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# Does disappearance mean extirpation? The case of right whales off Namibia

**Jean-Paul Roux**,[1] Ministry of Fisheries and Marine Resources, Lüderitz Marine Research, PO Box 394, Lüderitz, Namibia and Animal Demography Unit, Department of Biological Sciences, University of Cape Town, Private Bag X3, Rondebosch, Cape Town 7701, South Africa; **Rod J. Braby**, Namibian Coast Conservation & Management Project, PO Box 7018, Swakopmund, Namibia; **Peter B. Best**,[†] Mammal Research Institute, University of Pretoria, % Iziko South African Museum, Cape Town 8000, South Africa.

## Abstract

Right whales off Namibia were severely depleted by early 19th century whaling, and rarely featured in modern whaling catches in the 1920s. Aerial surveys of the Namibian coastline from 1978 and onwards revealed increasing numbers of right whales, but few cow-calf pairs. Aerial surveys off South Africa since 2009 showed a major decline in the availability of animals without calves. Twenty individual matches were made between 94 whales photographed off Namibia/Northern Cape in 2003–2012 and 1,677 photographed off South Africa in 1979–2012. Eight were adult females that calved in South African waters, but only one was also seen with a calf off Namibia. Twelve out of 13 individuals off Namibia with distinctive dorsal pigmentation were first seen as calves off South Africa. These results strongly indicate connectivity between the two regions, while the presence off Namibia of three adult females from the South African population in the season in which they are believed to conceive suggests that there is unlikely to be any genetic differentiation between the two areas. We conclude that the reappearance of right whales off Namibia represents range expansion from South Africa rather than the survival of a few remnants of an originally separate stock.

Key words: southern right whale, *Eubalaena australis*, Namibia, South Africa, movements, subpopulation, recovery.

During the history of whaling there have been many occasions when a whale population in a region was heavily exploited, to the extent that after a number of years its abundance had been so reduced that it ceased to be of commercial importance: it effectively became "commercially extinct." In some of these cases there were very few subsequent overt signs of recovery, despite decades of official protection, leading to pessimistic assessments of its prospects of survival. Clapham *et al.* (2008) listed several examples of subpopulations of baleen whales that they considered extirpated and for which no recovery or repopulation had occurred since. Examples of these include Northeast Atlantic right whales, eastern North Pacific right whales, and Spitsbergen

[1]Corresponding author (e-mail: jprouxnamibia@gmail.com).

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bowhead whales; in some of these cases, individual sightings are now being made (Martin and Walker 1997, Wiig *et al.* 2007, Wade *et al*. 2011) leading to the question of whether these represent small remnants, or instead recolonization by animals from a currently more robust population (IWC 2013).

Another such instance involves the "rediscovery" of southern right whales off Namibia (Roux *et al*. 2001). In this paper we (1) describe the historic decline of right whales off Namibia using available whaling records and summarize what is known about the seasonality and composition of the catches; (2) document the numbers and distribution of right whales seen on aerial surveys of the Namibian coast since 1998, and compare these trends with those off South Africa; and (3) investigate to what extent the reappearance of right whales off Namibia has involved individuals originating from the South African population, comparing photo-identification images taken on aerial and boat-based surveys in Namibia from 2003 to 2012 with the South African right whale catalog that dates from 1979 to 2012.

## Material and Methods

In order to obtain a baseline understanding of historic right whale occurrence and distribution along the Namibian coast, we consulted a number of historical sources. We examined a time series of open-boat whaling effort in Namibian waters from 1788 to 1803 published by Richards and Du Pasquier (1989), and extended it to 1850, principally using voyage summaries in Starbuck (1878), Jones (1986), and Du Pasquier (1982), but also using abstracts of logs of French whaling ships between 1831 and 1836. The latter records were accessed on microfilm in the International Marine Archives (IMA), Nantucket, in 1977, and were particularly useful in clarifying the destinations visited by whaling vessels, often expressed in voyage summaries as simply "Côte d'Afrique," but actually involving visits to Spencer Bay, Elizabeth Bay, Angra Pequena (Lüderitz), Sims Bay, Walvis Bay, and Tiger Bay (Fig. 1). In extending the time series, therefore, voyages listed as "Côte d'Afrique" or "Coast of Africa" were included with those with the destination listed as Walvis Bay, on the assumption that they all referred essentially to the Namibian coast. The abstracts also provided more detail on catches by whaling ground than was available from voyage summaries.

Dedicated aerial surveys of the Namibian (and in some years the Northern Cape) coast were flown in 1978, 1998, 1999, 2003, 2004, 2005, 2008, 2009, 2010, 2011, and 2012. Except for 2003, all these flights were single surveys, flown between 15 September and 21 October. The flights covered variable stretches of the coast between the Kunene River mouth and 30°S, so for the purposes of constructing a trend series we chose a stretch of coast reasonably consistent between surveys (St Francis Bay, 25°00′S, to the Orange River, 28°33′S), termed the "Southern Survey Area." While the two surveys of 2003 partially overlapped, only the September survey covered the "Southern Survey Area" in its entirety and the counts from this survey were used in the trend analysis.

The aerial survey program off South Africa consists of a single coastwise flight annually by helicopter along the same stretch of coast at the same time of year. The basic protocol has remained consistent since 1979, *i.e.*, flights are confined to days of light wind and low swell, all animals seen are recorded but (with few exceptions) photography is restricted to adult females with calves (Best 1990*a*). The exceptions are those individuals that are associated with cow-calf pairs, and (since 2005) albinistic

