ICES Journal of
Marine Science

ICES Journal of Marine Science (2020), doi:10.1093/icesjms/fsaa205

The missing whales: relevance of “struck and lost” rates for the impact assessment of historical whaling in the southwestern Atlantic Ocean

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Vighi, M., Borrell, A., Jackson, J. A., Carroll, E. L. , Pennino, M. G., and Aguilar, A. The missing whales: relevance of “struck and lost” rates for the impact assessment of historical whaling in the southwestern Atlantic Ocean. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsaa205.

Received 5 June 2020; revised 2 October 2020; accepted 4 October 2020.

The massive impact that open-boat historical whaling (18th to 20th centuries) had on whale populations has been traditionally estimated from records of oil and baleen plate production. However, an unknown proportion of hunted whales were struck, wounded, eventually killed, but lost, and not included in these records, suggesting that whaling impact may be critically underestimated. Whaling logbooks provide a key source for assessing past catches and losses. Here, we extract detailed records of 19875 days of activity in the southwestern Atlantic Ocean from 255 logbooks of offshore whaling voyages. During the period considered (1776–1923), whalers first targeted southern right whales (*Eubalaena australis*, 2497 sightings and 658 catches), gradually substituted by sperm whales (*Physeter macrocephalus*, 1157 sightings and 843 catches) after 1840. Loss rate factors, calculated to account for the number of “struck and lost” whales, decreased across time for both species, and were particularly high (ranging 1.09–1.6) for the southern right whale, whose population was drastically reduced by whaling, as compared to previous estimates based on rough catch records. Accurate accounting for these “lost” individuals is essential for reconstructing the impact of whaling on cetacean populations and for a proper assessment of their initial population size and demographic trends.

Keywords: cetacean populations, demography, *Eubalaena australis*, logbooks, open-boat whaling, *Physeter macrocephalus*

Introduction

Whale hunting has been one of the most well documented exploitation activities in the history of marine resource exploitation. Rudimental whaling has been carried out for millennia (e.g. by Norwegian Norse and Inuit whalers; Douglas *et al.*, 2004; Hennius *et al.*, 2018), with the earliest records evidenced by Neolithic petroglyphs and excavations revealing bones of captured whales from 5500 to 4700 BC (Sang-Mog and Robineau, 2004). However, it only became a large-scale industrial activity after the 11th century, with Basque whalers (Aguilar, 1986). The reach of the whaling industry spread rapidly after the industrial revolution and assumed a global scale during the 18th and 19th centuries, with the advent of open-boat whaling, which involved the pursuit of whales by small open boats launched from large vessels that could sail for several months and process whales onboard. During this period, the leading country in the industry was the United States, whose large whaling fleet was based in the harbours of Nantucket, New Bedford, and other cities of New England (Davis *et al.*, 1997; Smith *et al.*, 2012). Great Britain, France, Germany, and on a smaller scale, Portugal and other countries also contributed to a lesser degree to the operations, although sources of information and catch records are fragmentary or unavailable (Dawbin, 1986; Du Pasquier, 1986; Schokkenbroek, 2008; Vieira *et al.*, 2019).

Open-boat whaling, aiming mainly for commercially valuable oil and baleen plates, targeted several cetacean species. During the late 18th and 19th centuries, the right whale (*Eubalaena* spp.) and the sperm whale (*Physeter macrocephalus*, hereafter SW) were considered among the most profitable species (Reeves and Smith, 2007; Smith *et al.*, 2012). Indeed, right whales produced large quantities of oil and high-quality baleen and were relatively easy to catch due to their generally unaggressive behaviour and the positive buoyancy of their corpse; while the sperm whale was targeted for the high value of the spermaceti oil contained in its head and its positive buoyancy. Open-boat whaling had a heavy impact on these species worldwide and was occasionally so intense that led some populations to the edge of extinction (Clapham *et al.*, 2008; Thomas *et al.*, 2016). Despite the nominal protection of the right whale in 1935 (illegal hunts by USSR were still taking place into the 1960s, Ivashchenko and Clapham, 2014), the virtual cessation of SW exploitation after the moratorium on commercial whaling adopted by the International Whaling Commission (IWC) came into force in 1985–1986 (Whitehead, 2018), and the recent implementation of regulations to protect cetaceans worldwide, some populations, such as those of right whales in the North Pacific, North Atlantic, and southeastern Pacific, have never recovered (Cooke and Clapham, 2018; Cooke, 2020; Cooke and Zerbini, 2018).

Estimating the actual number of whales killed by whaling is important for assessing historical baselines (i.e. how many animals were removed from the population) and the extent of subsequent recovery, which is key for the effective management and conservation of whale populations. The importance of historical data for the interpretation of current trends in marine ecosystems has been underlined by several authors (e.g. Lotze and Worm, 2009; McClenachan *et al.*, 2012). Reconstructions of pre-modern (i.e. pre-20th century) catches have been commonly based on the records of total catches delivered at the end of each whaling voyage, or on the number of oil barrels or baleen plates discharged at port (e.g. Best, 1983, 1987; Dawbin, 1986; Du Pasquier, 1986; de Morais *et al.*, 2017). However, many whaling voyages lasted several years, and whaling vessels were often sailing far and wide, visiting different whaling grounds in different oceans, and stopping at different harbours where they could trade part of the production to get provisions, or forward it to the port base to empty the ship's hold. Therefore, the counts of whales killed based on total discharge at the end of a given trip usually included catches made over a few years in geographically distinct regions and may be underestimated. Such tallies can provide an approximate global assessment of catches, but their allocation to source populations requires detailed assessment of the logbook records to resolve the geographical and temporal details (e.g. Carroll *et al.*, 2014).

