Coastal and offshore movements of southern right whales on the South African coast revealed by satellite telemetry

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ABSTRACT

Twenty-one satellite-monitored radio tags were deployed on southern right whales in South African coastal waters in September 2001, and transmissions were received for 25 - 161 days from 15 of them. Most coastwise movement after tagging in St Sebastian Bay on the south coast occurred in a westerly direction, with cow-calf pairs moving slowest. Two individuals travelled far enough west to round Cape Point and onto the west coast, where one was tracked as far north as St Helena Bay. Of the five whales tagged at Saldanha Bay on the west coast, one travelled rapidly south and east, rounded Cape Point and reached St Sebastian Bay 10 days after tagging. Another also travelled south round Cape Point and into False Bay, while the remaining three animals moved north into St Helena Bay. These animals (and the one from St Sebastian Bay) remained within St Helena Bay for between 36 and 100 days, indicating the importance of this area as a probable feeding ground. Only six animals left the coast with their transmitters still functioning, departing from various sites along the coast and over dates ranging from 24 September to 8 January. All five whales subsequently tracked left the coast on a bearing of 201-220^{o} before branching out over the southeast Atlantic. Each animal travelled between 3,800 and 8,200 km over the ensuing 53 – 110 days before transmissions ceased, covering the region from 37 to 60^{o}S and between 13^{o}W and 16^{o}E. Locations were categorised as being ‘migrating’ or ‘non-migrating’ based on the relative orientation of the track and on the net speed. After removal of ‘migrating’ locations, there were 42 to 127 locations per whale that might represent other behaviour such as feeding. Of these 414 ‘feeding’ locations, 41.3% were between 37 and 45^{o}S and 54.1% from south of 52^{o}S, with only 4.6% in the intervening 7^{o} of latitude. The more northerly group seemed to be associated with the Sub Tropical Convergence, and the more southerly with the Antarctic Polar Front: Soviet whaling data suggest feeding largely on copepods at the former and euphausiids at the latter. Switching between widely separate feeding grounds was a strategy, with obvious cost-benefit implications: two whales that migrated between high and low latitude zones had appreciably fewer “feeding’ locations (29.2 – 35.9%) than the three others that stayed either in low or high latitudes (60.3 – 74.7%).

INTRODUCTION

Many published statements on the seasonal distribution and movements of southern right whales *Eubalaena australis* have relied to a large extent on data emanating from late eighteenth- and early nineteenth-century whaling (Bannister, 2001; Best, 1970, 1981), supplemented to some extent by information from illegal twentieth-century whaling (Tormosov *et al*., 1998). While patterns of apparent migration can be derived from such data, their interpretation depends heavily on assumptions regarding the process of whaling and how it might have been affected by influences other than the abundance of whales. Other indirect lines of evidence used to investigate possible movement patterns include stable isotope ratios in baleen (Best and Schell, 1996).

More recently, direct evidence of individual movement has been obtained from photo-identification matches (Best, 1997; Best *et al*., 1993; Bannister *et al*., 1999), but the timing, routes and speeds of migration still remain speculative.

In this paper we report on the movements of a number of southern right whales on and away from the South African coast following the deployment of satellite tags in September 2001. These were the first southern right whales and the first large whales of any species to be successfully tracked in the Southern Hemisphere using this technology.

MATERIAL AND METHODS

In September 2001, satellite transmitters were deployed on 21 southern right whales in South African waters. These were intended principally as trials of a modified tag before its deployment on North Atlantic right whales.

The tags were stainless steel cylinders 1.8 cm in diameter and 24 cm long, deployed from a crossbow and designed to be almost completely subdermal (with a stopper preventing the tag from becoming completely embedded). The outer end of the tag carried a 15 cm aerial and a 4 cm saltwater switch, while two sets of spring tines radiating from the body of the tag increased tag retention. The tag was coated with a long-lasting antibiotic prior to deployment (Mate, *et al*, 2007).

Sixteen of the tags were deployed in St Sebastian Bay on the south coast of South Africa between 8 and 13 September, and five outside Saldanha Bay on the west coast between 21 and 26 September. Eight tags were placed on cows with calves, all in St Sebastian Bay, while the remaining 13 were placed on animals without calves (Table 1). The gender of a tagged whale was established either because it had an accompanying calf, from visual inspection of its genital area, or from a skin biopsy by PCR amplification followed by *Taq*I digestion of the ZFX/ZFY region of the sex chromosomes (Palsbøll *et al.*, 1992).

All tagging was done in terms of a permit issued to PBB by the South African Department of Environmental Affairs and Tourism in terms of Regulation 58 of the Marine Living Resources Act (no. 18 of 1998) dated 10 January 2001. The subsequent sighting history of some of the tagged individuals has already been published (Best and Mate, 2007).

Tags were monitored by Argos Data Collection and Location Service receivers on NOAA TIROS-N weather satellites in sun-synchronous polar orbits. Locations were calculated by Argos from Doppler-shift data when multiple messages were received during the 7 to 16 mins of a satellite's passage overhead. Argos assigns the following theoretical location class (LC) accuracies (of one standard deviation) to locations calculated when at least four messages are received during a satellite pass: LC1

= 350 - 1,000 m; LC2 150 -350 m; LC3 = <150 m. These are considered high-quality locations. In some instances four or more messages may be received during a pass but the accuracy of such locations is considered to be > 1,000 m (LC0). Argos does not assign accuracy when less than four messages are received during a satellite pass (LCA – three messages, LCB – two messages, LCZ – single message). Based on results from previous tests (Mate *et al*., 1997), we have assigned an 11.5 km error around these poor quality locations (but see filtering process below).

Altogether, 2,132 locations were obtained from all tags combined, composed of 47 (2.2%) LC3, 185 (8.7%) LC2, 406 (19%) class 1, 472 (22.1%) LC0, 352 (16.5%) LCA, 589 (27.6%) LCB, and 81 (3.8%) LCZ. Locations were edited using the assigned accuracies as radial errors. Locations on land further than the assigned error distance from the ocean were not used (n = 53). Poor quality locations within one hour of high-quality locations were not used, nor were LC1 locations received within 10 minutes of LC2 or LC3 locations {n = 279). If two poor quality locations were received less than an hour apart, or if two LC1 locations were less than 10 mins apart, only the location providing the shortest distance between previous and subsequent locations of acceptable quality was used (n = 3). Minimum distances and speeds were then calculated between acceptable locations, and additional locations were eliminated if the estimated swimming speed of the whale between a location and the prior one was more than 15 km/h (after adjusting for radial error, and allowing for movement around headlands where appropriate (n = 42), or more than 10 km/hr for more than 5 hours (n = 2). And finally, given that they are normally classed by Argos as invalid, all remaining locations classified as LCZ were eliminated (n = 48).

In total, 427 locations were rejected, or 20% of those received (Table 1). The percentage rejection rate by location class was 3 (0%), 2 (0%), 1 (3.4%), 0 (23.5%), A (24.4%), B (22.9%) and Z (100%).

The remaining locations were used together with the 18 GPS locations obtained when the tags were deployed, to construct tracks for each whale. Distances between locations were calculated using the formula

$$d = \mathrm{acos}(\sin(lat_1).\sin(lat_2) + \cos(lat_1).\cos(lat_2).\cos(long_2 - long_1)).R$$

where d = distance in km and R = Earth's radius (6371 km).

These were used in combination with the elapsed time (recorded to the nearest second) to develop swimming speeds. These are net speeds, and unless the animal is consistently swimming in one direction will inevitably lead to an under-estimate of true speed over the ground, especially given the infrequency of successful uplinks to the satellite. Nevertheless, in combination with information about swimming direction, the net swimming speeds are useful as a comparative indication of animal behaviour in different habitats.

