Catch history, seasonal and temporal trends in the migrations of humpback whales along the west coast of southern Africa

Peter B. Best[1] and Cherry Allison[2]

[1]Mammal Research Institute, University of Pretoria, C/o Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa

[2]International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge, CB24 9NP, UK

Abstract

The catch history and seasonality of humpback whales are reviewed for four whaling grounds on the west coast of southern Africa, the SW Cape, Namibia, Angola and Gabon. Seasonal availability was distinctly bimodal in the three southern grounds (with the peaks converging with decreasing latitude) but unimodal in Gabon, a pattern that most contemporary observers considered indicative of migration. Differences in the timing of the peaks at Hangklip (SW Cape) and Cabinda (Angola) indicated an overall speed of movement of 441-553 km/week on both winter and spring migrations. Preceding WWI the catch history in all four whaling grounds was similar, with massive declines in humpback whale availability, but thereafter it differed, especially between Gabon (where there were apparent signs of recovery between three episodes of whaling) and the SW Cape (where there were no such signs between almost contemporary episodes of exploitation). Differences in mtDNA haplotype frequencies between Gabon and the SW Cape, and the movements of whales satellite-tagged in Gabon, have led to the suggestion of a separate breeding ground in southern Angola or northern Namibia, to which animals from the SW Cape migrate. Given 11 genetic or photographic matches between Gabon and the SW Cape, and the offshore migratory routes demonstrated by some tagged whales from Gabon, an alternative hypothesis of a single breeding ground in Gabon but separate, maternally-directed migratory routes to different feeding grounds is proposed.

Introduction

Large catches of humpback whales were made in the waters off the west coast of southern and central Africa, both in the late nineteenth century by open-boat whalers (Townsend 1935) and particularly in the early twentieth century by modern whalers (Best 1994). While formal catch statistics were not collected for the open-boat fishery, the catch of humpback whales by American vessels has been estimated as 14,600 – 18,200 worldwide between 1805 and 1909, with catches peaking at 2,500 – 5,000 over five years (i.e. 500-1,000 a year) in the late nineteenth century: these estimates are for landed catch and do not account for the proportion struck and lost which could be substantial in this species (Best 1987). The number of these taken in African waters has not yet been established. Although the statistics for modern whaling in the region are full of uncertainties for the early years of the modern fishery, an estimated 21,671 humpback whales were landed in operations on the west coast of southern Africa between 1909 and 1930 (Best 1994).

Despite these large catches, little has been published about the links between the various coastal whaling grounds or between these whaling grounds and those in the Antarctic, as there were no recoveries of Discovery whale marks and (until very recently) no confirmed matches between individuals through photo-identification or genetics. The situation has been complicated by the recent finding of significant genetic differentiation between whales sampled in the SW Cape and off Gabon, implying limited or very low gene flow between these two locations that were (supposedly) frequented by whales on the same migratory route (Rosenbaum et al., 2009). This has prompted the IWC to subdivide the humpback whales occurring on the west coast of southern Africa into Breeding Stock B1 (situated around Gabon) and B2 (situated in the SW Cape), with the boundary between the two situated around 18^{o}S, or at the Angola/Benguela Current Front (IWC 2007). At the same time, a number of photo-identification and genetic (microsatellite) matches have confirmed that individuals do indeed move between regions B1 and B2, despite the apparently limited gene flow (Carvalho et al., 2009).

In this paper we attempt to address the issue of the B1/B2 distinction by reviewing information on the seasonality of historical catches and recent sightings at different localities, and comparing trends in the apparent availability of humpback whales over time at these same localities. This information is combined with the results of ongoing photo-identification, genetic and satellite-tagging studies to develop an alternative hypothesis for stock-structuring on the west coast of southern Africa.

Methods

The catch series used here for humpback whales on the west coast of southern Africa is based on that developed by Allison (2007), being *inter alia* a re-evaluation of the information provided by Best (1994). During the preparation of this paper, however, the catch series in Allison (2007) has been revised following the provision of new information and the resolution of inconsistencies. It is available as Appendix 1. The data have been divided into four separate regions, corresponding to largely separate whaling grounds and to some extent with similar divisions used in the International Whaling Statistics: S W Cape (stations at Hangklip, Donkergat and Salamander), Namibia (stations at Luderitz and Walvis Bay), Angola (stations at Tiger Bay, Porto Alexandre, Mossamedes, Elephant Bay and Lobito) and Gabon (stations at Cap Lopez, Libreville, and including the islands of Fernando Po and Sao Thome (Fig. 1).

Until very late in the catch series there are no specific data available on catching effort, such as number of catcher days or searching hours; indeed, early in the catch series it is sometimes difficult to establish even the number of catchers operating with an expedition. There is also the problem that although the industry originally started with humpback whales as its main target, several operations switched to other species as soon as the availability of humpback whales declined. Thereafter it is difficult to establish how much of the catching effort was directed towards humpback whales: undoubtedly they would be taken whenever encountered, but the search for other species may have taken the catchers further offshore and away from at least the coastal stream of migrating humpbacks, so effectively reducing the chances of encountering them. Some operations, however, notably those off Gabon, seem to have retained humpback whales as their principal target throughout their history.

Our approach to developing indices of abundance for these two types of operation has therefore differed. For whaling grounds with obvious prey-switching, annual indices of humpback whale availability have simply been expressed as the number of whales landed per

catcher per season. For whaling grounds where humpback whales remained the target of pursuit we have attempted a more detailed accounting of effort: the length of the season in days has been converted to daylight hours and then adjusted for the time spent handling the catch so that an estimate of time spent searching is approximated. This in turn is converted to distance searched using an average cruising speed. Both the handling time per whale and cruising speed are assumed to vary with the size of the catcher boat, so compensatory adjustments have been made for the increasing size of the catchers over time (following the approach of Best, 1981).

The relationship between handling time (time spent chasing, killing and securing) in hours for each humpback whale (y) and catcher gross tonnage (x) has been taken as

$$y = -0.0013x + 1.9332.$$

These imply average handling times per whale of 1.8 h for a 100 ton catcher reducing to 1.54 h for a 300 ton catcher. Because of their small contribution to the total catch, no separate calculations of handling time have been made for other species and they have been assumed to be the same as that for humpback whales. Based on data for 70 catchers ranging from 162 to 625 in gross tonnage, catcher speeds have been taken as varying with catcher size according to the following relationship –

$$y = 4.258\ln(x) - 11.81,$$

where y = maximum speed in knots and x = catcher gross tonnage ($r^2 = 0.778$). This translates to a speed of 9.5 knots for a catcher of 150 tons and 12.5 knots for a catcher of 300 tons. These speeds have been adjusted downwards by 20% to approximate that used in searching (following information in Best, 1981).

Finally, where data are available for more than one expedition operating on the same whaling ground in the same season, these have been considered as independent samples of whale availability and their mean and standard error calculated. Exceptions are made in the case of the operations at the islands of Fernando Po and Sao Thome in the Congo whaling ground, which are considered distinct enough to be illustrated separately.