During the early decades of open-boat whaling, whaling was often inefficient and whales were often struck, slightly or severely injured, and subsequently lost by whalers. Scammon (1874) estimated that ~10% of SW and 20% of the baleen whales were lost after being killed, but these were rough estimates and it is known that percentages may have varied over time in certain periods or fisheries. For example, the exploitation of North Pacific right whales (*Eubalaena japonica*) during the 1840s was so inefficient that <50% of whales struck were eventually processed (Webb, 1988). Reasons for the loss of a whale could include the breaking or loss of a harpoon, a line that accidentally parted or was intentionally cut to prevent the whaleboat from being capsized, or accidents related to the aggressive behaviour of the whale defending itself (Scammon, 1874; Starbuck, 1878). "Struck but lost" whales could get away with a slight injury and recover with no consequences, or eventually die because of the wounds caused by the harpoons. These unaccounted deaths contributed to different extents to increase the impact of whaling on many cetacean populations, very significantly in some cases.

Accurate determination of the significance of these failed whaling attempts is critical to improve the estimate of total kills and thus the assessment of the overall impact of whaling. Many attempts have been made since the late 19th century to determine the so-called "loss rate factors" (hereafter LR), which are corrections applied to total catch numbers to account for whales struck but not landed (e.g. Best, 1983; Bockstoce and Botkin, 1983; Mitchell and Reeves, 1983). These rates vary greatly between species, regions and periods, ranging from values very close to 1 in recent modern whaling (i.e. all whales struck are landed, Smith and Reeves, 2010) to values up to 2.5 or even higher in certain open-boat whaling operations or the early modern fishery (i.e. for each landed whale, 1.5 whales are lost, Tønnessen and Johnsen, 1982; Scarff, 2001). However, most LR calculations were based on summaries provided at the end of whaling trips and included only a limited number of voyages (e.g. Kugler, 1981; Reeves *et al.*, 1999; Scarff, 2001; Aguilar and Borrell, 2007).

Here, we perform a detailed calculation of struck and lost rates for southern right whales (*Eubalaena australis*, hereafter SRW) and SW during open-boat American whaling in the southwestern Atlantic Ocean. This area has been exploited for one of the longest periods among the Southern Hemisphere areas because it hosts several whale species, including both wintering and feeding grounds for SRW and SW, and is relatively close to the North American coast, from where most whaling voyages originated. The southwestern Atlantic Ocean therefore provides an excellent case study for investigating differences between species and temporal variations in whaling loss rates: understanding them is key for an accurate assessment of the magnitude of past impacts on the main target species.

Data used for our calculations were directly extracted from 255 whaling logbooks preserved in historical archives. Logbooks contained detailed evidence of whaling activities, including daily positions and the descriptions of tasks onboard, which enabled the extraction of accurate catch and loss data and the calculation of LRs for SRW and SW. The data series, embracing almost 150 years, was complete enough to allow the investigation of the relative trends across the period ranging from the late 18th century to the early 20th century and to address time-specific corrections of catch estimates, as well as collateral indications of the potential evolution of whaling efficiency.

Material and methods

Study area and data collection

The study area was defined according to the whaling charts produced by Maury (1851), Clark (1887), Ashley (1926), Townsend (1935), and Kugler (New Bedford Whaling Museum, NBWM) to encompass the main open-boat whaling grounds for the two species in the southwestern Atlantic Ocean: *La Plata* or *Platte Ground*, *Brazil Banks*, *False Banks*, and *Falklands Islands Ground*. This area extends latitudinally from Southern Brazil (25°S) to the tip of Cape Horn (60°S) and longitudinally from the eastern coast of South America to 35°W, with a narrower 50–70°W range in the southern portion, corresponding to the Drake passage (Figure 1).

Initial identification of the available logbooks of whaling expeditions liable to have visited these whaling grounds was made through Starbuck (1878), Hegarty (1959), Savours and Brown (1977), Sherman *et al.* (1986), the Whalemen's Shipping List and Merchants' Transcript, the Abstracts of Whaling Logs and Journals compiled by J. S. Cumpston (preserved at the NBWM), Dennis Wood's abstracts 1831–1873 (preserved at the New Bedford Free Public Library), and the archival data from the NBWM, the New Bedford Free Public Library, the Providence Public Library, the Mystic Seaport Museum, the Scott Polar Research Institute (University of Cambridge), the UK National Maritime Museum at Greenwich, and the London Royal Geographical Society. Examination of logbooks was carried out either in person in these libraries or through their microfilm loan and online services. As the data extraction progressed, further relevant whaling expeditions were identified through the names of the vessels raised or spoken to in the study area. Relative logbooks were located through the compilations by Sherman *et al.* (1986), Lund (2001), and Lund *et al.* (2020). Because the study area was also crossed by vessels bound to the Pacific Ocean, to avoid expeditions that were merely in transit, only logbooks of voyages spending >40 active whaling days in the area (i.e. reporting sightings and/or catches) were included in the database.

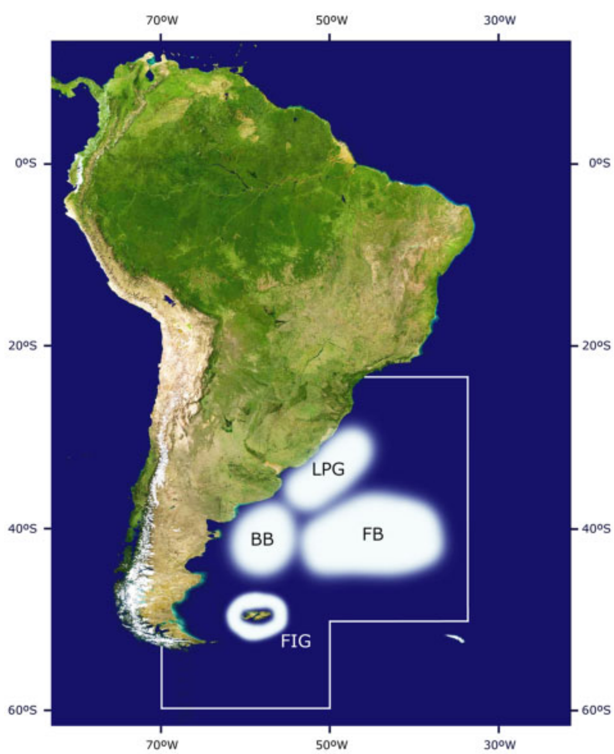

Figure 1. Study area showing the location and approximate extension of the main whaling grounds included in it (Brazil Banks, BB; False Banks, FB, La Plata or Platte Ground, LPG, and Falkland Islands Ground, FIG) based on Maury (1851), Ashley (1926), Townsend (1935), the chart of whaling grounds by Kugler (NBWM), and Bannister *et al.* (2008).

