S. Afr. J. mar. Sci. 22: 43–55
2000

COASTAL DISTRIBUTION, MOVEMENTS AND SITE FIDELITY OF RIGHT WHALES *EUBALAENA AUSTRALIS* OFF SOUTH AFRICA, 1969–1998

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Counts and photographs of right whales *Eubalaena australis* taken on aerial surveys of the southern coast of South Africa between 1969 and 1998 have been used to examine patterns of coastal distribution between successive 20-minute bins of longitude. Some bins had consistently higher densities of whales than others, either of cows with calves or of unaccompanied adults. Apart from an overall increase in density, the centre of distribution shifted 40–60 minutes of longitude to the west over the 30-year period. Most (>93.4%) female calves born on the South African coast returned there to have their first calf, but only 52.9% were photographed with their first calf in the same or an adjacent bin as that of their natal year. This compares with 60.9% of multigravid females that occurred in the same or an adjacent bin as that of their previous calf, with significantly more westward (368) than eastward (255) shifts in distribution between calves. Approximate residence times for cow-calf pairs in the De Hoop region were 12–105 (average = 59.0 ± 3.9) days: dispersal rates were low between July and September but increased thereafter. Incidental records of coastwise movement were mainly to the west, but were probably influenced by the survey direction. Distances moved ranged from 6 to 202 km, at average speeds of 0.08–2.89 $km \cdot h^{-1}$. Theodolite tracking of undisturbed groups of right whales from Cape Columbine produced a similar range of swimming speeds. Inter-calf movements of cows between the survey area and the coasts to both east and west indicated that the entire South African coast could be considered as one homogeneous winter assemblage area for right whales.

Southern right whales *Eubalaena australis* visit the coasts of continents and oceanic islands during the austral winter and early spring, where some individuals (especially cows in a perinatal condition) may reside for several weeks to months, apparently for the purposes of giving birth to and nursing their calves, and possibly mating. In this process, certain bays or stretches of coastline are more favoured than others. The predictability of this distribution was probably one of the contributory factors to the rapid depletion of most populations of southern right whales by the mid-19th century, as whalers could deploy their effort with corresponding efficiency.

The distribution of right whales on the South African coast in winter has already been described, based on sightings made during fixed-wing aerial surveys between 1969 and 1987 (Best 1981, 1990a). In this paper, data from helicopter surveys on the South African coast between 1979 and 1998 are analysed for patterns of coastal distribution, and the results are compared with those from the earlier fixed-wing surveys. In addition, photographs of cow-calf pairs taken on the helicopter surveys are used to study shifts over time in the coastal distribution of individual cows, both within a season and between seasons with successive calves. Apparent rates of movement within a season are compared with swimming speeds calculated from shore-based theodolite readings at Cape Columbine in 1993. The site fidelity of cows first photographed as calves is also examined. Monthly photogrammetric surveys in 1988 and 1989 provide information on residence times of cow-calf pairs at (and dispersal rates from) the De Hoop region.

Such information on the coastal distribution, movements and site fidelity of right whales over the last 20–30 years could form useful baseline data against which to examine some of the possible long-term effects of boat-based whale watching in South Africa, for which permits were introduced for the first time in 1998.

MATERIAL AND METHODS

From 1969 to 1987, a fixed-wing aerial survey was flown each year along the southern coast of South Africa between Muizenberg, False Bay, and Woody Cape, Algoa Bay (and sometimes beyond these limits), in late September or early October (Fig. 1). These surveys had as their principal objective the recording of the distribution, numbers and classes (cow plus calf, adult, juvenile) of all right whales seen. Details of survey procedures have been given earlier (Best 1990a).

From 1979 to 1998, a helicopter survey was flown each year along the same stretch of coast, but between

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Manuscript received August 1999; accepted December 1999

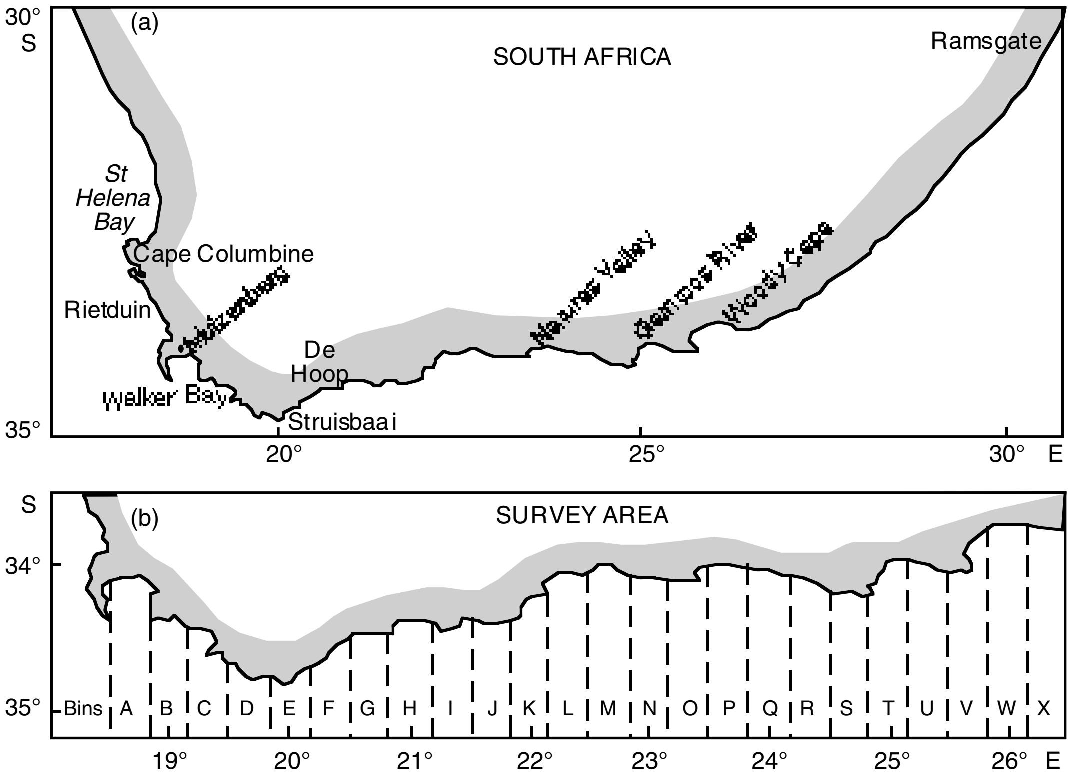

Fig. 1: Southern coast of South Africa, showing (a) place names mentioned in text and (b) the survey area, indicating position of longitudinal bins. Fixed-wing surveys (1969–1987) covered Bins A–X, helicopter surveys (1979–1998) covered Bins A–O

Muizenberg and Nature's Valley, Plettenberg Bay, around the middle of October. These surveys had as their principal objective the photography of whales for individual identification purposes. All whales seen were recorded, but photography was confined to cow-calf pairs. Details of survey procedures are given in Best (1990b).

