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Southern right whale (*Eubalaena australis*) population demographics at major calving ground Head of Bight, South Australia, 1991–2016

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Abstract

1. Demographic parameters were estimated for southern right whales (SRWs), *Eubalaena australis,* using photo-identification (ID) and count data collected during annual cliff-based surveys at the Head of the Great Australian Bight (HoB), South Australia between 1991 and 2016. Photo-ID and count data were contributed from the annual aerial surveys of the south-western population in Australia (1993–2016).
2. The HoB photo-ID database included 1,186 non-calf individuals, with 459 reproductive females. HoB is an open population and represents a relative proportion (0.48–0.21) of the overall south-western population, which is decreasing with population growth.
3. No change was detected in the growth rate at HoB over time (1992-2016) and there was no significant difference when compared to the overall south-western population. The estimated mean rate of increase for all SRW was 3.2% (± 1.3) per annum (p.a.) and for females with a calf

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was 4.6% (± 1.7) p.a. at HoB, compared to 5.5% (95% CI 3.78, 7.36) and 6.01% (95% CI, 3.78, 7.36), respectively for the south-western population during the same period.

4. The apparent mean calving interval was 3.3 years (SD = 0.78, ± 0.14, 95% CI), (1996-2016), and a significant increase to 4 years was observed since 2015. The apparent mean age at first parturition was 9.0 years. The minimum estimated age of the oldest whale was 50 and oldest lactating female 41 years old.
5. The SRW demographic data provides information for monitoring recovery, population status, species conservation management and global comparative studies. There is a need to understand fluctuations in calving intervals, threats to the population and implications for species recovery.

KEYWORDS: Australia, conservation management, demographics, photo-identification. recovery, southern right whale.

1. Introduction

Population demographics and life history parameters are fundamental to the assessment of species assessments and conservation management of marine mammals (Cooke, Rowntree & Payne, 2001; Skalski, Ryding & Millspaugh, 2005; Zerbini, Clapham & Wade, 2010; Brandão, Best & Butterworth, 2011; Brandão et al., 2018). Demographic parameters are subject to variability due to density dependence, habitat occupancy, or other influences such as prey availability, health and body condition (Best, Brandão & Butterworth, 2001; Cooke, Rowntree & Payne, 2001; Leaper et al., 2006; Bradford et al., 2008; Pirzl et al., 2009; Miller, 2011; Carroll et al., 2014a; Meyer-Gutbrod et al., 2015; Seyboth et al., 2016). Long-term monitoring of southern right whales (SRWs), *Eubalaena australis*, using photo-identification (ID) life history data provides information for assessment of population estimates (Whitehead, Payne & Payne, 2000; Best, Brandão & Butterworth, 2001; Cooke, Rowntree & Payne, 2001; Torres et al., 2017; Bannister, 2017), calving intervals (Burnell, 2001; Best, Brandão & Butterworth, 2001; Cooke, Rowntree & Payne, 2001; Burnell, 2008; Davidson et al., 2018), age at first parturition (Burnell, 2001; Best, Brandão & Butterworth, 2001; Cooke, Rowntree & Payne, 2001; Burnell, 2008), site fidelity (Burnell, 2001; Carroll et al., 2014a; Charlton, 2017), movement patterns (Burnell, 2001; Pirzl et al., 2009; Carroll et al., 2014a; Roux, Braby & Best, 2015; Torres et al., 2017) and human impacts (Corkeran et al., 2018; Pace, Corkeron, & Kraus, 2017; Harcourt et al., 2019).

In the 19th and 20th centuries SRWs were depleted to near extinction by commercial whaling (Dawbin, 1986; Carroll et al., 2014b). SRW became protected internationally from commercial whaling in 1935 and Jackson et al. (2008) suggest that abundance increased between 1935 and 1960. However, illegal catches by the Soviet Union slowed the increase in their abundance until the 1970s (Tormosov et al., 1998; International Whaling Commission, 2013). The global population estimate of SRWs recorded in 2009 was 13,600 individuals (International Whaling Commission, 2013). SRWs are found in Southern Hemisphere latitudes of 16° S to 65° S, with genetically distinct populations in Australia, New Zealand (NZ), South Africa, Argentina/Chile and Brazil (Baker et al., 1999; Carroll et al., 2011; Patenaude et al., 2007; International Whaling Commission, 2013; Carroll et al., 2014b). SRWs migrate to coastal winter grounds and stay close to shore to breed, calve and rest during the austral winter and early spring and then return to offshore locations to feed in their summer grounds (Bannister, 2001; Zerbini et al., 2016).

Following overexploitation by commercial whaling, SRWs were only rediscovered in Australia through anecdotal reports of a small number of whales between 1955 and 1968 (Chittleborough, 1956; Bannister, 1986). In Australia, SRWs are divided into two populations or management units, the south-western and south-eastern Australian populations, based on genetic differentiation in mitochondrial and microsatellite DNA haplotype frequencies (Carroll et al., 2011; Carroll et al., 2015), geographical diversity and contrasting rates of population increase (Bannister, 2001). The south-western population occurs in coastal waters off Western Australia (WA) and South Australia (SA), extending >1,700 km and the south-eastern population occurs off Victoria, New South Wales and Tasmania (>2,000 km).