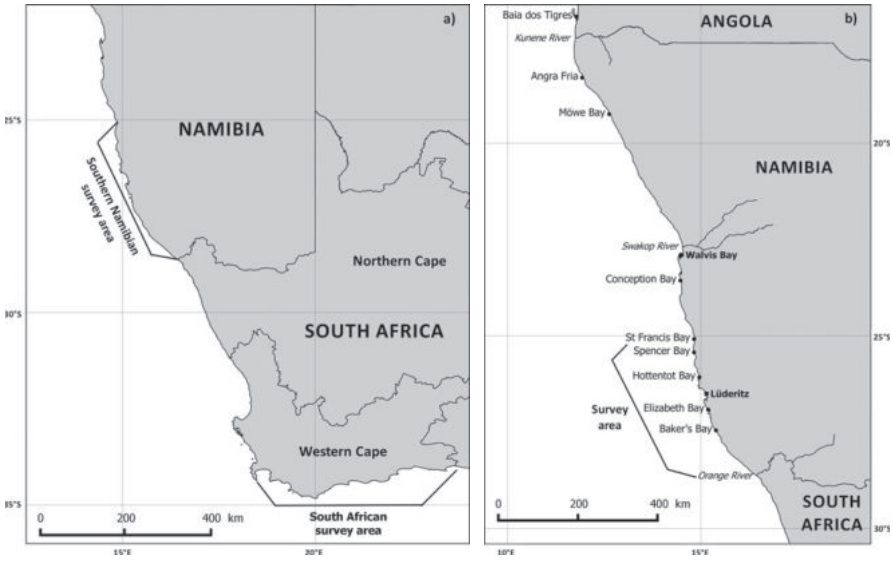


*Figure 1.* Coast of (a) southern Africa and (b) Namibia showing places mentioned in text.

individuals, believed to be >90% male (Schaeff *et al*. 1999). As callosity patterns of calves are not currently utilized, this means the catalog is dominated by adult females (a known minimum of 78.4%). Measures of search effort on these surveys are not straightforward, as it is difficult to distinguish searching from photographic effort. However, the rate of population increase estimated from the numbers of adult females identified on these surveys was not significantly different from the intrinsic rate of population increase estimated from a demographic population model (Best *et al*. 2001), so we feel that the assumption that search effort has essentially remained constant over the duration of the surveys is justified. Hence trends in the numbers of other individuals seen and counted but not photographed on the surveys should also be a valid reflection of their relative abundance.

Apart from photographs taken on the dedicated aerial surveys off Namibia since 2003, incidental boat-based and aerial photographs taken in the vicinity of Lüderitz by whale watching operators, yachtsmen, and other members of the public from 2007 to 2010 were available. Images were not scored for quality or distinctiveness, but those subjectively considered unmatchable were rejected before matching. In total, images of 92/94 individuals from Namibia or the Northern Cape were considered of acceptable quality. In addition, another two whales were matched from pigmentation only, as no suitable callosity pictures were available, making a final total of 94 individuals from Namibia/Northern Cape.

This catalog was compared with the South African aerial catalog held at the Mammal Research Institute, University of Pretoria, that included photographs taken from 1979 to 2012 ($n$ = 1,677 individuals). Callosity matching was mainly done using the Hiby-Lovell procedure (Hiby and Lovell 2001), adapted by Mike Harfoot, where image extracts are rated for similarity with those in the catalog using an overall index of similarity from 1.00 to 0; matching continued until this index had fallen to 0.50 (involving the comparison with 146–545 individuals from the South African catalog). When interpreting the results, it should be noted that (as explained above) the

South African aerial catalog is dominated by images of adult females, so that the likelihood of matching a male is much less than that for a female.

The sex of animals was determined from the presence of a calf in attendance (adult female), or from pigmentation patterns, where all partially albinistic individuals are considered to be female and >90% of albinistic individuals male (Schaeff *et al*. 1999).

## Results

### *Whaling for Right Whales in Namibian Waters*

Aside from a brief episode of exploratory voyages to Walvis Bay by the Dutch West India Company from 1726 to 1731 (Dekker and de Jong 1998), commercial taking of right whales on the Namibian coast may have resumed as early as 1773, when 14 American whaling vessels returned from the coast of Africa (Starbuck 1878), although their exact whaling grounds are unknown. The first French whaling vessels arrived on the west coast of southern Africa in 1787 (Du Pasquier 1990), and were active in Walvis Bay in 1788 (Fig. 2). This is a more definite date for the beginning of intensified whaling on the Namibian coast (Richards and Du Pasquier 1989). Between 1788 and 1803 a total of 76 American, 39 French and 71 British whaling vessels were identified as being present on the Walvis Bay whaling ground, reaching an annual maximum of 28 in 1796. Because not all vessels on the ground were identified, these are probably minimum numbers: in 1796, for instance, contemporary accounts stated that there were 35 vessels present on the ground, and "near forty" in 1793 (Richards and Du Pasquier 1989).

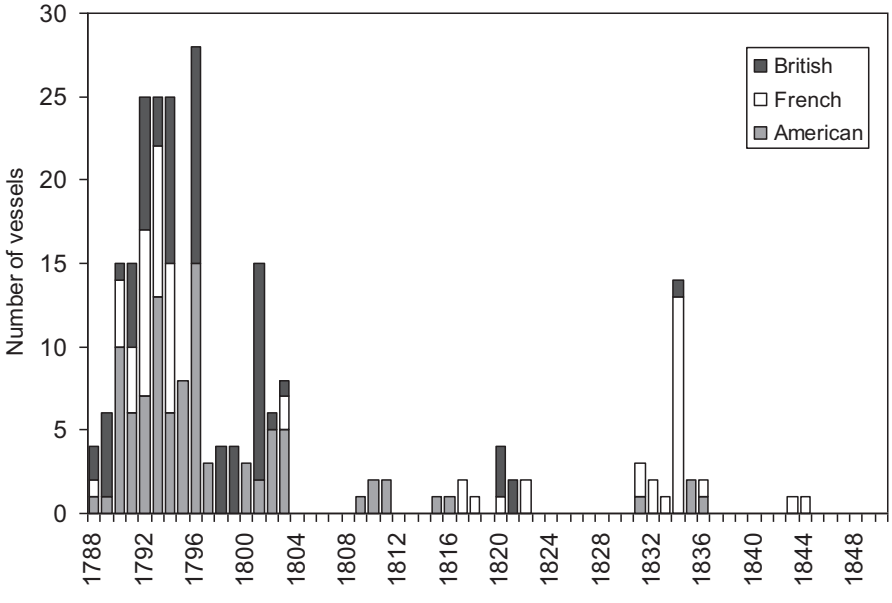


*Figure 2.* Numbers of identified whaling vessels visiting the Walvis Bay whaling ground per year, 1788–1850.