Apart from the 1997 survey, when the helicopter used was fitted with a Global Positioning System, the locations of all whales seen were recorded relative to convenient adjacent landmarks. Although this means that most positions are not geographically precise, their accuracy is certainly sufficient for the purposes of studying overall coastwise distribution and movement on the scale used in this paper.

Because the coast ran in an essentially east-west direction, the survey area was divided into successive bins of 20 minutes of longitude (24 bins for the surveys prior to 1988, and 15 bins for later surveys). These bins have been labelled from west to east as A–X (Fig. 1). Within each bin the length of coastline was measured, ranging from 30.6 to 68.5 (average = 41.4) km in extent, and the density of whales expressed as the number of pairs (for cows with calves) or individuals seen per km of coastline.

To study shifts in distribution with time, the survey series was divided into three periods, 1969–1979, 1980–1987 and 1988–1998. The first two periods were chosen for comparability with published data (Best 1990a) and only involve data collected on fixed-wing surveys (because of their greater geographical coverage than helicopter surveys). The last period only involves data collected on helicopter surveys.

Between 1979 and 1995, 432 right whale cows were individually identified from photographs taken on the helicopter surveys. Of these, 83 were seen with only one calf, and so were excluded from further analysis. The remaining 349 cows produced a total of 1 250 calves between 1979 and 1998 and can potentially provide information on 901 between-calf movements.

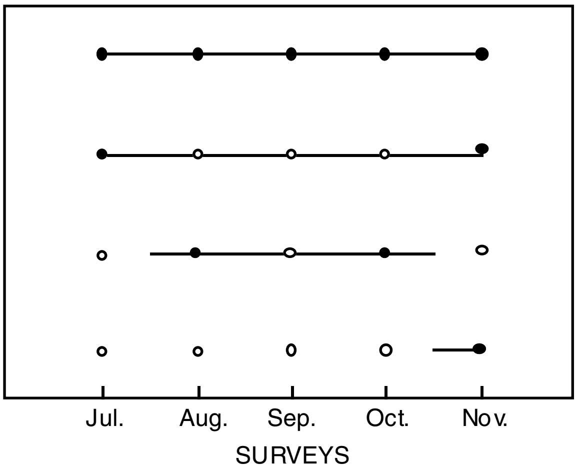

Fig. 2: Diagrammatic representation of residence time calculations from right whale surveys at De Hoop, July–November 1989 (solid circles = whale seen, open circles = whale not seen, solid lines = residence time)

The distribution of these movements has been analysed by 20-minute bins of longitude. Site fidelity was measured as the frequency with which successive calves for the same cow were photographed in a particular bin. In addition, 34 of the cows were first photographed as calves, enabling the fidelity to their natal stretch of coast to be examined.

Monthly photogrammetric helicopter surveys were flown in the De Hoop area of the coast from August to November 1988 and from July to November 1989 (Best and Rüther 1992), on which 100 different cow-calf pairs were photographed. Resightings of these pairs off De Hoop (or elsewhere during the October surveys in 1988 and 1989) produced information on same-season dispersal and approximate residence time. In calculating the latter, only the 1989 data were used because of their more comprehensive seasonal coverage. As the observations were episodic, assumptions had to be made about intervening periods (hence the designation of "approximate" residence time). Whales seen in successive months were assumed to have been present for the whole of the intervening period, as were whales seen in alternate months. Whales that "appeared" or "disappeared" between surveys were assumed to have arrived or departed at the mid-point between surveys. However, no allowance was made for residence time prior to the first survey (for whales seen for the first time in July), nor for residence time after the last survey (for whales seen for the last time in November). A diagrammatic re-

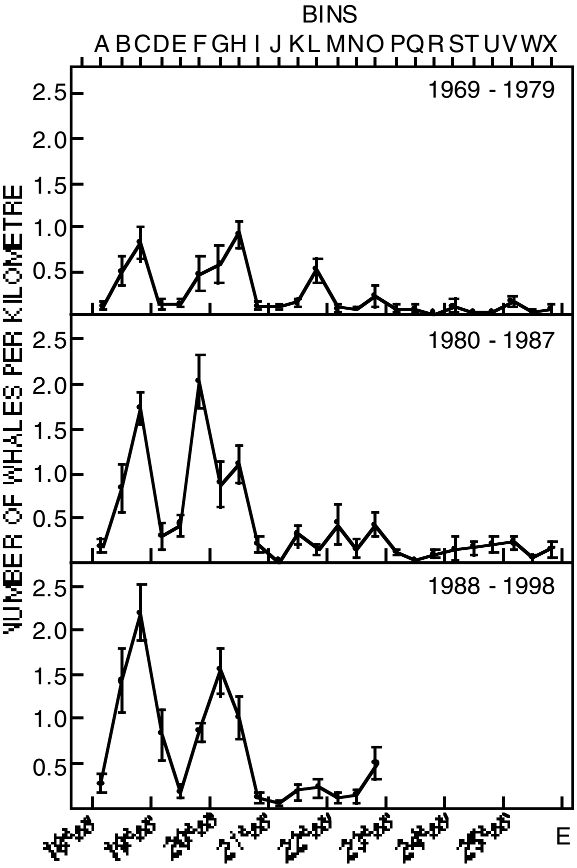

Fig. 3: Mean density (± *SE*) of unaccompanied right whales per longitudinal bin in the survey area on the southern coast of South Africa, expressed as the number seen per km of coastline on three sets of aerial surveys

presentation of these residence time calculations is shown in Figure 2.

