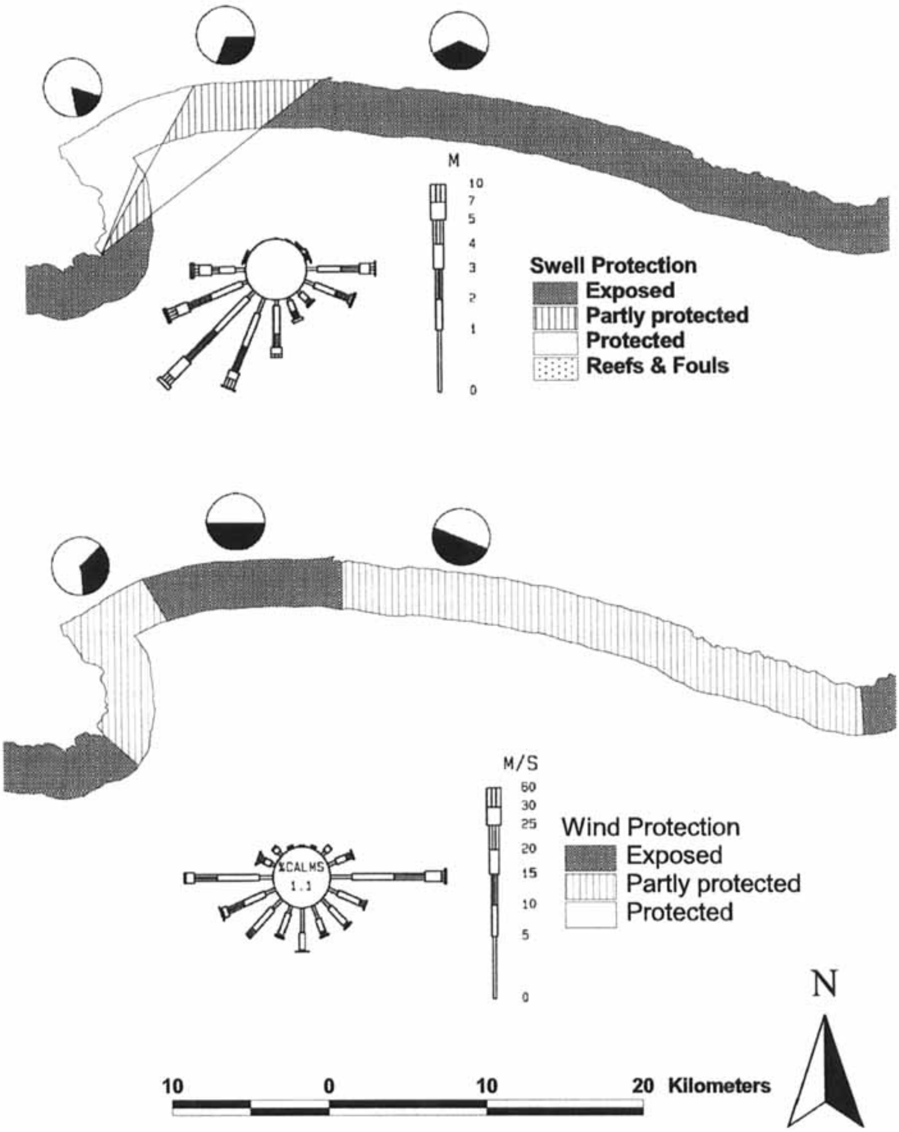

Figure 2. St Sebastian Bay shown as an example of how protection from swell (top) and wind (bottom) was worked out. Respective "roses" (and scales) of raw data for the area shown as well as pie charts reflecting direction from which wind and swell were regarded to be striking each section of coastline (black).

