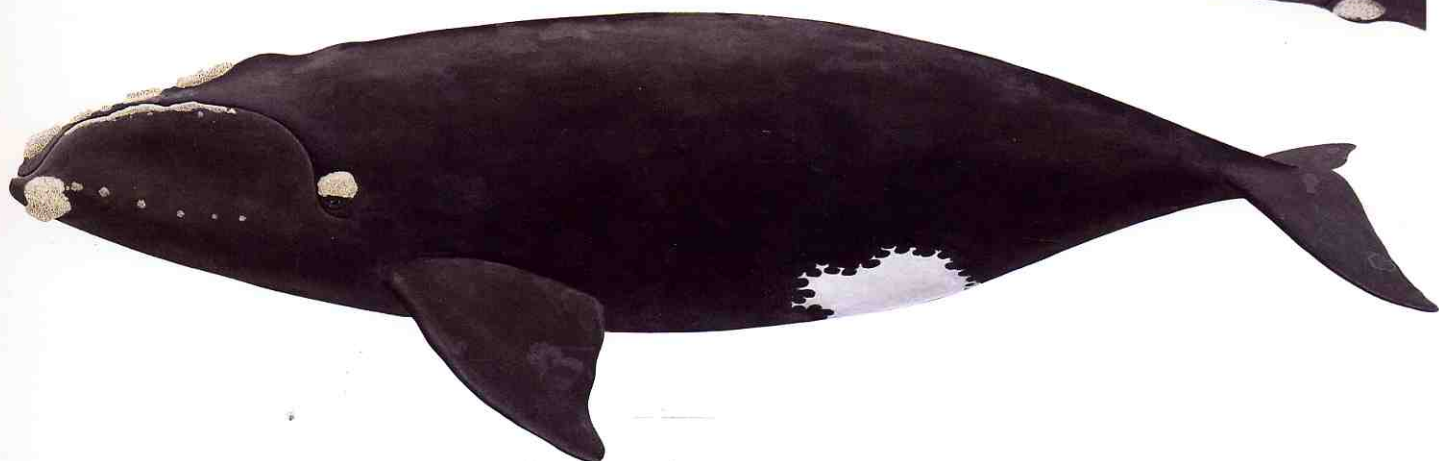


Family BALAENIDAE

Southern Right Whale

Eubalaena australis

Dorsal view of head and callosity pattern



'RIGHT' OR 'TRUE' were epithets applied by early whalers to balaenid whales, apparently in recognition of their commercial value, especially the long tapering baleen that was superior to that of other whalebone whales. The fact that they were slow-moving, produced high oil yields, (usually) floated when dead, and showed fidelity to nearshore calving grounds, must also have helped. Right whales in the southern hemisphere are now regarded on phylogenetic grounds as a distinct species from those in the North Atlantic (*E. glacialis*) and North Pacific (*E. japonica*), although reliable morphological criteria for distinguishing between the three species are still lacking.^{1,2}

Appearance

Right whales are hard to confuse with any other large whale. Firstly, they lack a dorsal fin, and, secondly, their head is covered with a pattern of yellowish-white wart-like callosities – sometimes referred to colloquially as the 'rock garden'. The blow is also characteristically V-shaped, although like all blows this can be affected by wind and whale behaviour, and humpback whales are also able to produce a similar blow. When lying at rest on the surface, which they tend to do a lot, right whales resemble overweight hippos.

Adult females average 13.9 m in length with a maximum of 15.5 m,³ and are perhaps slightly larger than males.⁴ The head is big, forming 27–31% of the length in adults, the upper jaw narrow and the lower lips strongly arched upwards. The flippers are large (16–21% of the body length) and broad (maximum width 50–58% of flipper length). Although they are sometimes described as paddle-shaped, in reality the flippers are more rectangular in outline, but with a pointed tip.⁵ The flukes are pointed rather than hooked at the tip (as in humpback whales), and in adults their width averages 36% of body length.³ Right

whales are not shy to expose both their flippers and flukes above the surface.