Resightings of individual cow-calf pairs during annual helicopter surveys (and occasionally on incidental photographic flights) also provided information on within-season movement. Ignoring resightings within the same day (on the basis that such short-term movement could have been influenced by disturbance during photography), there were 52 resightings from 1 to 31 days apart. The distances travelled by these animals were measured on 1:250 000 charts, on the assumption that movements took place coast-wise (i.e. following the general topography of the coast), rather than from headland to headland. Local times of sightings were recorded to the nearest minute, and the time elapsed

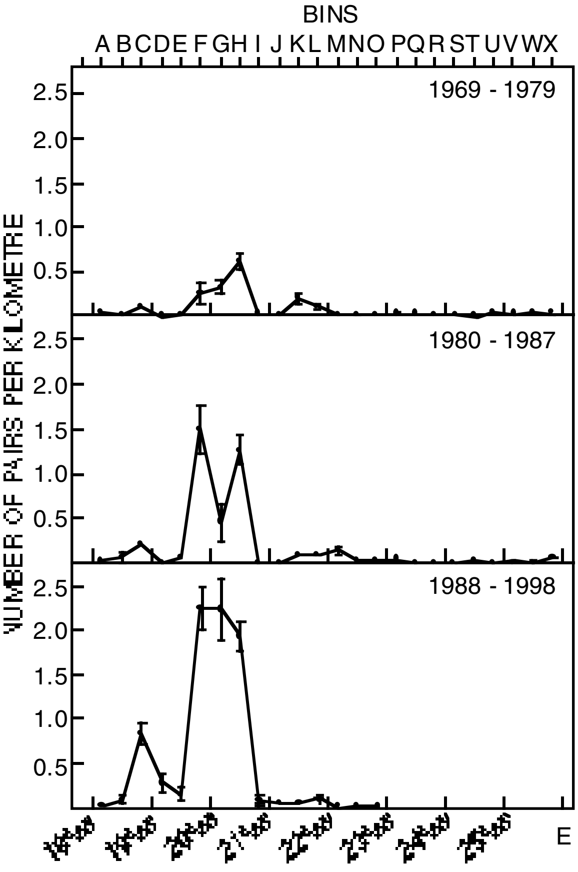

Fig. 4: Mean density (± *SE*) of cow-calf pairs of right whales per longitudinal bin in the survey area on the southern coast of South Africa, expressed as the number seen per km of coastline on three sets of aerial surveys

between sightings used to calculate average speed of movement.

Between 5 October and 19 November 1993, 47 groups of right whales (including four cow-calf pairs) were seen from the lighthouse at Cape Columbine, on the west coast of South Africa, and tracked by theodolite. Field and analytical techniques used for humpback whale observations from the same site have been detailed by Best *et al.* (1995), and those used for right whales were identical. The average swimming speed was defined as the sum of the distances covered between each theodolite position divided by the time interval between the first and last theodolite position. The net swimming speed was defined as the linear distance travelled between the first and last theodolite positions divided by the corresponding time interval.

RESULTS

Coastwise distribution

The mean densities of right whales per 20 minutes of longitude with their associated standard errors are shown for each of the three survey periods in Figure 3 (for adults without calves) and Figure 4 (for cows with calves).

As noted previously (Best 1990a), the coastwise distribution is not random. In all three time periods, some bins have consistently higher or lower densities than others, indicating that certain sections of the coast are habitually more favoured by right whales than others. In addition, some of the favoured areas are characterized by higher densities of cows with calves (Bins F–H) and others with higher densities of unaccompanied adults (Bins B–D), corresponding perhaps to "nursery" and "mating" areas respectively.

A comparison between the three time periods indicates that, for both unaccompanied adults and cow-calf pairs (but more especially for the latter), densities have increased over time. As an example, peak densities for cow-calf pairs increased in Bins F–H from an average of $0.63{\cdot}km^{-1}$ in the period 1969–1979 to $1.48{\cdot}km^{-1}$ in 1980–1987 and $2.24{\cdot}km^{-1}$ in 1988–1998. This is presumably a corollary of the general increase in reproductively active females that has been documented for this population over the same overall time period (Best *et al.* in press). For unaccompanied adults, peak densities have increased from an average of about $0.9{\cdot}km^{-1}$ in 1969–1979 to $2{\cdot}km^{-1}$ in 1980–1987 and $2.2{\cdot}km^{-1}$ in 1988–1998. This is not such a consistent increase as for cow-calf pairs, but in this case the helicopter surveys in 1988–1998 may not be completely comparable to the earlier fixed-wing surveys, because they occurred slightly later (1–2 weeks) in the season. Off Australia, unaccompanied right whales have shorter residence times on the coast than females with calves (means of 20.4 and 70.9 days respectively – Burnell and Bryden 1997), so the later helicopter surveys may not be as representative of the peak abundance of unaccompanied whales as were the earlier fixed-wing surveys.

Apart from the overall increase in densities, there seems to have been a shift in the distribution of the population over time. In Table I the numbers of whales seen in each period have been summed over three successive bins (i.e. within one degree sector of longitude), and the total number of observations in each of these sectors compared across surveys, using the x^2 test. For all combinations tested (1969–1979 v. 1980–1987, 1969–1979 v. 1980–1987 v. 1988–1998, unaccompanied adults or cows with calves), the pro-

Table I: Numbers of right whales seen on aerial surveys on the south coast of South Africa, by one-degree sector of longitude (proportions of total between 18°30’ and 23°30’E shown in parenthesis)

Sector	Number of unaccompanied adults			Number of cows with calves		
	1969–1979	1980–1987	1988–1998	1969–1979	1980–1987	1988–1998
18°30’–19°30’E	256 (0.369)	370 (0.384)	700 (0.494)	39 (0.155)	41 (0.105)	202 (0.182)
19°30’–20°30’E	96 (0.139)	271 (0.281)	246 (0.174)	39 (0.155)	156 (0.399)	368 (0.332)
20°30’–21°30’E	191 (0.276)	188 (0.195)	302 (0.213)	119 (0.472)	158 (0.404)	490 (0.442)
21°30’–22°30’E	106 (0.153)	49 (0.051)	68 (0.048)	48 (0.190)	18 (0.046)	35 (0.032)
22°30’–23°30’E	44 (0.063)	85 (0.088)	101 (0.071)	7 (0.028)	18 (0.046)	13 (0.012)
23°30’–24°30’E	12	15	–	18*	9*	–
24°30’–25°30’E	16	46	–			–
25°30’–26°30’E	35	41	–			–
Chi-square	1969–1979 v. 1980–1987: 104.1, $p < 0.0001$, $df = 7$; 1969–1979 v. 1980–87 v. 1988–1998: 170.2, $p < 0.0001$, $df = 8$			1969–1979 v. 1980–1987: 74.8, $p < 0.0001$, $df = 5$; 1969–1979 v. 1980–87 v. 1988–1998: 149.3, $p < 0.0001$, $df = 8$		

* Bins between 23°30’ and 26°30’E combined

portions of observations in different surveys differed significantly between sectors. The overall impression is that the populations of both cow-calf pairs and unaccompanied adults have tended to shift somewhat to the west with time.

