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ENVIRONMENTAL FACTORS INFLUENCING THE DISTRIBUTION OF SOUTHERN RIGHT WHALES (*EUBALAENA AUSTRALIS*) ON THE SOUTH COAST OF SOUTH AFRICA II: WITHIN BAY DISTRIBUTION

SIMON H. ELWEN[1]
PETER B. BEST
Mammal Research Institute, University of Pretoria,
Pretoria, 0002 South Africa
E-mail: elwen@iziko.org.za

ABSTRACT

Environmental factors are thought to strongly influence the distribution and predictability of the coastal distribution of southern right whales (*Eubalaena australis*) off South Africa. Preferred habitat had generally shallow sloping sedimentary floors and was characteristically protected from open ocean swell and prevalent seasonal winds. This study investigated whether habitat choices at smaller scales (within bays) were similar. Fine scale distribution patterns (GPS) from three years' surveys (1997, 1999, 2000) were analyzed separately within the three main concentration areas St Sebastian Bay, De Hoop, and Walker Bay (containing ~73% of cow-calf pairs and ~49% of unaccompanied adults in the whole survey region). Whale density at this scale of within particular bays did not correlate well with predicted variables, but Chi-squared analysis strongly supported results at broader scales, in all bays. *Post-hoc* "choice" tests between similar areas differing in only one variable revealed that cow-calves preferred (presumed) sandy substrates and especially protection from swell. The strength and predictability of preferences shown at fine scale (where individual movement and weather variability could have great influence) provide strong support for findings at larger scales and emphasize the importance of environmental factors in the habitat choice of wintering right whales.

Key words: environmental factors, *Eubalaena australis*, right whale, distribution, GIS, river mouths, South Africa.

Southern right whales (*E. australis*) were extremely depleted along the coasts of southern Africa due to whaling between about 1770 and 1940 (Best and Ross 1986). Although considerably fewer right whales are now found along the coasts of South Africa, their distribution is still predictable and markedly discontinuous

[1] Mailing address: Whale Unit, c/o South African Museum, P. O. Box 61, Cape Town, 8000, South Africa.

(Best 2000). In addition to maternal philopatry, environmental conditions appear to determine coastal distribution (Best 2000). Most right whales along the southern coast of South Africa today 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 (Elwen and Best 2004).

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 large scales (Jaquet and Whitehead 1996, Jaquet *et al.* 1996) and fine scales (Siegfried and Abrams 1977). Variations in the habitat of whales at meso scales (10s of km) can have important implications for their distribution and biology, especially in the breeding/calving grounds. Potential impacts such as boat-based whale-watching, fishing, vessel traffic and certain environmental changes can all occur at these scales, so understanding factors influencing finer scale whale distribution is important for predicting and interpreting impacts. For example, extensive changes in bottom topography following powerful storms are thought to underlie the abandonment of the Outer Coast nursery ground by right whales at Peninsula Valdés, Argentina (Rowntree *et al.* 2001). The abandonment of Laguna Guerrero Negro by gray whales in the late 1960s is thought to be due mainly to increased shipping and dredging activities in the lagoon (Gard 1974) and in San Ignacio Lagoon, Mexico, boat-based whale-watching vessels were banned from only the small section most frequently occupied by gray whales with calves (Jones and Swartz 1984).

Right whale distribution along the South African coast is mainly concentrated in two 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 study, we examined right whale distribution within these three bays for the three years for which GPS data were available, to ascertain whether the factors influencing large scale distribution are also important at a fine scale. We tested the same environmental factors used by Elwen and Best (2004) namely, protection from swell and wind, depth, slope of sea floor, and shore type. In addition, we tested for proximity to river mouths given the potential benefits of a) high sediment load resulting in a soft seabed, and b) possible thermal benefits of the warmer rivers, especially during molting (Watts *et al.* 1991). Finally, we compared adjacent areas differing in only one environmental variable, to better understand the influences of specific variables.

Methods

Since 1979, right whales have been counted and photographed each year, during early to mid October, by helicopter along the southern Cape coast (Fig. 1) between Muizenberg (18°30′E) and Natures Valley (Plettenberg Bay, 23°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). The timing of the surveys was planned for the period of peak calf abundance (Best 1990) and flown in conditions of relative calm (Beaufort 3 or less). The survey was flown in a predominantly east to west direction with each part of the coast being searched once, thus "effort" was equivalent within and between all three bays. Precise whale positions from GPS data were only available for the 1997, 1999, and 2000 surveys. Since environmental data used were either static or long-term averages, it was not

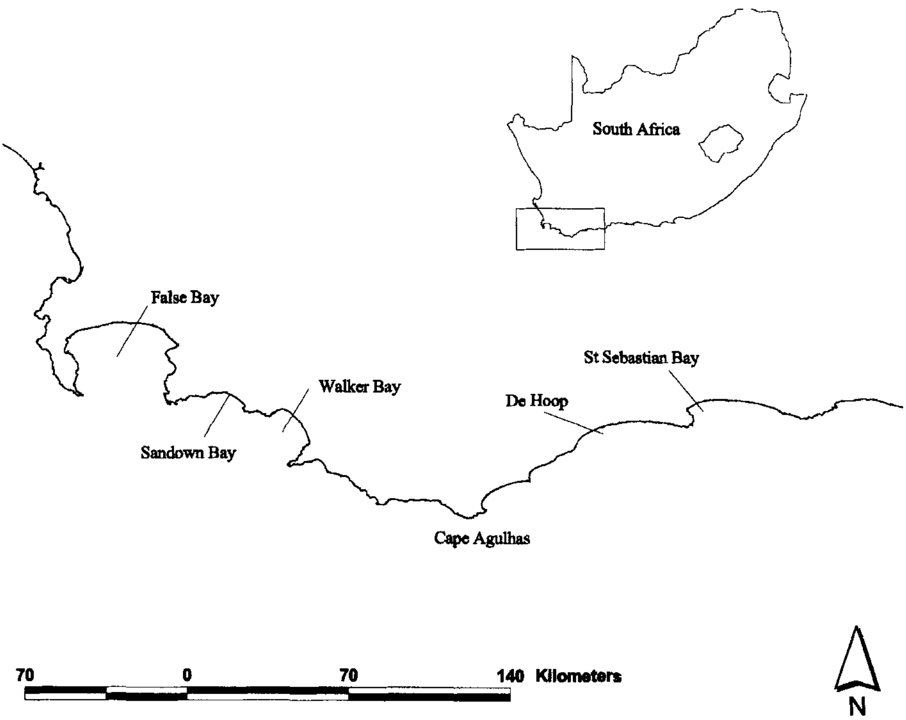

Figure 1. South-western coast of South Africa showing study area and place names referred to in text.

possible to test for variation between years and all three years of whale data were summed to increase sample sizes.

Environmental Data

To describe the variation in each environmental factor to which whales within the surveyed area were exposed, we defined the seaward extent of the surveyed area within each bay. Inspection of GPS positions of whales from the aerial surveys showed that all sightings were contained within 3,000 m of the coast, although most were substantially closer inshore. This was regarded as the extreme limit of the surveyed area from the coast and all analyses refer to data collected within this region. Data were processed using a GIS software package (Arcview 3.2, ESRI, Redlands, CA).