The callosities are distributed over the head in a distinct pattern, but with sufficient variation to make them extremely useful in identifying individuals. The most prominent sits at the

Length:weight relationship

For 19 North Pacific right whales, $W = 0.0124L^{3.06}$, where W = weight in tonnes and L = total length in metres.¹¹ As these weights have been unadjusted for weight loss during cutting up, about 6% should be added.

Weights of only three southern right whales are available, all from South Africa. A 4.8 m female neonate weighed 1.1457 tonnes, a 9.85 m female 9.975 tonnes, and a 10.78 m female 16.34 tonnes: the first was weighed in pieces and the others whole.⁸ If these are added to the weights for eight North Atlantic right whales (which are more like southern right whales in size than North Pacific right whales) already corrected for weight loss during dismemberment (6.8%),¹² then $W = 0.0116L^{3.037}$, where W = weight in tonnes and L = total length in metres. This implies that a 10 m whale would weigh 12.6 tonnes and a 15 m whale 43.3 tonnes.

Skeletal data

Vertebral formula: 7 cervical, 15 thoracic, 9–11 lumbar and 21–27 caudal; total 54–57.¹³

All cervical vertebrae are fused.

Phalangeal formula: I₂₋₃, II₅, III₆, IV₅₋₆, V₄.¹³

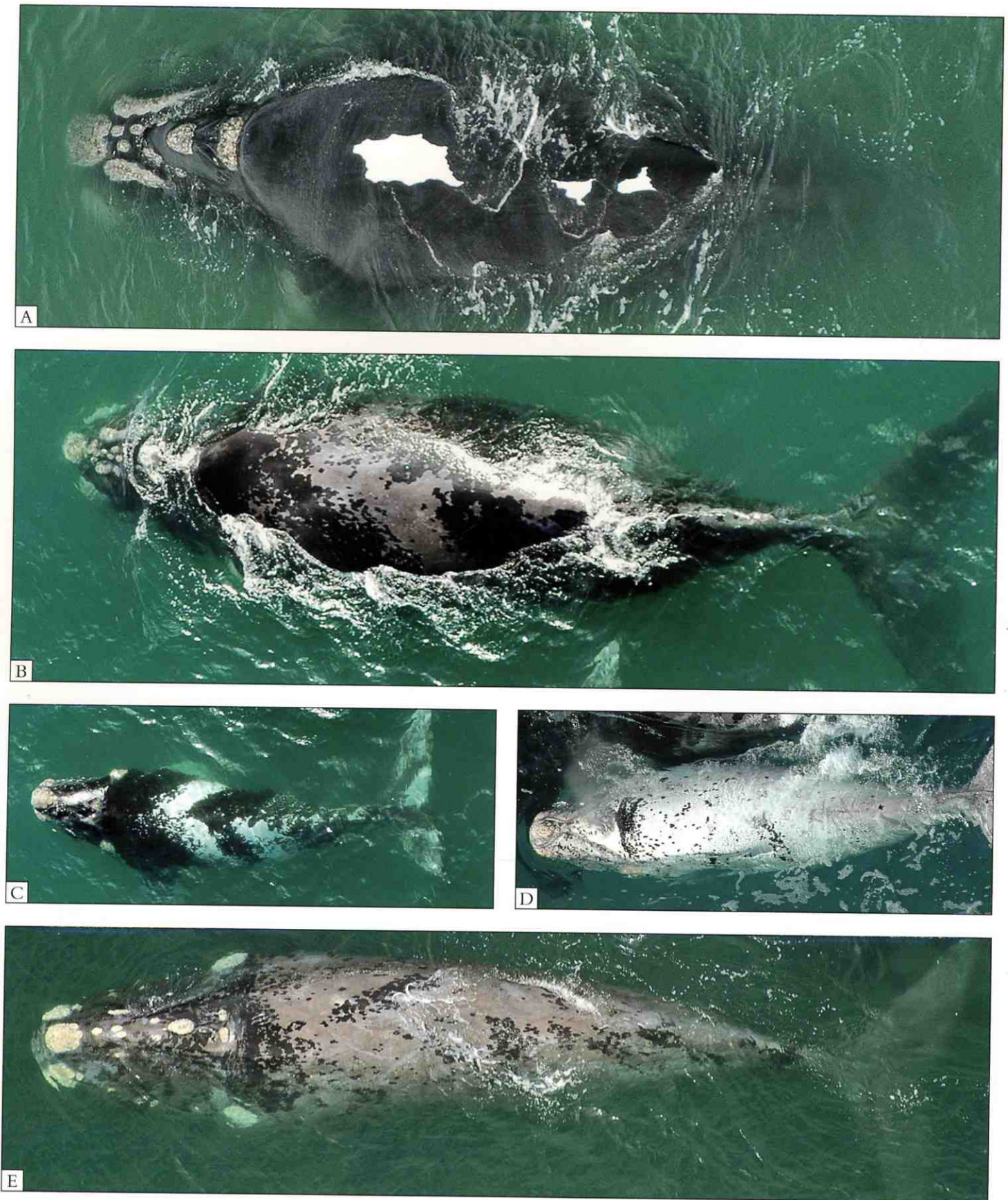


FIG. 7 Variations in pigmentation patterns of southern right whales: (A) White blazes stay permanently white and are found equally on both sexes; (B) Irregular markings such as these are white in the calf (C) but gradually darken with age, and are only found in females; (D) A few calves are born almost completely white (apart from a black collar and variable spotting), but also darken with age (E). Such 'brindled' animals are nearly always male.

tip of the snout and is known as the 'bonnet'. In front of the blowhole there is a 'coaming', and behind the blowhole a pair of 'post-blowhole' callosities. Between the bonnet and the coaming are a variable number of smaller, scattered 'rostral islands'. Above each eye is an 'eyebrow' callosity, on each side of the chin a 'chin callosity', and on the side of the lower jaw a number of small 'mandibular callosities'. Finally, and more typical of southern than northern right whales, there are often 'lip callosities' along the upper edge of each lower lip. These tend to be asymmetrical, being bigger on the right than on the left side of the head. Each callosity corresponds to the position of one or more rudimentary hairs that can be seen in stranded animals protruding bristle-like from the centre. Much of the contrast between the colour of the callosities and the surrounding black skin comes from the layer of external parasites (mostly cyamids) that cover the callosities (see page 32).⁶