Data were extracted from logbooks following the methods described by Shuster (1987) and Mitchell (1983). Detailed information was reported in Excel spreadsheets for each active day spent by each selected vessel in the study area, including: date (day, month, year, and Julian day), geographical position (latitude and longitude), sightings of SRW, SW and other cetaceans, whaling activities (including whaling attempts, successful and unsuccessful catches, and processing activities), name and characteristics of the vessel (type and tonnage), and sighting of other whaling vessels ("spoken to" or "raised" boats).

Whaling statistics

For any SRW or SW sighting, notes about whaling activities were further categorized following the indications provided by IWC (1986) and Reeves and Mitchell (1986), as:

Sightings = every occasion a whale was seen, irrespective of whether there was an attempt to capture it;
L = lowerings, i.e. the number of times boats were lowered from the main boat to go in pursuit of whales;
C = catches, i.e. whales that were first struck, then killed, and finally processed;
S = struck and lost, i.e. whales struck and then lost without specification given of their likely fate (e.g. losses due to parted lines, harpoons drawn);
K = killed but not recovered, i.e. whales lost after being struck, for which it was explicitly reported that they were seen "spouting blood", "drowned", or "sunk" before being lost (all of which indicate a very high likelihood that the whale was killed or mortally wounded);
R = recovered carcasses, i.e. carcasses found floating, as the result of a previous whaling event in which the whale was struck but not retrieved, by the same or a different whaling crew.

Where C, S, and K are non-overlapping groups (i.e. groups composed by different animals) and R is assumed to be a subset of $(S+K)$ (Figure 2).

Total sightings, L, C, S, K and R across the study period, as well as their annual mean and annual ranges, were calculated separately for each species, summing data reported by the different vessels active each year in the study area. Sightings statistics were calculated considering all years when effort data were available ($n = 105$), while lowering statistics were calculated only considering years when sightings took place ($n = 69$ for SRW and $n = 96$ for SW). Catch statistics were calculated only considering years when lowering took place ($n = 55$ for SRW and $n = 91$ for SW).

To calculate annual whaling statistics (S, K, R), only data available from years when catches took place were considered for the two species (i.e. $C > 0$) to avoid biases related to null values of C. This resulted in 42 and 81 years for SRW and SW, respectively. We assumed that this operation had a negligible impact on overall results, as only two SRW ($n = 1$ in 1836 and $n = 1$ in 1852), and five SW ($n = 1$ in 1821, 1823, and 1833 and $n = 2$ in 1848) were struck and lost in the absence of reported catches.

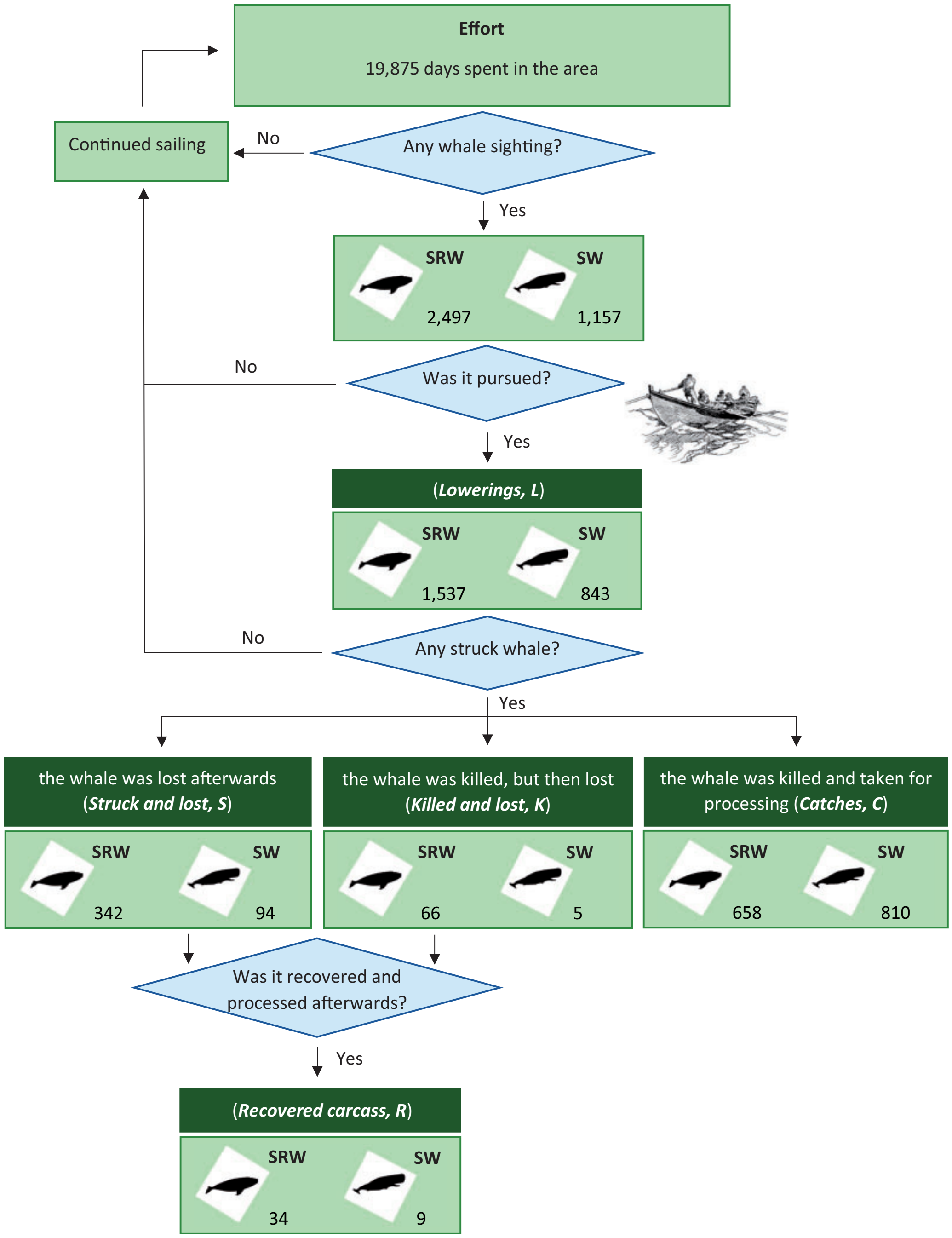

Figure 2. Flowchart summarizing the different whaling activities (from survey effort and sightings to whaling attempts) and possible fates of the struck whales, with relative overall figures for the two species.