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. Depth and slope values for whale sightings, as well as average values for areas, were calculated from an artificial sea floor surface (TIN) created in the GIS using these data, following Elwen and Best (2004).

Good quality data on the substrate type of the sea floor were not available for all three bays, thus shore type (Jackson and Lipschitz 1984) was used instead since this has been shown to be a useful analogy (Elwen and Best 2004). Shore types used were estuarine, sandy beaches, wave-cut rocky platforms and exposed rocky headlands.

Daily measurements of swell and wind were not available for the three studied bays, thus long-term averages (September–November of 1997–1999) of these variables were used, following Elwen and Best (2004). Offshore data of the frequency of wind and swell strength and directions are collected by voluntary observer ships and held in the CSIR Marclim database. These data were used to represent the offshore swell and wind climate in the absence of any land. The most appropriate degree square of data was used for each bay to calculate the frequency of swell striking the beach at any point. Protection from offshore swell and wind was defined using a three-tier level of protection, as in Elwen and Best (2004). Any stretch of coast protected from less than 30% of wind or swell was defined as exposed, from 30% to 60% 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 5-m depth contour on the GIS system (as opposed to the 0-m contour used in Elwen and Best 2004), since marginally better sea floor data were available for the specific areas analyzed here. The use of the 5-m 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) that potentially provided substantially more protection than that estimated from land alone.

Description of Study Sites

All three bays studied here have certain broad characteristics in common; they are reasonably protected from open ocean swell and wind, and have generally sedimentary bottoms and shallow sea floor slopes (Elwen and Best 2004). However, each of these factors varies within and between bays (Fig. 2, 4, 6).

The majority of swell on the South African coast comes from a southwesterly direction, and the resulting erosion causes the typical "log-spiral" or "half-heart" shape of the bays east of Cape Agulhas including De Hoop and St Sebastian Bay (Bremner 1991). 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 (Walker Bay) than in the eastern section. Protection levels in Walker Bay are thus higher than might be expected considering it faces in the opposite direction to the other two study bays.

To test the effects that river mouths may have on whale distribution it was necessary to find a region of high whale density that included a river mouth and where all other factors were relatively constant. In St Sebastian Bay, into which the Breede and Duiwenhoks rivers flow (Fig. 2, 3) and De Hoop (into which the Potberg River no longer flows but ends in a brackish pan 2 km from the sea; Fig. 4, 5), other environmental factors in the bay are too variable to be able to discriminate river mouth effects. In Walker Bay however, the entire bay is classified as partly protected from swell and wind and the Klein River flows into the northern end of a long sandy beach (Fig. 6, 7). The river ends in a large lagoon and often does not reach the ocean, but is periodically bulldozed open by the local municipality. It was artificially opened 13 wk before the survey in 1997, about two weeks before the 1999 survey, but in 2000 the river was opened only after the survey was completed.

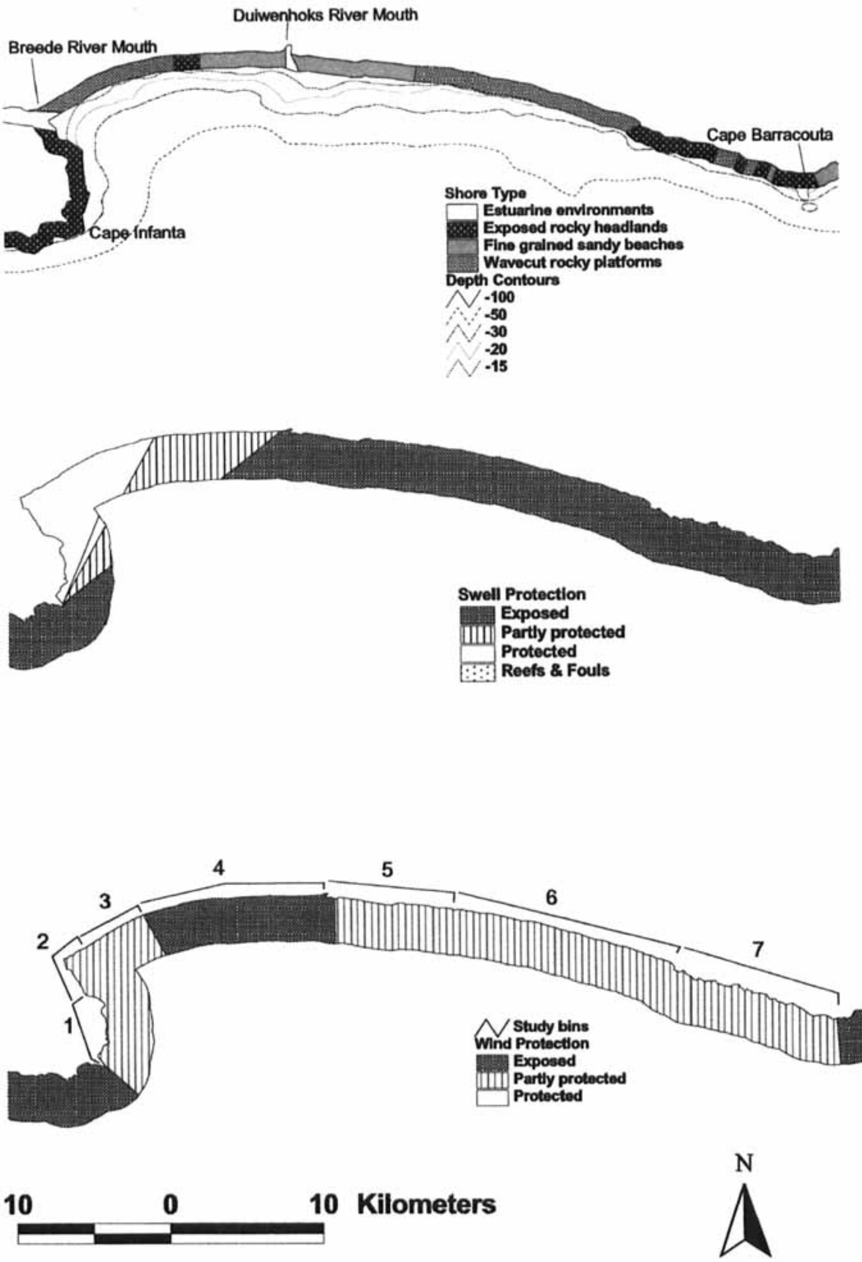

Figure 2. St Sebastian Bay showing environmental characteristics. Top: shore type and isobaths. Middle: Swell protection and reefs and fouls. Bottom: Wind protection and lines showing the subdivisions of the subareas used in analysis.