Although the overall Australian population is now increasing, there is a marked difference in population size and rate of increase between the different populations. The abundance estimate for the south-western population based on aerial surveys undertaken between 1993 and 2018, was 3,191 individuals and the annual rate of increase is approximately 5.56% (95% CI 4.06, 7.08) per annum (p.a.) for all animals and 6.24% (95% CI 4.10, 8.42) p.a. for females with a calf (Smith et al., 2019). The south-eastern population abundance is estimated at less than 300 individuals with an estimated increase of 4.7% p.a. between 1996 and 2017 for all individuals and no signs of increase in the reproductive females at the only recognized nursery ground at Logans Beach Warrnambool, Vic (Stamation et al., 2020). The maximum biological rate of increase for the species as a whole is 7.5 % p.a. (International Whaling Commission, 2001).

The Head of the Great Australian Bight (HoB), SA is a primary large established wintering aggregation area for SRWs in Australia, utilized for calving, nursing, resting and mating. HoB is in the eastern range of the south-western population. The rate of increase in the total number of whales at HoB was estimated at 4.3% p.a. between 1991 and 2007, whilst in the same period, the rate of increase in the overall the south-western population was estimated at 5.2% p.a. (Burnell, 2008). The lower rate of increase estimated at HoB, compared to the overall south-western population was an indicator of possible changes in occupancy and movement between coastal aggregation areas, and the open population at HoB (Burnell, 2001; Burnell, 2008).

Females display high site fidelity to calving grounds in the year of calving (Payne et al., 1990; Burnell, 2001; Charlton, 2017). A breeding cohort is referred to as the group of females accompanied by their calves in each year. SRW females form breeding cohorts based on their predominant three year calving intervals. It is assumed that the year of calving is followed by a rest year, and then a mating year when animals usually migrate to alternative areas to their selected calving ground (Best, 1994; Burnell, 2001; Cooke, Rowntree & Payne, 2001; Brandão, Best & Butterworth, 2011; Brandão et al., 2018), although mating is also observed in Australian aggregation areas including HoB (Burnell, 2001; Charlton, 2017). Annual monitoring is required to assess the trends in abundance and increase in each breeding cohort to understand the overall population trends and potential changes to the rate of increase over time (Bannister et al., 2011).

Southern right whales are listed as endangered under the Australian Commonwealth Environment Protection Biodiversity and Conservation Act (1999) and of Least Concern under the International Union for Conservation of Nature Red List (Cooke & Zerbini, 2018). The long-term annual cliff-based study at HoB provides an unbroken time series dataset of count data and photo-ID data. There is a critical need to utilize this dataset for assessment of SRW demographics in Australia. These datasets are needed to inform the Australian Government's Conservation Management Plan for the SRW (2011–2021), which has given high priority for understanding life history parameters and measuring population growth of both Australian populations (Department of Sustainability, Environment, Water, Population and Communities, 2012). The assessment of SRWs is also prioritized by the International Whaling Commission Science Committee Southern Hemisphere subcommittee.

The objectives of this study were to assess SRW demographics including relative abundance trend, rate of population increase and life history parameters at HoB over 26 years (1991–2016). Life history parameters assessed include apparent mean calving interval, apparent mean age at first parturition and longevity. The relative proportion of the HoB aggregation area compared to the overall south-western population was assessed as an indicator of the relative significance of the primary aggregation at HoB.

2. Methods

Data collection

Study site

The HoB is in the far west of SA (31° 29' S, 131° 08' E), (Figure 1), approximately 270 km west of Ceduna, SA and 210 km east of the WA border (using shortest swim distance). The site is adjacent to Yalata Aboriginal Land on the Bunda Cliffs (the escarpment of the Eucla Basin) of the Nullarbor Plain. The HoB aggregation area is within the Marine Mammal Protection Zone of the Great Australian Bight Commonwealth Marine Reserve and the Far West Coast State Marine Park. The Great Australian Bight Marine Reserve was established in 1995 to protect the SRW wintering ground at HoB. The study site is selected to include the primary aggregation area and extends approximately 15 km along the coast and 5 km offshore (Figure 1).

Study period

Field surveys have been carried out at HoB annually between June and October 1991–2016. During each year, a minimum of eight days were surveyed in the peak season between August 15 and 31, to provide interannual comparison of population trends at the site. Calving females (female with a calf from that year) are expected to have calved by the middle to end of August (Burnell, 2001; Charlton, 2017), and it was assumed that the study period provided access to all calving females that selected HoB as calving/nursing habitat in that season (Burnell & Bryden, 1997; Burnell, 2001; Charlton et al., 2019a). Outside of the consistent annual field study period (August 15–31), the survey effort varied between June and October (For more details, see Table 1 in Charlton et al., 2019a).