Initial bearings between locations were calculated using the formula

$$\theta = \mathrm{atan2}(\sin(long_2 - long_1).\cos(lat_2), \cos(lat_1).\sin(lat_2) - \sin(lat_1).\cos(lat_2).\cos(long_2 - long_1)).$$

A measure of the angular dispersion of movement, r, has been calculated for each set of 3 consecutive initial bearings ($a_1 \ldots a_3$), where

$$r = \sqrt{(\sum\cos(a_i)/n)^2 + (\sum\sin(a_i)/n)^2}.$$

The value of r varies inversely with the amount of dispersion, so that r = 0 indicates that there is total dispersion and r = 1.0 that all the bearings are identical (Zar, 1984).

RESULTS

Six of the tags either failed to transmit at all (#s 824, 834, 835) or for a day or less (#s 837, 1385, 10826), and have not been considered further in this paper. Four of these were deployed on cows with calves, and it is possible that their failure was due to aerial damage arising from the strong thigmotactic behaviour shown by neonatal right whales towards their mothers.

The remaining 15 tags transmitted for periods of between 25 and 161 days (Table 1). Those on cows with calves lasted for a shorter period (25-57, average 37 days) than those on other classes (35-161, average 84.5 days; Wilcoxon test, p=0.022). This is very probably the result of damage to the tag arising from the same interactive behaviour between cow- calf pairs as mentioned above.

Nine of the 15 tagged whales did not leave the coast before their tag stopped transmitting, 25 - 69 (average 43.6 days) after deployment. Four of these were cows with calves, one was an unaccompanied female and one a male. The remaining six whales (whose tags transmitted for between 64 and 161 days, averaging 114.2 days) all eventually left the coast, and all but one were then tracked to oceanic feeding grounds.

Because of the different geographic scales involved, and because the primary behaviours of the animals were likely to be different, the presentation of results has been largely divided into coastal and offshore movements.

Coastal movements

In order to depict the patterns of coastal movement of tagged right whales, the south-western coastline of South Africa has been stratified into adjacent segments corresponding to known favoured areas (Elwen and Best, 2004), and a time line of the number of days after tagging (DAT) spent in each segment constructed. As the tags were deployed separately in two discrete blocks of time and space, the time lines have been constructed separately for whales tagged in St Sebastian Bay (Table 2A) and Saldanha Bay (Table 2B).

From Table 2A it is obvious that most movement after tagging in St Sebastian Bay occurred in a westerly direction: only three of the 10 animals moved into the coastal segment adjacent to the east, and then only for a maximum of 8 days. Movement, however, was not always uni-directional; sometimes animals back-tracked into segments in which they had already been present (although some of these shifts may have been artefacts resulting from inaccurate locations). The westward movement of cow-calf pairs tended to be slower than for other classes: two cows were still in St Sebastian Bay 25 DAT or off De Hoop 27 DAT, while the other two finally rounded Cape Agulhas 23 and 43 DAT. By contrast, while one animal of unknown sex was still off Struisbaai 37 DAT, four other whales (a female, a male and two of unknown sex) rounded Cape Agulhas between 10 and 16 DAT, while a fifth (male) had already left the coast. The two cow-calf pairs tracked as far west as Walker Bay only arrived there 33 and 51 DAT, while four other animals reached the bay 12, 15, 20 and 22 DAT.

The clumped nature of the locations of the four tagged cows with calves (Fig. 1) suggests that their slower coastwise movement may be the consequence of socialisation or "waiting" for further calf development at particular, favoured sections of coastline.

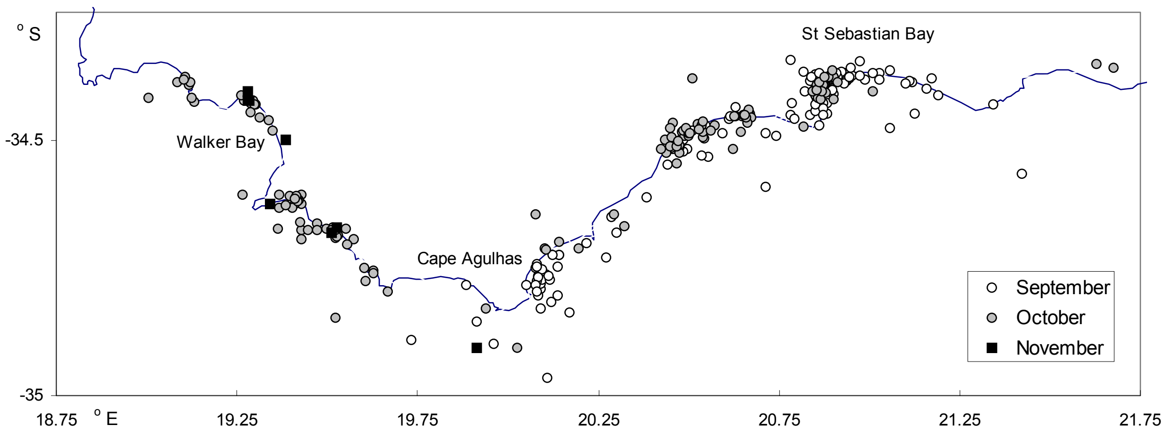

Fig. 1: Monthly locations received from four right whales with calves tagged in St Sebastian Bay on the South African coast, September to November 2001.

Two individuals (a male and one of unknown sex) tagged in St Sebastian Bay travelled far enough west to round Cape Point and move onto the west coast. One (23034) was tracked as far north as St Helena Bay, where it spent 39 days before transmissions ceased. This is the longest period of continuous occupancy of a single segment of coast by an animal tagged in St Sebastian Bay, and will be discussed further below.

The five whales tagged in Saldanha Bay consisted of a female, three males and one of unknown sex (Table 2B). The female travelled rapidly south and east, rounded Cape Point three DAT and Cape Agulhas eight DAT, and reached St Sebastian Bay 10 DAT. Two days later it left the coast. This is the fastest transit of the coast of any of the tagged animals.

One of the three males, after a brief visit to St Helena Bay, travelled south round Cape Point and into False Bay, from where it left the coast 27 DAT. The remaining two males and the animal of unknown sex moved north within a few days of tagging and entered St Helena Bay. Apart from an excursion into the Northern Cape by the animal of unknown sex (# 831), these animals seemed to remain within the bay (or off Saldanha Bay immediately to the south) for an extended period. The rate of information return for whale 831 (19 locations over 35 days) is lower than that for any of the other tagged whales, with a very high proportion (12/19) of category B locations, making it difficult to interpret its movements accurately. The two males (23031 and 23037) spent 100 days and 36-47 days (depending on interpretation of the incomplete location record) respectively within the bay, before they left the coast. Taken in conjunction with the movements of 23034 that had been tagged in St Sebastian Bay and spent a minimum of 39 days in St Helena Bay, it is clear this area was of some considerable importance to the whales. An inspection of the locations available for these four whales demonstrates an intense concentration in an area running roughly 50 km northeast from the headland at Cape Columbine (Fig. 2).

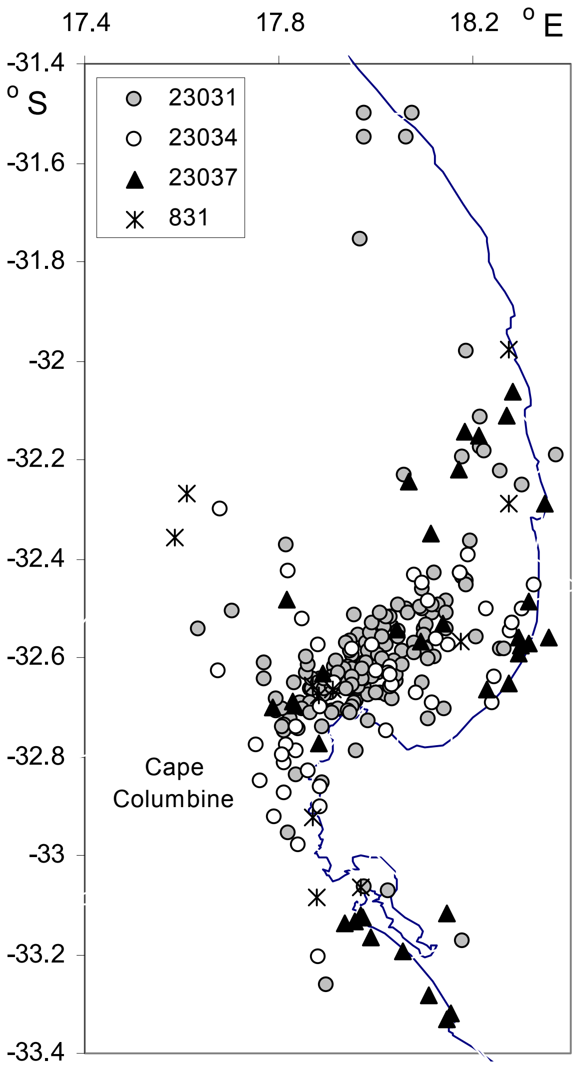

Fig. 2: Locations of four satellite-tagged right whales in the St Helena Bay area of South Africa, September 2001 – January 2002