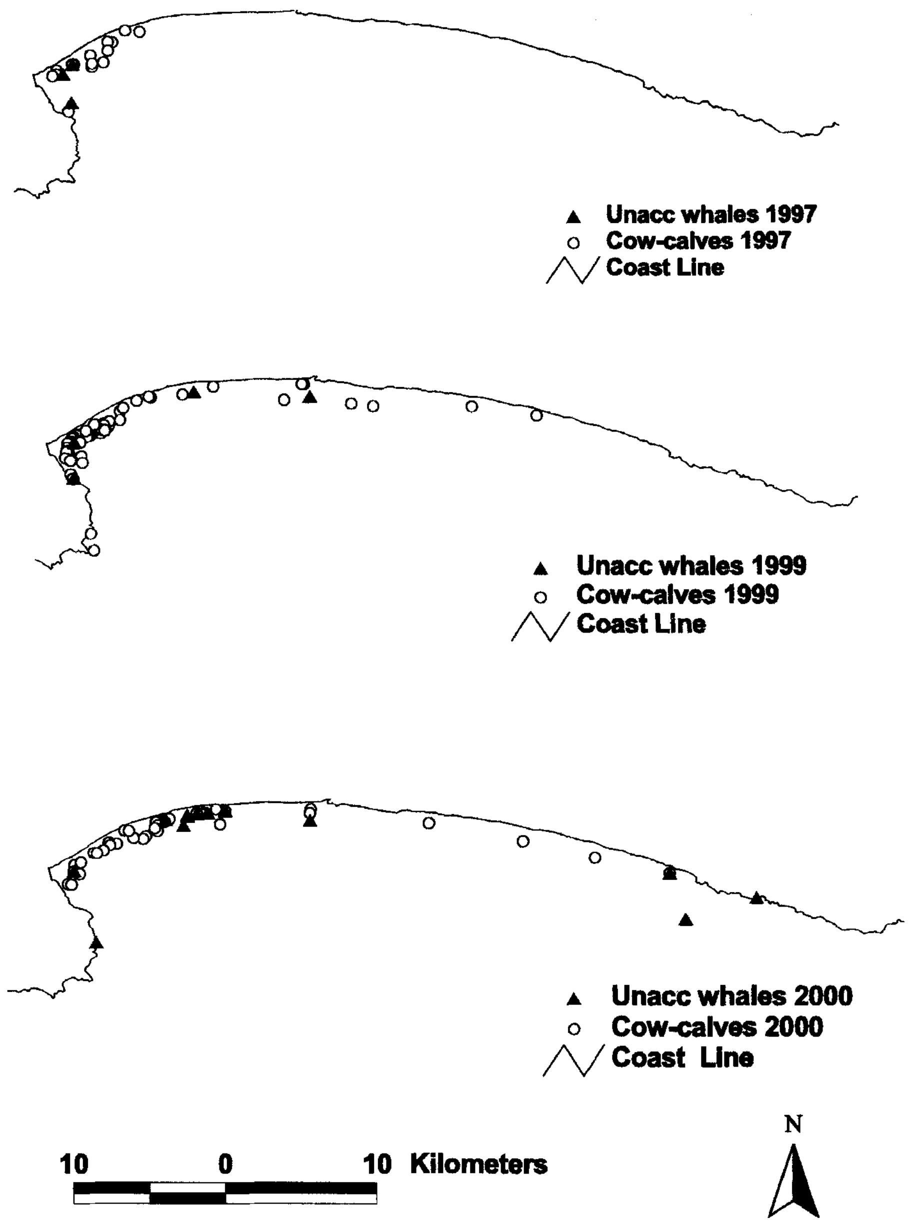

Figure 3. Distribution of right whales in St Sebastian Bay for each of the analyzed survey years.

Analyses

Each bay was subdivided into sub-areas that corresponded roughly to environmental factors, but primarily to shore type (St Sebastian Bay, $n = 7$; De Hoop, $n = 6$; Walker Bay, $n = 6$). The number of whales in each bay was correlated (Spearman Rank) against the environmental factors available for that bay (mean depth and slope

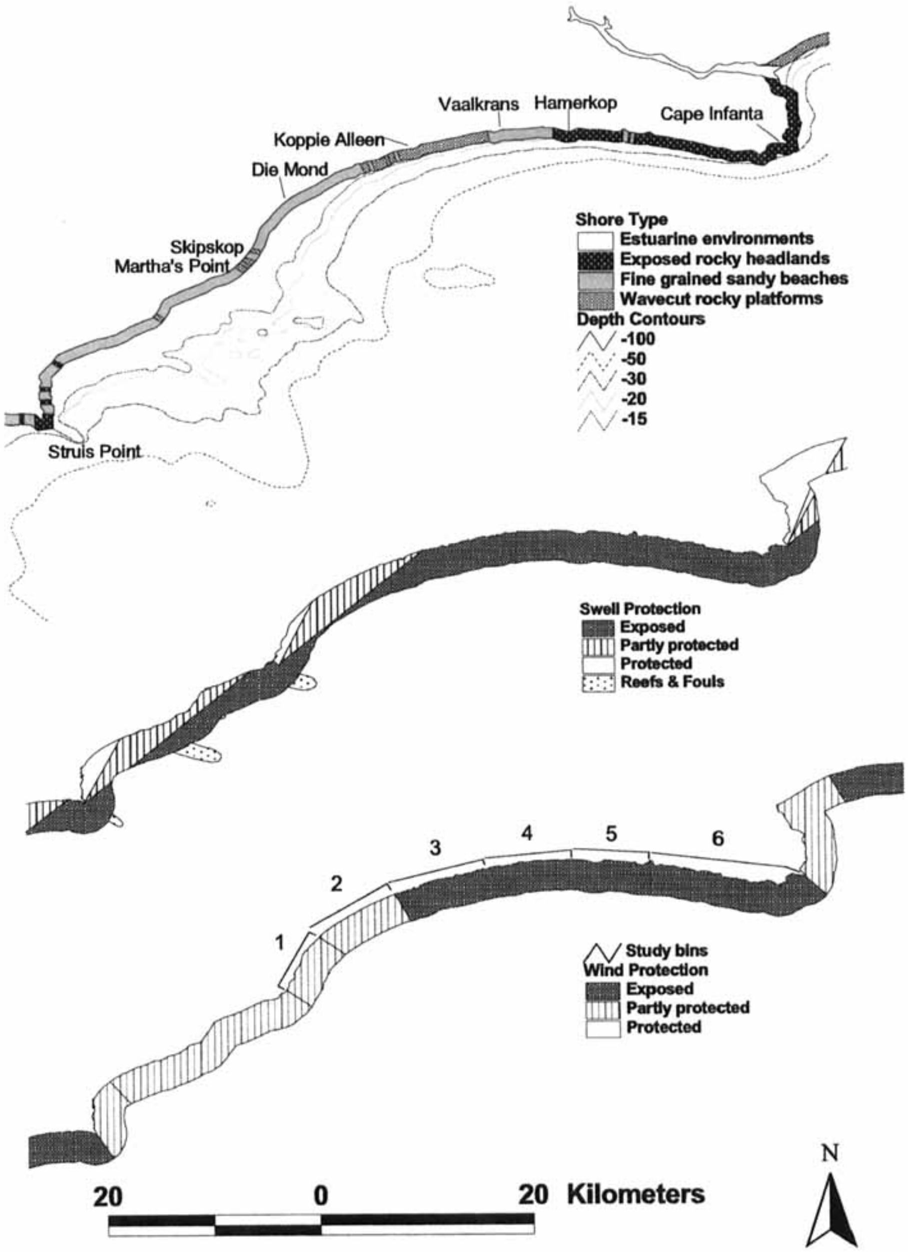

Figure 4. De Hoop and Marcus Bay regions showing environmental characteristics. Top: Shore type and isobaths. Middle: Swell protection and reefs and fouls. Bottom: Wind protection and lines showing the subdivisions of the subareas used in analysis.