Surveys

Southern right whale count and photo-ID data were collected during daily surveys from 16 land-based observation stations along a 15 km stretch of coastline, 0 to 5 km from shore (Figure 1). The elevation of observation stations ranged from 33 m above sea level in the east and 53 m in the west of the study site. At each observation station systematic scans were completed using 10x50 Bushnell binoculars and the naked eye at an angle of approximately 180° east to west and as far as the eye could see offshore to the south from the horizon down to the cliffs. Observation station locations were selected based on the shape of the cliff line to ensure that the observers had full coverage of the survey area to prevent missed or duplicate sightings, thus the distance between stations varies from 300-1,000m apart. To avoid duplicate sampling between adjacent stations, only individuals to the south or west of observation stations were recorded. To further reduce the risk of duplicate sightings, the location of sighted whales at each station was mapped in real time based on measurements of distance and compass bearing to whale, individuals were identified using photo-ID, and the location and ID was cross checked with sightings at a similar location at the next adjacent station where possible. Photo-ID could be obtained for individuals within ~500m from the shore. The time spent travelling (by vehicle) between stations ranged from two to six minutes.

All surveys were completed in Beaufort Sea States of three or less and wind speeds less than 15 kn to reduce bias in counts due to weather conditions. Environmental conditions including wind speed and direction in knots, cloud cover in percentage, sea state using the Beaufort scale and swell height were recorded qualitatively at the start and end of each survey. Glare was not recorded as observations were timed to avoid glare (>8:30am when the sun had risen and glare reduced). If weather conditions exceeded survey limits during the field day, the survey day was called off and the time and changes to conditions were recorded. Daily cliff-based survey effort ranged from 2.9 hrs to 4.9 hrs ($\bar{X}$= 3.6 hrs). Start time was roughly 08:30 and end time ranged between 12:30 and 16:00. Observations were timed to avoid glare in the early morning and sea breeze in the afternoon. Effort reported excludes travel times between observation stations. Detailed methods are outlined in Charlton et al. (2019a).

Counts provide abundance of SRW at HoB relative to the overall south-western population in Australia. Detection bias was not quantified. Most animals, particularly females accompanied by a calf, were easily observed in the clear and shallow waters at HoB. The maximum daily count reflects the number of individuals present in the HoB study site on a single day during the study period. While the maximum daily count is indicative of numbers using the site on a given day, it is likely to be an underestimate of the true maximum number using the site in a season, since whales move to and from the site throughout the season. (Burnell, 2001; Bannister, 2017; Charlton et al., 2019a). Observer bias was reduced by using two trained and experienced observers and minimizing rotation of researchers across the duration of the study. The visual detection range was quantified in Charlton et al. (2019a) as 5 km from shore, with the detection probability beyond that range reducing significantly. A minimum of 10 mins was spent observing at each station based on the assumption that SRWs were at the surface at some point during that period. This 10 min minimum also improved the detection probability of animals at a distance from the observation stations while ensuring that whale movements were visually tracked to avoid double counting. Female and calf pairs spend the majority of their time on the surface. Measured respiration rates for lactating females and calves at HoB are 0.5 and 2 breaths per min, respectively (Nielsen et al., 2019). Surface active behaviour is common for young calves with a mean rate of 9 occurrences per hr recorded at HoB (Nielsen et al., 2019). The data were biased towards potentially having greater detection probability for females and calf pairs than unaccompanied whales (juveniles or adults not accompanied by a calf). However, the overlap in observation stations and methodology moving west to east with overlapping visuals at each observation station, increases the likelihood of sighting all individuals. Longer time periods were spent at a location if additional time was required to capture photo-ID.

The maximum daily count collected each year during the peak period (August 15–30) was used to inform population increase over time. Charlton et al. (2019a) reports that the peak period in relative abundance is consistent across years with the maximum daily count recorded during August 15–30 for female and calf pairs and unaccompanied adults. Therefore, the count data are comparable across years (1992–2016).

Sightings data recorded included: date, time, observation station, group composition (number and classification of individuals, i.e. female accompanied by calf, unaccompanied adult, unknown status (unknown if animal was with a calf or unaccompanied)), range and bearing.

Photo-identification

Photographs of individual whales were obtained for comparing and matching to previously photographed and catalogued individuals. Photographs used for identifying individuals (photo-IDs) taken from the 33–53 m high Bunda Cliffs provided the required vantage point for collecting high quality images of the whale's dorsal surface. Photographs of the dorsal surface allow callosity patterns on the head that are unique to an individual to be documented. Callosity patterns are keratinised skin patches colonized by cyamids that provide unique markings on the dorsal surface of the rostrum, the lip line of the lower jaw and just posterior to the blowhole that persist throughout life (Payne et al., 1983). To capture the unique callosity patterns, photographs of the rostrum from above and left and right lateral perspectives of the dorsal side of the whale were obtained when possible. The ventral side was also photographed if presented, to document the size and shape of ventral pigmentation (also persistent and unique) and the anogenital configuration (to give information on sex) (Burnell, 2001). Grey or white blaze or brindle coloration patterns, evident markings and scarring were also photographed on adults and calves. Photographs were taken using a Nikon 7100 or D100 digital SLR camera with a Nikon 500 mm (effective 750 mm) telephoto lens or Sigma 500 mm lens mounted on a tripod (in the 1990s film cameras were used with Nikon 500 mm telephoto lens).