Although the effects of wind on nearshore water are complicated by the influences of the height and shape of near shore land masses, any area of nearshore water was regarded as protected from all winds blowing in an offshore direction at that point along the coast. Although arbitrary, this protection was assumed to extend to 3,000 m offshore (*i.e.*, the same as the width of the survey area), on the grounds that a whale could easily move inshore from that distance to get shelter. Winds blowing in a longshore (parallel to the coast) or onshore direction were regarded as conditions that reduced the calmness of water and were thus classified as "exposed" (Fig. 2).

Analyses

The longshore distribution patterns of cow-calf pairs and unaccompanied whales were compared with each other using a "no difference" expected distribution with a Chi-squared analysis using the total number of animals per bin for both the 32-yr (15 bins) and 19-yr (24 bins) data sets. The onshore-offshore distributions of cow-calf pairs and unaccompanied whales were compared in relation to the depth, slope and distance from shore values that were available from the GIS for the three years where GPS data were available. Sightings from all three years were summed as there was no reason to expect any difference between years. A Mann-Whitney *U* test was used to compare cow-calf pairs with unaccompanied whales for each factor.

Because shore type has not been previously used as an alternative to nearshore bottom type, we felt it necessary to test its usefulness as an indicator. One of our original hypotheses was that right whales, especially cow-calf pairs would prefer sandier bottom types to rocky bottom types in order to reduce chances of injury when close inshore. We hypothesized that if shore type was equivalent to bottom type, then the depth and distance offshore of whales off the varying shore types would correspond to that predicted for bottom type (shallowest and closest to shore over sandy bottoms). Kruskal Wallis ANOVA with a *post hoc* Dunn's test was used to compare both distance from shore and depth of whales off the three main shore types (exposed rocky headlands, sandy beaches, wave-cut rocky platforms).

In testing whether whale distribution was related to environmental variables, the use of correlation/regression analyses was considered inappropriate, given that the population still has to re-occupy parts of its former range (Best and Ross 1986), leaving a number of bins of historical right whale habitat with zero or very low whale densities. These would have undue weight in any regression analyses. As an alternative, environmental variables were assigned to individual whale sightings and the number of whales per category for each environmental factor calculated and compared to numbers expected if they were distributed uniformly. For slope and depth "available" within the surveyed area, measurements were categorized into 0.2° and 2 m intervals, respectively. Since there was little of the surveyed area (and very few whales) beyond 30 m in depth or 3° in slope, categories beyond these measurements were pooled. For 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 in the environment was used to define the expected sighting frequency (total number of whales $\times$ surface area of variable class/surface area of whole study area). 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. If a significant difference was found, Chi-squared tests were subdivided (Zar 1984) by removing individual variable classes to determine which was causing most of the difference.

RESULTS

The longshore distribution patterns of unaccompanied whales (Fig. 3a) and cow-calf pairs (Fig. 3b) along the Cape coast were significantly different over both the