A simple indication of this is the location of the median animals within each survey period. In unaccompanied adults, the median animals were located in Bin G in 1969–1979, Bin F in 1980–1987 and Bin D in 1988–1998. For cow-calf pairs, the median animals were located in Bin H in 1969–1979, Bin G in 1980–1987 and Bin F in 1988–1998. The centre of

Table II: Coastwise movements between successive observed calvings of right whales off South Africa, 1979–1998. Bold numbers indicate site fidelity

Initial calf	Subsequent calf																Total
Bins	Bins																
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	*Z*	
A	**1**		2				1										4
B			7		1	1	2	5									16
C	2	5	**42**	2	8	23	15	17	1		1	2	1			1	120
D			1	**1**	1	2	3	2			1	1					12
E			4		**1**	1	2		1						1		10
F	1	1	20	6	3	**52**	46	30		1			1			1	162
G	1	4	23	11	1	73	**85**	55	1		1	1	1				257
H	1	3	26	3	5	41	69	**90**	1		2	3	2		2		248
I			1	2		1	2	4	**1**								11
J				1					1								2
K						1	1	4	1		**1**	1	1				10
L			2			2	6	10				**1**					21
M			1			1	4	4					**3**				13
N		1															1
O						2	1	5		1							9
Z		1	1			1		1	1								5
Total	6	15	130	26	20	201	237	227	8	2	6	9	9	0	3	2	901

Z = calving observed outside normal survey area

Table III: Distribution of right whale cows first photographed as a calf, both as a calf and when seen with their first calf, South Africa. Bold numbers indicate site fidelity

Photographed as calf	Photographed as cow with first calf															Total
Bins	Bins															
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	
A																
B																
C		1	**2**				1	2								6
D							1									1
E																
F																
G			3			1	**3**	3								10
H			2		2	2	4	**4**								14
I																
J																
K																
L			1													1
M							1									1
N																
O											1					1
Total		1	8		2	3	10	9			1					34

coastal right whale distribution therefore seems to have shifted 40–60 minutes of longitude to the west over the last 30 years.

Individual movements of cow-calf pairs

BETWEEN-SEASON MOVEMENTS – SITE FIDELITY

To investigate the movements of individual cows over time, the positions at which they were seen with successive calves have been compared (Table II). The combined records indicate that the bin in which cows were most frequently photographed with their next calf (30.9% of the time) was the same as that for the previous calf. Another 30% were photographed in an adjacent bin to either east or west, and in total, 72.3% of cows were resighted within two bins either east or west of that in which they were photographed with their previous calf. Other cows, however, were photographed up to 13 or 14 bins apart from their previous calf. Site fidelity (as measured by the frequency with which cows were photographed with successive calves in a particular bin) was highest in those areas with the highest densities of cow-calf pairs (Bins C, F, G and H), where it ranged from 32–36%. The highest value for any other bin was 25% (Bin A), but most were 10% or less.

Overall, there were more westward (368) than eastward (255) shifts in distribution, and a comparison between the distributions of "initial" and "subsequent" calves indicates that there was a significant difference in the proportions in Bins A–G (westward) and H–O (eastward) between the two (x^2 = 7.104 with Yates correction, p = 0.0077).

Of the 34 cows first photographed as calves, only nine (26.5%) were photographed with their first calf in the same bin as that of their natal year, although an additional nine were photographed in an adjacent bin (Table III). Some individuals were photographed with their first calf as much as nine bins (3° of longitude) away from the bin in which they were photographed as a calf. Such movements took place to both east and west, and the distribution of the animals seen as calves and with their first calf in the western bins (A–G) and eastern bins (H–O) is not significantly different (Fisher's exact test, p = 0.1364).

EXTRA-LIMITAL MOVEMENTS

Since 1980, nine cow-calf pairs have been photographed outside the standard survey area on the South African coast, and one outside the helicopter area but within the fixed-wing survey area. Five of these records indicate coastwise movement of cow-calf pairs between the helicopter survey area and other sectors of the southern African coast.

On 23 October 1980, two cows were photographed with calves on the standard survey, one (R80/28A) at Struisbaai in Bin F and the other (R80/32A) in Walker Bay (Bin C). On 19 October 1983, R80/28A was photographed with another calf at Rietduin (33°24.3´S,

Table IV: Same-season resightings of right whale cow-calf pairs photographed off De Hoop during photogrammetric surveys, 1988 and 1989. Values in parenthesis represent whales seen off De Hoop in subsequent months but not seen in current month

Date of survey	Number photographed for first time	Rephotographed off De Hoop				Rephotographed elsewhere in October
		Aug.	Sep.	Oct.	Nov.	
28 Jul. 1989	15	12 (2)	8 (2)	8	1	4
24 Aug. 1988	15		13 (2)	9	2	4
21 Aug. 1989	14		10 (2)	9 (1)	5	1
18 Sep. 1988	15			6 (1)	3	3
26 Sep. 1989	9			5	2	4
15 Oct. 1988	7				1	
13 Oct. 1989	11				2	
10 Nov. 1988	9					8*
10 Nov. 1989	5					4
Total	100	12 (2)	31 (6)	37 (2)	16	

* In addition, one female was photographed in October 1983 at Gough Island, South Atlantic, as one of two adults

18°13.5´E) on an extension of the survey up the West Coast, and was rephotographed 12 years later (on 19 October 1995) with a third calf, east of Danger Point in Bin C of the survey area. On 28 September 1985, R80/32A was photographed with a calf at the mouth of the Gamtoos River (33°58.2´S, 25°05´E) in Bin T of the fixed-wing survey area. It was seen subsequently with calves in the survey area in 1988 (Bin B), 1991 (Bin H), 1995 (Bin H) and 1998 (Bin F). On 22 October 1985, two cows (R85/53A and R85/54A) were photographed with calves-of-the-year in St Helena Bay on the west coast of South Africa (at 32°41.5´S, 18°13.5´E and 32°36.7´S, 18°17.2´E respectively) during an extension of the normal aerial survey. Neither female had been seen previously. Both individuals were subsequently photographed with calves-of-the-year in 1988, 1991, 1994 and 1997, all within the survey area (R85/53A in Bins H, G, H and H; R85/54A in Bins I, G, D and C respectively). On 10 August 1989 a cow-calf pair of right whales was photographed from the air off Ramsgate, KwaZulu-Natal (30°54´S, 30°21.4´E) by a private photographer. This individual cow (R89/163A) had also not been seen previously. On 13 October 1993, the same cow was photographed with another calf in Bin F of the survey area.

WITHIN-SEASON MOVEMENTS AND APPROXIMATE RESIDENCE TIME

For the 54 cow-calf pairs photographed at De Hoop in 1989 on monthly photogrammetric surveys, approximate residence times on the coast ranged from 12 to 105 days (average = 59.0 ± 3.9 days). This estimate includes data from animals photographed at De Hoop between July and September, but seen elsewhere during the October survey. Because no allowance has been made for residence before the July or after the November surveys, these values may be underestimates of the true residence time.