Collection of photo-ID of lactating females and unaccompanied adults was prioritized because their callosity patterns are well developed. Photo-ID effort for calves increased later in each season (August–October) when their callosity patterns are developed enough to enable accurate future resights. This study currently provides the only individuals of known age for the Australian SRW population because photo-ID images of calves in their year of birth could be collected. Calves were resighted as subadults or adults in subsequent years using callosity patterns and grey or white blaze or brindle coloration patterns. Position, behaviour, group composition, age class and reproductive status were recorded for each whale. In 2016, photo-ID images of SRW at HoB were also collected using Unmanned Aerial Vehicles (UAVs or drones) in collaboration with Murdoch University (See Christiansen et al., 2018 for UAV methods).

Digital photo-ID images were sorted daily in the field, including within season cross matching of individuals to document the total number of individuals identified. Quality of images was assessed by following an image quality protocol and grading images into categories (excellent, high, average, poor, and very poor quality), as defined in the protocols for the Australian Right Whale Photo Identification Catalogue (ARWPIC). The ARWPIC protocol grading was applied retrospectively with the long-term data. All images were stored but only average or above images were selected for future matching. Photo-ID resights were identified through a desktop cross matching exercise to compare photographs to the long-term photo-ID catalogue developed in the Big Fish v6 Microsoft Access database (Pirzl et al., 2007). Individuals were predominantly only matched when identifiable features were recorded sufficiently to identify both sides of the rostrum. This ensured that callosity patterns present (including features: bonnet, coaming, islands, lips and post blow hole islands) were recorded and that the individuals could be identified and matched in the future. Only individuals with complete profiles were added to the master catalogue. Identification images were compared manually by 2-3 experts in right whale photo-ID and matching. All matches were independently verified by at least one expert scientist.

Life history and annual count data were contributed from the Western Australian Museum (WAM) photo-ID catalogue from annual aerial surveys completed between Cape Leeuwin, WA, and Ceduna, SA, along an area of approximately 1,700 km (1993–2016). Although the northern extent of SRW distribution is Exmouth, WA, the aerial surveys covered the primary aggregation areas from Perth to Ceduna. For detailed methods on the WAM aerial surveys see Bannister (2017). Photo-ID data were also contributed by WAM prior to 1993, when the aerial surveys had a smaller survey area between Perth and Cape Leeuwin, WA, and sometimes as far as Twilight Cove, WA, covering ca 700–900 km (1977–1992). Inter-catalogue cross matching was completed for all WAM and HoB photo-ID data using reconciled HoB data from 1991–2007 and WAM data from 1993–2004 (Burnell, 2008). The cliff top HoB and the WAM aerial survey count and photo-ID data have a different set of biases. For example, aerial surveys capture a greater area across a five day period and photo-ID is limited to the animals at the surface when the plane is flying overhead. The photo quality has increased remarkably, however, images from the 1990s were not always of the greatest quality, meaning poor quality images were unable to be used. Aerial surveys provide an absolute count of SRW between Cape Leeuwin, WA, and Ceduna, SA, (inclusive of HoB) and capture photo-ID images of approximately 50% of individuals counted.

Data Analysis

Trends in long-term relative abundance and rate of increase

Long-term trends in annual rate of increase at HoB were estimated using all years of count data (1992–2016), except for 1991 where numbers of groups were recorded rather than individuals, and thus data for this year are not comparable for inclusion in the analysis. The linear regression of the natural logarithm of count data was used to allow comparison to count data previously analysed for HoB (Burnell, 2008) and the south-western population (Bannister, 2017). Data were presented as a linear regression of the natural logarithm of the annual count data for all animals and for females with a calf, and the 95% confidence intervals calculated for the rate of increase, along with the R^2 value. The significance of relationships was given by the F critical value.

Proportion of southern right whales at Head of Bight relative to the overall south-western population

Head of Bight is recognized as the key calving aggregation area within the south-western population. It is important to understand the relative proportion that HoB represents of the total south-western population to understand drivers for shifts in distribution and density dependence areas along the Australian southern coastline. The maximum daily count of calving females counted at HoB each year relative to the overall south-western population recorded through WAM annual aerial surveys between 1993 and 2016 was compared to see how the proportion varied with time. The relative proportion was displayed as a scatterplot with year as the independent variable and proportion as the dependent variable and regression lines were tested in XLStat using a simple one way ANOVA Tukey (HSD) test in XLStat and presenting the P value and R^2.

Life history parameters

Apparent calving interval and age of first parturition

Life history parameters including apparent mean calving interval and apparent mean age at first parturition were estimated using photo-ID resight data for individual whales collected over all years (1991–2016).