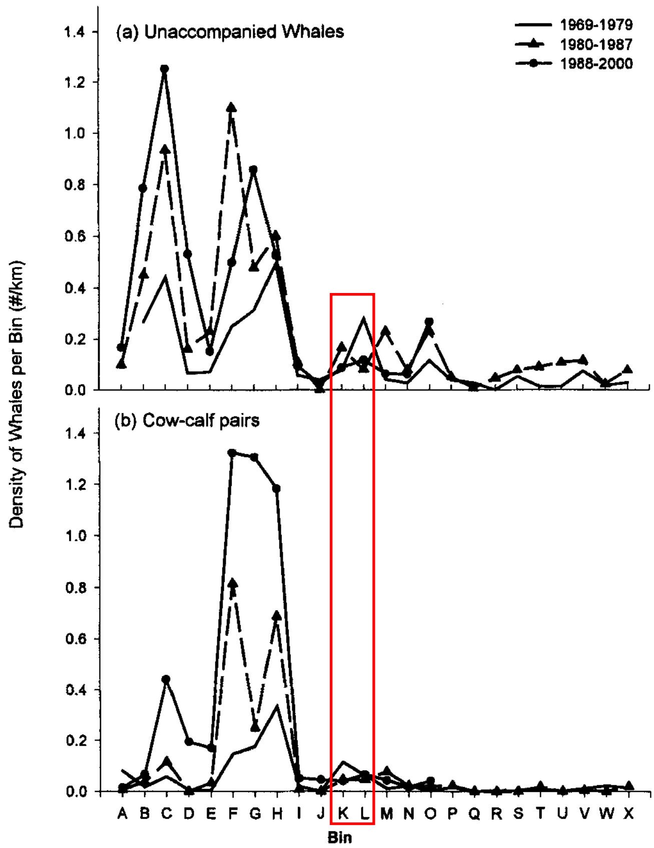

Figure 3. Mean density (whales sighted per kilometer of coastline) of unaccompanied whales (top) and cow-calf pairs (bottom) for the full surveyed length of coast. Densities for each time period shown separately.

19-yr ($\chi^2 = 328.1$, $P < 0.0001$, df = 47) and 32-yr ($\chi^2 = 842.5$. $P < 0.0001$, df = 29) data sets. In particular, the relative numbers of cow-calf pairs and unaccompanied whales west of Cape Agulhas (bin E) were very different.

The offshore distributions of cows with calves and unaccompanied whales differed significantly for depth ($U = 45425.0$, $P < 0.001$), slope ($U = 109088.5$, $P < 0.0001$) and distance from shore ($U = 95198.0$, $P < 0.001$). In all three years, cow-calf pairs were significantly closer to shore and in shallower water, but in only two years over significantly gentler slopes than unaccompanied whales (Table 1).

Shore type appeared to be closely related to adjacent bottom type as there was a significant variation in the depth (Fig. 4a) and distance from shore (Fig. 4b) at which whales were found off the three tested shore types (unaccompanied whales—distance from shore: $H = 13.81$, $P < 0.001$; depth: $H = 13.69$, $P < 0.0011$; cow-calf pairs—distance from shore: $H = 26.83$, $P < 0.0001$; depth: $H = 37.98$, $P < 0.0001$). Cow-calf pairs were found in shallowest waters off sandy beaches, but only significantly so relative to wave-cut rocky platforms, and were closer to shore off exposed rocky headlands than either sandy beaches or rocky platforms.

Table 1. Mean distance from shore, depth and slope values for cow-calf pairs and unaccompanied right whales from the helicopter surveys of 1997, 1999, and 2000.

Variable	Survey year	Cow-calves *n*	Cow-calves Mean	Cow-calves SE	Unaccompanied whales *n*	Unaccompanied whales Mean	Unaccompanied whales SE	*U*	*P*
Distance from shore (m)									
	1997	120	728.3	728.3	181	1094.6	742.9	14815.0	<0.0001
	1999	172	584.3	690.9	162	737.6	527.4	29436.0	0.012
	2000	164	621.3	404.0	237	899.2	635.9	28295.0	<0.0001
Depth (m)									
	1997	120	8.2	5.3	181	13.8	9.7	22010.5	<0.0001
	1999	172	6.9	5.4	162	11.5	6.47	20411.5	<0.0001
	2000	164	6.7	3.6	237	12.4	6.98	43340.0	<0.0001
Slope (degrees)									
	1997	120	0.67	0.66	181	0.68	0.389	16700.0	0.360
	1999	172	0.71	0.47	162	0.95	0.954	311100.	<0.0001
	2000	164	0.69	0.34	237	0.87	0.654	30127.0	0.025

Unaccompanied whales were found in deeper water and further offshore off exposed rocky headlands than either of the other two shore types.