In 1988 and 1989, 100 individual cows were identified during photogrammetric flights in the De Hoop area (a 44-km stretch of coast, including the whole of Bin G and about 25% of Bin F). A total of 96 resightings of these animals was made in the same area in August, September, October or November surveys (Table IV). On the assumption that a whale not resighted on an intervening survey was probably in the De Hoop area, but not detected (such aerial surveys having overall sighting efficiencies of 75–80% – Best *et al.* in press), this total could be increased to 106 resightings. Using these two totals as likely extremes, resighting rates at De Hoop can be calculated as 80–93% for August (n = 15), 70–84% for September (n = 44), 54–57% for October (n = 68) and 19% for November (n = 86), where n is the total number of whales photographed for the first time in the preceding month(s). This pattern suggests that dispersal rates away from the De Hoop region were low between July and September but increased between September and October, and particularly from October to November.

On the October surveys in 1988 and 1989, 16 cow-calf pairs previously photographed off De Hoop between July and September were encountered elsewhere in the survey area. If these are added to the total resighted off De Hoop in October, it brings the re-

Table V: Coastwise movements of cow-calf pairs of right whales on the South African coastline during October (and some incidental) aerial surveys

Whale #	Date	Time	Estimated position	Distance travelled coastwise (km)	Average speed (km·h^{-1})
R79/13A	20 Oct. 1992	11:30	34°33.8'S, 20°24.6'E		
	21 Oct. 1992	08:49	34°36.4'S, 20°19.8'E	9	0.42
R79/17A	14 Oct. 1998	10:25	34°37.2'S, 19°18'E		
	15 Oct. 1998	09:42	34°25.5'S, 19°17.7'E	25	1.07
R79/26A	16 Oct. 1990	13:49	34°22.6'S, 20°53.5'E		
	21 Oct. 1990	11:49	34°28.8'S, 20°30'E	47	0.40
R80/03A	16 Oct. 1990	15:08	34°28.8'S, 20°50.8'E		
	21 Oct. 1990	11:27	34°28.5'S, 20°32.5'E	28	0.24
R80/17A	16 Oct. 1990	13:33	34°22.3'S, 20°56.8'E		
	21 Oct. 1990	08:56	34°27.9'S, 20°45.8'E	27	0.23
R80/31A	9 Oct. 1998	09:07	34°22.3'S, 20°56.8'E		
	12 Oct. 1998	10:28	34°27.2'S, 20°39.4'E	36	0.49
R80/34A	17 Oct. 1995	09:35	34°24'S, 20°52.3'E		
	19 Oct. 1995	09:20	34°28'S, 20°48.6'E	14	0.29
R81/11A	16 Oct. 1990	13:19	34°22.2'S, 20°59'E		
	21 Oct. 1990	13:52	34°32.8'S, 20°25.1'E	62	0.51
R81/24A	14 Oct. 1998	11:35	34°29.2'S, 19°20.8'E		
	15 Oct. 1998	08:22	34°35'S, 19°20.8'E	11	0.53
R81/26A	21 Oct. 1996	11:34	34°24'S, 20°51.7'E		
	24 Oct. 1996	13:43	34°27.9'S, 20°34.7'E	34	0.46
R81/31A	12 Oct. 1993	15:26	34°50'S, 19°59'E		
	13 Oct. 1993	08:55	34°39.3'S, 20°15'E	38	2.17
R82/10A	12 Oct. 1991	11:06	34°22.6'S, 20°53.5'E		
	15 Oct. 1991	08:43	34°50'S, 19°59'E	113	1.62
R84/63A	12 Oct. 1991	11:24	34°24.2'S, 20°51.8'E		
	12 Nov. 1991	~16:00	34°29.2'S, 19°20.8'E	202	~0.26
R84/77A	14 Oct. 1998	11:54	34°26.2'S, 19°18.7'E		
	15 Oct. 1998	11:53	34°21.5'S, 19°04.4'E	29	1.21
R85/15A	12 Oct. 1994	09:04	34°22'S, 20°58.2'E		
	13 Oct. 1994	09:02	34°27.2'S, 20°44.4'E	38	1.59
R85/49A	17 Oct. 1997	11:30	34°22.4'S, 20°54.3'E		
	19 Oct. 1997	08:10	34°27.9'S, 20°47.4'E	20	0.45
R87/08A	16 Oct. 1990	14:09	34°24.2'S, 20°51.8'E		
	21 Oct. 1990	08:41	34°28.5'S, 20°50.2'E	11	0.10
R87/10A	21 Oct. 1996	11:40	34°24.2'S, 20°51.8'E		
	24 Oct. 1996	15:57	34°29.5'S, 20°29'E	44	0.58
R87/30A	16 Oct. 1990	13:57	34°23'S, 20°50.2'E		
	21 Oct. 1990	11:11	34°28'S, 20°33.9'E	40	0.34
R87/33A	12 Oct. 1998	12:19	34°31'S, 20°27.4'E		
	13 Oct. 1998	08:27	34°35.5'S, 20°23.3'E	13	0.65
R88/41A	14 Oct. 1991	11:54	34°31'S, 20°27.4'E		
	12 Nov. 1991	~16:30	34°29.2'S, 19°20.8'E	155	~0.22
R88/57A	17 Oct. 1997	12:20	34°23.1'S, 20°52'E		
	19 Oct. 1997	10:11	34°27.4'S, 20°36.3'E	33	0.72
R89/02A	17 Oct. 1995	09:35	34°24'S, 20°52.3'E		
	19 Oct. 1995	11:51	34°32.4'S, 20°25.5'E	51	1.01
R89/30A	17 Oct. 1997	12:27	34°24.1'S, 20°51.3'E		
	19 Oct. 1997	09:49	34°27.2'S, 20°39.3'E	28	0.62
R89/53A	12 Oct. 1991	12:03	34°25.6'S, 20°52.6'E		
	14 Oct. 1991	10:47	34°29'S, 20°31'E	39	0.83
R89/105A	19 Oct. 1995	16:44	34°37'S, 19°24.2'E		
	20 Oct. 1995	10:15	34°29.2'S, 19°20.8'E	33	1.88
R89/118A	17 Oct. 1995	09:16	34°23.2'S, 20°52'E		
	19 Oct. 1995	09:13	34°28.5'S, 20°50.2'E	14	0.30
R91/18A	12 Oct. 1991	11:59	34°25.6'S, 20°52.6'E		
	14 Oct. 1991	11:21	34°31'S, 20°27.4'E	45	0.95
	12 Nov. 1991	~16:15	34°29.2'S, 19°20.8'E	158	~0.23
R91/46A	14 Oct. 1991	11:04	34°29'S, 20°31'E		
	13 Nov. 1991	~06:50	34°32.6'S, 19°22.3'E	152	~0.21
R91/46A	12 Oct. 1994	08:43	34°22.2'S, 20°59'E		
	13 Oct. 1994	08:40	34°28.5'S, 20°50.2'E	23	0.96