Right whales were often referred to as 'black whales' by open-boat whalers, and indeed most individuals are black in colour, at least on the back. On the belly, however, most animals possess a white blaze in the region of the navel, varying in size from a small spot to a large irregularly-shaped blaze that may extend up the side and sometimes even onto the back. Separate white blazes on the back are found in 4.8% of adults and seem to be evenly distributed between the sexes. Some animals also carry grey streaks or flecking on the back, usually highly irregular in outline, and often in the shape of a V or partial V, pointing forwards. These marks are white at birth and sometimes difficult to distinguish from a white blaze, but unlike the blazes they gradually darken with age to become grey in adults. Such markings are only found in females, and 10.5% of adult cows carry them (including 1.4% with both white blazes and grey markings). Most interesting of all, perhaps, are the 3.5% of calves that are born almost completely white. They are never completely white, always having a collar of black around the neck and a variable amount of black spotting on the adjacent back, but they are invariably reported as 'white' calves. As in the grey markings of females, the white colour gradually fades to become grey in adults (but with the black collar and spotting still visible), giving a sort of 'brindled' appearance. About 94% of these brindled animals are male; females of this colour phase can only be produced by the union of a brindled male with a female with grey markings. In North Atlantic right whales neither white nor grey dorsal markings, nor white calves, have been recorded, and in the North Pacific only whales with a white dorsal blaze.⁷

Southern right whales carry an average of 222 (range 196–246, $n = 11$) baleen plates on each side of the upper jaw,^{5,8} with a conspicuous gap between the series at the front of the mouth. The plates are characteristically long and narrow, reaching a maximum length (including the gum) of 2.38 m and a width at the base of 0.20 m. They are a greyish-black and the fringe a yellowish-brown in colour, while the baleen gum (which is often exposed above water during skim-feeding) is a pale whitish-grey. Baleen plates are already erupted in newborn whales but only as a meagre 9 cm or so: by the time the whale is one year old the baleen may have reached a length of 70 cm (including the gum). In the second year the plates begin to wear away at the tip, but still continue to grow in overall length.⁹ In young right whales the baleen bristles are among the finest in all baleen whales, averaging 0.13–0.19 mm in diameter and being spaced at about 45–55/cm.¹⁰