Calculation of mean apparent calving interval considers calving intervals between one and five years only. It is assumed that individuals with a calving interval of six years or greater were likely to have either calved somewhere else or were missed by observers (Burnell, 2001; Cooke, Rowntree & Payne, 2003; Brandão, Best & Butterworth, 2011). The inter-calving interval data for 1996–2016 (calving events were recorded from 1991) were analysed to allow for a five-year lead time.

The following assumptions that were made in Brandão, Best & Butterworth (2011), and are relevant in this study:

1. Observed calving intervals are biased representations of the true calving frequency, because females on longer intervals are under-represented in the sample (having a greater proportion of incomplete calving intervals).

2. No allowance is made for calving events missed by the observer. A female calving in a year might not be photographed because (a) the calf died before the survey, or was born after the survey, or (b) the female plus calf were outside the survey area at the time of the survey, or (c) they were in the survey area but were missed.
3. Age at first parturition is biased in that some first calving events will go undetected.

To account for the assumptions described above, the observed calving intervals or ages of first parturition were apparent intervals, with the possibility that a calving event was missed in surveys. Apparent mean calving intervals were displayed in a box and whisker plot in RStudio with time period (1996–2016) as the independent variable and calving interval as the dependent variable, displaying the distribution as a continuous variable, summarizing the median, upper and lower quartiles, maxima and minima, and extremes the median for the raw data (all calving intervals). Variation in mean observed calving intervals across years was calculated using a simple one-way ANOVA Tukey (HSD) test in XLStat and presenting the P value, R^2, standard deviation and 95% confidence intervals. The statistics were completed for calving intervals two to five for all years (1996–2016).

Cross matching completed between the HoB and the WAM catalogues (Burnell, 2008) were analysed to assess the apparent mean calving interval using combined data. Cross matching of the catalogues to date includes years 1991–2007 of the HoB catalogue with 1993–2004 (and some individuals to 2007) of the WAM catalogue. Sighting histories available from the HoB and WAM catalogues for the 267 matched individuals were then updated to include all available sightings up to 2012 for WAM and 2016 for HoB catalogue. The results for apparent mean calving interval calculated for the HoB dataset (1991-2016) were compared with the analysis of HoB and WAM data combined. The analysis was needed to assess the error in estimates calculated for the HoB catalogue; given that HoB is an open population.

To identify outliers in the data that could negatively bias the result for the assessment of the age of first parturition, the homogeneity of the data was tested using a simple Grubbs test and the *P* value was presented. Data were presented in a frequency histogram.

New calving females not previously sighted at Head of Bight

New calving females not previously sighted at HoB each year was calculated as a proportion to assess immigration and emigration of breeding females to the population over time. The trend in number of new individuals being sighted, and the trend in proportion of new individuals vs resights were assessed using a simple one-way ANOVA Tukey (HSD) test in XLStat, presenting the *P* value, R^2.

Longevity, reproductive age and maximum calving events

The longevity of SRW was assessed using early sighting records from within the long-term photo-ID resight database. Sightings included images and sightings collected opportunistically from as early as 1970, matching was completed between the HoB and the WAM catalogues. The reproductive longevity of SRW females was assessed using records of the last recorded calving events for the eldest known females in the dataset. Whilst longevity is likely to exceed the duration of this dataset (1970-2016), the information is considered valuable for comparison to right whale species globally that have seen a decline in longevity and reproductive age due to human induced impacts (Corkeran et al., 2018).

3. Results

Trends in long-term relative abundance

A total of 805 daily cliff-based surveys were completed between 1992 and 2016 at the HoB aggregation area. An average of 35 surveys was completed per year, ranging from a minimum of eight in 2013 to a maximum of 112 in 1993. Surveys resulted in 42,725 whale sightings over the 25 year study period. Of the total whale sightings recorded, 80% were females accompanied by a calf, 16% unaccompanied adults and 4% were of unknown status.

The annual maximum count of SRW increased from 43 in 1992 to 172 in 2016 at a mean rate of 3.2% ($R^2 = 0.54$, ± 1.3, 95% CI) based on a simple exponential regression (a linear regression of the natural log of the count on year) (Figure 2). The maximum count of 172 individuals were sighted on one day in in 2016 in the HoB study area (Figure. 3). In 2016, maximum daily counts of 81 females accompanied by a calf, and 29 unaccompanied adults were recorded, on separate days. Prior to 2016, the highest relative abundance was recorded in 2011 when a total of 172 individuals were also sighted on a single day. In 2011 a maximum daily count of 67 females accompanied by a calf, and 35 unaccompanied adults were recorded, on separate days. The growth rate of SRW at HoB showed no significant difference (P value >0.05) when calculated incrementally across years (Figure 4).