Using Richards and Du Pasquier's estimate of 20 whales taken per vessel voyage, this level of effort would have resulted in the removal of at least 3,700 right whales from Namibian waters over the 16 yr period. This figure excludes any allowance for whales struck and lost that might have subsequently died. Although these catches were all referred to the "Woolwich Bay" ground, in reality whaling in this era probably took place at a number of localities along the Namibian coast (Fig. 1). During a subsequent episode of French whaling from 1831 to 1834, the pattern was for vessels to arrive on the coast at either Angra Pequena (= Lüderitz) or Elizabeth Bay in May/June and remain on the coast until August/September, visiting Sims Bay,[2] Spencer Bay, Walvis Bay, and as far north as Tiger Bay (Baia dos Tigres) at 16°37′S in southern Angola (Best 1981).

This initial pulse of whaling from 1788 to 1803 seemed sufficient to deplete the local stocks to the extent that most vessels shifted to other, more profitable grounds (Richards and Du Pasquier 1989). The subsequent history of exploitation for right whales on this coast in the 19th century is not well documented, although French whaling vessels are known to have visited the Walvis Bay area between 1817 and 1843 (Du Pasquier 1982), and in four such voyages to the African coast in 1831–1834 a total of 40 whales (believed to be right whales from their oil yield) were taken (Best 1981). Catch rates, however, had fallen substantially, with between 0 and 18 (mean 5.6, $n$ = 16) whales per voyage between 1831 and 1836 (Voyage Abstracts, French National Archives).

With the increasing interest paid to humpback whaling from the 1830s, and particularly after 1850 (Best 1987), whaling vessels continued to visit the west coast of southern Africa in the second half of the nineteenth century in search of humpback whales. Although the history of this fishery is also poorly documented, it seems almost certain that as the seasonality of occurrence inshore of both species is similar, right whales with their greater intrinsic value would have continued to be taken incidentally. This could have been sufficient to have prevented any effective recovery from taking place.

At the start of modern whaling on the African coast in 1908, right whales must still have been very rare. No right whales were recorded in the 4,063 whales landed in Namibia between 1913 and 1930, and only one in the 14,475 whales landed in Angola between 1909 and 1928 (Best 1994*a*), although many of these catches (especially those pre-WWI) were unspecified. Nevertheless, after 1923, when catches were almost completely specified, no right whales were recorded amongst the 2,630 whales landed in Namibia up to 1930, nor amongst the 2,411 whales landed in Angola up to 1928 (the 17 right whales reported in the Bureau of International Whaling Statistics as being taken in 1925 in Angola proved to be a typographical error (Best 1990*b*): the catch was of Bryde's whales). This contrasts with the situation further south, where 39 right whales were amongst the 22,642 whales landed in the Western Cape (Southwestern Cape + Southern Cape; Best 1994*a*) between 1909 and 1930, 11 of which were taken between 1923 and 1930. It seems almost certain therefore that by 1930 right whales had effectively disappeared from Namibian inshore waters, although they were still present in small numbers along the South African coast in winter.

[2]At 26°10′S (Thierry Du Pasquier, 6, rue de la Mission Marchand, 75016, Paris, France, in litt. 29 June 1983), probably Hottentotsbaai.

*Seasonality and Composition of the Historical Catch*

Unlike modern whaling, open-boat whaling kept no official catch records, so determining what they caught depends almost entirely on examining the surviving unofficial records such as the logbooks and journals kept by individual crewmen. The detail in these is extremely variable and so open to interpretation: a lack of a record may simply represent a lack of interest in recording it, for example. These uncertainties have to be borne in mind in the following analysis.

French whaling vessels bound for Walvis Bay between 1791 and 1803 left port between September and the following May (most [8/12] between January and March), and returned between September and the following March, mostly (5/7) between November and January (Du Pasquier 1990). British whaling vessels similarly bound between 1791 and 1794 followed an almost identical pattern, leaving port between October and the following April (most [7/10] between January and March), and returning between November and the following May, mostly (9/14) in November and December (Jones 1986). Allowing about three months for the passage each way to and from the whaling grounds (Best 2006), this implies the vessels were mainly active on the coast between April/June and August/October. Actual dates of arrival and departure from Walvis Bay are available from nine logbooks (mostly French) between 1788 and 1796 (Richards and Du Pasquier 1989): arrivals ranged from 31 March to 28 May (mean arrival 3 May) and departures from 20 May to 14 October (mean departure 26 July). However at this early stage of the industry the departure dates were obviously influenced by a vessel's success, so that once it was full it would depart for home, despite there still being plenty of whales around. As an example of this, the *Anne* of Dunkirk processed her last whale in the 1792 season on 19 July, but waited until 23 July when three other whale ships were also full before departing the bay in their company (Richards and Du Pasquier 1989).

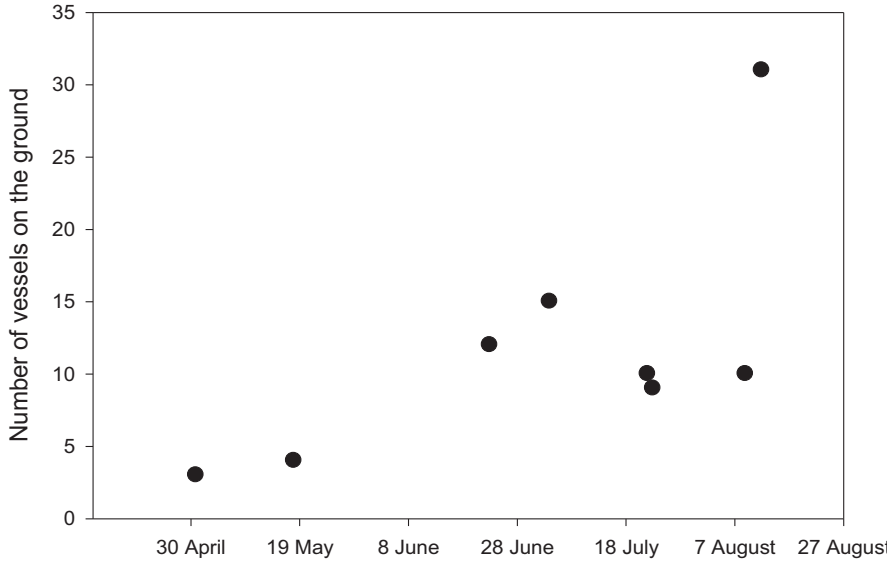


*Figure 3.* Numbers of whaling vessels present on any one day on Walvis Bay whaling ground, 1788–1796.