Results

Catch history and estimates of relative abundance

SW Cape

Modern whaling started on the west coast of South Africa in 1909 at Saldanha Bay, and continued with only a single year's interruption (1921) until 1930, with a maximum of three stations in operation in any one year. Whaling resumed with a single station (Donkergat) from 1936 to 1937, 1947 to 1953 and 1957 to 1967. Humpback whales formed the bulk of the catch from 1909 to 1911, but CPUE fell sharply thereafter and from 1914 (with the exception of one or two seasons) the species failed to exceed 4% of the catch for nearly all the remaining years that the stations operated (Fig. 2).

Not everyone considered this decline an index of depletion. In a letter to the Administrator of the Cape's office dated 16 January 1918, Carl Ellefsen, the manager of the Salamander

whaling station, commented “We only had two [humpbacks] in 1917. They were very small, only about 30 ft long. It is of course a well known thing that the Humpbacks are very shy, and soon disappear from any place where they are hunted. Wherever whaling has been carried on the Hbcks have left after two to three years. It has often been suggested that this is due to extermination, but that idea is absolutely unfounded. It is directly contradicted by the fact that a certain number of this species always are to be found around the coasts where whaling is carried out, only they are too cute to be trapped, and the whales which are shot constitute only a small figure compared with the vast numbers passing by. But with the Humpback more than with other whales it is the case that they change their habitat. They find it the easiest way to safety to clear out and this coincides with the fact that these whales are met in the most remote regions… We have no doubt that Humpbacks are passing our coast, because they are still in great numbers along the tropical coast of West Africa, and they often pass our coast very near”. The significance of the last sentence will become clear later.

There was no sign of a significant recovery of the species up to the time it received international protection (1963). The low availability of humpback whales in the SW Cape whaling ground at that time was confirmed by fact that over seven whaling seasons between 1961 and 1967, only five sightings of six humpback whales were made in 3,829 hours of searching by the spotter aircraft associated with the Donkergat whaling company, when operating between March and November each season. Two of these sightings were in June, one in July and two in August. As all species of large whale were recorded, whether of current commercial interest or not, these data suggest that indeed humpback whales were rare and not just ignored by the catcher fleet at this time (although of course this still refers principally to an area offshore from the main coastal migratory route).

Namibia

Modern whaling commenced in Namibian waters in 1912 with the mooring of a factory ship and the construction of a land station, both in Walvis Bay. A second land station opened at Luderitz in 1913. Following the outbreak of World War I, all operations were brought to a halt in September 1914 by the arrival of German troops in Walvis Bay and British troops in Luderitz. Whaling only resumed again in 1923 when the land station at Walvis Bay reopened: its closure in 1930 marked the end of legal whaling in Namibian waters.

The effects of the pre-WWI episode of whaling are difficult to establish with any certainty because of its brief duration and the abbreviated nature of the third season. Nevertheless, the data do seem to suggest a sharp decline in humpback whale abundance, and this is perhaps confirmed by the increased interest in other species in 1914 (Fig. 2). A statement by the Acting Magistrate in Walvis Bay, Mr FW Bult, dated 15 July 1915, supports this conclusion – “My predecessor, in his annual report on this District for the year 1914, stated that, since whaling started here towards the end of 1912 (just about two years), 1 218 whales had been caught by the two companies, who utilize six steam whalers between them. In 1914 whales had become very scarce and were only to be found at considerable distance from the shore”.

Humpback availability still seemed reasonable when whaling resumed in 1923, but catches thereafter were dominated by other species (particularly blue whales) and the progressive decline in humpback CPUE may be a reflection not only of a real diminution in humpbacks but also a preference to hunt blue whales when available (see remarks under Seasonality).

Angola

Whaling began in Angola in 1909 with the arrival of the *Viking* expedition, and escalated from two expeditions in 1910 to six in 1911 and seven in 1912. Catches at first were almost entirely of humpbacks, but their availability clearly started to decline from 1912 onwards, so that by 1915 their average CPUE was only 5-6% of that at its peak in 1912 (Fig. 2). This relative scarcity of humpbacks was accompanied by an increasing proportion of other species (particularly sei whales) in the catch so that by 1914 humpbacks were in the minority. After the 1916 season, when only two expeditions operated, whaling temporarily ceased in the region.

Strong (1914) estimated that about 14,000 whales passed the coast of Angola in 1911, of which 4,000 were killed. In 1912 equivalent estimates were 12,000 and 4,250 killed. He predicted that such catches were unsustainable, and that the fishery would collapse within six years. In 1913 he calculated that 30% less whales passed the coast compared to the previous year (Strong, 1915), implying a reduction of 40% in the population over two years. The average CPUE calculated in this paper declined from 225.9 whales per boat in 1911 to 121.5 whales per boat in 1913, or a 46% reduction over the same time period, essentially supporting Strong's claim.

Whaling resumed in Angolan waters between 1923 and 1928, but humpbacks formed only 11% of the catch in 1923 and declined to 1-7% from 1926 to 1928, and their availability (as measured by CPUE) was at levels similar to or lower than those seen in 1915 and 1916. Although initial catching attempts used a factory ship just outside territorial waters, from 1924 a land station was in operation most years, so presumably the coastal stream of humpback whales was available to be exploited. The abundance of humpbacks therefore must have continued to be low, unless there was a major switch in species preference. However the whaling off Angola in the 1920s is notorious for the low levels of oil production per Blue Whale Unit: in 1926, for instance, when 76.5 % of the catch consisted of blue whales, only 17 barrels were produced per BWU (Tønnessen and Johnsen, 1982). Such extremely low yields from species other than humpback make active selection against taking humpback whales extremely unlikely.

All whaling ceased in Angolan waters at the end of the 1928 season.

Gabon

Whaling commenced off Gabon in 1912 and took place essentially in four phases, 1912-1914, 1922-1926, 1934-1937 and 1949-1952, with separate single years of operation in 1930 and 1959. Single whaling seasons also occurred at Fernando Po (1914) and Sao Thome (1951). In contrast to the other west coast whaling grounds discussed here, humpback whales formed the bulk of the catches in all four phases, and other species only started to increase in prevalence towards the end of the 1922-26 and 1949-52 time series, reaching maxima of 20.2% and 39.2% respectively. This means that indices of availability such as CPUE are more likely to be a valid reflection of humpback whale abundance throughout the time series than in the other whaling grounds.

All four principal phases of whaling in the region were characterized by sharp declines in CPUE, with some suggestions of stock recovery between each, although this may partly reflect a failure to correct for increasing catching efficiency over time (Fig. 2). The rise in CPUE from 1949 to 1950 seems to go against the trend, but can be at least partly explained by

an increase in processing capability between the two seasons, from 12-15 to 18-22 whales per day: this meant that whereas in 1949 a stop-catch was enforced almost every day for nearly two months because the factory could not handle the catch, this was only necessary for three weeks in 1950 (Budker and Collignon, 1952). To try and compensate for such an effect, it has been assumed that half a day's search effort was lost on each of the 40 extra stop-catch days in 1949, but such a correction may not have been sufficient to allow for the overall increase in factory processing capabilities between the years.