The maximum number of females accompanied by a calf increased from 18 in 1992 to 81 in 2016 at a mean rate of 4.6% ($R^2 = 0.57$, ± 1.7, 95% CI) using the linear regression of the log value (Figure 2). There was high annual variability in the relative abundance of females with calves, due to pulses in calf production ($\bar{X} = 39$, SD = 17.8). The long-term annual counts demonstrate cohort structured calving cycles, with distinct peaks of calving females apparent every three to five years after 1998 (Figure 3). Triennial peaks in relative abundance were most commonly observed, representing three primary calving cohorts; for example, the largest breeding cohort occurs in 2005, 2008, 2011 and 2014.

Fewer SRW were recorded in 1998, 2007 and 2015 than the previous annual count, and the previous cohort year (3 years prior), these low years resulted in a reduced rate of population increase. For example, in 2015, the maximum number of females accompanied by a calf (n = 29) was 51% lower than in 2014 (n = 60) and 47% lower than the same cohort year in 2012 (n = 55).

The number of unaccompanied whales sighted within the HoB study area increased at a mean rate of 1.7 % ($R^2 = 0.1$, ± 2.0, 95% CI) p.a. between 1992 (n = 7) and 2016 (n = 29) (Figure 2 and Figure 3). The maximum number of unaccompanied whales recorded on one day during the study period was 35 individuals in 2011 (Figure 3). Few animals of undetermined status were recorded, ranging from three in 1996, 2011, 2015 and 2016, to 15 in 2005 (range = 3–15, $\bar{X}$ = 6, SD = 3).

Proportion of southern right whales at Head of Bight relative to the overall south-western population

The number of calving females sighted at HoB each year relative to the overall south-western population recorded through the WAM annual aerial surveys between 1993 and 2016 varied with time (Figure 5). The relative proportion that SRW at HoB represented of the overall south-western population declined from a maximum of 0.48 in 1994 to a minimum of 0.21 in 2002 ($\bar{X}$ = 0.32, SE = 0.01) and then stabilized after that. However, the regression fit was poor and the trend was not significant (R^2 = 0.05 with a polynomial best fit *P* value >0.05).

Life history parameters

Matching was facilitated using the HoB digital photo-ID catalogue containing 10,879 images that included high quality images of 1,186 individual non-calf SRW and 362 individuals that were first sighted as a calf. A total of 459 individual reproductive females and 727 individual unaccompanied adults were identified. Of the 459 reproductive females photo-ID'd, 70% (range = 46–94%, SD = 15.5) were resighted in subsequent years (Figure 6).

New calving females to Head of Bight

New calving females photo-ID'd at HoB increased with time. The mean annual percentage of new calving females not previously sighted at HoB was 33% ($\bar{X}$ 13 individuals) and ranged from 6% (1/18 individuals) in 1999 to 80% (16/20 individuals) in 2009 (Figure 6). The proportion of new individuals compared to resighted individuals had a significant increasing trend (R^2 = 0.65 *P* value = <0.0001) (Figure 6).

Apparent mean calving interval

A total of 459 individual reproductive females were identified at HoB between 1991 and 2016, of which 186 (41%) were recorded with a calf on two or more occasions, providing 471 inter-calf intervals (n = 663 calves) for analysis of mean apparent calving interval. Seventy-nine per cent were five years or less and 21% of intervals recorded were greater than five years. Intervals of greater than five years were excluded from the analysis as they may represent a missed calving event.

The apparent mean calving interval for individual reproductive females at HoB was 3.47 years (SD = 0.7, ± 0.24, 95% CI) (Figure 7). The most frequent mean annual calving interval across all years between 1996 and 2016 was three years representing 59.6% of intervals, followed by four-year intervals (26.5%), five-year intervals (9.7%) and two-year intervals (4.2%) (Figure 8). There was a significant difference in the mean recorded calving interval across years ($R^2 = 0.018$, *P* value 0.018). The mean apparent calving interval was 4.2 and 4.1 for 2015 and 2016, respectively which was statistically different from prior years. The mean observed calving interval increased to above four years in 2015 and 2016 for the first time in the 26 years dataset. There were no three years calving intervals recorded for calving females at HoB in 2015 and the second fewest three years intervals were recorded in 2016 (21% of calving females). No two years intervals were recorded in 2015 or 2016. The last four years displayed a greater spread of data compared to prior years (Figure 7).

The inter-catalogue cross-matching exercise using the HoB and WAM photo-ID catalogues (Burnell, 2008) resulted in a total of 267 individual females from the HOB catalogue being positively matched with the WAM catalogue. When sighting histories for the 267 matched individuals were updated from the WAM catalogue (1993–2012 inclusive) and the HoB catalogue (1991–2016 inclusive), 207 calving events were recorded in the WAM catalogue. The matching exercise resulted in 27 additional reproductive females, these individuals were sighted by the surveys team at HoB as unaccompanied adults and by the WAM surveys as calving females in different years (these females were sighted with a calf along the aerial survey transect between Cape Leeuwin, WA, and Ceduna, SA).

The mean observed calving interval for individual females with calving intervals of five years or less recorded for the HoB and WAM data combined was 3.3 years (SD = 0.78, ± 0.14, 95% CI), which showed no significant difference when compared to the calving interval recorded for HoB data only of 3.47 years (SD = 0.7, ± 0.2, 95% CI).