An alternative indicator of the extent of the season might be the numbers of vessels on the ground at any one time. Such incidental observations are available on eight occasions during the 1788–1796 seasons (Jones 1986, Richards and Du Pasquier 1989), and indicate that there were still large numbers of vessels present until late in August (Fig. 3). Although there are uncertainties surrounding the exact timing of the southern right whale's breeding season, given the lack of information on the rate of early fetal growth, most conceptions are believed to occur between June and September (Best 1994*b*). This implies that the presence of right whales in the Walvis Bay region at least overlapped with their postulated breeding season.

The composition of the catch can be assessed from the oil yield of individual whales recorded in contemporary logbooks ($n$ = 16), or from voyage averages for vessels visiting the ground ($n$ = 6). These provide very similar results, with individuals ranging from 50 to 100 (mean 69.6) barrels, and voyage averages ranging from 47.4 to 92.4 (mean 69.6) barrels (Table 1). With full-grown right whales in the South Atlantic said to yield 40–60 barrels if male and 60–80 barrels if female (Clark 1887), these values suggest that the catch was composed largely if not exclusively of "adults," many of which were probably females.

Richards and Du Pasquier (1989) commented on the lack of reference to the presence or taking of dependent calves in one informative logbook from the Walvis Bay ground (*Anne* of Dunkirk 1791–1792). The same can be said for the logbook of the *Kingston* of Spitshead, 1800–1801, whaling in Tiger Bay from June to mid-September (PBB, personal observation). These observations together with the oil yield data

*Table 1.* Individual and voyage average yields of right whales taken on the Coast of Africa, 1788–1832.

| Vessel | Year | Ground | No. of whales | Barrels | Average yield | Source |
|---|---|---|---|---|---|---|
| *Aimable Marie* | 1831 | Angra Pequena | 1 | 100 | | Voyage abstract, IMA Nantucket |
| | 1831 | Tiger Bay | 1 | 87 | | Voyage abstract, IMA Nantucket |
| | 1832 | 22°–27°S | 12 | ∑ = 915 | 76.25 | Voyage abstract, IMA Nantucket |
| *Courrier des Indes* | 1832 | Elizabeth Bay–Walvis Bay (+ Saldanha Bay) | 8 | ∑ = 739 | 92.38 | Voyage abstract, IMA Nantucket |
| *Woodrop Sims* | 1831 | 16°–26°S | 18 | ∑ =1,504 | 83.56 | Voyage abstract, IMA Nantucket |
| *Kingston* | 1801 | Tiger Bay | 14 | 50, 57, 59, 60, 60, 70, 70, 70, 80, 90, 126,[a] 135[a] | | Logbook, Kendall Whaling Museum, Sharon, MA, 1977 |
| *Harmonie* | 1788 | Northern Cape, Walvis Bay | 15 | ∑ = 800 | 53.33 | Richards and Du Pasquier 1989 |
| *Esperance* | 1789 | Saldanha Bay, Walvis Bay | 24.75 | ∑ = 1,172 | 47.35 | do |
| *Anne* | 1792 | Walvis Bay | 11 | | 65 | do |

[a]Pair of whales.

would suggest that this was not an area frequented by many cow-calf pairs. However this conclusion should be treated with caution given the unofficial and idiosyncratic nature of the logbooks themselves, and the possibility that at this stage of the industry calves, if taken as a lure for the mother, might simply have been discarded without any attempt to process. Du Pasquier (1990), however, believed that the processed catch on the west coast of Africa must have included a percentage of calves, because the overall average oil yield per whale taken there by French whaling vessels (40.5 barrels) was distinctly less than on the coast of Brazil (53 barrels). With births peaking in August (Best 1994*b*), neonates could certainly be expected to be present at the time whaling took place. The issue of whether Namibian waters ever hosted a substantial number of mother-calf pairs needs to be resolved through the examination of additional primary historical records.

*Recent Sightings of Right Whales in Namibian Waters*

Apart from a right whale taken in Gabon in 1951 (Budker and Collignon 1952), there were no further reports of southern right whales on the west coast of southern Africa north of the Orange River until 1971, when a cow-calf pair was seen on an aerial survey of seal colonies (Best 1981). The subsequent reappearance of right whales in Namibian waters has been described by Roux *et al*. (2001), including results from the first three aerial surveys. Counts made on all the aerial surveys of the Namibian coast are listed in Table 2 and apparently indicate an increasing trend, at least for unaccompanied whales. Fitting an exponential regression to data from the Southern Survey Area only (excluding 2011), the rate of increase in total counts from 1978 to 2012 is estimated as 6.1%/yr (95% CI −0.6%, 12.8%, one-tailed $P = 0.035$). Because the 1978 data point might exercise undue influence owing to its separation in time, a second regression was fitted without this point (*i.e*., from 1998), producing a nonsignificant slope of 3.6%/yr (one-tailed $P = 0.2997$). The counts of cow-calf pairs have clearly not increased over the same time period, with none being recorded on surveys between 2008 and 2012.

Although aerial surveys of northern Namibia have not been undertaken consistently over time, there has only been one sighting on these surveys north of Meob Bay, a cow-calf pair seen at Conception Bay (23°57.75′S) on 19 September 2003. The present-day distribution of right whales therefore seems to be concentrated largely in southern Namibia, with the historical whaling grounds at Walvis Bay (22°51′S) and presumably Tiger Bay area (16°37′S) still to be populated (marine tour operators in Walvis Bay have reported a few right whale sightings every winter over the last decade, suggesting that this process may have already started).