Coastal "residence time" and departure from the coast

Departure from the coast was documented for six whales. The first (a male) left on 24 September, the second (an unsexed individual) on 30 September, the third (female) on 4 October and the fourth (male) on 25 October. The last two animals (both male) only left the coast after visiting the feeding ground in St Helena Bay, the first leaving some time between 20 and 25 November, and the second on 8 January 2002. Coastal residence times since tagging were therefore 16, 22, 13, 29, 59-64, and 108 days respectively (mean = 41-42 days).

Minimum residence times for the other tagged whales, whose transmitters ceased functioning before they left the coast, ranged from 25 to 57 days for four cow-calf pairs (average 37 days), and from 35 to 69 days (average 48.8 days) for five other whales, one of which was a male (66 days) and the other a female (36 days).

Departure points from the coast varied from the Cape Columbine area on the west coast (two animals) to Cape Point, Walker Bay, Cape Infanta and the Yservarkpunt region. No specific departure points were therefore favoured. The courses followed by the whales as they left the coast were however surprisingly consistent. For the first 700-800 km of their journey away from the coast, the distance-weighted average of bearings between locations for all five animals only varied from 201.2 to 220.5^{o}, with a mean of 211.2^{o} (Table 3). Irrespective of when or from where they left the coast, all whales seemed initially to head southwest into the South Atlantic. Thereafter, however, their behaviour varied greatly.

Rate and direction of movement

Net speeds of movement documented for cow-calf pairs were generally low, ranging up to 10.5 km/hr, but with 85.6% being less than 2 km/hr and 95% less than 5 km/hr; the overall mean was 1.3 km/hr (n = 314). Other classes of whale while in inshore waters exhibited a somewhat similar overall range of net speeds, but with relatively fewer in the slowest range class (<0.5 km/h) and more in the higher classes; their overall mean speed was 1.4 km/hr (n = 614). Such net speeds contrasted markedly with those seen once the whales moved offshore (Fig. 3, and see below).

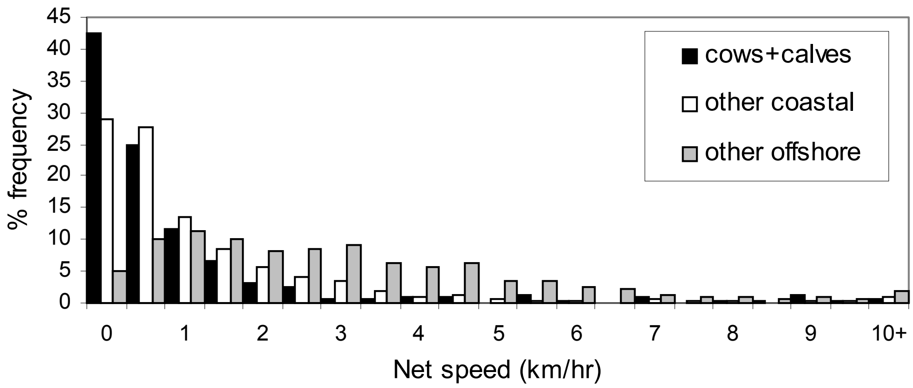

Fig. 3: Per cent frequency distribution of net speeds of movement of tagged southern right whales, comparing cow-calf pairs with other classes inshore and in offshore waters.

The distribution of r values between locations for both cow-calf pairs and other whale classes in coastal waters has a distinct mode at 0.3-0.4, indicative of little concerted directionality of movement (Fig. 4). This is what might be expected with animals whose main preoccupation seems to be moving along and around the coastline and between bays, rather than in one particular direction. The distribution of r values for whales that moved offshore however is quite different, with a small mode also at 0.3-0.4 but a much larger one at values of 0.9-1.0. This suggests two different behavioural modalities, the first corresponding to bouts of undirected movement and the second to bouts of concerted directional movement.

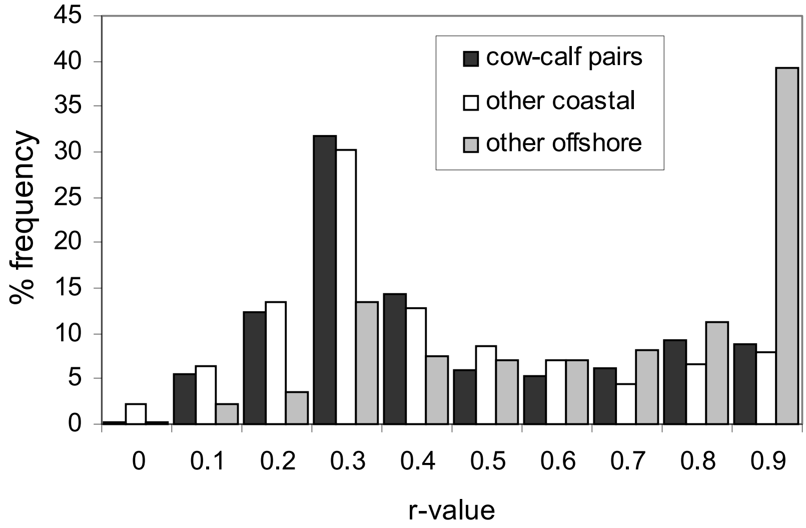

Fig. 4: Per cent frequency distribution of r-values for direction of movement of tagged southern right whales, comparing cow-calf pairs with other classes inshore and in offshore waters.

Choosing a value of r = 0.9 or above would therefore seem to be a useful way of discriminating between whales that are on the move and those that are indulging in some other activity (feeding, resting, reproduction). However, r values of this magnitude also occur, presumably by chance, in coastal waters where right whales are generally not considered to be migratory. In order to discriminate between whales with a high r value that are actively on the move and those that are not, the distribution of net speeds of movement of these animals has been compared between individuals on the coast and those offshore (Fig. 5). The distributions are clearly different, with 75.7% of animals travelling with this directionality inshore showing net speeds of less than 2 km/hr, whereas 83.9% of such animals offshore exhibit speeds in excess of 2 km/hr.

The criteria adopted for determining whether a section of track represents migratory behaviour or not have therefore been chosen as locations with an r value ≥ 0.9 and a net speed ≥ 2 km/hr.

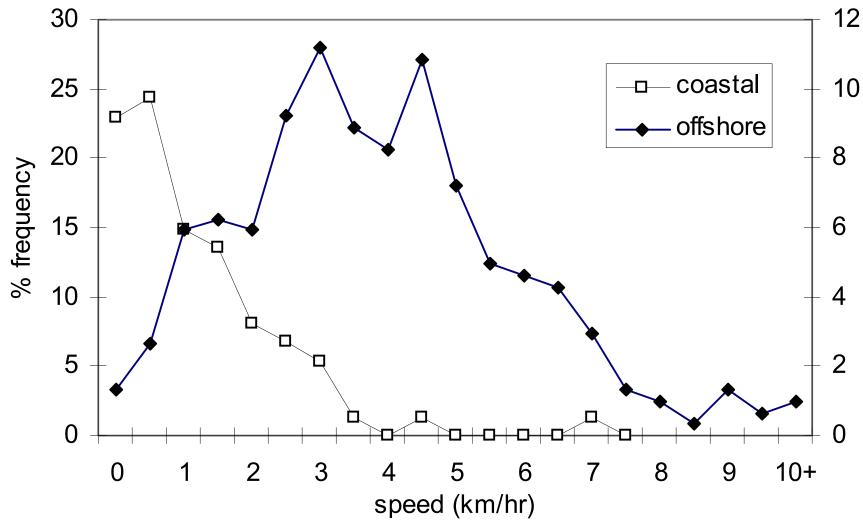

Fig. 5. The percent frequency distribution of net speeds of tagged right whales for locations with r values of 0.9 or more, compared between animals in coastal waters and those offshore.