There seems little doubt that each of these declines in CPUE represented a real reduction in humpback whale abundance. As corroborating evidence of this from 1949 to 1952, Budker (1953) cites the gradual reduction in size of the individuals killed and the shift in the sex ratio of the catch from predominantly male to predominantly female over the four-year time period.

Seasonality of occurrence

Apart from the shore-based study in the S W Cape reported on by Barendse et al. (2010), there has been no formal attempt to document the seasonal occurrence of humpback whales on the west coast. In this section I have therefore largely used data arising from the whaling industry or statements from whaling operatives.

S W Cape

Olsen (1914) commented on the length of the humpback "season" off Saldanha Bay, starting at the end of May and lasting until the middle of December, although single animals could be found as early as March. Catches for the 1911 and 1912 seasons combined show peaks in late June and late October (Fig. 3a) that Olsen equated with the northern and southern migrations respectively.

Catches for the Hangklip whaling station for the 1913 season (the last when humpback whales formed the majority of the catch) show a similar pattern to those for Donkergat but with a suggestion of a slightly earlier first peak (mid June) and later second peak (early-mid November) to the distribution (Fig. 3a).

The manager of the Salamander whaling station, Carl Ellefsen, commented that humpback whales generally passed the coast closest of all the whale species. They always seemed to come in from the S-SW or West all along the coast and then head North, very near land as a rule (C. Ellefsen, in litt. to Director, South African Museum, 23 Feb 1915).

Namibia

In a report entitled "Whaling – 1923" to the Secretary of the Fisheries Survey Committee, Dept of Mines and Industries, in Cape Town, the magistrate at Walvis Bay, Mr K.R. Thomas, reported that whaling was carried out from 12 June to 26 November with 4 small steamers.

> "The Blue whales caught in July and August were going North apparently and the Humpbacks in September, October and November were going South but I could not ascertain whether and when the Blue whales came back and when the Humpbacks went North. It may be of course that humpbacks going North and blue whales going South travelled further out from the coast. …..

> I understand some believe the humpback whale to be more timid and others more intelligent than other species of whales, and it is considered it avoids regions where whalers are found. If this is so it is curious only a few humpbacks were captured in June and July and none in August when active operations were being carried out daily and then a fair number were caught in September and the whole catch of 100 in October were humpbacks. The numbers began to fall off in November when only 59 were caught, only 15 being captured after the 15th and most of these were caught further out at sea. It may be of course that in early part of season whalers finding blue whales plentiful preferred catching these and only caught humpbacks later when former got scarce." (K.R Thomas, in litt. 4 Feb 1924).

The 1923 individual catch data given by Thomas for humpback whales are illustrated by 10-day period in Fig 3b, and clearly show the small peak in June /July and the much larger peak in October and November. The data plotted for blue whale catches show the reciprocal nature referred to by Thomas and lend support to his hypothesis of prey-switching by the catchers.

Thomas also gave monthly catch figures for the earlier episode of whaling from Walvis Bay in 1913 and 1914, when it is believed that the catch was predominantly of humpback whales (Best 1994). The most complete data set (that for the Durban Whaling Company for 1913) is included in Fig. 3b, and it shows a similar dip in catching in August and September.

Angola

According to information received in 1912 from the owner of the whaling station at Elephant Bay, the agent for the whaling companies at Mossamedes and Port Alexander, and the captain of the British floating factory (*Restitution*) operating at the same two localities, humpbacks on the Angolan coast were on their northward run from May till the end of July, and on their return journey from the middle of August until the middle of November, usually following the line of the coast and not going more than about 12 miles off (Strong, 1914). Olsen (1914) also commented that definite northern and southern migrations were noticeable at Porto Alexandre. Humpbacks arrived each year about 6 June and rapidly increased in numbers: the majority passed northward between the end of June and the first half of July, and southward in October, with the last whales passing at the beginning of November. When exploitation first started there were so many whales off Porto Alexandre that catch rates were unaffected by the change in migration, but after 1911 and a marked decline in whale availability the slack period between the northern and southern migrations became apparent.

Data presented by Lea (1919) for catches of humpback whales off Porto Alexandre in 1911 and 1914 indicate a similar seasonal pattern in the two years despite vastly different values owing to the intervening collapse in the humpback stocks. Catching occurred between June and November, with peaks in July and October and an intervening "slack period" in August and September. Risting (1922) referred specifically to this slack period and provided data on catch rates (as measured by barrels per catcher per day) for the *Viking* expedition to Porto Alexandre in 1913 in support (Fig. 3c). The seasonal bimodality in humpback catches persisted in the 1920s, with peaks apparent in July and October (Harmer 1931).

More recent observations of humpback whale abundance are available as incidental sightings collected during 1995 from oil platforms off Angola (Best et al., 1999). These were mainly collected from northern Angola and especially off Cabinda, so have been illustrated separately

from the catch data from Porto Alexandre (Fig. 3d). Sightings extended from the week ending 1 June to the week ending 25 November, Two clear peaks in sightings can be seen, the first (and larger) in the week ending 5 August, and the second in the week ending 30 September. The valley between the peaks extended from the week ending 26 August to the week ending 9 September. Assuming that effort was uniform (or varied randomly), the bimodality may represent successive waves of northward-moving and southward-moving whales. Observations made from an oil platform situated at 6^{o} 51.63'S 12^{o} 23.41'E (or approximately 15 n. miles offshore and about 50 n. miles due South of the Congo River mouth) from 17 to 28 September 1998 indicated that the majority (or 68.4%) of groups were moving southwards and the remainder northwards at this time of year (Best et al., 1999).

Gabon

According to Risting (1922), there was no sign of a seasonal slack period in humpback whale catches off Gabon, and he provided catch rate data (expressed as barrels/catcher/day) for the *Aekvator* expedition to the Congo in 1913 in support of this (Fig 3e). A single mode in catches in July/August was also reported for four out of five seasons (unspecified, but presumably 1922-26) by Harmer (1931).

Budker and Collignon (1952) provided information on the timing of whaling operations off Gabon by 12 operations over nine seasons between 1924 and 1950. The earliest starting and latest ending dates were 21 June and 14 November respectively, and one can assume that this corresponded to the period over which humpbacks were most abundant. Weekly data for the 1950 season (in which 1,404 humpback whales were landed) indicate a virtually unimodal catch distribution with a peak in early August (Fig. 3e).

Discussion

In the early years of modern whaling for humpback whales on the west coast of South Africa, those involved seemed in little doubt about the migratory nature of the whales (Strong, 1914, Olsen 1914, and remarks in contemporary correspondence noted above). The seasonal distribution of catches or sightings in the four whaling grounds is also suggestive of an overall northward migration in early winter and a southward movement in spring. Thus (from south to north) peaks are seen in mid-June (Hangklip), late June (Saldanha Bay), June/July (Walvis Bay), end of June – first half of July, or July (Porto Alexandre) and 30 July – 5 August (Cabinda), while (from north to south) peaks occur 23 – 30 September (Cabinda), October (Porto Alexandre), October/November (Walvis Bay), late October (Saldanha Bay) and early-mid November (Hangklip). The northernmost ground (Cap Lopez) had a single peak in July/August or early August.