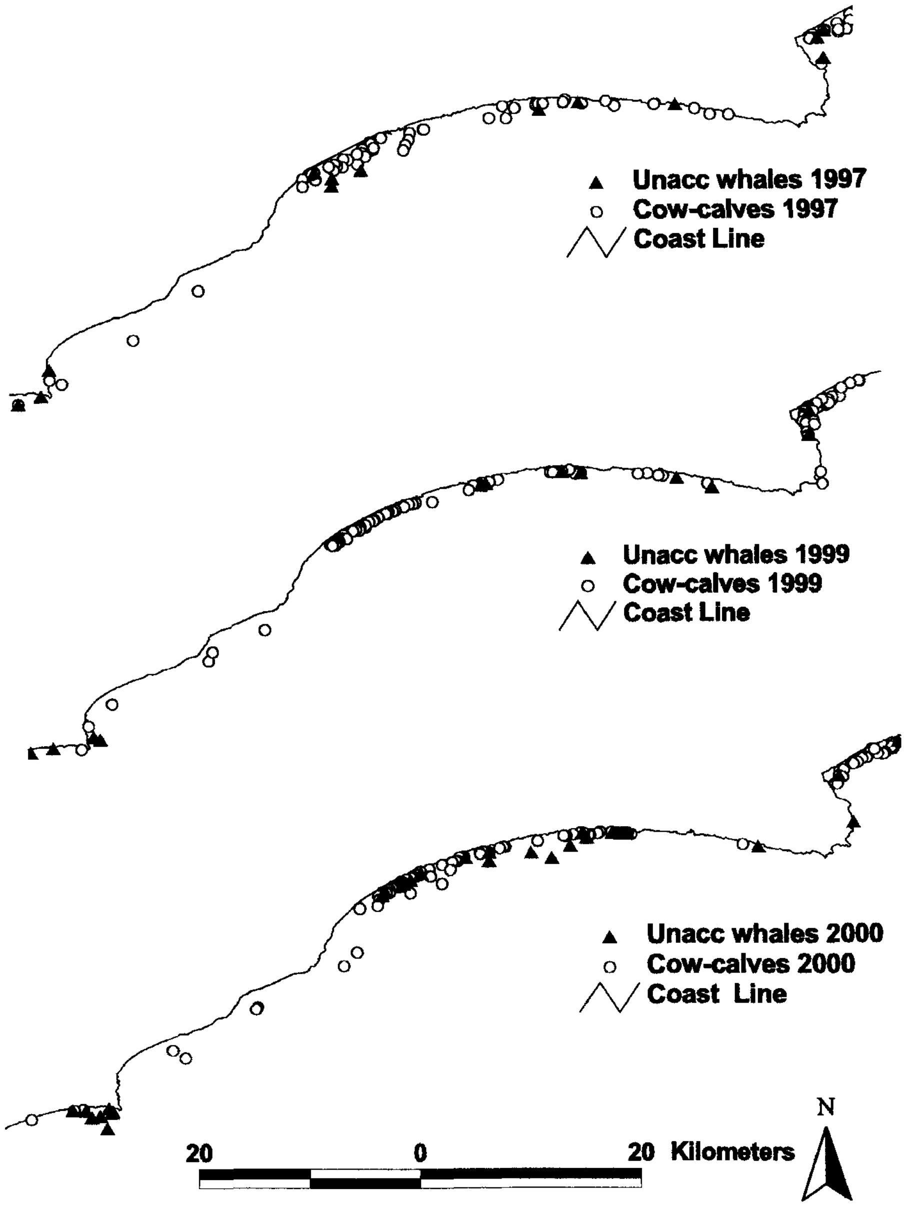

Figure 5. Distribution of right whales in the De Hoop and Marcus Bay regions for each of the analyzed survey years.

of each subarea, proportion of water exposed to swell and to wind and proportion of unattractive shore type).

A Chi-squared analysis was used to compare the numbers of whales at each level of each environmental factor within the bays to the proportion that would be expected from a uniform distribution across the whole area. Apart from De Hoop

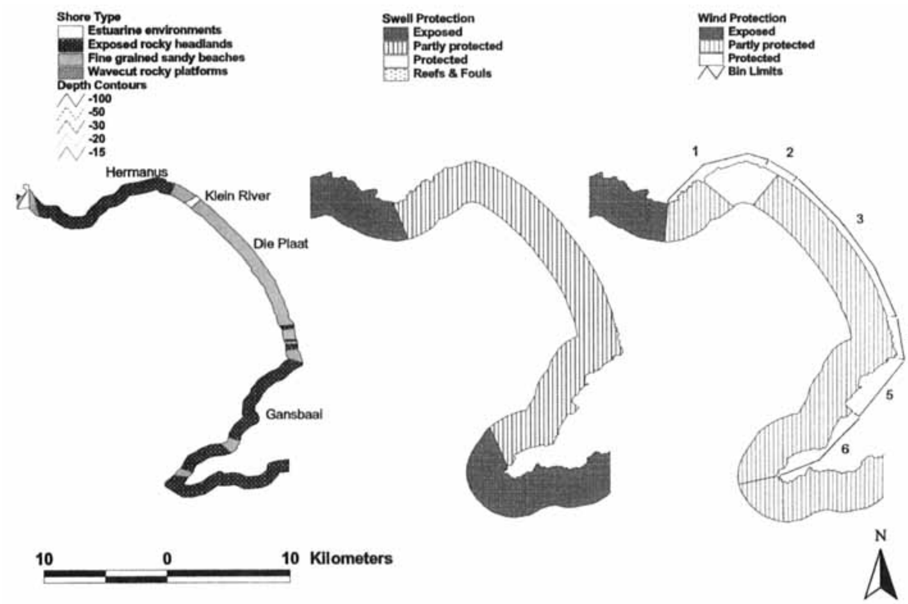

Figure 6. Walker Bay showing environmental characteristics. Left: Shore type and isobaths. Middle: Swell protection and reefs and fouls. Right: Wind protection and lines showing the subdivisions of the sub-areas used in analysis.

and St Sebastian Bay (where there were too few unaccompanied animals) analyses were performed for both cow-calf pairs and unaccompanied adults. In Walker Bay swell protection is virtually constant throughout the bay so distribution with respect to this factor was not tested. In situations where the assumptions of a Chi-squared test were violated due to small sample sizes, log-likelihood tests were used as suggested by Zar (1984).

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 categorizing them into 2-m and 0.2°-intervals respectively and establishing the distribution pattern of the categories within each of the bays. Due to low sample sizes, the categories were sometimes summed to allow for valid Chi-squared testing (Zar 1984).