Offshore movements

The movements of five of the six tagged right whales that departed the coast could be monitored – the transmitter of the sixth only produced one location of reasonable quality following departure. The whales comprised one female (836), three males (848, 4172 and 23031) and one of unknown sex (839).

Because of their consistent southwesterly heading upon leaving the coast, all five whales moved out into the South Atlantic, with the furthest east location south of 40°S being 18° 44'E (or well to the west of the longitude of Cape Agulhas). The five animals independently covered a large part of the South East Atlantic, from 37 to 60°S and between 13°W and 16°E, or roughly an area of 5. 3 million sq km. Each animal travelled between 3,800 and 8,200 km over the ensuing 53 – 110 days.

Although right whales are generally considered relatively slow-moving, some of the portions of offshore tracks that were classified as "migrating" showed an unexpected rate of travel (Table 3). Here the overall track lengths have been obtained by summing the component sections between locations, and dividing by the known time elapsed to give an average speed over the ground. Three of the tagged whales maintained an average speed of 5.1 to 5.7 km/hr over 9 to 20 days, while the fourth maintained an average of 4.4 km/hr over 22 days. All four were moving in a southerly direction away from the South African coastline.

Broadly speaking, there appeared to be three overall strategies for dispersal (Fig. 6). Two whales (848 and 23031) travelled more or less directly to high latitudes, with 77% and 79% of their locations coming from below 50°S. All locations from another whale (4172) were north of 46°S while the final two (836 and 839) moved between localities south of 50°S and north of 45° (up to 40°S). One of the latter two whales (839) made a second sortie down to nearly 60°S before its transmitter stopped.

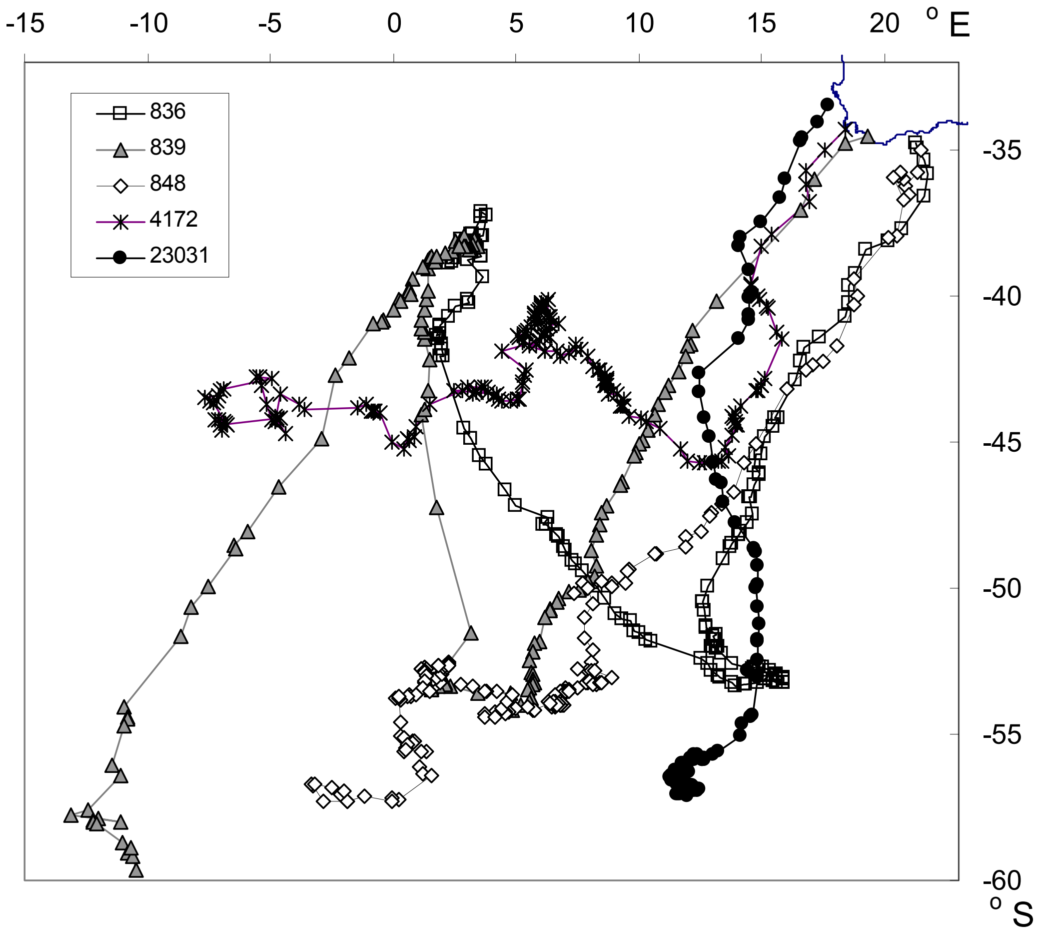

Fig. 6: Locations and tracks of five tagged right whales after leaving the South African coastline, September 2001 – March 2002.

Once all the locations that meet the criteria of a whale on migration were removed, there were 42 to 127 locations per whale remaining that might represent episodes of other behaviour such as feeding (Fig 7). These have been termed "feeding locations". Per individual these represent 29.2% to 74.7% of all locations received, with the two whales that migrated between high and low latitude zones (836 and 839) having appreciably fewer such locations (29.2 – 35.9%) than the other three (60.3 – 74.7%).

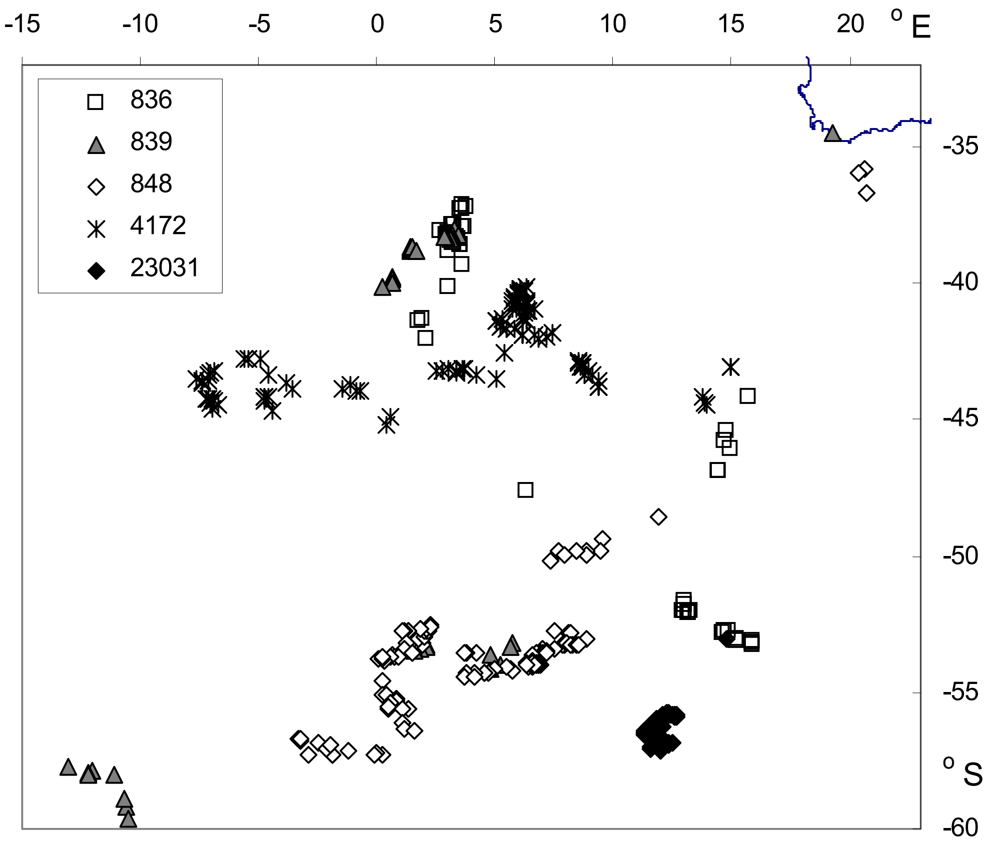

Fig. 7: Distribution of offshore "feeding locations" by latitude for tagged right whales in the Southeast Atlantic