Approximate rates at which the proposed waves of migration moved can be calculated using the two extreme localities where separate peaks could be detected (Cabinda and Hangklip), which are about 3,150 km apart if a direct route around headlands is assumed. Peaks in these two localities are about 40-50 days apart in both winter and spring, giving an overall rate of movement of 63-79 km a day, or 441 – 553 km a week in both "migrations". This compares with estimates of 220 n miles (407 km) or 180 n miles (333 km) a week estimated in a similar way by Dawbin (1956, 1966) for the migrations of southern humpback whales off New Zealand.

If the successive peaks in availability in adjacent whaling grounds along the west coast of southern Africa represent the migration of a single homogeneous stock of humpback whales, then one might expect the effects of exploitation at any one locality on that migration route to be equally felt throughout its range. However it is clear from the catch histories discussed above that this was not the case. The initial decline in humpback whale abundance before WWI seems to have been experienced in all four major whaling grounds, though the decline off Gabon was possibly less extreme than in the other three regions. After 1920, however, there were sharp differences in the catch histories between grounds.

The biggest contrast was between Gabon and the SW Cape, the regions with the longest catch histories and at the extreme ends of the "migration". Off Gabon, three successive episodes of whaling on humpbacks suggested at least partial recovery of the population in the intervening periods, whereas roughly contemporary episodes of whaling in the SW Cape revealed no such indication. Even given the different nature of the operations (Gabon - humpbacks as principal target; SW Cape - humpbacks as secondary target), it is difficult to visualize that these operations were targeting the same component of the population.

The catch histories in Angola and Namibia in the 1920s are more ambiguous. Whaling resumed in Namibia in 1923, one year after Gabon, and humpback catches in the first season were high and formed two-thirds of the catch, but fell rapidly thereafter. Although CPUE was also high in Gabon in 1923, and fell in 1924, a greater decline took place in 1925. It is possible that the greater decline in 1924 in Namibia reflected some degree of prey-switching to blue whales. In Angola whaling resumed in 1924, two years after Gabon and one year later than Namibia, but humpback availability was extremely low, and nominally less than when whaling ceased there in 1926. The contrast here with Gabon seems greater than in Namibia, but prey-switching had already taken place and humpbacks comprised only 10.9% of the catch in 1924.

This contrast between the whaling histories for humpbacks in Gabon and other whaling grounds on the west coast of southern Africa has been noted by other authors. Tønnessen and Johnsen (1982) state that while the presence of migrating whales past the Angolan coast would lead one to suppose that stocks of whales existed to the north off Gabon, and the more stationary nature of the whales there (without evidence of a pause between northward and southward migrations) would suggest that this was the terminus of the migration, "it was undoubtedly incorrect to believe that whales off the Congo were the same (humpback) stocks as those that proceeded past Angola". As apparent evidence in support of this they cite research showing that there were separate stocks of humpback in the Antarctic, each proceeding north to its own particular area.

In a recent analysis of humpback whale population structure in the South Atlantic and Indian Oceans using mtDNA, Rosenbaum et al. (2009) detected significant differentiation between whales sampled in Gabon and those sampled in the SW Cape, and postulated the existence of a second unsurveyed breeding population, possibly off Angola, to which whales from the SW Cape were linked via a coastal migration through the waters of Namibia.

However the paper did not mention the existence of 10 microsatellite matches between Gabon and the SW Cape (Carvalho et al., 2009), involving nine individuals (four males and five females), four of which implied a direct southward movement (August/September in Gabon, following October -January in SW Cape). An additional two matches have been made via photo-identification (Barendse et al., paper to meeting). There is therefore no doubt that some

humpback whales in Gabon travel to the SW Cape, presumably via a coastal route that takes them through the waters of both Angola and Namibia.

Further data on the movements of whales in the Gabon whaling ground have been obtained through satellite telemetry (Rosenbaum and Mate, submitted). Fifteen whales tagged there in August/September 2002 showed a variety of different movement patterns before their transmitters failed. Seven whales moved further north and west, extending the known range of the breeding ground in the Gulf of Guinea, while five whales swam south into Angolan waters. Two of the latter left the central Angolan coast and travelled southwest along the Walvis Ridge for 1,200 km before reaching 40^{o}S where they diverged and continued south as far as Bouvet Island (54^{o} 26'S 3^{o} 24E) or 56^{o}S, close to the prevailing ice edge. Both these females travelled 43-400 km off the Angolan coast. The authors suggest that the boundary between the two putative breeding stocks on the west coast may coincide with the Walvis Ridge, which would presumably mean somewhere in the vicinity of the Angolan/Namibian border (18^{o}S).

These results, taken in conjunction with the photo-identification and microsatellite data, indicate that whales from the Gabon breeding ground may take very different routes to feeding grounds, with some moving down the coast and others taking an offshore route. The latter took whales well outside the probable catching range of operations in the SW Cape and Namibia, and in some cases Angola.

This point was noted by Olsen (1914), who stated that relatively few humpbacks came inshore on the south coast of Africa and from there followed either the east or west coasts to the north: most came in from the sea further north and did not touch southernmost Africa during migration. In support, he pointed out that because humpback whale availability at Saldanha Bay was reduced after only a few years and moderate catches it could only have been a small proportion of the population that chose to travel close to the coast at these latitudes, possibly those whales that over-summered in the Antarctic due south of South Africa. The rest of the population presumably chose the shortest, offshore route between feeding and breeding grounds.

In the North Atlantic, humpback whales feed in a number of relatively discrete subpopulations in summer, but mix on a common breeding ground in winter. Fidelity to the feeding grounds is maternally directed (Clapham and Mayo, 1987), and has persisted long enough to be reflected in the population's genetic structure (Larsen et al., 1996). Less is known about the situation in the Southern Hemisphere, but the recovery of Discovery tags suggested that the majority of whales that feed in Area IV of the Antarctic migrate to Breeding Ground D on the West Australian coast, and the majority in Area V to Breeding Ground E on the East Australian coast, and that while some intermingling may occur on the feeding ground, this does not result in much permanent exchange between populations (Chittleborough, 1965). More recent photo-identification and satellite-tracking data indicate that humpback whales feeding in the vicinity of South Georgia and the Sandwich Islands over-winter off Brazil, while those feeding in the Western Antarctic Peninsula and the Weddell Sea south of the South Orkneys and west of 35W have been associated with Breeding Stock G on the west coast of South America (Zerbini et al., 2006; Dalla Rosa et al., 2008). Other individuals from Breeding Stock G may use feeding grounds in the Magellan Strait and not migrate to the Antarctic (Acevedo et al., 2007). Although the numbers of re-sightings and telemetered individuals are still small, the evidence is beginning to suggest a

greater fidelity to feeding grounds by individuals from a breeding ground than was previously considered for southern humpback whales.