When the observed distributions of whales taken from the GPS data were compared to the distributions that would be expected if the animals distributed uniformly with respect to levels of protection from swell, the positions of both unaccompanied whales and cow-calf pairs differed significantly from expected when tested individually or across the years (cow-calf summed for 3 yr: $\chi^2 = 726.4$, $P < 0.0001$, df = 2; unaccompanied whales summed for 3 yr: $\chi^2 = 259.7$, $P < 0.0001$, df = 2) (Fig. 5a). Subdivision of the these tests showed cow-calf pairs were found less often than expected in "exposed" areas than in partly protected ($\chi^2 = 254.1$, $P < 0.0001$, df = 1) or protected areas ($\chi^2 = 109.8$, $P < 0.0001$, df = 1). Unaccompanied whales were found more often than expected in "partly protected" areas than in exposed ($\chi^2 = 683.7$, $P < 0.0001$, df = 1) or "protected" areas ($\chi^2 = 146.1$, $P < 0.0001$, df = 1).

Similarly, both cow-calf pairs and unaccompanied whales were distributed significantly differently than expected for levels of protection from wind, whether tested by years or across all three years (cow-calves summed for three years: $\chi^2 = 96.58$, $P < 0.0001$, df = 2; unaccompanied whales summed for 3 yr: $\chi^2 = 126.52$, $P < 0.0001$, df = 2; Fig. 5b). Subdivision of these tests showed that cow-calf pairs were found more often than expected in "partly protected" areas than in "protected" ($\chi^2 = 41.9$, $P < 0.001$, df = 1) or "exposed" ($\chi^2 = 6.96$ $P = 0.008$, df = 1). Unaccompanied whales occurred more often than expected in "partly protected" areas that in "exposed" areas ($\chi^2 = 125.8$ $P = <0.001$, df = 1) or "protected" areas ($\chi^2 = 7.73$, $P = 0.005$, df = 1)

Both cow-calf pairs and unaccompanied whales were distributed at significantly different ratios than expected with respect to shore type, if tested singly or summed across all three years (cow-calf: $\chi^2 = 176.95$, $P < 0.0001$, df = 3; unaccompanied whales: $\chi^2 = 119.79$, $P < 0.0001$, df = 3; Fig. 5c). Subdivision of these tests showed that there was no longer a significant difference in cow-calf distribution if "exposed rocky headlands" was removed from the analysis ($\chi^2 = 3.715$, $P = 0.29$,

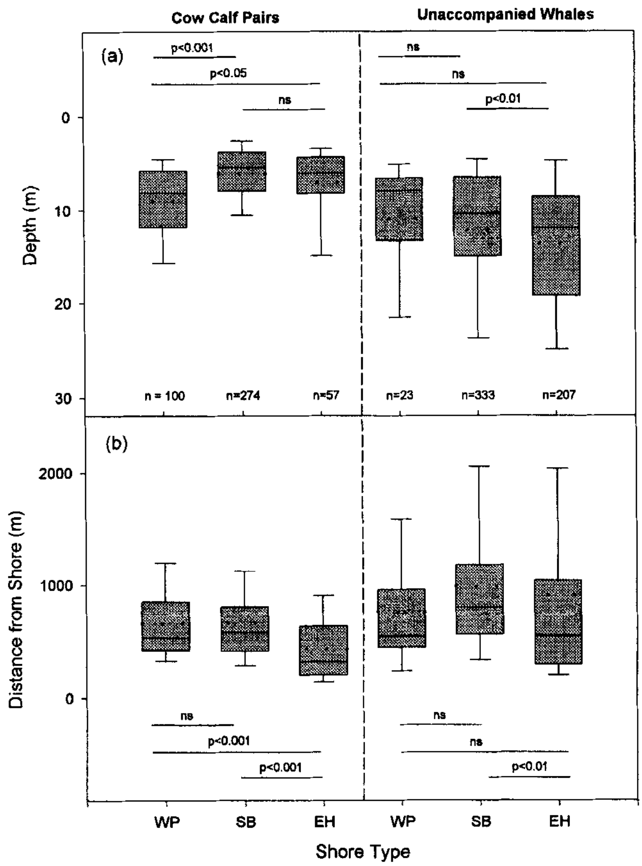

Figure 4. Depth (top) and distance from shore (bottom) of whales off the three main shore types (WP = Wave cut rocky platforms, SB = Sandy beaches, EH = Exposed rocky headlands). Cow-calf pairs shown on the left and unaccompanied whales on right. Graphs show 10th, 25th, 75th, and 90th Percentiles, with median (solid line) and mean (dashed line).