Illustrating the distribution of these feeding locations by latitude over time from September to March makes the separation of the feeding zones clear (Fig. 8). In total, 41.3% of feeding locations were from between 37 and 45°S and 54.1% from south of 52 °S, with only 4.6% in the intervening 7° of latitude, and this separation persisted throughout the period of the feeding season monitored. At the same time, the situation of the southern zone seemed to shift gradually into higher latitudes as the season advanced.

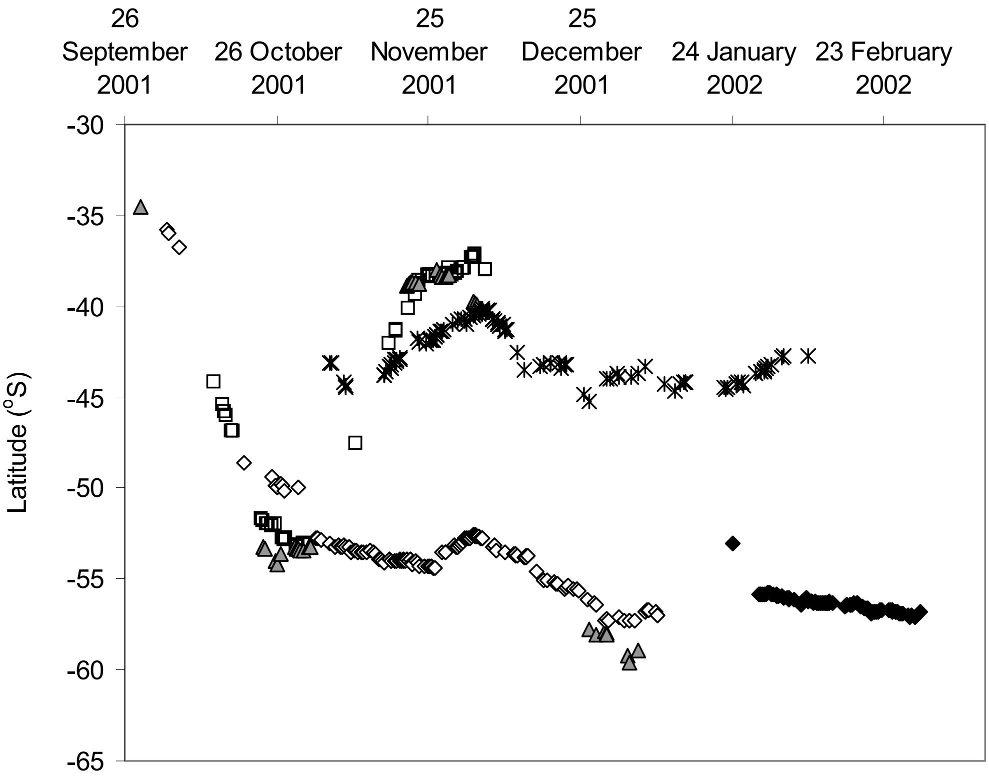

Fig. 8: Seasonal trends in the offshore latitudinal distribution of feeding locations of tagged right whales, September 2001 – March 2002.

DISCUSSION

The deployment of satellite tags provided an unprecedented opportunity for gaining insight into the patterns of movement of southern right whales on and away from the South African coastline. Nevertheless, limitations to the information provided include uncertainty in location accuracy, the limited number of satellite uplinks per day and the relatively short duration of transmitter function relative to the species' annual cycle.

Several different approaches to the filtering of marine mammal Argos locations to remove those of dubious accuracy have been developed based on estimates of swimming speed, distance between successive locations, turning angle, situation over land, Argos location quality, or a combination thereof (e.g. Austin *et al.*, 2003; Freitas *et al.*, 2008; Keating, 1994; McConnell *et al.*, 1992). All to some extent represent a compromise between an increase in accuracy and a loss of information, and so perhaps logically the approach to filtration should take account of the rate of data accrual and the use to which it is being put.

Our approach here has been based on the fact that the average number of locations received per day before filtration was 2 (reduced to 1.6 thereafter). This compares to some other marine mammal situations where as many as 5.7 locations (4.1 after filtration) may be received per day (Austin *et al.*, 2003). With the greater interval between locations resulting from duty cycles used to identify long-term seasonal distributions, it becomes problematic to use very aggressive filtering procedures.

We agree with Freitas *et al.* (2008) that in an animal occurring close inshore for sustained periods (such as a right whale) the automatic exclusion of all locations over land is not recommended as it could lead to an asymmetric offshore skewing of tracks: we prefer our approach here of using nominal location error to accept or reject a terrestrial location given that it is within a certain distance of the sea. We also concur with Austin *et al.* (2003) that the use of an approach involving turning angles and distances, such as that developed by Keating (1994) and Freitas *et al.* (2008), is problematic when applied to occasions in which signals may not be received from a tagged animal for an extended period of time (such as in this case). As stated by Austin *et al.*, given enough time large movements are possible by most marine mammals and to discard these apparent 'displacements' may be inappropriate, especially when (as is the case with right whales in coastal waters) the animal is not necessarily moving in a predictable direction.

The initial quality of locations received in this study (70% location classes <1) was at the upper end of the range frequently received from marine mammal tracks (69-93% for nine marine mammal species investigated by Freitas *et al.* (2008), for example). So although the filtration process only removed 20.3% of locations, the final tracks used contained 63.4% of locations of class <1. This compares to values of 60.2 – 86.8% for nine marine mammal species after they had been analysed using the SDA filter developed by Freitas *et al.* (2008), and 75.2% for the gray seal data after they had been subjected to the three-stage filtering algorithm of Austin *et al.* (2003).

The grouping of the locations from cows with calves in specific areas along the coastline is evident, especially in St Sebastian Bay, off De Hoop, in Struisbaai, around Quoin Point, in Walker Bay and Sandown Bay. These correspond to known concentration areas for cow-calf pairs along the southern coast of South Africa

(Elwen and Best, 2004). The obvious movements between them now suggest that these are areas of congregation where cow-calf pairs tend to linger to socialize or because conditions are somehow favourable.

This seasonal shift of cow-calf pairs to the west confirms what was suspected from re-sightings of individually-identified whales on aerial surveys (Best 2000), but could not be confirmed due to bias in the survey protocol. A similar westward shift of right whales along the southern Australian coast in winter was suggested by nineteenth-century whalers (Bannister, 1986), and subsequently confirmed by the movements of individually identified animals of both sexes, as part of a postulated annual anti-clockwise "circulation" of whales south of Australia (Burnell, 2001).

Unfortunately none of the tagged cow-calf pairs left the coast before its transmitter failed, but the apparent predominance of a south-westerly movement away from the coast by all five of the other animals that were tracked offshore might suggest that the there is some link between the westward coastal shift in winter and the south-westerly departure from the coast in spring. Given the prevailing West Wind Drift in the Southern Ocean south of Africa, utilisation of feeding grounds to the west of the continent in summer might make energetic sense (and would be consistent with a similar circulation pattern to that proposed by Burnell).