Struck and loss factors

Annual struck and lost rates

For each year of activity, maximum (LR_{max}), medium (LR_{med}), and minimum (LR_{min}) ranges of LR for the two species were calculated by varying the mortality rate for whales lost (S) from 1 (all whales struck and lost eventually died) to 0.5 (half of the struck and lost whales died, as in IWC, 1986), and 0 (none of the whales struck and lost died, and only the whale struck, killed, and lost are accounted as deaths), respectively:

$$LR_{max} = (C + S + K)/C,$$

$$LR_{med} = (C + 0.5\ S + K)/C,$$

$$LR_{min} = (C + K)/C.$$

To properly apply LRs to estimate total mortality from data obtained from landed catches, the number of lost whales subsequently recovered and processed should also be considered. Thus, the proportion of struck and lost whales (by the same whalers or by neighbour whaling vessels) that were subsequently recovered was calculated as:

$$R_{COR} = R/(S+K).$$

As a complementary indication of the whaling efficiency, the proportion of whales caught for each lowering (*C*/*L*) was also calculated for the two species, for each year when lowering took place ($n=55$ for SRW and $n=91$ for SW).

Annual mean values with relative standard errors and annual ranges throughout the study period were calculated for each of the above factors. The normality of distribution of LRs and *C*/*L* ratios was tested through a Shapiro-Wilk test. As these parameters were proportions and none of them was normally distributed ($p<0.001$), correlations between LRs, *C*/*L*, and time were explored for the two species through a non-parametric Spearman correlation. Correlation significance was set at 0.05 and values of rho were plotted for LR_{med} and the *C*/*L* ratio for the two species. Correlations were computed using the "corrplot" package of the R software (R Core Team, 2019).

Overall struck and lost rates

To avoid possible bias related to excluding years with no catches reported and allow a broader comparison with published estimates, overall loss rate factors (LRF) were also calculated according to the method applied by Carroll *et al.* (2014), adapted from Smith and Reeves (2010) and Reeves *et al.* (2010). The method assumed that all struck whales were killed, so it provides an upper bound on potential losses due to whaling inefficiency. The approach was applied both for (i) the entire catch period and catches (ii) up to 1850 (i.e. the peak right whaling period) and (iii) after 1850. First, the proportion of losses (PL) was calculated as follows:

$$\mathrm{PL} = (S+K-R)/(C+S+K).$$

The loss rate was treated as a binomial random variable, and standard errors calculated for each PL value as follows:

$$\sigma = \sqrt{\frac{\mathrm{PL}(1-\mathrm{PL})}{C+S+K}}$$

The LRF was then calculated as:

$$\mathrm{LRF} = 1/(1-\mathrm{PL}).$$

The error of this estimate was approximated from the standard error of PL, using a first-order Taylor series expansion as follows:

$$\sigma_{\mathrm{LRF}} = \sqrt{\frac{\sigma^2}{(1-\mathrm{PL})^4}}.$$

Generalized additive models

Being a compromise between the most conservative LR_{min} and the less conservative LR_{max} in terms lost whales that eventually died, annual LR_{med} was selected as the factor that most likely described the actual losses taking place for the two species. Generalized additive models (GAMs) were used to analyse the influence of four independent variables on the annual values of LR_{med} and the *C*/*L* ratio (dependent variables) of the two species, namely, year, effort (number of days), the type of vessel, and the medium tonnage of vessels active in the area for each year. As both dependent variables are proportions, all GAMs were fitted using a beta distribution. Proportion data are frequently modelled by transforming the dependent variable using the arcsine square root transformation (Paradinas *et al.*, 2016), but this approach has several drawbacks and inferences can be misleading (Ferrari and Cribari-Neto, 2004). The beta distribution, in contrast, is very flexible in terms of shape and fulfils the required characteristics (Paradinas *et al.*, 2018). However, as the beta distribution assumes data ranging from 0 to 1, and LR_{med} reached higher values, each LR_{med} and *C*/*L* was divided by its maximum value to obtain a range of annual values varying from 0 to 1.

Models by species and factor were run for each of the possible combinations of terms. Variables were selected with forward and backward stepwise procedures based on two different criteria including Akaike information criterion (AIC) and explained deviance (D^2). The best (and most parsimonious) model was ultimately chosen for each case based on the compromise between low AIC and high D^2 values, and significant predictors (i.e. Wald factor).

GAMs were performed using the "mgcv" package in R (R Core Team, 2019).

Results

Summary of data extracted and whaling statistics

Data used for this study were extracted from 255 logbooks of whaling voyages visiting the southwestern Atlantic Ocean from 1776 to 1923. Information was scattered across years, with effort data scarce in the period between 1776 and 1815 and concentrated across 105 years within the overall period of almost 150 years. SRW sightings concentrated during 69 years over the early decades of the 19th century (over 90% happened before 1850), while SW sightings distributed across 96 years, especially during the second half of the 19th century and beginning of the 20th century (87% of them taking place after 1850). The total sightings of SRW and SW were 2497 and 1157, respectively, and total catches for the two species were 658 and 810, respectively (Figure 2). Total, annual ranges, and mean values with relative standard errors for sightings, and the whaling statistics *L*, *C*, *S*, *K*, and *R*, for the two species, are reported in Table 1.