Distribution and migrations

With blubber up to 36 cm thick on the back, southern right whales are reluctant to venture into the tropics. Their distribution is often described as south of 20° S, but in regions where a cold current extends into the tropics (such as off the west coasts of southern Africa and South America) right whales will venture further north. On the west coast of southern Africa, for example, the northernmost known whaling ground for the species was at Baia dos Tigres in southern Angola (or c. 16° S), whereas on the east coast the most northern whaling ground was Maputo Bay (or c. 26° S). Obviously these are not absolute limits, since an individual was taken off Cap Lopez, Gabon (c. 1° S) in 1951¹⁴ and a sighting was made in Antongil Bay, Madagascar (15°31' S) in 1997.¹⁵

There has also been some controversy over the southern limit to right whale distribution, which has often been portrayed as the Antarctic Convergence, or about 50–55° S. There is little doubt, however, that a substantial number of whales penetrate further south than this in late summer – up to 64° S, judging by Soviet catches.⁴ This may or may not be a recent development: the restriction of nineteenth century catches mainly to north of 50° S may have reflected operational avoidance of ice-filled waters.

The right whale migration paradigm is that the whales move into the coastal waters of southern continents and some island groups in winter, the females apparently being constrained to give birth and nurse their newborn in sheltered areas protected from swell and wind, and frequently in shallow water over gently sloping soft substrate.^{16,17} At other times of the year the whales are present on feeding grounds away from the coast, usually to the south of the nursery areas. The higher latitude grounds may only be utilised in late summer/early autumn.

Within the subregion, winter concentrations of right whales have been recorded from Tristan da Cunha in the South Atlantic,¹⁸ and various localities along the coast of southern Africa, extending from Maputo Bay, Mozambique, in the east to Baia dos Tigres, Angola, in the west. Currently the most significant of these are located on the southern coast of South Africa, between Port Elizabeth and Cape Town,¹⁹ but historically there were significant catches made at other localities to the north, such as Lüderitz and Walvis Bay in Namibia and Maputo Bay in Mozambique. While there are signs of right whales returning to Tristan da Cunha¹⁸ and some of their historic haunts in Namibia,²⁰ there has so far been no such sign in Mozambique or Angola. Right whales arrive in coastal waters on the south coast of southern Africa in June, build up to a maximum in September/October and then depart again by December:²¹ a similar pattern has been described for Tristan da Cunha.¹⁸ Historically, however, a significant component of the southern African population moved up the west coast in spring and spent the summer in the area of St Helena Bay and Saldanha Bay. Re-occupation of this apparent feeding ground has been observed recently.²²

Pelagic concentrations of right whales in the subregion have been recorded (A) in a band between 30° S and 40° S from Cape Town to Tristan da Cunha, (B) around the Crozet Islands in the southern Indian Ocean,²³ and (C) in an area between 50° S and 60° S from 0° E to 20° E.⁴ Whales were caught in A mainly from October to December, and in C from December to April. At the Crozets, nineteenth century catches were largely made in February and March, but Soviet whalers also took substantial catches in December. It is likely that these were mainly feeding grounds.

Some long-distance movements between these grounds have been recorded. Three whales satellite-tagged on the South African coast in September 2001 subsequently moved down to area C,²⁴ and a whale photographed in C (at 58° S 2° E) in 1997 was a female that had (and has subsequently) calved on the South African coastline.²⁵ Three satellite-tagged animals (including two that had already visited C) moved from the South African coastline to area A,²⁴ and a whale photographed at Gough Island (south of Tristan da Cunha) was photographed with a calf on the South African coast five years later.²⁶ No links between the South African coastline and B have yet been demonstrated, but it is possible that the Crozet Islands are a destination for whales from the east coast of southern Africa.