Apparent age at first parturition

A total of 362 individuals in their year of birth were photographed and identified based on callosities and/or dorsal coloration pattern, of which 69 were re-sighted in at least one subsequent year, providing data on known age of individual whales within the south-western population. Whilst the catalogue included 362 calves, a calf was only considered a part of the master catalogue when it was resighted in at least one subsequent year. This is because calf callosity patterns were not always developed sufficiently to classify for inclusion in master catalogue, but it is considered valuable to store the data in the calf catalogue in case the animal can be resighted in future, in order to address questions on age of first parturition, and natal site fidelity. Within the catalogue of known aged individuals, 23 were subsequently sighted with a calf providing information on age at first parturition. The minimum age at first parturition recorded in this study was six years, showing that SRW can become sexually mature as early as five years old, assuming a gestation of about one year (Best, 1994). The homogeneity of the data was tested using double Grubs test in XLStat and the years 13 and 18 were both identified as outliers in the data with statistical significance (p value = 0.0001) and were therefore excluded from the analysis. Therefore, the age of first parturition was based on 20 individuals. The mean apparent age of first parturition was of 9.0 years (n = 20, SD = 1.9, ± 0.33, 95% CI) (Figure 9).

Longevity, reproductive age and maximum calving events

The oldest known female in the HoB catalogue is an adult female (H9220) first photographed in 1970 off Boston Bay, SA. She was sighted 14 times always without a calf across 40 years between 1970 and

2010, and 12 of those times were at HoB with the first sighting in 1983. The female was reported as an adult (based on her large size and the description in the catalogue was that female appeared old in 1970) and her age at first sighting in 1970 is assumed to be 9 years, making her approximately 50 years old at the last sighting in 2010. The next oldest SRW is a female (H9318) first sighted with a calf in 1984 and returned to HoB 10 times, accompanied by a calf each time, between 1984 and 2016, and therefore estimated to be at least 41 when last sighted (assuming age of first parturition of 9 years). Another three females were identified with a calf in 1984 and were last sighted at HoB in 2014, 2007 and 2005, respectively (the last sightings of these individuals were all with a calf). There are no records of females with a calf at HoB prior to 1984. Assuming an age of first parturition of 9 years, the oldest known reproductive female was 41 years old. The last sighting of the four females from 1984 were all with a calf, therefore the age at which female SRW no longer reproduce cannot be assessed. The maximum number of calves recorded for a single female was 10.

4. Discussion

Long-term population trends and life history parameters provide critical information for assessment of species conservation status, population recovery, and and monitoring of changes to a population over time from natural and anthropogenic factors. This study presents 26 years of annual cliff-based count and photo-ID data collected for SRW at HoB between 1991 and 2016. Demographic data including rate of population increase and life histories including apparent mean calving interval, age of first parturition, natal site fidelity and observed longevity were reported.

The estimates of the life history parameters presented in this analysis update those previously reported for this population for the years 1991 to 2007 (Burnell, 2001; Burnell, 2008). Burnell (2008) presents rate of increase, calving rate and age of first parturition for data 1991-2007 in an unpublished report to the IWC Science Committee. Burnell (2001) presents mean calving intervals, estimated birth dates and movement data for SRW at HoB during 1991-1997. Bannister (2001), Bannister et al. (2011), Bannister (2017) and Smith et al. (2019) present abundance estimates for the south-western population in Australia. This study provides the most comprehensive assessment of SRW life histories in Australia using 26 years of unbroken time series data. These data contribute directly to the national assessment of SRW abundance currently underway with funding from the Australian Department for Environment National Environmental Science Programme, and the International Whaling Commission Scientific Committee (IWC SC) species assessment for SRW.

Trends in long-term abundance

Long-term monitoring in the order of decades is required for management of long-lived and slow to recover marine mammals. To detect changes in the rates of increase and recovery of SRWs, assessment of each breeding cohort is required (Burnell, 2001; Bannister et al., 2011). At HoB, the updated estimated mean annual rate of increase for females accompanied by a calf between 1992 and 2016 was consistent with prior estimates (Figure 2) between 1991 and 2006 (Burnell, 2008). For reproductive females, the updated rate of increase at HoB was slightly lower than the previous estimate for the years 1991–2006 (Burnell, 2008). When compared to the overall south-western population, the estimated rate of increase for SRW females accompanied by a calf and all population classes at HoB was lower than for the overall south-western population, although within the bounds of the confidence intervals (Bannister, 2017). Charlton et al. (2019a) reported that HoB has likely reached capacity based on density dependence, which could explain why the growth rate is lower for HoB which is an open population, compared to the south-western population.