Struck and loss factors

Annual ranges and means with relative standard errors of LRs, R_{cor}, and *C*/*L* ratios and associated statistics are shown for the two species in Table 1.

Annual values of LRs ranged from 1 to 3 for both species, with overall mean values of LR_{max}, LR_{med}, and LR_{min} higher for SRW than for SW. R_{cor} values were low for both species; however, *K* and *R* values for SW were in general lower than those of SRW (Table 1). A Spearman's rank-order correlation was run to determine the relationship between LRs, *C*/*L*, and year of whaling activity for the two species, considering only years when such indexes were available. Results showed a significant negative correlation of LRs over time for the SRW ($\rho = -0.59$, $p<0.01$ for LR_{max}; $\rho = -0.62$, $p<0.01$ for LR_{med}, and $\rho = -0.56$, $p<0.01$ for LR_{min}). For SW, LRs showed a slight negative correlation with time ($\rho = -0.1$ for LR_{max}, $\rho = -0.12$ for LR_{med}, and $\rho = -0.15$ for LR_{min}), but this pattern was not significant ($p=0.38$, 0.37, and 0.17 for LR_{max}, LR_{med}, and LR_{min}, respectively). The *C*/*L* ratios showed no significant correlation with time ($\rho = 0.06$, $p=0.57$) for SRW, while a significant positive correlation of this

Table 1. Summary of the whaling statistics for SRW and SW calculated from the information contained in the logbooks.

	Southern right whale				Sperm whale			
	***n* (years)**	**Mean ± SE**	**Range**	**Total**	***n* (years)**	**Mean ± SE**	**Range**	**Total**
Sightings	105	23.78 ± 5.02	0_237	2 497	105	11.02 ± 1.19	0_58	1 157
Lowerings	69	22.28 ± 4.59	0_154	1 537	96	8.78 ± 0.9	0_37	843
Catches	55	11.96 ± 2.16	0_59	658	91	8.9 ± 1.13	0_51	810
Struck and lost (S)	42	8.1 ± 1.84	0_58	342	81	1.1 ± 0.19	0_8	94
Killed and lost (K)	42	1.57 ± 0.41	0_11	66	81	0.06 ± 0.03	0_2	5
S + K	42			408	81			99
Recovered carcass	42	0.81 ± 0.2	0_5	34	81	0.11 ± 0.04	0_2	9
LR_{min}	42	1.09 ± 0.03	1_2		81	1.01 ± 0.01	1_1.3	
LR_{med}	42	1.29 ± 0.05	1_2.5		81	1.08 ± 0.02	1_2	
LR_{max}	42	1.49 ± 0.08	1_3		81	1.16 ± 0.03	1_3	
R_{cor}	42	0.07 ± 0.02	0_0.38		81	0.06 ± 0.03	0_1	
C/L	55	0.61 ± 0.05	0_1.5		96	0.83 ± 0.07	0_3.9	
$LRF_{All\ years}$	44	1.54 ± 0.04			85	1.11 ± 0.01		
$LRF_{1776–1850}$	27	1.60 ± 0.04			26	1.30 ± 0.08		
$LRF_{1851–1923}$	17	1.09 ± 0.04			59	1.09 ± 0.01		

Upper rows: mean annual values (± standard error), range of annual values, and total number of: sightings, lowerings (*L*), catches (*C*), struck and lost whales (*S*), killed and lost whales (*K*), and recovered carcasses (*R*) for SRW and SW. Central rows: Mean annual values (± standard error), and range values of loss rate factors (LR_{min}, LR_{med}, LR_{max}), correction factor R_{cor}, and *C*/*L* ratios for the two species. Lower rows: overall struck and lost rates (*LRF*) (± standard error) calculated for the entire catch period (*All years*), and for catches up to 1850, and after 1850. n = sampling period (in terms of number of years considered for calculations).

ratio with time (ρ = 0.55, $p < 0.01$) was observed for SW (Figure 3).

The temporal variation of mean LR_{med} and *C*/*L* for the two species is shown in Figure 4, where whaling effort is grouped into seven periods. Higher LR_{med} values can be observed for the two species during the first four periods, ending in 1855, while *C*/*L* values increase substantially for SW during the last three periods, starting from 1872.

A similar pattern is seen when considering the overall *LRF* (Table 1), whose values were significantly higher in the earlier 1776–1850 period for both SRW and SW and decreased to similar values for both species after 1850. Overall proportions of struck animals that were lost (PL) over the whole period were much higher for SRW (0.35, SE = 0.015) than for SW (0.099, SE = 0.01). However, up until 1850 the proportion of losses for both species was higher, at 0.37 (SE = 0.015) for SRW and 0.23 (SE = 0.046) for SW and dropped after 1850 to PL = 0.083 (SE = 0.03) and PL = 0.086 (SE = 0.01) for the two species.

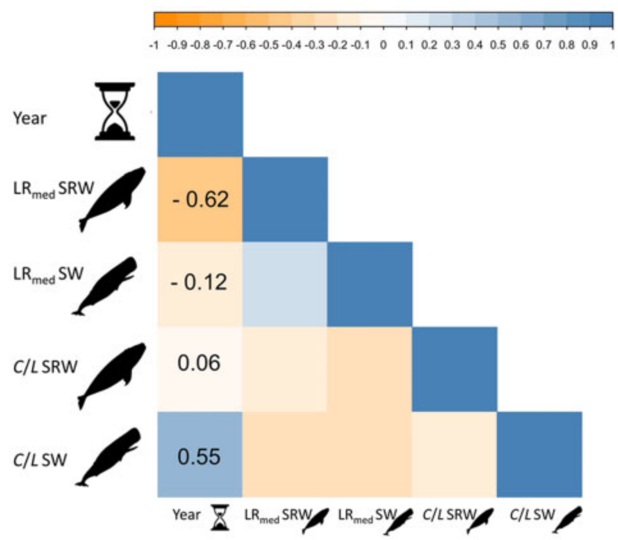

Figure 3. Matrix of the Spearman correlation between time (years), LR_{med}, and the *C*/*L* ratio for the two species. Correlation coefficients (ρ) are showed only for pairwise correlations between time and LR_{med} and time and *C*/*L* for the two species. Orange and blue tones indicate negative and positive values of ρ, respectively, as shown by the above scale.