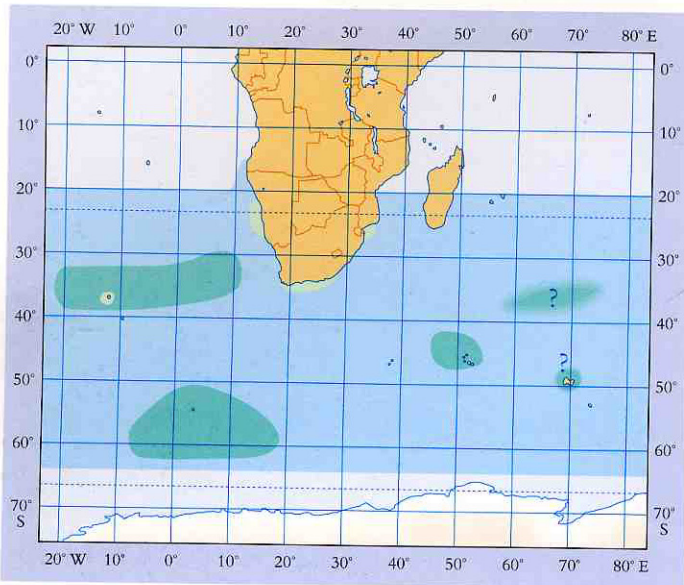


FIG. 8 Distribution map for southern right whale.

A genetic (mitochondrial DNA) comparison of right whales from wintering grounds in Argentina, South Africa, Western Australia and Campbell Island (New Zealand subantarctic) with feeding ground samples from South Georgia and south of Western Australia demonstrated differentiation between all four wintering grounds (although somewhat less between South Africa and Argentina). In general this indicated a strong maternal fidelity to a particular wintering ground. There appeared to be very little gene flow between the South Atlantic and Indo-Pacific ocean basins, and most gene flow occurred primarily between the adjacent populations in one ocean basin. The two feeding ground samples each contained representatives from both wintering grounds to the north of it, suggesting that mixing of breeding populations occurred on these grounds in summer.²⁷

Right whale cow-calf pairs on the South African coastline tend to move westwards as the season progresses.

Right whales are not exactly the Ferraris of the whale world: animals tracked by theodolite from the shore in South Africa have been found to move at average speeds of 1.7 km/hr (maximum 3.6 km/hr).¹⁹ This slow rate of movement was undoubtedly one reason why they were so easily taken by open-boat whalers, and currently may be a contributory factor to their vulnerability to ship strikes.

External commensals and parasites

Southern right whales are infested with cyamids or so-called whale lice virtually from the moment of birth. Three species are usually present, *Cyamus ovalis*, *C. gracilis* and *C. erraticus* (although *C. catodontis*, a species normally found on male sperm whales, was recorded from a stranded adult in South Africa²⁸). These three species have different habitats on the whale. The first two are confined to the callosities, with *gracilis* predominating in the deeper pits of the callosity and *ovalis* in the more open areas. They reach such abundance that the whole callosity turns chalky white. *Cyamus erraticus* is normally elsewhere on the body surface, but particularly around the genital slit and anus or in fresh wounds. Shortly after birth, however, large patches of *erraticus* (of a reddish-orange colour) may be found on the head of the calf, but these disappear as the calf grows, to be replaced by *ovalis*. It has been speculated that the initial infestation of *erraticus* may be related to a high rate of skin production on the calf's head,²⁹ or to the dramatic post-natal ecdysis (moult) that occurs.³⁰

The barnacle *Tubicinella* is only found on right whales, and then only in their callosities. It is unique in that it 'burrows' into the skin as far as its junction with the blubber, rather than sitting on the skin's surface.³¹ *Tubicinella* seems to be universally present on adult southern right whales in southern African waters, though their incidence elsewhere in the southern hemisphere is either lower or under-reported. Historically, *Tubicinella* has been recorded from North Atlantic right whales, but not apparently in recent times, and there are no records from North Pacific right whales.³² This seems to be another piece of evidence confirming the long separation of northern and southern right whales. There are few authentic records of coronuline barnacles on southern right whales.³³

Films of the cold-water diatom *Bennettella* (= *Cocconeis*) *ceticola* either occur rarely on southern right whales or are difficult to detect macroscopically because of the dark colour of the skin.