Although it is not possible to perform well-controlled, classical "two-choice" behavioral tests on free swimming right whales, whale numbers can be compared between two adjacent areas differing in only one factor, thereby mimicking a two-choice situation. Such data were analyzed using the Chi-squared comparison between observed whale numbers in each area and expected frequencies assuming no difference between areas.

The influence of swell protection on cow-calf distribution was tested where two sandy beaches in De Hoop have differing levels of exposure to swell, but an otherwise reasonably uniform environment. Relative preferences for the three main shore types were tested 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 levels of wind and swell protection. In both comparisons, the expected

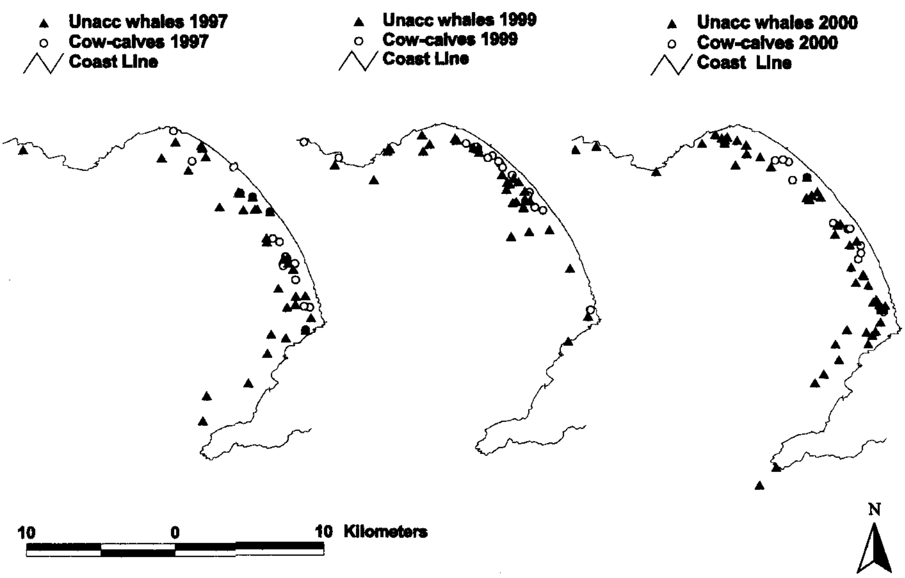

Figure 7. Distribution of right whales in Walker Bay for each of the analyzed survey years.

number of whales in each sub-area was adjusted for the size of the sub-area, using the relative length of the particular segment of coastline.

The relative use of river mouths by whales was tested within a part of Walker Bay where all environmental factors were relatively constant except for the presence of the Klein River mouth (Fig. 6, 7). The beach area of the bay was divided into six 3-km segments, all of which had predominantly (71%–100%) sandy shores with a similar gentle slope (0.5–0.6°). Both unaccompanied whales and cow-calf pair numbers within each 3-km segment were compared to an expected "uniform" distribution. Because the Klein River mouth was not open to the sea during the 2000 survey, analysis was performed on the data both with and without the 2000 data since one of the presumed benefits of river mouths (sedimentary sea floor due to alluvial deposition) still occurred even with the river mouth closed.

Results

St Sebastian Bay

Cow-calf pairs in St Sebastian Bay were predominantly clustered at the head of the bay, in the lee of the headland (Fig. 2, 3). In 1997, all whales in the bay used the "protected" corner of the bay. In 1999 and 2000, whales were more dispersed with some (1999, $n = 5$; 2000, $n = 3$) clustered around the Duiwenhoks River mouth, but most whales were at the head of the bay (1997: 100%; 1999: >80%, 2000: >70%).

Numbers of both cow-calf pairs and unaccompanied whales were significantly correlated with the proportion of protection from swell in each subarea, but there was no relationship with any of the other tested factors (Table 1).

Table 1. Spearman-Rank correlations (R_s) between environmental factors and the distribution of right whales in subareas of St Sebastian Bay.

	Unaccompanied		Cow-calves	
	R_s	P	R_s	P
Slope	0.14	0.72	−0.36	0.39
Depth	−0.09	0.78	−0.54	0.18
Shore type	0.71	0.055	0.47	0.26
Wind exposure	0.00	0.97	0.00	0.97
Swell exposure	−0.87	0.006	−0.95	<0.0001

Because of inadequate sample size, Chi-squared analysis could not be performed on unaccompanied whales. Cow-calf distribution was more strongly clustered in the swell protected water than expected ($\chi^2 = 278.03$, df $= 2$, $P < 0.0001$) (Fig. 8a), but was no different from the expected pattern with respect to protection from wind ($\chi^2 = 0.92$, df $= 2$, $P = 0.17$) (Fig. 8a). Most animals were clustered in the partly wind-protected region 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 pairs occurred more frequently off the "estuarine environments" and "wave-cut rocky platforms" at the head of the bay than expected, and less frequently off sandy beaches (middle section of bay) and "exposed rocky headlands" (Infanta headland and the foot of the bay) ($\chi^2 = 61.86$, df $= 3$, $P < 0.0001$) (Fig. 8a). Cow-calf pairs were also found more often than expected in the shallower waters within the observed portions of the bay (depth intervals were summed to 4 m due to small sample size) ($\chi^2 = 316.59$, df $=$ 8, $P < 0.0001$). This is largely a result of their proximity to shore (see Elwen and Best 2004). The distribution of cow-calf pairs relative to the slope of the sea floor was significantly different from the expected distribution ($\chi^2 = 29.02$, df $= 6$, $P <$ 0.0001; slope categories larger than 1.2° summed due to small sample size), with animals apparently avoiding the areas with very gentle slopes.

De Hoop

Certain patterns of distribution were obvious and consistent within the De Hoop region for the three surveyed years (Fig. 4, 5). Few whales used the northerly stretch of coast at the western edge of the analyzed region. At the De Hoop vlei (Die Mond), whale density increased to the highest observed along the coast. At the end of the dune field/beginning of the wave-cut rocky platform area (near Koppie Alleen), whale density began to decrease but remained fairly high as far east as Vaalkrans. For the ~5 km between Vaalkrans and Hamerkop, the area with a sandy beach, whales maintained a regularly higher density. Once east of Hamerkop, in the exposed rocky shore of the Infanta headland, whale density dropped off rapidly.