Generalized additive models

When modelling annual LR_{med} of SRW, the GAM selected based on the lower AIC and higher percentage of D^2 retained only the year as significant factor ($p = 0.001$), explaining ~30% of the total LR_{med} variation. LR_{med} was negatively affected by the year, while effort, type of vessel, and average vessel tonnage had no significant effect (Table 2). The GAM analysis of SW LR_{med} also showed that the best fitting model retained only the year as a significant factor ($p = 0.05$), explaining 5.68% of its total variation. As for SRW, the year was negatively correlated with LR_{med}, while none of the other variables had a significant effect on LR_{med} variability (Table 2).

For GAMs built with *C*/*L* ratios as response variable, none of the explored variables is significant in explaining *C*/*L* total variability for SRW (Table 2). In contrast, the best and most parsimonious GAM for the *C*/*L* ratio of SW retained only the year as significant variable ($p = 0.00$), showing a positive relationship over time and explaining 35.5% of the total variability (Table 2).

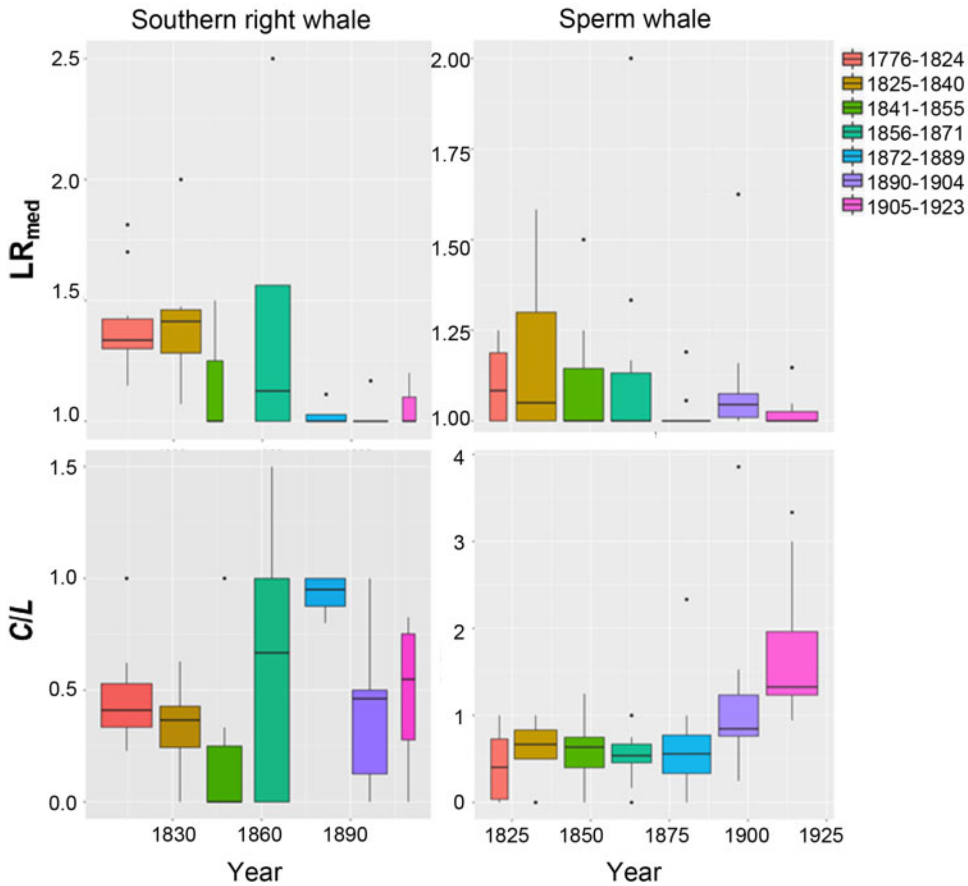

Figure 4. Boxplot showing the variation of mean values of LR_{med} (top) and *C*/*L* ratio (bottom) for SRW (left) and SW (right) across time. Whaling effort is grouped in seven periods, each spanning ∼15 years (except the first period, which includes years between 1776 and 1824 due to the scarcity of data between the end of the 18th century and the beginning of the 19th). Darker horizontal lines correspond to the median; lower and upper hinges correspond to the 25th and 75th percentiles; whiskers extend to the largest value no further than 1.5*IQR from the hinge; outliers are plotted individually as circles.

Table 2. Numerical summary of the model selection for LR_{med} and *C*/*L* ratios of SRW and SW.

	Model	AIC	D^2%
Southern right whale LR_{med}	$1+Y^*+E+TV+MT$	−48.05	33.7
	$1+Y^*+E$	−51.00	31.8
	$1+Y^*+MT$	−50.33	29.3
	$1+Y^*$	−50.29	29.8
Sperm whale LR_{med}	$1+Y^*+E+TV+MT$	−151.94	6.81
	$1+Y^*+E$	−153.03	4.65
	$1+Y^*+MT$	−153.63	6.58
	$1+Y^*$	−154.37	5.68
Southern right whale *C*/*L*	$1+Y+E+TV+MT$	−7.91	24.7
	$1+Y+E$	−7.91	4.64
	$1+Y+MT$	−6.86	15.5
	$1+Y$	−8.25	14.3
Sperm whale *C*/*L*	$1+Y^*+E+TV+MT$	−79.45	40.2
	$1+Y^*+E$	−81.72	35.5
	$1+Y^*+MT$	−80.02	30.2
	$1+Y^*$	−83.7	35.5

Variable acronyms: Y = years, E = effort, TV = type of vessel, MT = medium vessel tonnage. Statistical acronym: D^2% = total deviance explained by the model. The final selected model is highlighted in bold.
* represent significant variables.