df = 2), indicating that it is primarily the low numbers of cow-calf pairs off this shore type influencing the over all results. Cow-calf pairs were found more often than expected off sandy beaches and less often than expected off wave cut rocky platforms and exposed rocky headlands, and were close to expected numbers off estuarine environments. Unaccompanied whales were found more often off sandy beaches and less often than expected off all other shore types, subdivision of the analysis did not clarify results any further.

When compared to a uniform depth distribution, both cow-calf pairs and unaccompanied whales occurred in significantly different proportions than expected (cow-calf: $\chi^2 = 952.6$, $P = <0.0001$, df = 17; unaccompanied whales: $\chi^2 = 352.7$, $P < 0.0001$, df = 17; Fig. 6a). Both cow-calves and unaccompanied whales were clustered toward the shallower waters of the surveyed area and fewer than expected were found in deeper water.

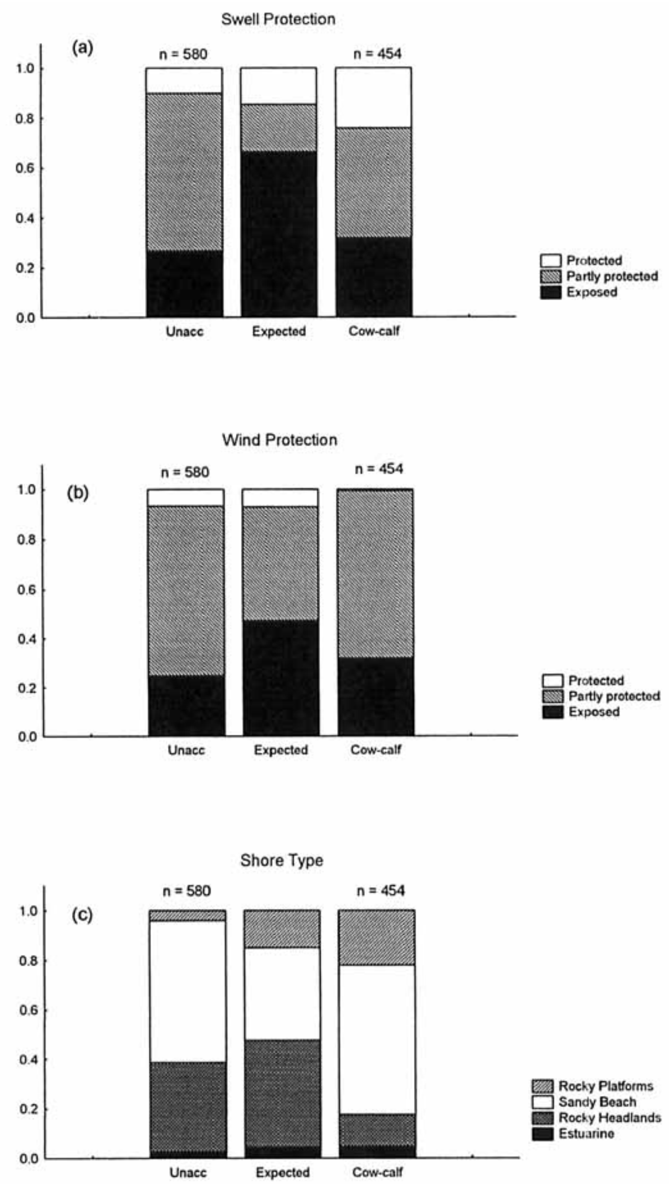

Figure 5. Proportion of unaccompanied whales (left) and cow-calf pairs (right) shown alongside expected proportions (middle) for (a) swell, (b) wind and (c) shore type. Data presented as proportions for ease of comparison.