In the western-most sub-area the water is extremely shallow: the 15-m isobath is 3.7 km offshore, farther than in any other part of the coastline used in this analysis. It is possible that this shallowness forced whales farther offshore (as suggested by the only two sightings in the sub-area, which were near the 3-km limit). It is also adjacent to the extensive Martha's Reef, and the sea floor may be more rocky than

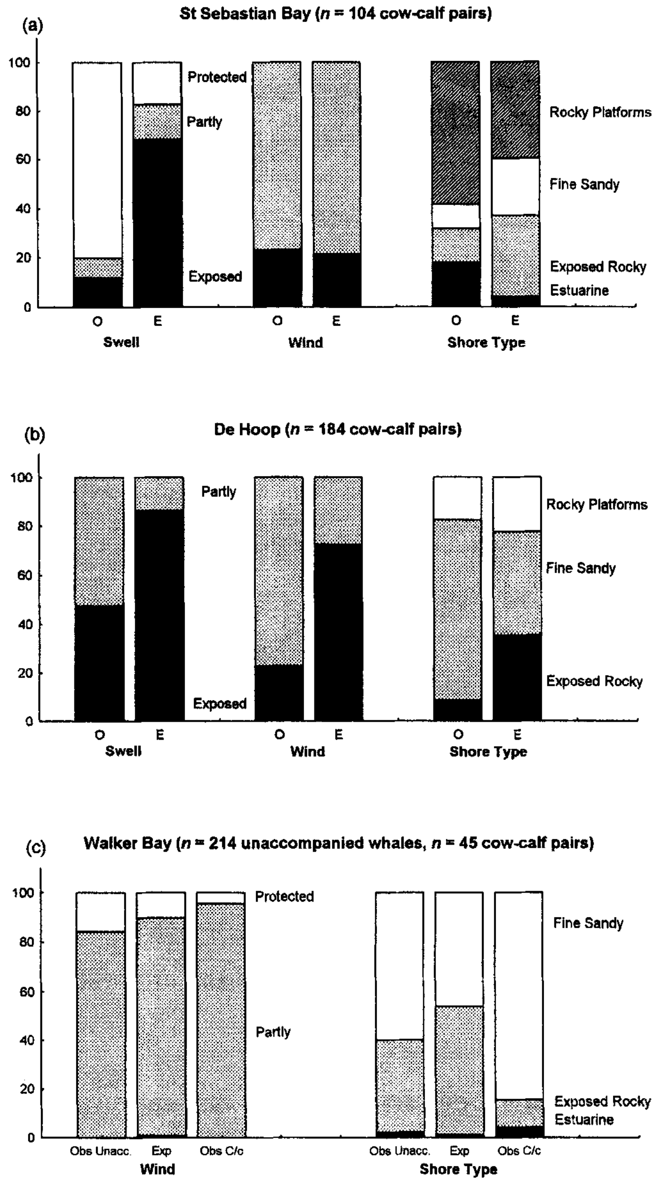

Figure 8. Comparison of observed (O) and expected (E) distributions of whales with respect to swell and wind protection and shore type, for cow-calf pairs (St Sebastian Bay, De Hoop, and Walker Bay) and for unaccompanied whales (Walker Bay only).

the adjacent shore type suggests. For these reasons the western most sub-area was omitted from the correlation analysis.

The pattern of unaccompanied adult distribution was not significantly correlated with any of the environmental factors (Table 2). Although cow-calf numbers tended to be greater in the sub-areas with gentler slopes and shallower sea floors and with

Table 2. Spearman-Rank correlations (R_s) between environmental factors and the distribution of right whales in subareas of the De Hoop region.

	Unaccompanied		Cow-calves	
	R_s	P	R_s	P
Slope	−0.70	0.233	−0.90	0.08
Depth	−0.70	0.233	−0.90	0.08
Swell exposure	−0.34	0.516	−0.89	0.08
Wind exposure	−0.11	0.783	−0.22	0.68
Shore type	−0.60	0.35	−0.70	0.23

a higher proportion of protection from swell, these correlations were not significant at the 5% level. There was no significant increase in whale numbers in the subareas with more attractive shores or greater protection from wind.

Significantly more cow-calf pairs were found in shallower water ($\chi^2 = 44.37$, df = 7, $P < 0.0001$) and in areas of gentler slope ($\chi^2 = 34.69$, df = 7, $P < 0.0001$) than expected (see Fig. 8b). There was also a clear tendency for most cow-calf pairs to be found in the more swell-protected western end of the bay than expected ($\chi^2 = 134.91$, df = 2, $P < 0.0001$), but not in areas with greater protection from wind only ($\chi^2 = 128.15$, df = 1, $P = 0.17$). Significantly more cow-calf pairs were found off sandy beaches and fewer off rocky shores than expected from a uniform distribution ($\chi^2 = 81.97$, df = 3, $P < 0.0001$) (Fig. 8b).

Walker Bay

Right whales in Walker Bay were at higher densities along the central sandy beaches (Die Plaat), tapering off gradually towards the headlands on either side of the bay (Fig. 6, 7). The distribution was similar between years, with cow-calf pairs being found predominantly off the sandy beaches of Die Plaat, while unaccompanied whales appeared to have a more scattered distribution within the bay.

Both cow-calf and unaccompanied whale numbers showed no significant correlations with any tested factor (although that for cow-calf pairs with shore-type was almost significant) (Table 3).

More cow-calf pairs were found off the sandy beach and estuarine environments and less off the exposed rocky headlands than expected from a uniform distribution ($G = 35.20$, df = 2, $P < 0.001$) (Fig. 8c). Although unaccompanied whales distributed more closely to the expected uniform pattern than cow-calf pairs, they still occurred significantly more often off sandy beaches and less often off rocky shores than expected ($G = 19.08$, df = 2, $P < 0.001$) (Fig. 8c).

Both unaccompanied whales ($\chi^2 = 80.81$, df = 5, $P < 0.0001$) and cow-calf pairs ($\chi^2 = 167.24$, df = 17, $P < 0.0001$) showed a significant preference for the shallower waters within the bay (categories summed into 6-m intervals to satisfy Chi-squared demands). Similarly, both unaccompanied whales ($\chi^2 = 49.83$, df = 8, $P < 0.0001$) and cow-calf pairs ($\chi^2 = 34.36$, df = 3, $P < 0.0001$) showed a significantly different distribution from expected for "slope" (categories $>1.4°$ summed in both tests to satisfy Chi-squared demands) and appeared to be clustered toward the medium rather than the extreme slopes (gentle and steep) within the bay. Distribution of cow-calf pairs with respect to wind protection did not differ

Table 3. Spearman-Rank correlations (R_s) between environmental factors and the distribution of right whales in subareas of Walker Bay.

	Unaccompanied		Cow-calves	
	R_s	P	R_s	P
Slope	−0.31	0.56	−0.66	0.14
Depth	−0.14	0.80	−0.58	0.24
Shore type	0.058	0.92	−0.82	0.058

from the expected uniform pattern ($G = 2.09$, df = 1, $P > 0.05$) (Fig. 8c), while unaccompanied whales were found more often in the partly protected area and less often in the protected areas of the bay than expected ($G = 6.22$, df = 1, $0.025 > P > 0.01$) (Fig. 8c).

Direct Comparisons under "Controlled" Conditions

Protected sedimentary bottom versus exposed sedimentary bottom—Both the lower section (sub-area 2) and the middle section (sub-area 4) of De Hoop have sandy beaches and are presumed to have a nearshore sedimentary substrate (Fig. 4). Sub-area 2 is 7.1 km long (slope: 0.36° ± 0.12°SE), 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 5.2 km long (slope: 0.74° ± 0.24°SE), but is entirely exposed to swell and wind and only contained 27 cow-calf pairs during the survey years. Assuming a uniform distribution, sub-area 2 would have contained (7.1/12.3 km × 127 whales) 73.3 cow-calf pairs and sub-area 4, 53.6 pairs. The observed numbers are significantly different ($\chi^2 = 22.9$, df = 1, $P < 0.001$) indicating that cow-calf pairs preferred a protected to exposed sedimentary substrate. Unaccompanied whales have a different pattern and less ($n = 13$) were found in sub-area 2 than sub-area 4 ($n = 16$), but (after adjusting for sub-area size) not significantly different from a uniform distribution ($\chi^2 = 1.93$, df = 1, $P = 0.16$). This suggests that the requirements for partly sheltered conditions over a sedimentary substrate is less for unaccompanied whales.