Food and feeding behaviour

We know relatively little about the food of southern right whales. Until recently there were only incidental records of their feeding on krill, copepods or the post-larva of lobster-krill. More substantive data became available when the information on stomach contents of 249 whales taken illegally in the 1960s was published. South of 50° S virtually all (99.4%) of individuals examined were feeding on krill (unidentified), while north of 40° S nearly all (91.7%) were feeding on copepods (unidentified). Between 40° S and 50° S, whales could be feeding on either copepods (71.4%), euphausiids (24.3%) or 'small crustacea' (4.3%). The only items specifically identified were the copepods *Calanus propinquus* and *Pleuromamma robusta*, from whales south of Tasmania.⁴ Faeces collected on the South African coast indicate feeding on copepods, probably *Calanoides carinatus* and (to a lesser extent) *Calanus agulhensis*.⁸

The results of stable isotope analysis of baleen plates from South Africa indicated a strong pattern of seasonality in feeding, falling off after May and only resuming again in August to December.⁹ Between November and April the incidence of food in right whale stomachs taken pelagically also showed a seasonal trend, with a peak from January to March.⁴ These observations seem to suggest that right whales follow the normal baleen whale paradigm in moving between summer feeding grounds in high



FIG. 9 Dorsal (A) and right lateral (B – retouched) views and vertex of skull (C); lateral (lingual) (D) and dorsal (reversed) (E) views of left mandible (USNM 267612); anterior view of left baleen (F) and baleen fringe detail (G) from a young right whale (ZM 05/15).

latitudes and winter breeding grounds in low latitudes, where feeding is minimal. However, right whales have recently been found feeding in spring and summer in regions of high productivity on South Africa's west coast, particularly St Helena Bay, with some individuals staying as long as 100 days in the vicinity.^{22,24} The importance of this ground has yet to be established, but it seems that not all intensive feeding takes place at high latitudes.

Right whales are designed as skim-feeders, that is to say they catch their prey by moving forward through the water column with their mouths open for protracted periods. This is in contrast to blue and fin whales, for example, which feed principally by engulfing their prey in one opening and closing of the mouth. Right whales have consequently developed a massive filtering

apparatus (their baleen) rather than an expanding throat system. In order to open the mouth, the large lower lips have to be swung out away from the head, and they presumably then act as guides for funnelling the plankton into the mouth. When feeding at the surface the whale will swim up and down a plankton swarm, much like someone mowing a lawn, periodically closing its mouth and swallowing. At these times there is a distinct head nodding, which may be the whale attempting to get rid of plankton accumulated on the baleen fringes by back-flushing. Such feeding bouts can continue for at least 1.75 hours. On the west coast of South Africa most feeding takes place at depth, where the behaviour cannot be seen, although head-nodding is seen at the surface.⁸

Reproduction and growth

After a gestation period of 12–13 months, most southern right whale calves off South Africa are born over a 118-day period, with a peak around late August.³⁴ The size of the calf at birth varies from 4.5 m to 6 m, and is correlated with the size of its mother. For the next 3–4 months the calf grows in length at an average rate of 2.8 cm/day. A differential exodus of larger calves from the nursery area seems to occur when the calf reaches a critical size³ (about 8 m), presumably when it is large enough to make the migration. Females usually give birth to their first calf when they are eight years old³⁵ and at least 12.4 m long.³ It is not known for how long the calf is nursed, but calves have been seen attempting to skim-feed in February,⁸ or at an estimated age of six months, and a few are still accompanying their mother at one year of age. Most subsequent calves are born at three-year intervals.³⁵

Right whales are among the best endowed of all mammals. The male North Pacific right whale has been recorded as having a penis 2.7 m long and a combined testis weight of 972 kg³⁶ (the largest corresponding measurements from a southern right whale are 2.24 m and a single testis volume of 198 litres³). By comparison, a mature blue whale might have testes one-tenth the size of the North Pacific right whale. The reason for this difference probably lies in differing mating strategies. From analogy with primates it is thought that the right whale may be practising sperm competition, which means that instead of physically preventing another male from mating, the right whale may simply be attempting to dilute its sperm by sequential mating.

Under this strategy, the larger the volume of sperm that can be produced, the better the chances of success, hence the evolutionary pressure for larger testes and a longer penis with which to contest access to the female.³⁷ Certainly the behaviour seen in surface-active groups (see below) would be consistent with such a strategy.