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; Fig. 6b). The majority of both whale classes were found less often in the shallowest slope categories than expected.

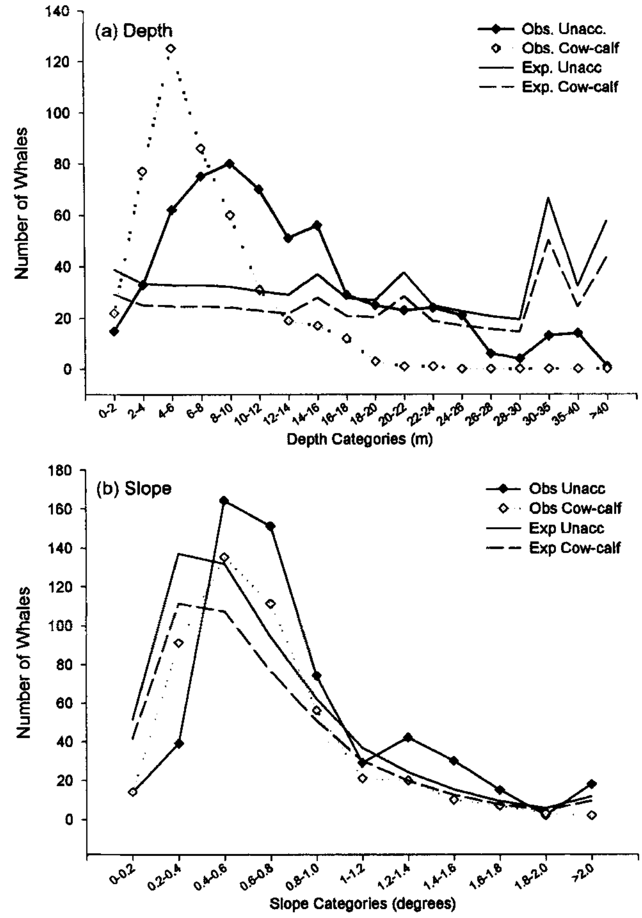

Figure 6. Distribution of all unaccompanied whales and cow-calf pairs across (a) depth and (b) slope categories for the full survey area. Observed numbers shown as well the distribution expected from a "uniform" distribution.

Discussion

In winter and spring right whale distribution patterns are non-uniform along the South Coast of South Africa and have shown the same general pattern for 32 yr 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 an area for unaccompanied whales. Although males, females, and juveniles visit the coast along with the near-term females, these "unaccompanied whales" have a different main congregation area (bin C, Walker Bay) to the "nursery area" of the cow-calf pairs (bins F–H, De Hoop and St Sebastian Bay), and although increasing numbers of both classes of whale are found in all regions of the coast, this differential distribution has been consistent over time. The apparent longshore segregation of cow-calf pairs from unaccompanied whales is supportive of previous work on both right whales (Best 1981, 1990; Payne 1986, Thomas 1987) and other species such as humpback whales (Smultea 1994) and gray whales (Swartz 1986). It is not clear in other studies if the whales distributed themselves based on abiotic environmental factors (*e.g.*, calmer waters or sandy substrate) or due to some behavioral or social benefit such as the dilution effect, increased predator detection (Connor 2000), but usually it is thought to be a combination of the two. Behavioral and social influences on distribution were not directly part of this study, although it is realized that they can have strong influences.

In this paper, longshore comparisons of distribution in relation to environmental factors have shown that right whales generally are found more often than would be expected in areas partly protected from wind and swell, off sandy beaches and in shallower waters. By contrast, they are found less often than expected in areas exposed to wind and swell, off exposed rocky headlands and in deeper water. In these comparisons, cow-calf pairs differed from unaccompanied adults primarily in their stronger avoidance of "exposed rocky headland" shore types.