Rocky headland vs. wave-cut platforms vs. sandy beach in an exposed environment—We used the De Hoop region to compare the relative use 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 (0.61°, 0.74°, and 0.93°; 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 5.2-km fine sandy beach, to the west of which there is a 7.0 km area of wave-cut platforms and to the east a 5.3-km area of exposed rocky headlands.

Assuming a uniform distribution the numbers of cow-calf pairs expected off the sandy beach, wave-cut rocky platforms and exposed rocky headlands would have been (5.2/17.5 km × 56 whales) 16.6, 22.4, and 17.0, respectively. The observed numbers ($n = 27$, $n = 18$ and $n = 11$ respectively) are significantly different ($\chi^2 = 9.50$, df = 2, $P < 0.01$). By subdivision (Zar 1984), we can conclude that the numbers off the two rocky shore types are not different from expected ($\chi^2 = 0.32$, df = 1, $P = 0.57$), so that the rejection of the initial null hypothesis must be due to the higher than expected number of cow-calf pairs off sandy beaches.

The apparent preference of whales for sandy-bottomed areas is further supported by the distribution patterns in the two adjacent areas of Marcus Bay (Struis Point to Martha's Point; ~12 km) and the lower De Hoop areas (Martha's Point to Koppie Alleen; ~14 km), both of which are protected from wind and swell (Fig. 4). While the lower De Hoop area is shallow sloped with a very sandy bottom, Marcus Bay is dominated by a number of reefs (including Saxon, Miles Barton, and Atlas reefs). Right whales in this region are strongly biased toward the De Hoop side ($n = 102$, summed for three years), compared to only eight in Marcus Bay.

Effects of river mouths—We used the Walker Bay region only for this analysis as explained above. Both unaccompanied whales and cow-calf pairs were found more often off the northern half of the sandy beach area (closer to the river) and less often off the southern half of the beach ($\chi^2 = 8.13$ and 5.23, df = 1, $P = 0.004$ and 0.022, respectively). On a finer areal subdivision (into six 3-km segments), the lowest numbers of unaccompanied whales occurred in the 3-km segment overlaying the river mouth itself ($n = 12$), while the highest numbers ($n = 38$) occurred in the adjacent 3-km segment (Fig. 9); distribution among the segments was not uniform ($\chi^2 = 26.86$, df = 5, $P < 0.001$). Cow-calf pair distribution did not differ from uniformity ($\chi^2 = 10.45$, df = 5, $P = 0.06$), although numbers were small (Fig. 9). This pattern was largely influenced by the 1999 survey year when most whales of both classes were clustered toward the northern side of the bay. Because 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 non-uniform distribution with more on the river side of the beach area ($\chi^2 = 28.5$, df = 5, $P < 0.001$), but cow-calf pairs showed no variation along the beach ($G = 7.5$, df = 5, $P > 0.05$; log-likelihood test due to small sample sizes).

Discussion

The three bays were chosen because together they contained 73% of the cow-calf pairs and 49% of the unaccompanied whales within the entire survey area, and represented the largest congregations of whales along the South African coast. All three bays have characteristics in common: they provide a fair degree of protection from swell and wind and they contain sandy or sedimentary bottoms and gentle slopes. These are all characteristics that on a wider geographical scale were predicted to be "attractive" to whales, especially cow-calf pairs (Elwen and Best 2004), but it was not clear whether such criteria would apply on a finer scale.

The correlation analyses were generally unsuccessful in detecting significant relationships with environmental variables within bays, apart from swell protection for both classes of whale in St Sebastian Bay. This failure may be the result of (1) the small number of data points (6–7) and (2) the choice of bins, which were based mainly on shore type and may not have provided the optimum contrast for all of the environmental variables.

The Chi-squared tests based on a null-hypothesis of a uniform distribution within the bays were more successful. Cow-calf pairs were found more often than expected off sandy beaches and/or wave-cut rocky platforms within all three bays. They were also found more often than expected in shallower waters and gentler slopes in all three bays, although in St Sebastian Bay and Walker Bay they also

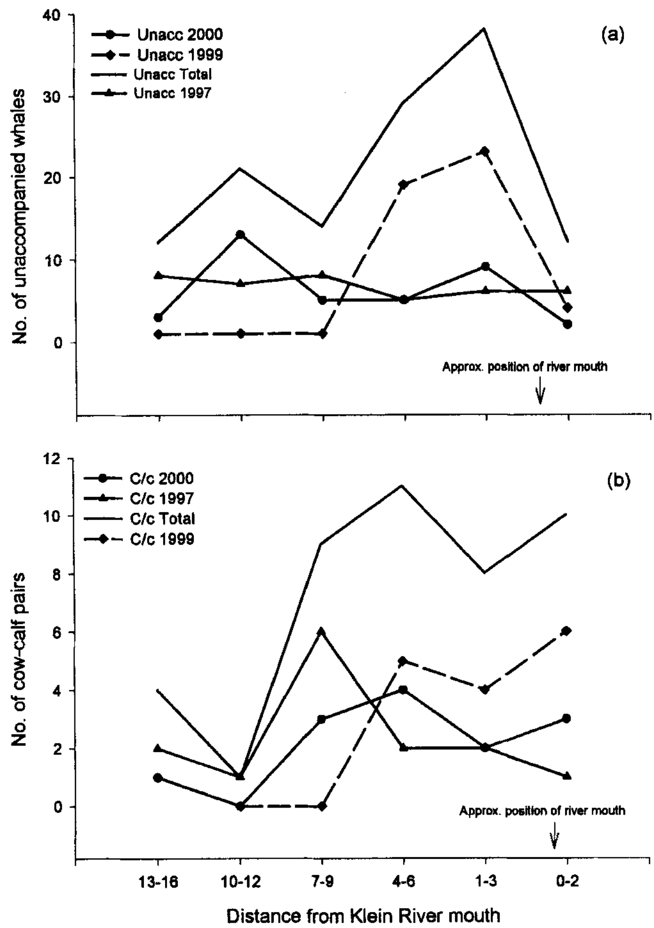

Figure 9. Distribution of unaccompanied whales (a) and cow-calf pairs (b) per 3-km segment of sandy shore in Walker Bay, relative to the Klein River mouth.

avoided the very gentlest sloping sea floors. In the two areas with some contrast in swell protection (St Sebastian Bay and De Hoop), cow-calf pairs were encountered more often than expected in swell-protected areas. Unaccompanied whales showed similar "preferences" for sandy beaches and shallower areas (avoiding very gentle and very steep slopes) as cow-calf pairs, but differed in being found more often than expected in areas partly protected from wind (these results refer to Walker Bay only).