Behaviour and vocalisations

While in South African waters, right whales are found in groups of 1–10 animals, with cow-calf pairs predominating in nursery areas. From July to October the proportion of single animals drops, while more animals become involved in surface-active groups (known as SAGs). These are aggregations of 2–10 interacting animals that are conspicuous from the amount of splashing and exposure of heads, bodies and flippers at the surface. Characteristically, one individual is the focus of attention, usually a female, while the other members of the group are mostly males. These groups can persist for an hour or more, and membership can wax and wane. While mating seems to be what is taking place (and can be seen occasionally), closer study of some of the groups has shown that the females are immature (2–5 years old) and none has been seen with a calf in the following year. Furthermore, SAGs occur in coastal waters during at least seven months of the year, while we believe that conceptions take place over a relatively brief period (four months). One can only speculate that some sort of mating strategy is being practised by

In dense fog

The southern right whale whose skull photographs are shown in Fig. 9 is the sole representative of its species in the Smithsonian Institution's Natural History Museum. It was taken in the South Atlantic (at 62°38' S 20°48' W) on 23 February 1938 and processed on board the US floating factory *Ulysses*. This was of course some time after the species had been protected by the League of Nations agreement of 1931 (that came into force in 1935), to which the United States was a signatory. According to a cablegram from the whaling inspector on board the *Ulysses* (Lt Q. R. Walsh of the US Coastguard) to Dr Remington Kellogg of the Smithsonian, the animal was 'accidentally killed in dense fog'. This explanation was accepted and Scientific Permit No. 1, for the importation of the specimen for scientific purposes, was issued by the US Bureau of Fisheries on 7 April 1938. The plausibility of the explanation is somewhat compromised,

however, by earlier wording in Walsh's cablegram—'For Doctor Kellogg Smithsonian Institution Stop Accordance your request if southern right whale sighted or accidentally killed ...!' implying (to the suspicious mind at least) that there was some element of premeditation in this take. These suspicions are not allayed by the fact that the period 21–26 February 1938 represented the most productive six consecutive days of the season for the *Ulysses*, during which 20–27 whales were processed daily, including 27 on 23 February itself: if there was any fog around it must have been very localised. Furthermore, no right whale takes were reported to the Bureau of Whaling Statistics in Norway.²

This is not to deny that southern right whales have been taken by accident. In 1963, a 13.1 m male right whale was taken by a catcher attached to the Union Whaling Company at Durban, South Africa. According to a later interview with a crew member, a group of sperm whales had been sighted

and during the chase a whale was seen coming up beneath the bow of the catcher. Although the sailor in the masthead barrel recognised that it was a right and not a sperm whale, his warning shout came too late to prevent the reflex firing of a harpoon by the gunner.³ As it happened, science also benefited from this capture, as Dr G. Pilleri of the Brain Anatomy Institute, Berne, Switzerland, was collecting neurological tissue at the Durban whaling station at the time, and was able to secure and publish a paper on the brain of this individual.⁴

No excuses (other than pure ignorance) can be found for other post-protection takes in the area. At Donkergat in the 1937 season, for instance, no fewer than seven southern right whales were landed, five of which were pregnant.⁵ Such takes of a protected species were termed 'deplorable' by the International Whaling Conference at its 1938 meeting,⁶ and thereafter (until the depredations of the Soviets in the 1960s) illegal takes of right whales were few and far between.

References

- | | | | | | | | |
|---|---|---|--|---|-----------------|---|--------------------|
| 1 | Accession no. 148006, US National Museum, Smithsonian Institution | 2 | Allison, C., International Whaling Commission secretariat, pers. comm. | 3 | PBB pers. comm. | 5 | Best and Ross 1986 |
| | | | | 4 | Pilleri 1964 | 6 | Anon. 1947 |

juvenile animals, so that breeding with the fittest male will eventually occur. In the Antarctic, group sizes are smaller and SAGs are not so apparent.³⁸