(continued)

Table V: *(continued)*

Whale #	Date	Time	Estimated position	Distance travelled coastwise (km)	Average speed (km·h^{-1})
R92/07A	12 Oct. 1998	12:27	34°31'S, 20°27.4'E		
	13 Oct. 1998	08:48	34°35'S, 20°23.3'E	10	0.49
R93/59A	17 Oct. 1997	12:44	34°25.3'S, 20°51.6'E		
	19 Oct. 1997	13:01	34°31'S, 20°26.6'E	50	1.04
R93/72A	9 Oct. 1998	09:17	34°23.2'S, 20°52.3'E		
	12 Oct. 1998	13:26	34°33.8'S, 20°24.6'E	54	0.71
	13 Oct. 1998	08:14	34°37'S, 20°19.4'E	11	0.59
			Overall	65	0.68
R93/90A	21 Oct. 1996	10:52	34°22.4'S, 20°55'E		
	24 Oct. 1996	15:06	34°28.6'S, 20°31.5'E	47	0.62
R95/24A	9 Oct. 1998	09:38	34°23.6'S, 20°51.9'E		
	12 Oct. 1998	10:44	34°27.8'S, 20°34.2'E	36	0.49
	13 Oct. 1998	08:08	34°37.8'S, 20°17.8'E	32	1.43
	14 Oct. 1998	08:27	34°46.1'S, 19°49'E	63	2.59
			Overall	131	1.10
R95/27A	9 Oct. 1998	09:58	34°25.5'S, 20°52'E		
	14 Oct. 1998	08:59	34°45.6'S, 19°37.5'E	146	1.23
R95/29A	12 Oct. 1998	11:42	34°28.2'S, 20°33'E		
	13 Oct. 1998	08:43	34°35'S, 20°23.3'E	20	0.95
R95/100A	9 Oct. 1998	09:43	34°24.7'S, 20°51.2'E		
	13 Oct. 1998	10:27	34°42.3'S, 20°09.9'E	87	0.90
R96/01A	21 Oct. 1996	08:45	34°22.6'S, 21°03.1'E		
	23 Oct. 1996	09:29	34°22.2'S, 21°29.3'E	43	0.88
R96/08A	21 Oct. 1996	09:20	34°22.2'S, 20°59.5'E		
	24 Oct. 1996	11:23	34°25.6'S, 20°52.6'E	16	0.22
R96/24A	21 Oct. 1996	11:10	34°24.7'S, 20°51.2'E		
	24 Oct. 1996	15:49	34°29.5'S, 20°29'E	42	0.55
R96/35A	21 Oct. 1996	11:51	34°25.3'S, 20°51.6'E		
	24 Oct. 1996	16:54	34°31'S, 20°27.4'E	45	0.58
R96/36A	21 Oct. 1996	11:57	34°25.3'S, 20°51.6'E		
	24 Oct. 1996	11:53	34°28.1'S, 20°51.6'E	6	0.08
R98/08A	9 Oct. 1998	09:10	34°22.3'S, 20°56.8'E		
	13 Oct. 1998	08:37	34°35'S, 20°23.3'E	66	0.69
R98/62A	12 Oct. 1998	13:07	34°31.8'S, 20°25.6'E		
	13 Oct. 1998	10:40	34°43.4'S, 20°06.3'E	38	1.76
	14 Oct. 1998	08:40	34°46'S, 19°43'E	49	2.23
	15 Oct. 1998	09:35	34°26.2'S, 19°18.3'E	72	2.89
			Overall	159	2.32
R98/67A	12 Oct. 1998	13:21	34°32.4'S, 20°25.5'E		
	13 Oct. 1998	08:17	34°37.2'S, 20°19.9'E	13	0.69

sighting rate for that month up to 80–81%, similar to that for August and September. This indicates that, although dispersal rates may increase between September and October, cow-calf pairs still remain in coastal waters at that time. Dispersal took place to Bins C (five animals), F (one animal), H (nine animals), and I (one animal). The only long-distance dispersals (more than the adjacent bins to east or west) were one to the east (Bin I) and five to the west (Bin C).

Of the 14 cows photographed in November that had not been seen earlier off De Hoop, comparison with the October survey photographs reveals that 12 (or 85.7%) had been photographed elsewhere in the survey area and so were recent immigrants to the De Hoop region. This confirms that dispersal rates increase between October and November. Individuals originated from Bins O (one animal), I (one animal), H (seven animals), G (one animal), F (one animal) and E (one animal). This represented two long-distance immigrants from the east (Bins O and I) and one from the west (Bin E). A thirteenth animal had been previously photographed as one of a pair of adults at Gough Island in the South Atlantic (40°17.7´S, 9°54.5´W) in 1983 (Best *et al*. 1993), and is likely to have been a transient animal.

There were 52 incidental records made during annual helicopter surveys that provide some information on coastwise movement from day to day (Table V). Of these records, 48 (92.3%) represent movement to the west and only two (3.8%) movement to the east, but this result is probably influenced by the fact that flights were usually undertaken from east to west (so that movements to the east between days would not be detected). Distances moved ranged from 6 to 202 km,

Table VI: Speed of movement of right whales as determined by theodolite tracking from the shore, Cape Columbine, October/November 1993