A reasonable hypothesis would be therefore that individuals from Breeding Stock B use different summer feeding grounds, and that fidelity to these feeding grounds is maternally directed. As intimated by satellite-tracking results, one of these feeding grounds is on the borders of Areas II and III, in the vicinity of Bouvet Island, and migration to and from that ground is quite remote from the African mainland for most of its route. Provided enough individuals habitually took this route, this could account for the different catch histories shown for the whaling ground off Gabon and others to the south. As suggested by photo-identification and genetic matches, other individuals may be linked with feeding grounds on the west coast of South Africa or south of the continent, and take a coastal migration route between breeding and feeding grounds. Genetic differences observed between samples from B1 and B2 could therefore be an evolutionary consequence of long-term maternally directed site-fidelity to specific feeding grounds. Under this hypothesis there is no need to postulate the existence of a separate breeding stock in southern Angola or Namibia, for which there is no other supportive evidence.

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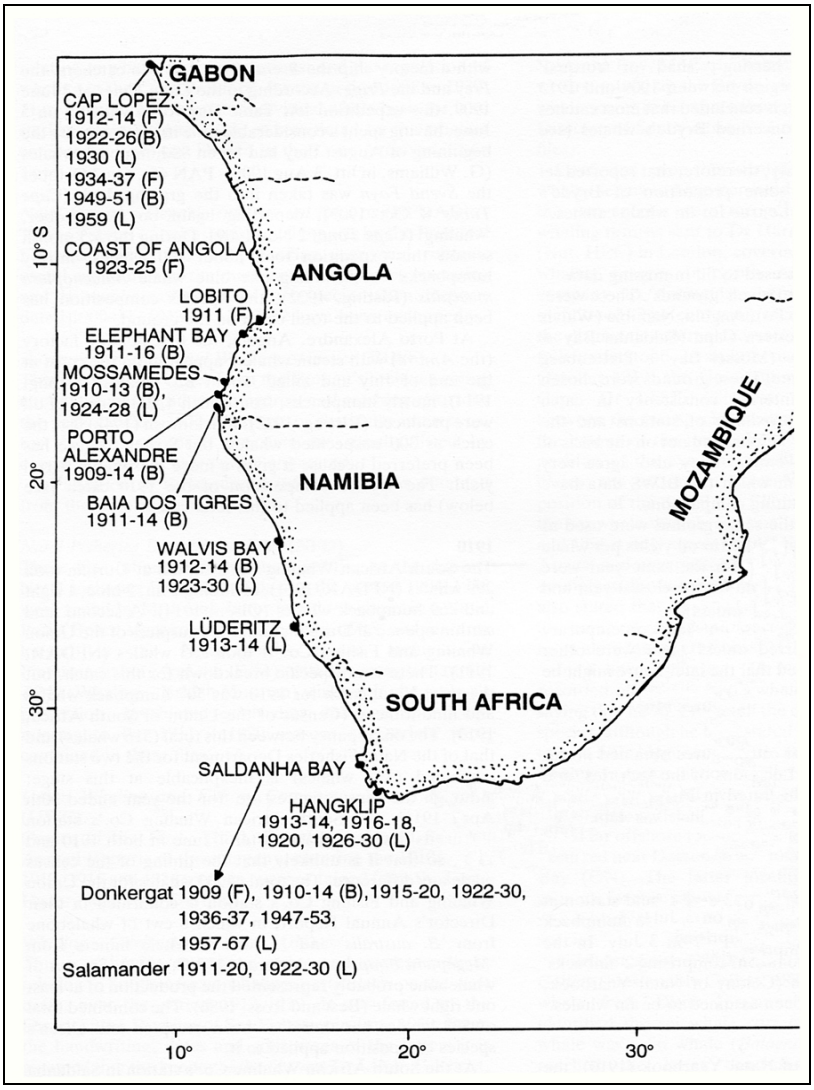

Fig. 1: Coast of southern Africa showing positions and years of operation of all modern whaling activities on the west coast

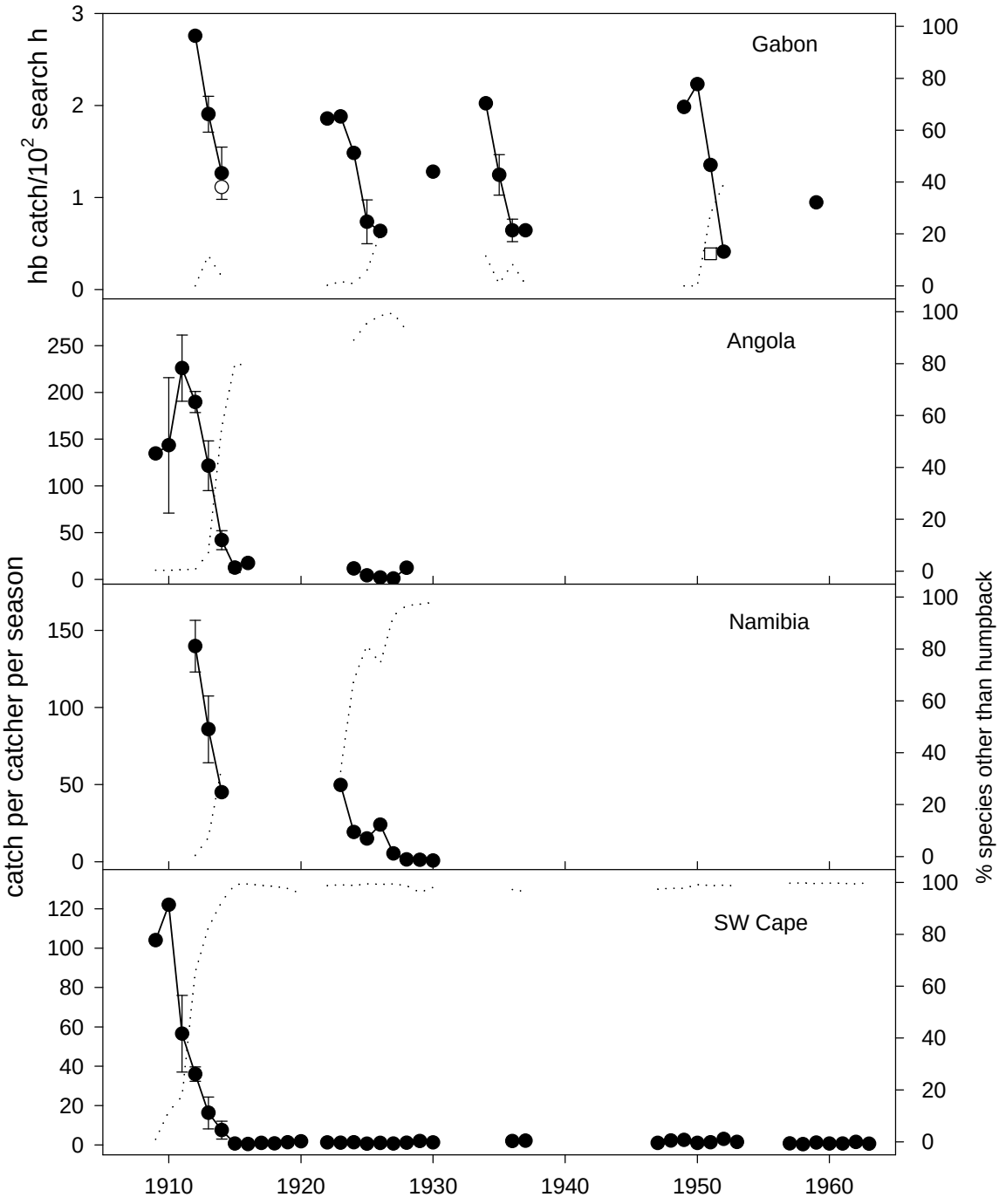

Fig. 2: Trends over time in humpback whale CPUE (solid line) and the % of other species in the catch (dotted line) in four whaling grounds on the west coast of southern Africa (vertical bars = SE of mean, open circle = Fernando Po, open square = Sao Thome).