The influences of slope on whale distribution are difficult to interpret. In De Hoop whales clustered above the gentle slopes, in Walker Bay above medium slopes, and on medium to 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, depth 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, and 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 avoidance of the very gentlest slopes (which are normally found closest to shore), however, may be a direct recognition of a physical hazard. In this connection, the very shallow and gently shelving area in subarea 1 off De Hoop may be perceived as a "trap," in which it is relatively easy (especially for neonates) to become disoriented and trapped by a falling tide.

The influence of the river mouth on whale distribution in Walker Bay is not clear, perhaps because it was not in a similar state of flow between years, but there seems to be some degree of attraction to an estuarine environment shown in both Walker and St Sebastian bays. The benefits of river mouths for right whales are unknown but could potentially include assisted exfoliation of skin as has been observed in beluga whales (*Delphinapterus leucas*) (Watts *et al.* 1991) or loss of external parasites. It is more likely that the principal benefit of river mouths for right whales is the nature of the substrate in the vicinity due to the fluvial transport and subsequent deposition of sediment. This is supported by the distribution of whales both during the 2000 survey in Walker Bay (when the river mouth was closed) and in all three years off De Hoop, where the river mouth has not been open for at least a century.

Cow-calf pairs in fact chose sandy beaches rather than rockier shores even when there was no apparent benefit from swell protection. As proposed by Elwen and Best (2004), a sedimentary substrate may provide some protection for the calf from both injury (avoidance of obstacles) and predation (acoustic damping).

Although long term and wide scale distributions are not likely to be affected by short-term weather changes, 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 in those areas, since whales could easily move from one part of the bay to another. This is not as likely to apply to depth, substrate type or distance from shore, as these factors are less likely to be related 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. This preference is shown even when the substrate is presumed to be sedimentary in both protected and exposed areas of the bay.

The preferential occupation of at least partly protected areas even under apparently calm (survey) conditions is interesting. 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 possible that there was still an active benefit to be gained from the swell-protected 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. This conclusion has some support in the failure to detect a significant departure from the presumed uniform distribution in relation to wind protection shown by cow-calf pairs in all three bays.

Evidence of whale preference for calm water is not exclusive to South Africa. The majority of right whales off Argentina occupy the Peninsula Valdés area (Payne 1986), which is dominated by two large gulfs that presumably provide some degree of protection from open ocean wind and swell. Rowntree *et al* (2001) show whale numbers (mostly cow-calf pairs) to peak sharply in one part of their distribution within Golfo Nuevo, Argentina (almost twice the density of anywhere else in the study site). This particular 5-km 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, 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 hypothesized "preferred" activity) close to shore off shallow sloping sandy beaches in preference to cliff areas or areas exposed to strong currents.

An apparent preference for calmer waters has been observed in southern right whales off the Auckland Islands (Patenaude and Baker 2001) as well as in humpback whales off Hawaii (Whitehead and Moore 1982, Smultea 1994) and gray whales off Mexico (Swartz 1986). 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 and Taber 1984). 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 (Whitehead and Moore 1982, Corkeron and Connor 1999, Clapham 2001).

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Literature Cited

Best, P. B. 1990. Trends in the inshore right whale population off South Africa, 1969–1987. Marine Mammal Science 6:93–108.

Best, P. B. 2000. Coastal distribution, movements and site fidelity of right whales *Eubalaena australis* off South Africa, 1969–1998. South African Journal of Marine Science 22: 43–55.

Best, P. B., and G. J. B. Ross. 1986. Catches of right whales from shore-based establishments in southern Africa, 1792–1975. Report of the International Whaling Commission (Special Issue 10):275–289.

Bremner, J. M. 1991. Logarithmic spiral beaches with emphasis on Algoa Bay. Pages 147–164 in J. M. Bremner, A. Du Plessis, J. G. K. Glass and R. W. Day, eds. Algoa

Bay—marine geoscientific investigations, eds. Bulletin of the Geological Survey South Africa 100.

CLAPHAM, P. J. 2001. Why do baleen whales migrate? A response to Corkeron and Connor. Marine Mammal Science 17:432–436.

CORKERON, P. J., AND R. C. CONNOR. 1999. Why do baleen whales migrate? Marine Mammal Science 15:1228–1245.

ELWEN, S. H., AND P. B. BEST. 2004. Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the south coast of South Africa I: Broad scale patterns. Marine Mammal Science 20:567–582.

GARD, R. 1974. Aerial census of gray whales in Baja California lagoons, 1970 and 1973, with notes of behavior, mortality and conservation. California Fish and Game 60:132–144.

JACKSON L. F., AND S. LIPSCHITZ. 1984. Coastal sensitivity atlas of southern Africa 1984. Department of Transport, Pretoria, South Africa.

JAQUET, N., AND H. WHITEHEAD. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135:1–9.

JAQUET, N., H. WHITEHEAD AND M. LEWIS. 1996. Coherence between 19th century sperm whale distribution and satellite-derived pigments in the tropical Pacific. Marine Ecology Progress Series 145:1–10.

JONES, M. L., AND S. L. SWARTZ. 1984. Demography and Phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. Pages 375–387 *in* M. L. Jones, S. L. Swartz and S. Leatherwood, eds. The gray whale *Eschrictius robustus*. Academic Press, Orlando, FL.

PATENAUDE, N. J., AND C. S. BAKER. 2001. Population status and habitat use of southern right whales in the sub-Antarctic Auckland Islands of New Zealand. Journal of Cetacean Research and Management (Special Issue 2):111–116.

PAYNE, R. 1986. Long term behavioral studies of the southern right whale (*Eubalaena australis*). Report of the International Whaling Commission. (Special Issue 10): 161–167.

ROWNTREE, V. J., R. S. PAYNE AND D. M. SCHELL. 2001. Changing patterns of habitat use by southern right whales (*Eubalaena australis*) identified on the nursery ground at Peninsula Valdes, Argentina. Journal of Cetacean Research and Management (Special Issue 2):33–144.

SIEGFRIED, W. R., AND R. ABRAMS. 1977. Cape fur seals riding the waves. South African Journal of Science 73:237–239.

SMULTEA, M. A. 1994. Segregation by humpback whale (*Megaptera novaeangliae*) cows with a calf in coastal habitat near the island of Hawaii. Canadian Journal of Zoology 72:805–811.

SWARTZ, S. L. 1986. Gray whale migratory, social and breeding behaviour. Report of the International Whaling Commission (Special Issue 8):207–229.

THOMAS, P. O. 1987. Social behavior, habitat use and interspecific interactions of southern right whale (*Eubalaena australis*) mother-calf pairs. Ph.D. dissertation, University of California, Santa Cruz, CA. 133 pp.

THOMAS, P., AND S. TABER. 1984. Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. Behavior 88:42–60.

WATTS, P. D., B.A. DRAPER AND J. HENRICO. 1991. Preferential use of warm water habitat by adult beluga whales. Journal of Thermal Biology 16:57–60.

WHITEHEAD, H., AND M. J. MOORE. 1982. Distribution and movements of West Indian humpback whales in winter. Canadian Journal of Zoology 60:2203–2211.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, NJ.

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