Date	Sighting number	Group size	Total time tracked (mins)	Number of theodolite fixes	Average speed (km·h^{-1})	Net speed (km·h^{-1})
5 Oct. 1993	1	Cow/calf	88.8	7	3.02	2.66
13 Oct. 1993	1	2	70.0	8	2.19	1.76
18 Oct. 1993	3	2	89.3	9	1.49	0.48
21 Oct. 1993	1	2	201.2	9	1.51	0.86
21 Oct. 1993	6	2	67.7	7	3.22	3.04
23 Oct. 1993	5a	3	109.1	6	1.64	0.72
23 Oct. 1993	5d	2	85.1	3	1.34	0.83
23 Oct. 1993	7a	1	97.2	5	3.20	1.25
23 Oct. 1993	7b	1	62.1	5	1.75	0.89
27 Oct. 1993	4	2	369.1	4	0.93	0.26
28 Oct. 1993	2	5	82.4	2	1.70	1.70
28 Oct. 1993	4a	2	110.0	3	1.58	0.98
28 Oct. 1993	4b	2	126.7	6	1.22	0.80
30 Oct. 1993	1	2	126.7	5	0.93	0.48
30 Oct. 1993	2	Cow/calf	201.1	13	1.41	1.14
3 Nov. 1993	1	1	71.6	4	0.61	0.03
3 Nov. 1993	2	Cow/calf	180.4	15	3.25	3.09
6 Nov. 1993	3	2	135.3	11	2.48	2.46
6 Nov. 1993	5	1	71.5	8	1.21	0.35
6 Nov. 1993	6	1	61.9	4	0.99	0.89
6 Nov. 1993	7	2	139.4	11	3.62	3.10
7 Nov. 1993	2	2	554.9	27	1.42	0.24
7 Nov. 1993	4	3	143.2	3	0.76	0.71
7 Nov. 1993	5	2	428.1	15	0.87	0.38
7 Nov. 1993	6	3	406.8	17	1.10	0.14
9 Nov. 1993	1	2	121.1	13	2.36	2.15
12 Nov. 1993	1	2	385.4	16	1.25	0.42
12 Nov. 1993	3	2	63.3	5	0.50	0.44
13 Nov. 1993	1	2	216.0	14	1.83	0.17
13 Nov. 1993	3	Cow/calf	391.6	8	0.40	0.27
15 Nov. 1993	1	2	203.9	13	0.85	0.01
17 Nov. 1993	1	1	223.5	12	1.17	1.07
17 Nov. 1993	2	1	76.7	6	2.12	0.30
17 Nov. 1993	8	1	82.4	11	2.54	0.57

at average speeds of 0.08 to 2.89 km·h^{-1}. Speeds were generally inversely proportional to the time delay. Thus, at intervals of one day, average speeds ranged from 0.42 to 2.89 (mean = 1.34 ± 0.75) km·h^{-1}, at two days 0.29 to 1.01 (mean = 0.71 ± 0.27) km·h^{-1}, at three days 0.08 to 1.62 (mean = 0.58 ± 0.37) km·h^{-1} and at longer intervals 0.1 to 1.23 (mean 0.42 ± 0.32) km·h^{-1}. These mean speeds are significantly different (Kruskal-Wallis One-Way ANOVA on ranks, $H = 19.2277$, $p = 0.0002$): pair-wise multiple comparisons reveal significant differences between average speeds at one-day and at three-day or longer intervals.

Shore-based observations of movement

Of the 47 groups of right whales tracked by theodolite from the shore during October/November 1993, 13 were tracked for less than an hour and so have been omitted from further analysis. Average speeds of movement for the remaining 34 groups (Table VI) ranged from 0.4 to 3.62 (mean = 1.67 ± 0.85) km·h^{-1} and net speeds of movement from 0.01 to 3.10 (mean = 1.01 ± 0.91) km·h^{-1}. For four cow-calf pairs, average speeds ranged from 0.4 to 3.25 km·h^{-1} (mean = 2.02 ± 1.17 km·h^{-1}) and net speeds from 0.27 to 3.09 km·h^{-1} (mean = 1.79 ± 1.14 km·h^{-1}).

DISCUSSION

The overall pattern of distribution of right whales on the south coast of South Africa has remained the same during the period 1988–1998 as in the preceding 19 years, in that whales there still seem to favour the same stretches of coastline. Reasons for choosing these preferred areas are still unknown.

In general terms, philopatry in female right whales visiting the South African coast must be strongly developed. An analysis of resightings of female calves born on the South African coastline produced an overall survival rate to the mean age at first parturition of 0.827 (0.913 for the first year and 0.986 for the subsequent seven years – Best *et al.* in press). Emigration and natural mortality are indistinguishable in such calculations, but if the (reasonable) assumption is made that juvenile survival can be no higher than adult survival (0.986), a lower limit to the degree of philopatry can be set as

$$1 - (0.986^8 - 0.827) = 0.934 \quad ,$$

i.e. at least 93.4% of female calves born on the South African coast return there to have their first calf.

Fidelity to the actual stretch of coast where the calf was first photographed, however, does not appear to be as strong. Only 52.9% of females were photographed with their first calf in the same or an adjacent 20-minute longitudinal bin to that in which they had been photographed in their natal year. However, it must be appreciated that the surveys mostly took place in October, some two months later than the peak calving season (Best 1994), so that substantial movement could have taken place in the interim. For instance, Burnell and Bryden (1997) referred to a female right whale with a neonatal calf that moved 600 km along the Australian coast within a month, and Thomas and Taber (1984) described a developmental stage for newborn right whales characterized by constant travel.

Fidelity of multigravid females to the same stretch of coast with successive calves is similar to that shown by females with their first calf, with 60.9% returning to the same or an adjacent bin. Off Argentina, Rowntree *et al.* (in press) showed that 52% of females exhibited fidelity to the same region of concentration with successive calves: these regions of concentration were roughly 55–75 km in extent, or equivalent to 1–2 longitudinal bins in this study.

Inter-calf fidelity in South African waters seemed to be region-related, so that it was highest in the most popular nursery areas. Therefore, the tendency for certain stretches of coast to be more favoured than others is presumably not so much a consequence of individual site fidelity *per se*, as a consequence of certain characteristics of the bay itself that make it attractive to right whales in general.

Because of unequal survey coverage outside his study area, Burnell (in press) described the fidelity of right whales to the Head of the Bight aggregation area in Australia in relative terms. Whales that had been seen in more than one year at the Head of the Bight, and at most in as many years at other coastal localities, were considered as showing some level of fidelity. This is a very different and not directly comparable approach to that used in this study. Nevertheless, there is no reason to challenge Burnell's conclusion that, in relative terms, unaccompanied whales showed a lower site fidelity to the Head of the Bight aggregation area than calving females. Rowntree *et al.* (in press) described a similar pattern for right whales off Argentina, in that females in calving years and subadults moved significantly less between regions of concentration than males or females in non-calving years.

In any particular year, cows with calves tended to show relatively little directed coastal movement until late in the season. In a shore-based study of right whales in Australia, Burnell and Bryden (1997) established from daily observations that cow-calf pairs remained within a 20-km long coastal aggregation area continuously for up to 118 days (average over a three-year period was 70.9 days). According to Rowntree *et al.* (in press), females with calves off Argentina stayed in coastal waters for an average of 77 days (range = 15–170 days). As might be expected, these values are somewhat greater than the approximate residence times calculated in this study for De Hoop (mean = 59 days, maximum = 105 days), which are believed to be underestimates.