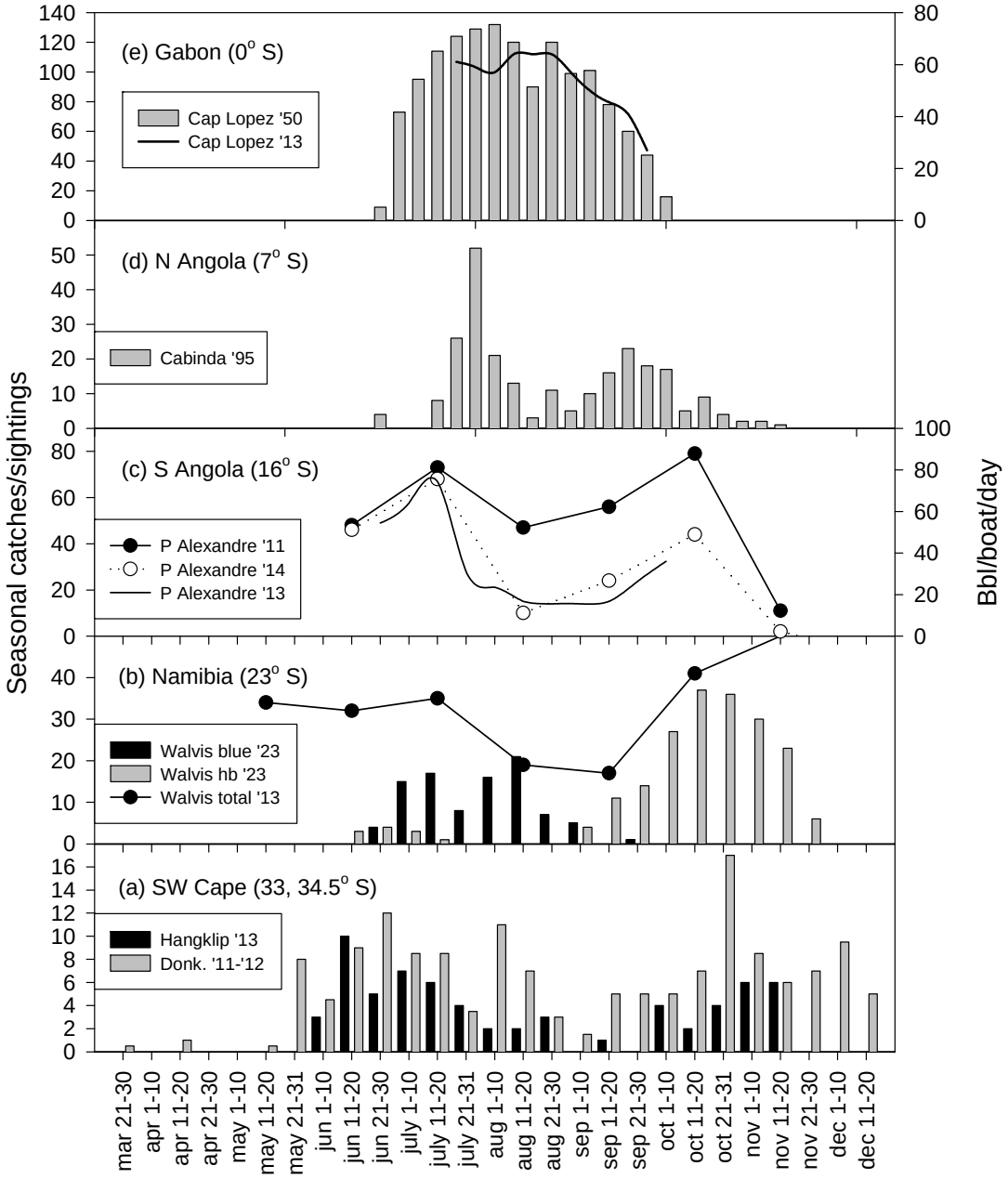

Fig. 3: Seasonal variations in availability/catch rates of humpback whales on the west coast of southern Africa

Updated catch data for humpback whales on west coast of Africa, 1909-1930

NB – The compilation of these statistics represents a distinct advance in general on those published by Best (1994), in that more sources have been consulted and some errors corrected. However as in many historical reconstructions this is very much a work in progress, and should not be considered the final word on the subject.

Where the data are essentially unchanged from Best (1994) the latter has been given as the default source, even though it is almost always not the original source. In some of these cases data for species other than humpbacks may have changed.

All catch figures represent landed (i.e. processed) catch, with no allowance for other animals that may have been killed or mortally wounded and lost before processing. Oil production refers to whale oil only (not sperm), if declared as such.

To give some idea of uncertainty, catches shown in italics mean they are estimated rather than enumerated by some source.

1909

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Angola	*Ambra*, A/S Viking	Porto Alexandre	4500 4200	237	*236*	IWS II, IV give catch as 237 wh, Strong (14) ~270, Macintosh 42 ~ 300, sp comp from 1910. Higher estimates could incl some sperm whales
SW Cape	*Vale*, SA Whaling Co.	Donkergat	4000	210	*208*	NHT 18:138 gives catch 169 wh (4000 bbl) +16 = 185 wh, sp comp from *Svend Foyn*
	Svend Foyn, A/S Sydhavet	Saldanha Bay	3500	~100	99	Best 94

1910

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Angola	*Ambra*, A/S Viking	Porto Alexandre	13,500	~650	647	Best 94
	Ambar, Pesca de Balaena	Mossamedes	1 638	71	71	IWS XVI (Rist 22 – 60 wh 1400 bbl)
SW Cape	SA Whaling Co	Donkergat	20500	276	244	Best 94

1911

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Angola	*Ambra*, A/S Viking	Porto Alexandre	19300	950	946	Tønn 67 Lea 19 have 950 as total, Rist 22 has 946 hb, Lea 19 has 4 non-hb in Tables 34,35.
	Ambar, Pesca de Balaena	Mossamedes	4062	217	217	IWS XVI
	Alonso, A/S Bas	Lobito Bay	2 000	*85*	*85*	Subtract *Ambra*, *Ambar* and *Augwald* catches from IWS total (2289) = 643, divide using rel oil prodn. Adopt sp composition from *Ambra* catch
	Alonso, A/S Bas	Elephant Bay	1 500	*64*	*64*	Ditto
	Vasco da Gama, A/S Spermacet	Elephant Bay	11 600	*494*	*492*	Ditto
	Augwald, Haugesunds Hvalf.	Tiger Bay	11 200	479	*477*	Ditto, but use total no whales from Rist 22 (479)
SW Cape	SA Whaling Co	Donkergat	11 000	276	*228*	Best 94
	Hans Ellefsen Ltd	Salamander	4 000	135	*111*	Best 94