*Changes in Relative Abundance of Right Whales off South Africa*

Since aerial surveys for right whales began on the South African coast in 1971, there has been a general overall increase in the numbers of whales seen annually, at least until very recently. Figure 4 illustrates trends in the numbers of cow-calf pairs and other whales (termed "unaccompanied whales") seen on fixed-wing surveys from 1971 to 1987 and helicopter surveys from 1979 to 2012.

The areas covered by these surveys were different, with the fixed-wing surveys extending some 250 km further east than the helicopter surveys. This difference in distance searched explains why the counts of unaccompanied whales from fixed-wing surveys were usually higher than those on the helicopter surveys in the same year.

*Table 2.* Numbers of right whales seen on aerial surveys off Namibia and the Northern Cape, by latitude, with dotted lines indicating limits of Southern Survey Area.

| Latitude (°S) | 1978 28-29 September | 1998 29–30 September | 1999 7–8 October | 2003 15–19 September 20–23 October | 2004 27 September–8 October, 14 October | 2005 15 September–5 October | 2008 30 September–1 October | 2009 4–6 October | 2010 19–21 October | 2011 6–8 October | 2012 1–3 October |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 17.5–18 | 0 | | | | 0 | | | | | | |
| 18–18.5 | 0 | | | | 0 | | | | | | |
| 18.5–19 | 0 | | | | 0 | | | | | | |
| 19–19.5 | 0 | | | | 0 | | | | | | |
| 19.5–20 | 0 | | | | 0 | | | | | | |
| 20–20.5 | 0 | | | | 0 | 0 | | | | | |
| 20.5–21 | 0 | | | 0 | 0 | 0 | | | | | |
| 21–21.5 | 0 | | | 0 | 0 | 0 | | | | | |
| 21.5–22 | 0 | | | 0 | 0 | 0 | | | | | |
| 22–22.5 | 0 | | | 0 | 0 | 0 | | | | | |
| 22.5–23 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | | |
| 23–23.5 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | | |
| 23.5–24 | 0 | 0 | 0 | 2[a] | 0 | 0 | | | 0 | | |
| 24–24.5 | 0 | 0 | 0 | 0 | 0 | 0 | | | 0 | | |
| 24.5–25 | 2[a] | 0 | 0 | 0 | 0 | 0 | | 2 | 0 | | |
| 25–25.5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 25.5–26 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| 26–26.5 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 |
| 26.5–27 | 0 | 0 | 0 | 4[a] | 0 | 0 | 16 | 0 | 0 | 3 | 0 |
| 27–27.5 | 1 | 2[a] | 0 | 0 | 0 | 2 | 1 | 0 | 15 | 7 | 3 |
| 27.5–28 | 0 | 2[a] | 0 | 1 | 2[a] | 0 | 0 | 1 | 10 | 0 | 1 |
| 28–28.5 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| 28.5–29 | 0 | 0 | 10[a] | 1 | 0 | 1 | 0 | 1 | 0 | | 0 |

*(Continued)*

*Table 2. (Continued)*

| Latitude (°S) | 1978<br>28-29 September | 1998<br>29–30 September | 1999<br>7–8 October | 2003<br>15–19 September<br>20–23 October | 2004<br>27 September–8 October, 14 October | 2005<br>15 September–5 October | 2008<br>30 September–1 October | 2009<br>4–6 October | 2010<br>19–21 October | 2011<br>6–8 October | 2012<br>1–3 October |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 29–29.5 | | | | | 0 | 1 | 1 | 0 | | | 0 |
| 29.5–30 | | | | | 4 | | 2 | | | | |
| 30–30.5 | | | | | 0 | | | | | | |
| Total | 3[a] | 5[b] | 10[a] | 8[b] | 6[a] | 4 | 22 | 5 | 26 | 11 | 6 |

[a]One cow-calf pair.
[b]Two cow-calf pairs.

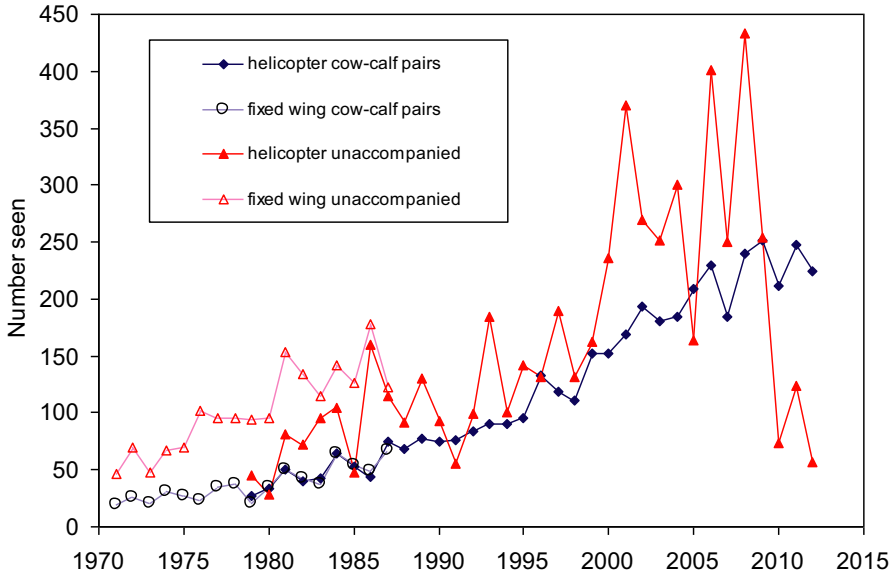


*Figure 4.* Trends in the counts of cow-calf pairs and unaccompanied right whale adults in the South African survey area, 1971–2012.

The counts of cow-calf pairs, however, were generally in good agreement between the two surveys, despite the difference in distance searched. This was because nearly all the cow-calf pairs were sighted in the western section of the survey area, so that exclusion of the eastern sector on the helicopter surveys made little difference to the total seen. The data sets are also not strictly comparable, in that the numbers of cow-calf pairs were adjusted for duplicate sightings (using individual identification photographs), whereas the numbers of unaccompanied whales were unadjusted for duplicate sightings as they were not usually photographed.