Burnell and Bryden (1997) reported a rapid dispersal of female-calf pairs from the aggregation area in early October: the present data indicate a similar dispersal from De Hoop between mid to late September and mid October. However, although Burnell and Bryden (1997) claim that this dispersal of cow-calf pairs was associated closely with movement away from the coast, the present data do not fully support their claim. More than half the apparent emigrants from the De Hoop area between September and October were found elsewhere along the South African coast in October. The accelerated dispersal from De Hoop seen between October and November is consistent with the sudden onset of the pre-migratory stage in behaviour around mid November, described by Taber and Thomas (1982) and Thomas and Taber (1984) for right whales off Argentina.

Burnell and Bryden (1997) commented that, late in the season, cow-calf pairs had been detected moving away from the aggregation area, following the shoreline to the west. Burnell (in press) also reported that the great majority (95%) of within-year movements on the southern coast of Australia took place in a westerly direction. Data on within-season movement in this study are also suggestive of a westerly movement, but are difficult to interpret because most flights were carried out in a westerly direction.

One interpretation of the finding that speed of coastwise movement of cows with calves is inversely related to their time at large is that coastal movements in October are still relatively small scale (on the order of

30–40 km), and mainly completed within a day (equivalent to the "meandering" described by Thomas and Taber 1984 for cows with younger calves). Alternatively, the greater movement shown over the first 24 hours could represent an initial small-scale displacement as a result of disturbance from the aerial photography itself. However, speeds of travel estimated over the first 24 hours were similar to those calculated from shore-based theodolite tracking of cow-calf pairs on the west coast of South Africa. As the latter observations were of (presumably) undisturbed whales, it seems unlikely that the average speeds of coastwise movement recorded from the aerial surveys, even the fastest ones, can represent an artifact because of disturbance. Burnell (in press) also reported average speeds of 1.1–3.66 km·h^{-1} for three unaccompanied whales moving over distances of 351–1 490 km on the Australian coast, and gave details for a female plus calf that indicate an average speed of about 0.95 km·h^{-1} over a distance of 704 km. All these data were presumably from undisturbed whales.

Although the locations of favoured areas along the South African coastline have remained the same for the past 30 years, the relative numbers of right whales in the various areas have changed over time. In some bays (particularly those to the east), the density of whales has not increased at all, whereas in others (particularly in the west) the density has increased at a greater-than-average rate during the series of aerial surveys. Median whale analysis indicated above that the distributions of both cows with calves and unaccompanied adults have shifted some 40–60 minutes of longitude to the west over the last 30 years. Data from individual movements of cows with successive calves from 1979 to 1998 confirmed a significant shift westwards over time. Such an effect is not so apparent between birth and first parturition for females. This would suggest that the decision on which bay to use as a nursery area is one that may initially be based (perhaps loosely) on the natal site, but which in later years is modified on the basis of experience.

No environmental reasons can be advanced to explain the westward shift in right whale distribution off South Africa. Rowntree *et al*. (in press) have described the abandonment of one major concentration area for right whales on the coast of Argentina (Outer Coast) between 1971 and 1997 in favour of adjacent regions of concentration. Such abandonment involved all classes of whale, including cow-calf pairs. It was suspected that major changes in bottom topography occurred following storms on the Outer Coast, and that this might have caused the shift in whale distribution. In another instance off Argentina, a group of females using a particular nursery area shifted their preferred area 50 km to the west, in two successive calving years (1994 and 1997), although females in other calving years did not follow suit (Rowntree *et al*. in press). This move took the females away from the centre of the whale-watching industry, but into bays with a high incidence of gull attacks and close to a region of high vessel traffic. The authors concluded that such moves may be influenced more by individual preference and social cohesion than by disturbance. A similar conclusion might be reached regarding the South African situation.

Earlier aerial surveys of the wider South African coastline showed that an estimated 91.5% of cows with calves on the whole South African coast in late September/early October occurred within the standard survey area (Best 1990a). The extra-limital records in this study indicate that cows photographed in the survey area with calves can be found in subsequent years with a calf outside the survey area to both east and west (and return again with subsequent calves to the survey area). Conversely, cows photographed with calves outside the normal survey area to both east and west have been photographed in subsequent years with calves in the survey area. The entire South African coast can therefore be considered as one homogeneous winter assemblage area for cows in a perinatal condition. Burnell (in press) reached a similar conclusion for the geographically much more dispersed Australian population. How this South African assemblage might relate to those right whales that were taken historically in winter on the coasts of southern Angola, Namibia and southern Moçambique is still unknown. The degree of flexibility in habitat use and the extent of movement shown by cows in their calving years are encouraging signs that recolonization of these historic wintering grounds may still be possible.

ACKNOWLEDGEMENTS

I am indebted to a number of people who have unselfishly acted as assistants in the aerial surveys: these include Mr M. A. Meÿer, Dr K. Sekiguchi, Ms P. Meÿer, Ms D. Reeb, Dr K. P. Findlay, Messrs J. Bassett, M. E. Sanson, K. Smith, C. Potts, R. Weekes and R. Horne, Drs G. J. B. Ross and P. D. Shaughnessy, Mr N. Denton, Drs V. G. Cockcroft and D. L. Cram, Mr C. Boltman, Ms M. A. Best, Mr H. B. Crous and Ms A. von Loewensprung. The skill of pilots, Messrs S. Rowe, R. Matthews, M. Tilson, T. Pryor, J. Broberg, M. Franz, R. Richards, K. Hall, P. Savage, D. Notten, J. Lawson, C. Bartmann, B. Freylink, B. Curtin, G. Wilson, G. Wrigley, M. Fagan, K.Whittal, B. Walzer and S. Botha, was essential to the success of the surveys. Funding for the survey programme was provided by the South African Department of Environment Affairs (and its predecessors), the South African Scientific Committee for Antarctic Research, the South African Marine Corporation Ltd, World Wide Fund for Nature (South Africa), Exclusive Touch Pty Ltd, Southern Right Cellars, and Moby Dick Rum. For the photographs of the Ramsgate cow/calf pair I am indebted to the photographer, Mr F. Moodley, the pilot, Mr P. Buchell, and M. Fothergill of Durban Sea World. Observers at Cape Columbine included Mr A. la Cock, Ms G. Luyt, Messrs M. A. Meÿer and A. Rossouw, Ms K. Sink and Mr P. Zammit, while Dr K. Sekiguchi kindly assisted with the analysis of theodolite data. The support of the South African National Research Foundation (formerly the Foundation for Research Development) is gratefully acknowledged. This work was conducted under a series of permits issued to PBB in terms of the Sea Fisheries Act (Act 58 of 1973), Sea Fishery Act (Act 12 of 1988) and the Marine Living Resources Act (Act 18 of 1998).

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