1912

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Pythia*, Dominion Whaling	Cap Lopez	11 300	418	418	Best 94
Angola	*Ambra*, A/S Viking	Porto Alexandre	16 400	669	665	Best 94
	Restitution, Southern Wh&Seal.	Porto Alexandre	10 000	300	*298*	Tot from Strong (14), sp comp from *Ambra*
	Ambar, Pesca de Balaena	Mossamedes	8 450	425	425	IWS XVI
	Alonso, A/S Bas	Elephant Bay	7 750	*278*	*276*	Tot 2710 for Nor companies less *Vik, Espera, Beng* =769, alloc by oil prod, sp comp from *Ambra*
	Esperanza, A/S S Atlantic	Elephant Bay	18 700	760	*755*	Tot from Tønn 67, sp comp from *Ambra*
	Augwald, Haugesunds Hvalf.	Tiger Bay	13 650	*491*	*488*	[See *Alonso*]
	Benguela, A/S Kastor	Tiger Bay	13 880	512	*509*	Tot from Tønn 67; sp comp from *Ambra*
Namibia	*Pentaur*, Durban Whaling Co	Walvis Bay		315	*313*	Best 94
	Walfish Bay Whaling Co	Walvis Bay	5 000+	247	*246*	Best 94
SW Cape	SA Whaling Co	Donkergat	10 000	374	*119*	Best 94
	Vale (?), SA Whaling Co	West Coast		?	?	May be incl with Donkergat – see Best 94
	Hans Ellefsen Ltd	Salamander	7 000	258	*97*	Best 94

1913

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Pythia*, Dominion Whaling	Cap Lopez	13 000	470	*415*	Best 94
	Rakiura, NZ Whaling Co	Cap Lopez	11 200	*441*	*390*	Best 94 + Oct catch to make total of 2522 for all spp Congo from IWS, + sp comp from Lea 19
	Perth, W Australia Whaling Co	Cap Lopez	13 000	*504*	*445*	[see *Rakiura*]
	Vik, Aekvator Co.	Cap Lopez	10 650	*323*	*285*	[see *Rakiura*]
	Imo, S Pacific Whaling Co	Libreville	12 000	*528*	*466*	[see *Rakiura*]
	Aviemore, Alfa & Beta Co	Libreville	2 800	256	*226*	Best 94
Angola	*Ambra*, A/S Viking	Porto Alexandre	13 800	453	*421*	Best 94
	Restitution, Southern Wh&Seal.	Porto Alexandre	12 500	360	*335*	Tot catch Best 94, sp comp *Ambra*
	Ambar, Pesca de Balaena	Mossamedes	6 596	274	*255*	Tot catch IWSXVI, sp comp *Ambra* because of proximity
	Alonso, A/S Bas	Elephant Bay	8 400	612	*312*	Tot catch Best 94, sp comp same as *Esperanza* because of locality, assumed 300
	Esperanza, A/S S Atlantic	Elephant Bay	18 500	827	*427*	Tot catch Best 94, sp comp “almost half catch sei wh” Tønn 67, assumed 400.
	Augwald, Haugesunds Hvalf.	Tiger Bay	13 500	447	*415*	Tot catch Best 94, sp comp *Ambra* because of proximity
	Benguela, A/S Kastor	Tiger Bay	11 495	345	*321*	Tot catch Tønn 67, sp comp *Ambra* because of proximity
Namibia	*Pentaur*, Durban Whaling Co	Walvis Bay		231	*215*	Tot catch Best 94, sp comp *Ambra* because of proximity
	Walfish Bay Whaling Co	Walvis Bay	13 000	276	*256*	Tot catch Best 94, sp comp *Ambra* because of proximity
	A/S Sturmvogel	Luderitz	2 000	*54*	*50*	Tot catch Best 94, sp comp *Ambra* because of proximity
SW Cape	SA Whaling Co	Donkergat	11 270	353	*40*	Best 94
	Hans Ellefsen Ltd	Salamander	8 900	304	25	Best 94
	Southern Cross Whaling	Hangklip		198	65	Individual catch records – Lea 19 sp comp very different, esp humpbacks (148)

1914

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Pythia*, Dominion Whaling	Cap Lopez	10 400	*394*	*380*	Best 94
	Loch Tay/Thule, W Australia Whaling Co	Cap Lopez	14 800	*560*	*539*	Best 94
	Vik, Aekvator Co.	Cap Lopez	7 400	*281*	*270*	Best 94
	Imo, S Pacific Whaling Co	Libreville	8 000	*303*	*292*	Best 94
	Aviemore, Alfa & Beta Co	Libreville	2 500	*95*	*92*	Best 94
	Polynesia, A/S Antarctic	Fernando Po	7 400	280	*270*	Best 94
Angola	*Ambra*, A/S Viking	Porto Alexandre	8 150	197	85	Best 94
	Restitution, Southern Wh&Seal.	Porto Alexandre		*99*	*43*	Tot catch and sp comp pro-rated from *Ambra*'s catch rate ('cos proximity), assuming 2 catchers
	Ambar, Pesca de Balaena	Mossamedes	4 000	100	58	Tot from IWS, sp comp ???
	Alonso, A/S Bas	Elephant Bay	7 100	368	*159*	Tot after other ops deducted from IWS total, sp comp from other 3 Norwegian companies
	Esperanza, A/S S Atlantic	Elephant Bay	15 200	405	*87*	Tot from NHT 14, sp comp from Lea19 (5th boat)
	Augwald, Haugesunds Hvalf.	Tiger Bay	10 000	409	*265*	Tot and sp comp from IWS total after deduction of *Ambra* catch (and assumptions about sp comp of other expeditions)
Namibia	*Pentaur*, Durban Whaling Co	Walvis Bay		66	*44*	Best 94
	Walfish Bay Whaling Co	Walvis Bay	5 670	143	94	Best 94
	A/S Sturmvogel	Luderitz	4 000	*101*	*66*	Best 94
SW Cape	SA Whaling Co	Donkergat	11 600	576	*21*	Best 94
	Hans Ellefsen Ltd	Salamander	9 700			Best 94 [incl under Donkergat catch]
	Southern Cross Whaling	Hangklip		219	33	Individual catch records – size of catch from manager (85) and sp comp from Lea 19 (1 hb in 73 wh) very different