Despite the fact that they must inevitably be considered as minimal values, the coastal residence times of the tagged whales in this paper are still important as (unlike most earlier estimates based on photo-identification) they are not as subject to spatial or temporal limitations, and for some of them at least an exact date of departure is known. Not unexpectedly, given that neither arrival nor departure dates were monitored, the estimated residence times for cow-calf pairs (25-57 days, average 37 days) are much lower than those published from Australia (average 71 days, maximum 108 days – Burnell and Bryden, 1997) or indeed from South Africa (12-105 days, average 59 days – Best, 2000). The values for unaccompanied whales, however, are surprisingly high (13-108, average 41-42 days for those with known departure times, and 35-69, average 49 days for others) compared to those published for Australia (average 20.4 days, maximum 93 days – Burnell and Bryden, 1997). Part of this difference may be the inclusion of data for whales that visited St Helena Bay in spring: if these are excluded, the values for unaccompanied whales become 13 – 29 (average 20) days and 36-66 (average 47) days respectively.

Average and net swimming speeds for 34 groups of right whales in South African waters as recorded by theodolite from the shore ranged from 0.4 – 3.62 (mean 1.67) km/hr and 0.01 to 3.1 (mean 1.01) km/hr respectively. Net speeds estimated from re-sightings of individual cow-calf pairs at intervals of one day (n=17) ranged from 0.42 to 2.89, with a mean of 1.34 km/hr (Best, 2000). As these are of a similar magnitude to the majority of the net speeds estimated here for tagged whales in coastal waters, and well below the speeds recorded for offshore animals, it suggests that the satellite-derived data (although still conservative) are not unduly biased by location error or the interval between data points.

Swimming speeds recorded from satellite-tagged North Atlantic right whales ranged from 0.8 – 0.9 km/hr for two cow-calf pairs that remained within the Bay of Fundy to 1.5 – 4.6 (average 3.2) km/hr for seven other whales (including one cow-calf pair) that left the Bay and travelled widely in the western North Atlantic (Mate *et al*., 1997). This is a similar tendency to that observed here for whales monitored while inshore compared to those recorded when the whales moved offshore. The net speeds recorded during concerted southward movements of tagged whales (4.4 – 5.7 km/hr) are the first for "migrating" southern right whales, and are higher than all but one of the speeds recorded for North Atlantic whales by Mate *et al.* (1997), although they did not stratify the data in the same way to distinguish "migrating" from "non-migrating' sections of the tracks.

Perhaps the most interesting and unexpected result of the tagging was the discovery of the different feeding options available to right whales in the South Atlantic and the variety of strategies used to exploit them.

St Helena Bay was known as an historical whaling ground in the late eighteenth century (Best, 2006), and catches were concentrated there in summer and autumn, rather than in winter and spring. This suggests that its principal function was unlikely to be a nursery ground. The clumping of the tag locations shown in Fig. 2 corresponds with the position of a well-known upwelling plume that extends northwards from Cape Columbine and tends to curve eastwards towards the coast in apparent response to cyclonic wind curvature (Taunton-Clark, 1985). This region exhibits some of the highest levels of zooplankton abundance on the west coast (Verheye *et al*., 1998), and recent observations have confirmed the presence of whales feeding (largely on copepods) in the vicinity of the clump of tag locations in spring and early summer (PBB pers. obs.). There seems little doubt that this is a potentially important feeding ground for southern African right whales, although the exact number of animals using it still has to be established.

Of the two offshore zones utilised by right whales in summer, the more northerly seems to be associated with the Sub Tropical Convergence (STC) which in the South Atlantic has a mean position of 41^{o} 40'S and is an area known for its high primary productivity (Ansorge and Lutjeharms, 2007). In the south-east Atlantic in the vicinity of Tristan da Cunha, separate fronts have been associated with the northern and southern boundaries of the STC, with the northern front located at 35 – 37.3^{o}S and the southern at approximately 39^{o}S, although the positions of these fronts (especially the southern one) may shift seasonally by up to 2.5^{o} of latitude (Smythe-Wright *et al*., 1998). It is possible that the simultaneous "shadowing" of the feeding locations in the northern zone seen in November/December (Fig. 8) represents individuals foraging at the northern and southern boundaries of the STC, some 3^{o} of latitude apart. The stomachs of southern right whales examined north of 40^{o}S were dominated by copepods (91.7%), while 71.4% of those between 40 and 50^{o} S contained copepods, 24.3% euphausiids and the remainder small crustacea (Tormosov *et al*., 1998). This suggests that the whales' principal prey in this feeding zone was copepods.

Although the right whales' prey has not been specifically identified, a similar latitudinal succession of prey-types has been recorded for the Antarctic sei whale, and given the similar feeding behaviour and distribution of the two whales it is possible that the same food species are involved. Copepods (especially *Calanus tonsus* and *C. simillimus*) occurred in the sei whale diet from about 40°S to the middle of the SubAntarctic zone, dominating to the north but closer to 50°S being supplanted as the dominant food type by smaller euphausiids such as *Euphausia vallentini* or the amphipod *Themisto gaudichaudii* (Kawamura, 1974).

The more southerly feeding zone, running from 52-57°S, may correspond to the position of the Antarctic Polar Front (APF, otherwise known as the Antarctic Convergence). At this front, northward-moving Antarctic water sinks below warmer subantarctic water, forming strong horizontal gradients in temperature and salinity: its average location is at 52-53°S, although south of Africa it may lie at only 50°47'S (Ansorge and Lutjeharms, 2007). South of 50°S, right whale stomach contents consisted almost entirely (99.4%) of unidentified euphausiids (Tormosov *et al.*, 1998). Sei whales at these latitudes were feeding to the north on *Themisto gaudichaudii* and to the south on *Euphausia superba* (Kawamura, 1974), and these remain the most likely targets for right whales feeding in this zone.

The five southern right whales tracked here displayed four different feeding strategies involving three different feeding zones. Two individuals (836 and 839) travelled firstly to the APF and then to the STC, with 839 subsequently returning to the APF. One individual (848) travelled to the APF and was not recorded as leaving there before its transmitter failed. Another individual (4172) seemed to only visit the STC, while the last (23031) spent 100 days in St Helena Bay before moving directly to the APF. Some of these strategies may have converged, or new ones emerged, if any of the animals had been tracked for an entire summer season, but this remains an objective still to be achieved.

Only two of the whales visited any of the offshore nineteenth-century whaling grounds in the South Atlantic depicted by Townsend (1935). Whales 836 and 839 spent 22 November – 10 December and 19 November - 3 December respectively in the vicinity of 37-39°S 1-4°E, or roughly in the centre of a line of nineteenth-century catches extending from 15°E to 10°W and between 30° and 38°S: the timing of their visit agreed well with the historic catches which mostly took place between October and January. The remainder of the locations from these and other tagged animals were south of 40°S and down to 60°S, a region where Townsend's charts indicate little or no catching. Takes by Soviet whalers in the 1960s, however, did occur in a diffuse area between 51° and 63°S and from 15°W to 30°E (Tormosov *et al.*, 1998), which agrees reasonably well with the locations of the tagged whales in the southern feeding zone. The timing of the Soviet catches was between December and April with a peak in March, somewhat later than most of the locations recorded here, but the longest-lasting transmitter only functioned until 2 March. It remains an open question whether the greater incidence of higher latitude catches in the twentieth compared to the nineteenth centuries was the result of a shift in whale distribution or the consequence of differing operational constraints in the two eras of whaling (Tormosov *et al.*, 1998).

Also of interest is the lack of any migration to the south-east from the South African coast towards the nineteenth-century whaling grounds at the Crozets or Kerguelen, or towards the band of catches between 30 and 40°S to the north of those islands (Townsend, 1935). The presence of right whales at the Crozet and Kerguelen Islands was confirmed by Soviet catches in the 1960s (Tormosov *et al.*, 1998), and the lack of a link could simply be a consequence of the small number of whales tagged (or the timing of the taggings), although the general westward shift of the tagged animals suggests this is unlikely. Possibly these feeding grounds are frequented by right whales that over-winter in the East African region (e.g. Mozambique, Madagascar, Reunion/Mauritius), where recent sightings remain rare (Best 2007, Rosenbaum *et al.*, 2001).