Discussion

In this study, we provide an estimate of loss rates for SRW and SW catches across 150 years of American open-boat whaling activity in the southwestern Atlantic Ocean. Loss rates were positive for both species and during all periods, meaning that the number of whales killed was in all cases higher than the number of whales processed and whose products were taken to port. Our results show that LRs differed between the two species, and varied across decades, indicating differences in whaling efficiency potentially related to each target species as well as to improvements in whaling techniques over time. Such information needs to be accounted for when assessing the impacts of whaling in terms of individuals taken and, consequently, in any reconstruction of the demographic trends in these populations.

The sightings and catch data extracted from the whaling logbooks show that, during the first half of the period considered (spanning from the late 18th century to early 19th century), whalers in the southwestern Atlantic Ocean primarily targeted SRW. During this period, over 90% of the total sightings and 88% of the total catches reported were of SRW, while sightings and catches of SW were limited. From about 1850 onwards, SW became the focus of the whalers, with over 87% of sightings and 92% of catches made. Such changes cannot be attributed to a varying interest by whalers for one species or the other, because commercial prices of the various whale products did not show a significant shift during that period (Davis *et al*., 1997). Moreover, the observed trend in SW catches does not match the worldwide pattern, which shows a peak during the period 1820–1850 followed by a decline during 1850–1930 and a tenfold increase thereafter due to the advent of modern whaling (Best, 1983; Smith *et al*., 2008). This suggests that the time shifts observed here should be attributed to the almost complete eradication of SRW in the southwestern Atlantic Ocean. These were caused by the combined impacts of open-boat whaling and shore-based whaling along the coast of Brazil, which took place since the early 17th century (Hart and Edmundson, 2017) and contributed to the depletion of the species. In this scenario, after a few years experiencing a substantial decrease in the number of sightings and catches of SRW, the SW was left as the sole profitable target for open-boat whalers in the area.

The logbooks examination also showed that the number of individuals struck or killed, and subsequently lost, was high for the two species, with over 400 SRW and almost 100 SW having suffered this fate within the studied period. Not all these lost whales can be considered killed with certainty, but at least a proportion of them, which were reported to be "spouting blood" or to have "drowned" after being struck, likely died. The fate of the other struck whales is uncertain because the severity of the injuries could not be assessed. While an exact assessment of the fate of these struck and lost whales was not possible, the qualitative information extracted from the logbooks allowed the categorization of individuals according to the severity of their injuries or the cause of their loss. Thus, to keep an intermediate approach between considering as dead all the lost whales or only those drowned, and to allow comparison with previous studies (e.g. Du Pasquier, 1986; Dawbin, 1986), we based our temporal analyses on LR_{med}.

The LRs calculated here are overall higher for SRW than for SW. This difference is consistent with observations by earlier researchers contemporary with the fishery (e.g. Scammon, 1847; Hohman, 1928), who mentioned that the tendency of SW to sink was lower than that of baleen whale species, and is confirmed by more recent and accurate estimations based mostly on the same, or similar, equations to those used here (Table 3). The values calculated for the southwestern Atlantic Ocean fishery are overall consistent with those obtained for the same species across different whaling grounds during the open-boat whaling period. Thus, our mean LR_{med} of 1.29 and upper bound *LRF* of 1.54 for the SRW across the whole period are consistent with the values of LR_{med} and LR_{max} between 1.18 (Bannister, 1986) and 1.55 (Reeves and Mitchell, 1986) and between 1.25 and 2 (Reeves and Mitchell, 1986) reported in literature. The same consistency is found for SW, whose LR_{med} of 1.08 and upper bound *LRF* of 1.11 calculated in this study fall in the range between 1.04 (LR_{min}, Hope and Whitehead, 1991) and 1.61 (LR_{max}, Bannister *et al.*, 1981) reported in previous literature. However, it should be pointed out that the majority of authors based their calculations on the summaries reported at the end of logbooks, or on a very limited number of voyages, and, except for a few cases [i.e. LRs of New Zealand bay whaling, calculated by Carroll *et al.* (2014)] none did LR assessments based on a comprehensive analysis of a wide number of logbooks separated by whaling periods.

Compared to other areas of the Southern Hemisphere, total estimates of right whales struck but lost were particularly high in the southwestern Atlantic Ocean prior to 1850 (Table 1). The values obtained in this study are similar to regional estimates reported previously (Du Pasquier, 1986; Reeves and Mitchell, 1986), but in this case provide sufficient resolution to allow annual values to be calculated. Values of *LRF* prior to 1850 (1.60 ± 0.04) were higher than those reported during 1838–1839 off the western Australian "New Holland Grounds" (Bannister, 1986), and the total loss rate was higher than the average reported across the whole Southern Hemisphere using a large selection of American logbooks (Carroll *et al.*, 2014). This likely reflects the fact that southwestern Atlantic offshore right whaling began earlier than in other parts of the Southern Hemisphere and experienced higher loss rates prior to 1830 (Figure 4); a similar pattern can be seen in the loss rates reported by French vessels whaling in the South Atlantic Ocean between 1783–1794 and 1817–1837 (Du Pasquier, 1986).

Independently of specific differences in mean values, our results indicated an overall decrease in LRs across time for both species. Whaling vessels employed varying types of rigging and their tonnage increased across the study period, similarly as it occurred in the whaling fleet globally (Brown, 1887; Ashley, 1926). These changes permitted more efficient navigation, greater storage space and the carriage of more whaleboats, the latter being a determinant factor for the increase in catching effort. However, in our study, neither the type nor the average tonnage of vessels played a significant role in the variation of the indices of whaling success. Conversely, the losses for both species declined with time, and the number of whales caught per lowering of boats (*C/L* ratio), which is an indicator of whaling efficiency, increased with time for SW.

Improved whaling efficiency should be attributed to the introduction of improvements in the whaling technology that resulted in a reduction in loss rates. Although some developments, such as the shoulder gun for shooting harpoons, the Greener, or other types of harpoon guns installed at the bow of the whaleboats, were not apparently used in the offshore fishery in the

Table 3. LRs (mean values, ranges, or mean ± SE when available) calculated for different right whale and SW populations targeted by whaling, showed in chronological order of publication for each species.