1915

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Angola	*Restitution*, Southern Wh &Seal.	Porto Alexandre		*220*	*45*	Tot catch and sp comp pro-rated from other Angolan expeditions, assuming 3 catchers
	Ambar, Pesca de Balaena	Mossamedes	2 700	109	*22*	Tot from IWS, sp comp from Lea 19
	Alonso, A/S Bas	Elephant Bay	6 000	*288*	*59*	Tot from IWS for Nor, pro-rated by oil prodn, sp comp from Lea 19
	Esperanza, A/S S Atlantic	Elephant Bay	8 500	*408*	*83*	[see *Alonso*]
SW Cape	SA Whaling Co	Donkergat	14 550	395	3	Best 94
	Hans Ellefsen Ltd	Salamander	7 400	210	2	Best 94

1916

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Angola	*Ambar*, Pesca de Balaena	Mossamedes	3 348	224	*45*	Best 94
	Esperanza, A/S S Atlantic	Elephant Bay	2 000	96	*20*	Best 94
SW Cape	SA Whaling Co	Donkergat	17 871	286	1	Tot and sp comp = IWS less Ellefsen catch
	Hans Ellefsen Ltd	Salamander		276	2	Salvesen archive
	Shepstone Whaling & Fishing	Hangklip	5 400	148	*1*	Best 94

1917

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
SW Cape	SA Whaling Co	Donkergat	14 000	532	5	Best 94
	Hans Ellefsen Ltd	Salamander	5 705	213	2	Best 94
	Shepstone Whaling & Fishing	Hangklip		304	3	Best 94

1918

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
SW Cape	Irvin & Johnson	Donkergat	22 506	330	5	Harmer's records (other options 549-553 for total Donkergat and Salamander combined)
	Hans Ellefsen Ltd	Salamander		220	4	Harmer's records
	Shepstone Whaling & Fishing	Hangklip		93	1	Harmer's records (Best 94 four more sei)

1919

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
SW Cape	Irvin & Johnson	Donkergat	17 455	398	14	Best 94
	Hans Ellefsen Ltd	Salamander	9 506	253	3	Best 94

1920

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
SW Cape	Irvin & Johnson	Donkergat	17 509	358	33	Best 94
	Hans Ellefsen Ltd	Salamander	8 390	206	6	Best 94
	Shepstone Whaling & Fishing	Hangklip	7 320	107	1	Best 94

1922

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Prof Gruvel* A/S Congo, Gabon	Cap Lopez	20 000	614	613	Best 94
SW Cape	Irvin & Johnson	Donkergat		574	9	Tot from NHT 23 (Best 94 omitted Nov catch of 51 wh)
	Hans Ellefsen Ltd	Salamander	14 000	487	4	Best 94

1923

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Prof Gruvel* A/S Congo, Gabon	Cap Lopez	23 230	696	685	Best 94
Angola	*Bas II*	Off Angola	4 200	213	2	Best 94
Namibia	Lars Christensen	Walvis Bay	8 400	296	199	Best 94
SW Cape	Irvin & Johnson	Donkergat	23 942	901	9	Harmer records (Best 94 has 1 sei wrongly attributed to Salamander instead of Donkergat)
	Hans Ellefsen Ltd	Salamander	10 711	411	4	Harmer records

1924

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Prof Gruvel* A/S Congo, Gabon	Cap Lopez	19 300	523	519	Best 94
Angola	*Esperanza*, A/S Atlantic	Elephant Bay	8 710	430	47	Best 94
Namibia	A/S Africa	Walvis Bay	11 300	240	77	Tot from CI (1 more blue than Best 94)
SW Cape	Irvin & Johnson	Donkergat	32 674	1009	13	Best 94
	Hans Ellefsen Ltd	Salamander	17 248	538	6	Best 94

1925

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Prof Gruvel* A/S Congo, Gabon	Cap Lopez	13 000	382	360	Best 94
	Maudie, A/S Hvalen	Off Gabon	3 400	101	96	Best 94
	Lancing, A/S Globus	Off Gabon	9 500	308	300	Best 94
Angola	*Esperanza*, A/S Atlantic	Elephant Bay	6 077	288	17	Best 94
Namibia	A/S Africa	Walvis Bay	12 800	321	60	Best 94
SW Cape	Irvin & Johnson	Donkergat	30 615	901	6	Individual catch records (Best 94 omits 1 bl 3 fin late Nov)
	Hans Ellefsen Ltd	Salamander	21 874	683	3	Individual catch records (Best 94 one less fin)

1926

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	*Prof Gruvel* A/S Congo, Gabon	Cap Lopez	12 294	402	321	Best 94
Angola	Praia Amelia Co	Mossamedes	5 768	396	6	Best 94
Namibia	A/S Africa	Walvis Bay	13 200	375	96	Best 94
SW Cape	Irvin & Johnson	Donkergat	26 204	958	9	Individual catch records (Best 94 omitted data from 4 catchers from Hangklip that worked at Donkergat late season, also has 1 bl 1f 1 sei less)
	Hans Ellefsen Ltd	Salamander	20 092	842	9	Individual catch records (Best 94 four more sei)
	Irvin & Johnson	Hangklip	16 112	435	1	Individual catch records (see Donkergat)

1927

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Angola	Praia Amelia Co	Mossamedes	5 880	570	3	Best 94
Namibia	A/S Africa	Walvis Bay	1 800	444	32	IWS (Nov catch, 7 bl 1 f 5 hb, omitted in Best 94)
SW Cape	Irvin & Johnson	Donkergat	25 656	801	2	Individual catch data has discrepancies, total catch varies 799-802, hb catch always 2
	Hans Ellefsen Ltd	Salamander	21 373	711	6	Best 94
	Irvin & Johnson	Hangklip	19 224	529	4	Best 94

1928

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Angola	Praia Amelia Co	Mossamedes	8 340	514	37	Best 94
Namibia	A/S Africa	Walvis Bay	21 465	310	10	Best 94
SW Cape	Irvin & Johnson	Donkergat	26 163	621	7	Best 94
	Hans Ellefsen Ltd	Salamander	20 994	547	8	Harmer records (Best 94 omits 1 hb in error)
	Irvin & Johnson	Hangklip	19 867	473	6	Best 94

1929

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Namibia	A/S Africa	Walvis Bay	20 600	355	10	Best 94
SW Cape	Irvin & Johnson	Donkergat	19 419	436	10	CI data (Best 94 has 1 more bl 1 less f, 1 less sei, from obvious error in Harmer records)
	Hans Ellefsen Ltd	Salamander	14 119	300	25	Individual catch data (Best 94 omits 1 sp)
	Irvin & Johnson	Hangklip	21 123	474	5	Best 94

1930

Area	Operation	Location	Oil prodn	Total catch	Humpback	Remarks
Gabon	A/S Congo	Cap Lopez	19 536	585	578	CI (Best 94 has 6 sei also added to hb number)
Namibia	A/S Africa	Walvis Bay	16 200	303	6	Best 94
SW Cape	Irvin & Johnson	Donkergat	23 812	695	21	CI (Best 94 excl Nov catch of 86 wh & 1 fin entered as hb)
	Hans Ellefsen Ltd	Salamander	13 724	325	6	Best 94
	Irvin & Johnson	Hangklip	13 123	324	3	Best 94

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Abbreviations: IWS = International Whaling Statistics; NHT = Norsk Hvalfangststidende; CI = Individual IWS catch data