A comparison of offshore distributions, however, showed that cow-calf pairs are found closer to shore, in shallower water and above gentler sloping sea floors than unaccompanied whales. 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 is the killer whale (which presumably hunts by aural cues), although they are currently rarely seen in South African nearshore waters. Thomas (1987) found cow-calf pairs in Golfo San Jose, Argentina to be clustered close to the shore in shallow water more often than expected from chance. He suggested this behavior could be due to increased 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 35 km/h in some parts of Golfo San Jose). Neonates may be particularly vulnerable to killer whale predation because of their small size and naïve behavior. The noise and turbidity of the surf zone have potential masking or camouflaging effects from these predators, thus providing an area of reduced threat in close proximity to shore. Proximity to shore has also been suggested as an effective defense against killer whale predation in bottlenose and dusky dolphins (Würsig and Würsig 1979), especially in conjunction with continuous longshore movement (Würsig and Würsig 1979).

Secondly, proximity to shore serves to segregate cow-calf pairs from the rest of the population (Thomas 1986), any member of which could potentially injure the calf or interrupt suckling behavior. Thirdly, the shallowness of the water probably deters males from mating attempts, since in this species intromission generally occurs with the female lying at the surface and the male swimming upside-down underneath her (Kraus and Hatch 2001). In water depths frequented by cow-calf pairs (mean 6.7–8.2 m), barely deeper than the adult whales, this maneuver 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 defense.

Although cow-calves were farthest from shore off sandy beaches (contrary to initial hypotheses), this most likely reflects the generally shallower slope of sandy beaches making a wider surf zone than off steeper rocky shores. The tendency for cow-calf pairs to be found shallowest off sandy shores compared to the other principal shore types in the region supports 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. Right whale cow-calf pairs on the Peninsula Valdés, Argentina, occupy resting areas described as wide, gently sloping beaches where cows could drift in and out with the tidal change, a distance of 0.25–1 km in the region, the lack of underwater obstructions was suggested to be the reason for the attractiveness of the area (Thomas 1987). Subsequently, this area has been abandoned probably due to a high incidence of gull harassment (Rowntree *et al.* 2001), a factor that does not play a significant role in South Africa.

Calm water, with low swell and wind stress (chop), is obviously of an energetic benefit to whales, especially for neonatal stage-one calves that are weak swimmers and struggle in rougher waters (Thomas and Taber 1984). Energetic savings *post-partum* can allow calves to invest more heavily in growth and permit a more efficient transfer of energy from cow blubber to calf mass. Because calves apparently need to attain a minimum size before leaving coastal waters (Best and Rüther 1992), faster growth would potentially allow for a quicker departure to polar waters where feeding can begin for the cow. Right whales in Argentina are thought to have changed their nursery ground after a large sedimentary bulge that created a calm eddy that whales preferentially occupied was destroyed in a powerful storm in 1975 (Rowntree *et al.* 2001). Similarly, the highest concentration of right whales in the Auckland Island wintering ground was in a small area on the northeast side of the main island (Patenaude and Baker 2001). The northeast side of the island is likely, due to frontal weather systems similar to those of the western Cape, to be the most sheltered side of that island. North Atlantic right whales also show a preference for calmer waters, the area (off Georgia and Florida, U.S.A.), which is largely occupied by cow-calf pairs during their wintering months, is described by Clapham[2] to have the lowest sea state anywhere in the North Atlantic.

The South African right whale population shares a preference for sheltered, shallow water often with a low-relief sedimentary substrate in its winter nursery areas with other right whale populations. The potential benefits of these factors can be broken down into two important areas, energetic savings for the calf and mother gained from calmer waters, and improved survival and injury reduction of calves (and to a lesser extent cows) from both calmer waters and the preference for sedimentary substrates. Their proximity to shore further helps both mother and calf avoid and hide from predators and to some extent segregate themselves from unaccompanied whales. Given the low threat of killer whales in at least South African waters, the differential distributions of cow-calves and unaccompanied whales that occur in South Africa, Argentina (Payne 1986) and possibly off Brazil (Groch 2000), must provide some other long-term (evolutionary) benefit. 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.

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