Using the helicopter surveys since 1979 as being the longest series with the most consistent methodology, the increasing rates in cow-calf pairs and unaccompanied adults were similar up until 2009, exponential at 6.33%/yr ($r = 0.9232$) and 6.25%/yr ($r = 0.8561$), respectively. The numbers of unaccompanied animals tended to fluctuate more widely than the numbers of cow-calf pairs, presumably because (unlike near-term females) they are not constrained to visit coastal waters in winter. From 2009 onwards, however, the counts of unaccompanied adults declined sharply, reaching levels only seen 16–20 yr earlier. From being higher than the counts of females in 26 of the 31 preceding years, the counts of unaccompanied animals were as low as 25%–50% of the cow-calf counts over the last 3 yr.

### *Movements of Right Whales Between Namibia and South Africa*

In total, 20 whales were matched between the Namibian and South African survey catalogs (Table 3, excluding two internal Namibian matches between days in the same year). Two of these (L0316A and L0404A) were seen in the waters of the Northern Cape of South Africa, in an extension of the Namibian aerial surveys south of the Namibian/South African border. Three of the 20 whales were believed to be male

*Table 3.* Right whales matched between Namibian/Northern Cape and South African aerial catalogs (?M, ?F refer to sex determined from pigmentation only, and B = black, PA = partially albinistic, A = albinistic, WB = white blaze).

| Namibian/Northern Cape catalog | | | | | | South African aerial catalog | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Catalog number | Sex | Color | Date seen | Location | Grouping | Catalog number | Date seen | Location (A–H = longitudinal bins on SA coast) | Grouping | Age when first seen in Namibia |
| L0304A | F | B | 19 September 2003 | 23°57.75′S | C + calf | R06/65A | 13 October 2006 | H (20°50′–21°10′E) | C + calf | Adult |
| | | | | | | | 18 October 2009 | 34°40.80′S, 19°30.96′E | C + calf | |
| | | | | | | | 18 October 2012 | 34°45.98′S, 20°03.38′E | C + calf | |
| L0316A | F | PA | 21 October 2003 | 29°27.70′S | Non-SAG | R08/51A | 12 October 1999 | 34°30.59′S, 20°27.51′E | Calf | 4 |
| | | | | | | | 10 October 2008 | 34°24.54′S, 20°51.37′E | C + calf | |
| | | | | | | | 17 October 2008 | 34°45.41′S, 19°36.49′E | C + calf | |
| | | | | | | | 13 October 2012 | 34°29.29′S, 20°30.30′E | C + calf | |
| L0404A | F | B | 10 October 2004 | 29°59′S | Non-SAG | R11/06A | 5 October 2011 | 34°21.89′S, 21°31.65′E | C + calf | Unknown |
| | | | | | | | 11 October 2011 | 34°41.88′S, 20°10.61′E | C + calf | |
| L0701A | ?M | A | 21 October 2007 | 27°02.00′S, 15°13.00′E | Single | R01/80c | 11 October 2001 | 34°29.42′S, 20°29.38′E | Calf | 6 |
| L0703A | U | WB | 21 October 2007 | 27°02.00′S, 15°13.00′E | Single | R97/03c | 17 October 1997 | 34°22.35′S, 20°54.00′E | Calf | 10 |

*(Continued)*

*Table 3. (Continued)*

| Namibian/Northern Cape catalog | | | | | | South African aerial catalog | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Catalog number | Sex | Color | Date seen | Location | Grouping | Catalog number | Date seen | Location (A–H = longitudinal bins on SA coast) | Grouping | Age when first seen in Namibia |
| L0708A | ?F | PA | 22 October 2007 | 26°57.00′S, 15°14.00′E | Single | R03/241c | 22 October 2003 | 34°32.25′S, 19°22.31′E | Calf | 4 |
| L0713A | F | PA | 22 October 2007 | 26°57.00′S, 15°14.00′E | Group of 2 | R99/91A | 21 October 1990 | G (20°30′–20°50′E) | Calf | 17 |
| | | | | | | | 12 October 1999 | 34°30.07′S, 20°28.61′E | C + calf | |
| | | | | | | | 11 October 2002 | 34°28.35′S, 20°50.57′E | C + calf | |
| | | | | | | | 10 October 2005 | 34°38.42′S, 20°17.39′E | C + calf | |
| | | | | | | | 13 October 2008 | 34°29.51′S, 20°29.76′E | C + calf | |
| | | | | | | | 15 October 2010 | 34°25.20′S, 20°51.93′E | C + calf | |
| L0811A | U | B | 1 October 2008 | 26°34°.40′S | Group of 8 | R08/355A | 22 August 2008 | 30°20.79′S, 17°16.61′E | SAG | Unknown |
| L0812A | F | B | 30 September 2008 | 26°38.15′S | Group of 5 | R03/163A | 21 October 2003 | 34°42.92′S, 20°07.51′E | C + calf | Adult |
| | | | 1 October 2008 | 26°32.10′S | In pair | | 13 October 2006 | H (20°50′–21°10′E) | C + calf | |
| | | | | | | | 15 October 2006 | G (20°30′–20°50′E) | C + calf | |
| L0815A | U | B | 1 October 2008 | 26°34°.40′S | Group of 8 | R99/69A | 12 October 1999 | 34°27.93′S, 20°34.57′E | 3 + calf | >9 |