Southern right whales produce a variety of low frequency tonal and pulsive sounds. Most of these are indiscernible to an above-surface listener, but on occasion (and seemingly more often at night) a loud in-air moaning bellow, rather similar to a foghorn, can be heard. Their underwater vocabulary has been classified by starting frequency (low 55–110 Hz, medium 110–220 Hz, and high 220–440 Hz) and acoustic contour (up, down, flat and variable). Low up-calls, the commonest call-type, seem to serve as contact calls between individuals. Other calls, such as medium and high down-calls, seem to be produced mainly by surface-active groups, possibly by the focal female,³⁹ as a playback of the sounds can induce males to approach. A particularly distinctive call-type is the so-called 'gun shot', a very short, intense broadband cracking sound that can be painful to the listener. Nobody is sure how the whale can make such a sound, which appears to be produced by males as a type of threat.⁴⁰

Conservation status

The southern right whale was the first species to be targeted by commercial whaling in the southern hemisphere. In 1603 Basque whalers set up a shore-based enterprise in Brazil that lasted for over a century, with right whales as the target.⁴¹ In

about 1770 pelagic whaling vessels from America began operating south of the equator, and these were soon followed by British, French and other whalers. The fishery for right whales rapidly spread to all southern oceans, and although reliable catch figures are hard to obtain, it has been estimated that between 1770 and 1850 some 125 000–151 000 southern right whales were killed from an original population of 55 000–70 000. This produced obvious depletion, but because the species was not given international protection until 1935, the southern right whale at its lowest point (in 1920) may have been reduced to as few as 300 animals.⁴² Fortunately this protection, although by no means absolute,⁴ was sufficient to ensure the onset of a recovery. From 1979 to 1998 the population calving on the south coast of South Africa increased steadily at 7.1% a year,³⁵ and similar rates of increase have been recorded for Argentina and Australia.⁴² Recent sightings off Namibia,²⁰ Madagascar,¹⁵ Réunion⁴² and even Gabon⁴³ suggest that this recovery may be widespread. In 1997 the size of the South African population was estimated at 3 100 out of a total southern hemisphere population of about 7 500. The latter figure is 10–14% of the range of estimates for original population size,⁴⁴ indicating that the whales still have a long way to go.

Southern right whales are listed as Lower Risk: Conservation Dependent by the IUCN and as Least Concern in the South African Red Data Book. The species is also included on Appendix I of both CITES and CMS.

References

- | | | | | | |
|--------------------------------|---------------------------------|-------------------------------|---------------------------------|-----------------------------|---|
| 1 Gaines <i>et al.</i> 2005 | 10 Nemoto 1959 | 17 Elwen and Best 2004b | 25 Best 1997 | 34 Best 1994b | 41 Richards 1994 |
| 2 Rosenbaum <i>et al.</i> 2000 | 11 Lockyer 1976 | 18 Best 1988a | 26 Best <i>et al.</i> 1993 | 35 Best <i>et al.</i> 2001 | 42 Le Journal de l'Île de la Réunion, 26 Sept. 1991 |
| 3 Best and Rüther 1992 | 12 Moore <i>et al.</i> 2004 | 19 Best 2000 | 27 Patenaude <i>et al.</i> 2007 | 36 Omura <i>et al.</i> 1969 | 43 Darling, J., pers. comm. |
| 4 Tormosov <i>et al.</i> 1998 | 13 Van Beneden and Gervais 1880 | 20 Le Roux <i>et al.</i> 2001 | 28 Best 1970a | 37 Brownell and Ralls 1986 | 44 International Whaling Commission 2001a |
| 5 Matthews 1938c | 14 Budker and Collignon 1952 | 21 Best and Scott 1993 | 29 Rowntree 1996 | 38 Best <i>et al.</i> 2003b | |
| 6 Payne <i>et al.</i> 1983 | 15 Rosenbaum <i>et al.</i> 2001 | 22 Best 2006 | 30 Reeb <i>et al.</i> 2005 | 39 Hofmeyr-Juritz 2006 | |
| 7 Schaeff <i>et al.</i> 1999 | 16 Elwen and Best 2004a | 23 Townsend 1935 | 31 Marloth 1900 | 40 Parks 2003 | |
| 8 MRI Whale Unit data | | 24 Mate, B. R., pers. comm. | 32 Scarff 1986 | | |
| 9 Best and Schell 1996 | | | 33 Best 1991 | | |