Although Baumgartner and Mate (2005) undertook a similar telemetric study of North Atlantic right whales, a direct comparison with their results is difficult. Firstly, their tags were applied between July and October (61% in August), or late in the boreal summer, whereas the South African tags were deployed in September or the early austral spring. Secondly, the North Atlantic whales were tagged in the Bay of Fundy, a high-latitude feeding ground, as opposed to a lower latitude calving ground in this study. And lastly, the duration of the North Atlantic tags was much shorter (6 - 126, average 31.8 days, n = 18) than the South African tags (25 – 161, average 71.8 days, n = 15). Nevertheless, there are some striking differences. The distribution of the North Atlantic locations covered a much smaller area (about 7^{o} of latitude by 12^{o} of longitude) than in the South Atlantic. Although this might be partly attributed to shorter tag longevity, tagged animals visited all the major known feeding habitats in the western North Atlantic, namely Cape Cod Bay, Great South Channel, Bay of Fundy and Roseway Basin, so there is no *a priori* reason to suppose that the marked difference in the range area would have disappeared given equal tag duration (unless the range then included the unknown "Bay of Fundy-none" feeding ground (Schaeff et al., 1993)). As a corollary of this, most (ca 94%) locations in the North Atlantic were over the continental shelf in water less than 200 m deep, whereas once they left the coast, the whales tagged in South Africa were invariably in water over 200 m (and usually over 2,000 m) deep. Individual North Atlantic whales clearly cross deep water basins on occasion, and one of the satellite-tagged animals moved offshore into water 4,200 m deep before returning inshore (Jacobsen *et al*., 2004), but there does not seem to be any record of them habitually using an offshore, deep-water feeding ground, although numbers were taken historically in mid-summer on the Cape Farewell whaling ground south of Greenland (Reeves *et al*., 2007).

Attempts to characterise right whale feeding habitats have not been completely successful, possibly because their ultimate determinant must be the availability of the target prey species in high enough concentrations, and the factors that create these conditions may vary in space and time. Baumgartner *et al.* (2003), for instance, found that while water depth and the depth of the Bottom Mixed Layer (BML) might be important for right whales in the lower Bay of Fundy and Roseway Basin, water depth would not be as influential in the shallower Cape Cod Bay and the significance of the BML could disappear in spring. Furthermore, a horizontal gradient in sea surface temperature was important in determining both right whale spatial availability and inter-annual variability in occurrence in Roseway Basin but not in the lower Bay of Fundy. The current data also illustrate how different the physical conditions of foraging habitats may be for southern right whales, ranging from coastal upwelling plumes to major oceanic fronts.

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REFERENCES

Ansorge, I. J., and Lutjeharms, J.R.E. 2007. The cetacean environment off southern Africa. Pp 5-13 in *Whales and Dolphins of the southern African Subregion.* Cape Town, Cambridge University Press.

Austin, D.J., McMillan, J.I., and Bowen, W.D. 2003. A three-stage algorithm for filtering erroneous Argos satellite locations. *Marine Mammal Science* 19: 371-383.

Bannister, J.L. 1986. Southern right whales: status off Australia from twentieth-century 'incidental' sightings and aerial survey. *Report of the International Whaling Commission* (Special Issue 10): 153-158.

Bannister, J. 2001. Status of southern right whales (*Eubalaena australis*) off Australia. *Journal of Cetacean Research and Management* (Special Issue 2): 103-110.

Bannister, J.L., Pastene, L.A., and Burnell, S.R. 1999. First record of movement of a southern right whale (*Eubalaena australis*) between warm water breeding grounds and the Antarctic Ocean, south of 60^{o}S. *Marine Mammal Science* 15(4): 1337-1342.

Baumgartner, M.F., Cole, T.V.N., Clapham, P.J., and Mate, B.R. 2003. North Atlantic right whale habitat in the lower Bay of Fundy and on the SW Scotian Shelf during 1999-2001. *Marine Ecology Progress Series* 264: 137-154.

Baumgartner, M.F., and Mate, B.R. 2005. Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 527-543.

Best, P.B. 1970. Exploitation and recovery of right whales *Eubalaena australis* off the Cape Province. *Investigational Report of the Division of Sea Fisheries, South Africa* 80: 1-20.

Best, P.B. 1981. The status of right whales (*Eubalaena glacialis*) off South Africa, 1969-1979. *Investigational Report of the Sea Fisheries Institute, South Africa* 123: 1-44.

Best, P.B. 1997. *Whale watching in South Africa. The southern right whale*. Pretoria, Mammal Research Institute. Second Edition. 28 pp.

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. 2006. The presence of right whales in summer on the west coast of South Africa: the evidence from historical records. *African Journal of marine Science* 28 (1): 159-166.

Best, P.B. 2007. *Whales and dolphins of the Southern African Subregion*. Cape Town, Cambridge University Press, i-xiii + 338 pp.

Best, P.B., and Mate, B.R. 2007. Sighting history and observations of southern right whales following satellite tagging off South Africa. *Journal of Cetacean Research and Management* 9(2): 111-114.

Best, P.B., Payne, R., Rowntree, V., Palazzo, J.T., and Both, M.C. 1993. Long-range movements of South Atlantic right whales *Eubalaena australis*. *Marine Mammal Science* 9 (3): 227-234.

Best, P.B., and Schell, D.M. 1996. Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Marine Biology* 124: 483-494.

Burnell, S.R. 2001. Aspects of the reproductive biology, movements and site fidelity of right whales off Australia. *Journal of Cetacean Research and Management* (Special Issue 2): 89-102.

Burnell, S.R., and Bryden, M.M. 1997. Coastal residence periods and reproductive timing in southern right whales, *Eubalaena australis*. *Journal of Zoology, London* 241: 613-621.

Elwen, S., and Best. P.B. 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 (3): 567-582.

Freitas, C., Lydersen, C., Fedak, M.A., and Kovacs, K.M. 2008. A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science.*

Jacobsen, K., Marx, M., and Øien, N. 2004. Two-way trans-Atlantic migration of a North Atlantic right whale (*Eubalaena glacialis*). *Marine Mammal Science* 20(1): 161-166.

Kawamura, A. 1964. Food and feeding ecology in the southern sei whale. *Scientific Reports of the Whales Research Institute, Tokyo* 26: 25-144 + 3 pl.

Keating, K.A. 1994. An alternative index of satellite telemetry location error. *Journal of Wildlife Management* 58 (3): 414-421.

Mate, B.R., Mesecar, R., and Lagerquist, B. 2007. The evolution of satellite-monitored radio tags for large whales: one laboratory's experience. *Deep-Sea Research II* 54: 224-247.

Mate, B.R., Nieukirk, S.L., and Kraus, S.D. 1997. Satellite-monitored movements of the northern right whale. *Journal of Wildlife Management* 61(4): 1393-1405.

McConnell, B.J., Chambers, C., and Fedak, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarctic Science* 4: 393-398.

Palsbøll, P.J., Vader, A., Bakke, I., and Raafat El-Gewely, M. 1992. Determination of gender in cetaceans by the polymerase chain reaction. *Canadian Journal of Zoology* 70: 2166-2170.

Reeves, R.R., Smith, T.D., and Josephson, E.A. 2007. Near-annihilation of a species: right whaling in the North Atlantic. Pp 39-74 in (Kraus, S.D., and Rolland, R.M., eds) *The urban whale. North Atlantic right whales at the crossroads.* Cambridge, Mass., London, Harvard University Press.

Rosenbaum, H.C., Razafindrakoto, Y., Vahoavy, J., and Pomilla, C. 2001. A note on recent sightings of southern right whales (*Eubalaena australis*) along the east coast of Madagascar. *Journal of Cetacean Research and Management* (Special Issue 2): 177-180.