*(Continued)*

*Table 3. (Continued)*

| Namibian/Northern Cape catalog | | | | | | South African aerial catalog | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Catalog number | Sex | Color | Date seen | Location | Grouping | Catalog number | Date seen | Location (A–H = longitudinal bins on SA coast) | Grouping | Age when first seen in Namibia |
| L0820A | ?M | A | 30 'September 2008 | 26°37.60′S | Group of 5 | R06/308A | 12 October 2003 | 34°17.41′S, 21°55.34°′E | Calf | 5 |
| | | | | | | | 19 October 2006 | A (18°30′–18°50′E) | SAG | |
| L0904A | F | B | 6 October 2009 | 24°30.00′S | In pair | R11/45A | 6 October 2011 | 34°23.28′S, 20°52.90′E | C + calf | Unknown |
| L1001A | F | B | 19 October 2010 | 26°17.10′S | Single | R05/11A | 7 October 2005 | 34°23.07′S, 21°06.87′E | C + calf | Adult |
| | | | | | | | 12 October 2008 | 34°27.15′S, 20°39.65′E | C + calf | |
| L1002A | ?F | PA | 20 October 2010 | 27°01.27′S | Single | R05/02c | 7 October 2005 | 34°22.17′S, 20°59.73′E | Calf | 5 |
| | | | | | | | 9 October 2005 | 34°23.87′S, 20°51.74′E | Calf | |
| L1008A | ?F | PA | 20 October 2010 | 27°20.56′S | Group of 4 | R06/123c | 15 October 2006 | G (20°30′–20°50′E) | Calf | 4 |
| L1012A | U | B | 20 October 2010 | 27°47.04′S | SAG of 9 | R09/332A | 23 October 2009 | 34°25.26′S, 19°09.76′E | Group of 3 | Unknown |
| L1013A | ?F | PA | 20 October 2010 | 27°47.17′S | SAG of 9 | R01/13c | 10 October 2001 | 34°22.51′S, 20°54.35′E | Calf | 9 |
| L1015A | ?M | A | 20 October 2010 | 27°47.17′S | SAG of 9 | R94/15c | 12 October 1994 | H (20°50′–21°10′E) | Calf | 6 |
| L1019A | F | PA | 20 October 2010 | 27°47.17′S | SAG of 9 | R05/06A | 12 October 1999 | 34°30.17′S, 20°28.34°′E | Calf | 11 |

*(Continued)*

*Table 3. (Continued)*

| Namibian/Northern Cape catalog | | | | | | South African aerial catalog | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Catalog number | Sex | Color | Date seen | Location | Grouping | Catalog number | Date seen | Location (A–H = longitudinal bins on SA coast) | Grouping | Age when first seen in Namibia |
| | | | | | | | 7 October 2005 | 34°22.58′S, 21°02.01′E | C + calf | |
| | | | | | | | 14 October 2009 | 34°28.39′S, 20°51.20′E | C + calf | |
| | | | | | | | 17 October 2009 | 34°42.81′S, 20°09.94′E | C + calf | |
| | | | | | | | 23 October 2009 | 34°15.34°′S, 18°50.42′E | C + calf | |
| | | | | | | | 13 October 2012 | 34°30.51′S, 20°27.30′E | C + calf | |
| L1020A | U | WB | 20 October 2010 | 27°47.17′S | SAG of 9 | R06/247A | 21 October 2003 | 34°36.99′S, 19°25.05′E | Calf | 7 |
| | | | | | | | 16 October 2006 | C (19°10′–19°30′E) | Non-SAG | |
| | | | | | | | 18 October 2008 | 34°28.08′S, 19°20.24′E | Non-SAG | |
| | | | | | | | 16 October 2011 | 34°26.25′S, 19°18.56′E | Single | |
| L1204A | U | B | 12 October 2012 | 26°39.00′S, 15°09.60′E | ?SAG of 2 | R10/246A | 23 October 2010 | 34°22.36′S, 19°05.77′E | Single | Unknown |

(because they were albinistic), eight were known to be female (because they were or had been sighted with a calf), four were believed to be female (because they were partially albinistic) and the sex of five was unknown. Given the female bias of the South African catalog, all that can be said is that both sexes were represented in the intercatalog matches. Of the animals that could be accurately aged when first seen in Namibia (having been seen as calves), eight were 4–7 yr old (and so probably immature), three were 9–11 yr old (and so probably pubertal), and nine were either known adults (three), >9 or 17 yr old (two), or of unknown age (four).

The eight females had been or were seen with calves on the South African coast in a total of 20 surveys, but only one (L0304A) was also seen in a Namibian survey with a calf. This female was first photographed with a calf near Conception Bay in central Namibia, and 3 yr later with a calf in the nursery area in St Sebastian Bay on the south coast of South Africa, a coastwise geographical separation of some 1,500 km. It has subsequently been seen with two more calves at 3 yr intervals, both on the South African south coast, suggesting that the excursion to Namibia was atypical.

Three of the females, however, were present in Namibian waters in the winter preceding that in which they calved (L0713A) or in the winter two years after their previous calf (L0812A, L1001A); in other words, given a 3 yr calving interval, in the year in which they conceived or were predicted to conceive.

Of the 13 individuals photographed in Namibia/Northern Cape that were either partially albinistic (seven), albinistic (four) or carried white blazes dorsally (two), all but one (an albinistic individual) had been photographed as a calf in South African waters. Given that the probability of photographing an individual on any one survey in South African waters is usually between 0.6 and 0.8 (Brandão *et al*. 2013), such a high resighting rate (0.923) provides powerful support for the hypothesis that essentially all the animals currently being sighted in Namibia have originated from the nursery grounds on the southern coast of South Africa. This conclusion of course assumes that the atypically pigmented animals were representative of the total population.

A 21st match (L0811A) was not photographed on either survey program, but during filming of a television documentary series in the Northern Cape in August 2008. Forty days later it was photographed off Lüderitz on the Namibian survey, 400 km to the north. Although unsexed, on both occasions it was participating in surface active groups, of nine animals in August and of eight animals in October (Table 3).

A further example of linkage between the two areas is provided by an adult right whale of unknown sex found heavily entangled in rock lobster fishing gear (rope and attached floats) in Table Bay (33°52.83′S, 18°26.08′E) on 16 January 2013. Some of the gear removed was identified as originating from a rock lobster boat registered in Lüderitz, Namibia, and the trap was probably deployed between 28°12′S and 28°21′S, or about 650 km to the north.

In summary, 18 of the 22 individuals were first seen in South Africa (12 as calves) before moving to Namibia. Four of these were subsequently resighted in South African waters: three of these were females that returned to calve off South Africa. Four individuals (including the entangled whale) showed a movement from Namibia to South Africa but none of these has been resighted in Namibia yet.

## Discussion

Right whales off Namibia were subjected to the usual commercial whaling paradigm of discovery, over-exploitation, and commercial extinction. After being heavily

depleted by late 18th century whaling, they continued to be the targets of opportunistic exploitation for another 100 yr before finally being afforded official protection in 1935. For the first 70 yr of the twentieth century, including the first 35 yr of official protection, there are no records of the species in Namibian waters, although single specimens were taken further north in Angola (1913) and Gabon (1951). The species had for all intents and purposes disappeared from the region.