Species	Spatial/temporal extent	LR	Source
Multiple spp.			
Mysticete spp.	NE Pacific, 1851–1874	1.2[1]	Scammon (1874)
Right whale spp.	Globally, 1783–1898	1.26[2]; 1.46[1]	IWC (1986)
N Pacific right whale/SRW	N Pacific, S Atlantic, Indian Ocean, 1834–1880	1.27[3]; 1.55[2]; 1.84[1]	Reeves and Mitchell (1986)
N Atlantic/N Pacific right whale	N Hemisphere, 19th century	2.00 ± 0.115[5]	Carroll *et al.* (2014)
N Atlantic right whale	NW Atlantic, 1751–1790	2[1]	Reeves and Mitchell (1986)
	NW Atlantic, 1868–1899	1.5[1]	Reeves and Mitchell (1986)
	NE Atlantic, 1854–1880	1.25[1]	Reeves and Mitchell (1986)
N Pacific right whale	N Pacific, 1838–1860	1.39[3]; 2.46[1]	Scarff (2001)
	N Pacific, 1841–1846	1.9 (1.83–2.09)[4]	Reeves and Mitchell (1986)
Southern right whale			
Offshore	S Hemisphere, 19th century	1.45 ± 0.054[5]	Carroll *et al.* (2014)
	Indian Ocean, 1855–1856	1.52 (1.29–1.88)[4]	Reeves and Mitchell (1986)
	W Australia, 1838–1839	1.18[2]; 1.35[1]	Bannister (1986)
	S Atlantic, 1834–1880	1.66 (1–3.13)[4]	Reeves and Mitchell (1986)
	S Atlantic, 1783–1794	1.42[2]; 1.61[1]	Du Pasquier (1986)
	S Atlantic, 1817–1837	1.21[2]; 1.41[1]	Du Pasquier (1986)
	SW Atlantic, 1776–1923	1.29 ± 0.05[2]; 1.54 ± 0.04[5]	This study
Bay whaling	S Africa, 1804–1869	1.32[2]; 1.50[1]	Best and Ross (1986)
	New Zealand, 1834–1841	1.27 ± 0.050[4]	Carroll *et al.* (2014)
Sperm whale	Worldwide	1.1	Scammon (1874)
	Worldwide	1.1–1.15	Kugler (1981)
	NW Pacific, 1825–1846	1.2[3]–1.61[1]	Bannister *et al.* (1981)
	Galapagos, 1830–1850	1.04[3]–1.23[1]	Hope and Whitehead (1991)
	Indian Ocean, 1800–1888	1.28[1]	Wray and Martin (1983)
	NE Atlantic, 1863–1880	1.31[1]	Aguilar and Borrell (2007)
	SW Atlantic, 1776–1923	1.08 ± 0.02[2]	This study

Geographical and temporal ranges are provided when available. When specified, LR calculation methods are indicated with superscript numbers: [1]LR_{max}; [2]LR_{med}; [3]LR_{min}; [4]$[(C + K + 0.5 \text{ unspecified } S + 0.5 \text{ lost because iron drew} + \text{lost carrying whaling gear} + \text{calves orphaned})/C]$; and [5]*LRF*.

southwestern Atlantic Ocean, other elements were introduced. Parallel to the increase in the main vessel tonnage, whaleboats increased in size and began to be equipped with sails, improving their navigation and towing capacity; the traditional double or single flue harpoons (of sagittate shape) were replaced by toggle harpoons, which were less likely to draw from the body of the whale; bomb-lances shot with shoulder guns or darting guns replaced or were added to hand-lances for a faster and safer killing of harpooned whales; and the fibre type and quality of the lines used to fasten harpooned whales improved greatly, reducing the frequency of line parting and escaped whales (Brown, 1887; Ashley, 1938; Best, 1983; Lytle, 1984). As most of the above developments were introduced between 1840 and 1880, their effect could not be appreciated on the C/L ratios for the SRW, which was mostly exploited in the area before 1850. On the contrary, they did effectively increase C/L ratios for SW, which became the main target in the southwestern Atlantic Ocean after that date. These variations are consistent with previous studies in other whale fisheries, which showed a progressive reduction of LRs, particularly in the second half of the 19th century (e.g. Bockstoce and Botkin, 1983; Du Pasquier, 1986).

Our results underline the importance of accounting for the struck but lost individuals when assessing the number of deaths, which, for these species, represented approximately 1.1–1.5 the number of whales eventually processed and taken to port. The study also shows that the loss rates are species specific, time specific, and very likely, ground specific, or even specific to the group of whales encountered, as in the case of gregarious SW (i.e. lower LRs for single animals than for reproductive groups catches; Smith *et al.*, 2008), and this stresses the importance of determining case-specific LRs. These results highlight the importance of historical sources and their derived data to address ecological and conservation issues. Accounting for "lost" individuals is fundamental when reconstructing demographic trends of cetacean populations that were heavily over-exploited by whaling, such as the case of the SRW, which was drastically reduced by this activity. An accurate assessment of the individuals removed by whaling would enable more precise estimations of the size of these whale populations before their exploitation and can thus provide a relative indication of their current status, which is necessary to plan adequate and well-targeted conservation measures.

Data availability statement

The data underlying this article cannot be shared publicly due to their current use for further analyses and publications. The data will be shared on reasonable request to the corresponding author.

Funding

This research was partially supported by the Darwin PLUS project Where are they now? Right whales in South Georgia waters (Ref: DPLUS057).

Acknowledgements

Authors are indebted with the NBWM, the New Bedford Free Public Library, the Providence Public Library, the Mystic Seaport Museum, the Scott Polar Research Institute, the UK National Maritime Museum at Greenwich, and the London Royal Geographical Society for providing access to the logbooks preserved in their collections. We are particularly thankful to the NBWM for providing lodging during our research stays and to their personnel, particularly Mark Procknick and Michael Dyer, who granted us much patience and assistance. Sandra Sánchez Muñoz and Pau Esparó Larrégola contributed to the compilation and validation of the data base. We also thank Phil Clapham and two anonymous reviewers for their constructive feedback on the manuscript.

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Handling editor: Anita Gilles