Schaeff, C.M., Kraus, S.D., Brown, M.W., and White, B.N. 1993. Assessment of the population structure of western North Atlantic right whales (*Eubalaena glacialis*) based on sighting and mtDNA data. *Canadian Journal of Zoology* 71: 339-345.

Smythe-Wright, D., Chapman, P., Duncombe Rae, C., Shannon, L.V., and Boswell, S.M. 1998. Characteristics of the South Atlantic subtropical frontal zone between 15 ^{o}W and 5^{o}E. *Deep-Sea Research I* 45 167-192.

Taunton-Clarke, J. 1985. The formation, growth and decay of upwelling tongues in response to the mesoscale wind field during summer. Pp 47-61 in (Shannon, L.V., ed.) *South African Ocean Colour and Upwelling Experiment*. Cape Town, Sea Fisheries Research Institute.

Tormosov, D.D., Mikhaliev, Y.A., Best, P.B., Zemsky, V.A., Sekiguchi, K., and Brownell, R.L., Jr. 1998. Soviet catches of southern right whales, *Eubalaena australis*, 1951 - 1971; Biological data and conservation implications. *Biological Conservation* 86: 185-197.

Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica NY* 19(1): 1-50.

Verheye, H.M., Richardson, A.J., Hutchings, L., Marska, G., and Gianakouras, D. 1998. Long-term trends in the abundance and community structure of coastal zooplankton in the southern Benguela system. *South African Journal of Marine Science* 19: 317-332.

Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. Second Edition.

Table 1: Details of satellite tags deployed on southern right whales off South Africa, 2001

Tag	Class tagged	Date deployed	Where deployed	Date of last location	Days at large	No. of filtered locations, by location class							No. rejected	% rejected
						3	2	1	0	A	B	Total		
823	Cow + calf	08-Sep-01	St Sebastian Bay	03-Oct-01	25	3	9	10	7	2	10	41	4	8.89
824		08-Sep-01	St Sebastian Bay	n/a	0							0		
825		08-Sep-01	St Sebastian Bay	16-Oct-01	38		9	23	33	6	10	81	24	22.86
826	Female	08-Sep-01	St Sebastian Bay	14-Oct-01	36		4	6	5	8	9	32	4	11.11
827	Cow + calf	08-Sep-01	St Sebastian Bay	05-Oct-01	27	5	13	10	3	3	11	45	13	22.41
831		22-Sep-01	Saldanha Bay	27-Oct-01	35		1	1	3	2	12	19	9	32.14
834	Cow + calf	12-Sep-01	St Sebastian Bay	n/a	0							0		
835	Cow + calf	13-Sep-01	St Sebastian Bay	n/a	0							0		
836	Female	21-Sep-01	Saldanha Bay	11-Dec-01	81	4	13	51	39	24	49	180	44	19.64
837	Female	12-Sep-01	St Sebastian Bay	12-Sep-01	<1			1				1		0.00
838	Male	12-Sep-01	St Sebastian Bay	17-Nov-01	66	10	22	16	10	14	28	100	14	12.28
839		08-Sep-01	St Sebastian Bay	05-Jan-02	119	1	11	42	35	28	45	162	35	17.77
843	Cow + calf	08-Sep-01	St Sebastian Bay	17-Oct-01	39	9	23	45	15	6	6	104	34	24.64
847	Cow + calf	12-Sep-01	St Sebastian Bay	08-Nov-01	57	6	24	35	23	13	22	123	26	17.45
848	Male	08-Sep-01	St Sebastian Bay	09-Jan-02	123		9	23	42	40	72	186	40	17.70
1385	Cow + calf	08-Sep-01	St Sebastian Bay	09-Sep-01	1		1		1			2	2	50.00
4172	Male	26-Sep-01	Saldanha Bay	10-Feb-02	137	2	14	38	51	43	62	210	63	23.08
10826	Cow + calf	13-Sep-01	St Sebastian Bay	13-Sep-01	<1				1			1		0.00
23031	Male	22-Sep-01	Saldanha Bay	02-Mar-02	161	4	29	77	59	58	84	311	84	21.27
23034		12-Sep-01	St Sebastian Bay	20-Nov-01	69			7	27	9	24	67	25	27.17
23037	Male	22-Sep-01	Saldanha Bay	25-Nov-01	64	3	3	7	7	10	10	40	6	13.04
Total					1078	47	185	392	361	266	454	1705	427	20.03

Table 2: A summary of coastwise movements of tagged right whales off South Africa, expressed as the time in days post tagging spent in each area, or passing a certain feature. Apparent gaps in the time line reflect missing days of transmissions.

A. Whales tagged in St Sebastian Bay, 8 – 12 September 2001

Tag no.	Yservark punt area & offshore	**St Sebastian Bay**	De Hoop	Struisbaai	Round Cape Agulhas	Quoin Point area	Walker/ Sandown Bay area	Round Cape Point	West coast south of Saldanha	St Helena Bay area	Fate
Cow-calf pairs											
823	22 - 23	T + 14, 21 – 22, 24 – 25+	14 - 20								Signal lost
827		T + 19	20 - 27+								Signal lost
843		T + 4	4 -5, 16 - 18	5, 8 – 15, 19 - 22	<7, 23	24 - 32	33 – 39+				Signal lost
847		T + 1, 3 - 28	1, 28 – 30, 33 - 42	30 – 32, 43	43	43 - 51	51 – 57+				Signal lost
Other females											
826		T + 4, 8 - 11	5 – 7, 12 - 13		< 16	16 - 17	22 – 36+				Signal lost
Males											
838		T + 8	9 - 14	14	15	16 - 19	20 – 47	52	56 – 66+		Signal lost
848	10 - 18	T + 3, 8 - 9	3 - 4								Left coast
Unknown											
825		T + 13, 27 - 29	14 – 26, 30 - 33	34 – 37+							Signal lost
839		T	1 - 4	11 - 12	< 8, >12		15 - 21				Left coast
23034	4	T, 8	8		< 10	10	12 - 20	24	25 - 28	30 – 69+	Signal lost

B. Whales tagged in Saldanha Bay, 21 – 26 September 2001

Tag no.	Northern Cape	St Helena Bay area	**Saldanha Bay**	West coast south of Saldanha	Round Cape Point	False Bay	Walker/ Sandown Bay area	Quoin Point area	Round Cape Agulhas	De Hoop	St Sebastian Bay	Fate
Females												
836			T + 1	1 - 2	3	4	5 - 6	7 - 8	8	9 - 10	10 - 12	Left coast
Males												
4172		2 - 4	T + 1	7 - 21	21	22 - 27						Left coast
23031		7 - 107	T + 7									Left coast
23037		11 – 46, 59	T, 7 – 9, 52	1 - 4								Left coast
Unknown												
831	16 - 27	2, 13, 29 - 35+	T + 1, 8									Signal lost

Table 3: Some movement parameters for the five tagged right whales that moved offshore from the South African coast, 2001/2

Tag no.	Initial departure				Whole offshore period				Concerted southward migration				
	Date departed	Initial distance covered (km)	Number of locations	Average bearing, distance-weighted	Days away from coast	Number of locations (number migrating)	Distance travelled (km)	Overall speed (km/hr)	Start position	End position	No. of locations en route	Ground covered (km)	Ave speed over ground (km/hr)
836	4 October	731.4	10	201.2^{o}	67	153 (98)	5,606	3.48	34.773S 21.271E	44.15S 15.51E	17	1,284.7	5.7
839	29 September	853.6	5	220.5^{o}	100	143 (102)	8,197	3.43	34.782^{o}S 18.366^{o}E	53.101^{o}S 05.68^{o}E	44	2,467.6	4.4
848	27 September	703.9	12	215.7^{o}	105	170 (43)	5,766	2.29	37.915S 20.502E	48.256S 11.921E	18	1,534	5.1
4172	23 October	733	9	210^{o}	110	174 (69)	6,236	2.36					
23031	8 January	727	9	208.5^{o}	53	136 (50)	3,846	3.00	33.475^{o}S 17.669^{o}E	55.872^{o}S 12.678^{o}E	43	2,861.5	5.6