The first incidental sightings (four between 1971 and 1984) were followed by an apparent increasing rate of sightings over the next 15 yr (four from 1985 to 1989, nine from 1990 to 1994, and 20 from 1995 to 1999). Part of this resurgence was probably the result of increased public awareness and the development of a coastal diamond mining industry (Roux *et al*. 2001), but it was sufficient to motivate for the initiation of an aerial survey program in 1998. This has revealed an overall revival in the numbers of right whales off Namibia, at least in the southern half. This influx of animals has so far not included calving females to any great extent, and has been accompanied by a marked decline in the relative abundance of animals without calves off the south coast of South Africa from at least 2009. The discovery of 21 matches between these two area, 14 from 2008 onwards, with a best estimate of 92.3% originating from the South African nursery grounds as calves, confirms that the influx into Namibia has largely been at the expense of animals from the South African population.

At face value the phenomenon appears to be an example of range expansion as a depleted population recovers. However there are a number of qualifications to this conclusion. The nature of the original "Walvis Bay" whaling ground is still uncertain, even though there is little evidence of it functioning as a nursery ground. There is evidence that the right whale population off South Africa during the era of modern whaling (1908-1963) and even during open-boat whaling in the nineteenth century was dominated by adult females and their calves (Best and Ross 1986), which is a departure from the mixed population of cow-calf pairs and unaccompanied individuals that predominated until recently. Perhaps, therefore, the relocation of unaccompanied animals to Namibia is simply a recapitulation of the historic stock structure, with South African waters serving predominantly as a calving or nursery ground and Namibian waters as a breeding or mating ground. Separation of calving/nursery grounds from breeding grounds has also been described for the Northwest Atlantic right whale, with a breeding ground in the Gulf of Maine and a calving ground off the southeastern coast of the United States (Cole *et al*. 2013).

The number of animals so far seen off southern Namibia (<30 in any survey) is also far less than the numbers of unaccompanied animals "missing" on recent South African surveys—of the order of 200–300 animals per year. If these individuals have continued to visit coastal waters in winter and spring then they may have relocated to other, unsurveyed areas of both west and east coasts of southern Africa. There is evidence both from the southern extension of the Namibian surveys onto the west coast of Southern Africa (to *ca.* 30°S) and shore-based sightings off the west coast (at 33°S, Barendse and Best 2014) that right whales are present on the west coast of southern Africa in late winter and spring, some of which at least subsequently move into Namibian waters. Certainly there are potential feeding grounds in this area associated with the Namaqua, Columbine, and Peninsula upwelling cells, at about 29°, 32°, and 34°S, respectively (Lutjeharms and Meeuwis 1987). Some of these upwelling cells extend over 200 km offshore, meaning that feeding whales might well occur outside the normal seaward detection range of a coastal aerial survey. Furthermore, the charts of nineteenth century catch locations provided by Townsend (1935) indicate a broad

band of southern right whale captures in the southeast Atlantic between latitudes 30°S and 38°S, extending almost uninterrupted from the African coast for at least 3,500 km. Many of these catches were made between September and November, or contemporaneous with the timing of the aerial surveys, and provide a vast offshore habitat into which unaccompanied animals could "disappear." The extensive mobility of southern right whales along- and offshore, and their flexibility in use of apparent feeding grounds, has been demonstrated by the tracks of individuals satellite-tagged on the South African coast (Mate *et al*. 2011).

The possibility of the reappearance of right whales off Namibia representing the recovery of a few remnant individuals from a separate, original population seems remote, given both the scarcity of early 20th century sightings and the evidence of immigration from South Africa. Whether the Walvis Bay whaling ground in fact ever represented a reproductively isolated population from that off the Cape of Good Hope, rather than a separate population component (Best 2006), must remain a moot point. But the fact that adult females from the South African stock are to be found there in the season in which they are believed to conceive suggests that there is currently unlikely to be any genetic differentiation between the two areas.

A parallel situation exists in New Zealand, where the low numbers and disappearance of right whales along the mainland coast in the early 20th century compared with the New Zealand Subantarctic (Auckland Islands) have suggested that the species may have been extirpated from mainland New Zealand. Current genetic and photo-identification links between the two areas could be the result of recolonization from the Auckland Islands to New Zealand rather than involving the remnants of a single mainland stock, although analyses of historical genetic material are needed to establish whether the two areas were originally isolated (Carroll *et al*. 2011).

In the southwest Atlantic, right whales in southern Brazil showed an increase in sightings after 1997 that was too rapid to be accounted for by natural increase alone, and indicated a pulse of immigration that peaked in the early 2000s (IWC 2013). Genetic studies have revealed homogeneity between Peninsula Valdes, Argentina, and southern Brazil (Ott *et al*. 2011), and (although a full comparison of catalogs has not been completed) a few photo-identification matches have confirmed movement between the two regions (Best *et al*. 1993). However in this case there is less evidence of extirpation in the area receiving immigrants, with a Brazilian fishery for right whales running from at least 1950 to 1973 (IWC 1986, p. 29), in which as many as 26 right whales were taken between 1956 and 1959 (Watase 1959 in Castello and Pinedo 1979).

In the meantime, the process described here is consistent with the observation of Richards (2009) that southern right whales in general are extending their distribution northwards and occupying locations where they have not been seen for a century or more.

Clapham *et al*. (2008) concluded that when subpopulations of whales within relatively small geographic areas are extirpated or greatly reduced, no repopulation of the area occurs by immigration from adjacent subpopulations. They attributed this to loss of cultural memory, excessive exploitation of adjacent subpopulations, and/or social structure. The examples provided by Namibian and New Zealand right whales (although the recoveries are still embryonic in nature) suggest that this hypothesis may not be universally applicable. Whether some of the "repopulation" may in fact include an element of a remnant surviving from the pre-exploitation population is a larger issue, but observations of individual movement back and forth between the

high-density areas and the area being "repopulated" (as seen here) would not seem consistent with the behavior of members of a remnant population, that might be expected to show more site fidelity to a particular area (IWC 2013, p. 445).

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