The abundance trend data contributes significantly to conservation management of the species nationally by informing management on the presence of SRW inside and outside of marine parks and highlighting the need to monitor and protect whales outside of the large established aggregation areas such as HoB

(Charlton et al., 2019b). Whales at HoB are protected by the Marine Mammal Sanctuary Zone of the Great Australian Bight Commonwealth Marine Reserve, which provides a no-access zone during the whale season, May-November and is the only no-access zone providing protection for SRW in south-western Australia. The National Conservation Management Plan for the SRW identifies the need to improve legislation in order to increase the protection of southern right whales (DSEWPaC, 2012). In 1998, the IWC SC completed an extensive review of the status of SRW and assumed their biological maximum growth rate was 7.5% (International Whaling Commission, 2001). Over the past 20 years, the rate of increase has declined. The South African population of SRW is now increasing at an estimated 6.5% (± 0.3%) p.a. between 1979 and 2017 (Brandão et al., 2018). The Argentinean population growth rate decreased from *ca*. 7% for the period 1999–2007 to 0.06% and 2.30% for total number of whales and number of calves, respectively for 2016 (Crespo et al., 2019). In contrast, the NZ population and the eastern Australian population are estimated to be increasing at a different rate from other SRW populations. The difference in growth rates is likely caused by greater historical whaling pressure in the South Pacific than the South Atlantic (International Whaling Commission, 2013), but other factors may also be influencing the growth rate. The NZ population of SRW is estimated to have increased at a rate of 4.8% (95% CI, 2.4% to 6.4%) p.a. between 2006 and 2016 (Davidson, Rayment & Slooten, 2016), whilst the eastern Australian population is estimated to have increased at 4.7% p.a. between 1996 and 2017 for all individuals but is showing no signs of an increase in reproductive females (Stamation et al., 2020). The lower rate of increase recorded at HoB is likely reflective of the site being an open population with regular movement of individuals into and out of the area and the expansion into former calving grounds (Charlton et al., 2019b). Similarly, lower rates of increase were recorded for HoB compared with the overall south-western population for 1992–2006 reported in Burnell (2008). National and global comparative studies of demographic parameters inform conservation management; for example, abundance data contributed to a global comparative study to highlight the severe decline in North

Atlantic right whales compared to SRW populations in wintering grounds across the Southern Hemisphere (Corkeran et al., 2018).

Within the overall rate of increase at HoB, SRWs display three to five years peaks in relative abundance corresponding to different calving cohorts (Figure 3). Individual female calving intervals can vary in time and result in changes to the size of each breeding cohort and subsequently result in trends in peak abundance at the site (Burnell, 2008). For example, the high relative abundance recorded at HoB in 1998 and in 2005 was a direct result of a number of calving females from 1994 and 2001 switching from the typical three years interval to a four years interval and effectively redistributing into the 1995 and 2002 breeding cohorts, respectively (Burnell, 2008).

Female SRWs are known to display a high degree of philopatry, however, coastal movements and changes in selected calving habitat also occur (Best, Brandão & Butterworth, 2001; Burnell, 2001; Cooke, Rowntree & Payne, 2001; Pirzl et al., 2009; Charlton, 2017). Shifts in selected calving habitat from HoB to Fowlers Bay were reported by Charlton et al. (2019b). A shift in selected calving habitat of a known female with high site fidelity to Logans Beach, Victoria in south-eastern Australia was observed and the female relocated to HoB where she then displayed site fidelity over a nine year period (Watson et al., 2021). Similar changes in calving intervals and shifts in calving cohorts have also been observed in Argentina and South Africa (Best, Brandão & Butterworth, 2001; Cooke, Rowntree & Payne, 2001).

As the population increases, presumed historical winter grounds are re-established (Carroll et al., 2014a; Bannister, 2017; Charlton, 2017). The findings show that the proportion of the annual sightings of calving females from the south-western population occurring at HoB has decreased from approximately half to a fifth since the early 1990s, supporting the finding that HoB may have reached capacity based on density dependence and that whales are selecting alternative habitat to HoB as small and emerging aggregation areas establish along the southern coastline (Charlton et al., 2019a; Charlton et al., 2019b).

For example, increased relative abundance was observed at Fowlers Bay, SA (~170 km east of HoB), in years of high abundance at HoB (Charlton et al., 2019b). Head of Bight estimates were confounded by movements in and out of the site and from other coastal aggregation areas outside of the site.

New calving females not previously sighted at Head of Bight

The number of new calving females not previously sighted at HoB increased significantly with time (Figure 6). This increase in new breeding females to HoB relative to individuals sighted previously at HoB with a calf is due to increased immigration of new calving females into the study area. The reduction in the proportion that HoB represents of the overall south-western population (Figure 5) and simultaneous increase in new breeding females to HoB (Figure 6) leads to the hypothesis that within and across seasonal movements increases with increased abundance of SRW in Australia. Further modelling is required to compare the expected recruitment of first-time breeders versus the immigration and emigration of calving females to and from the study area. Whilst the number of new individuals visiting the area has increased, the rate of increase in count data remains unchanged. This supports Charlton et al. (2019a) which suggests that the HoB has reached saturation based on density dependence at the site. As the population increases, so does the movement into and out of the area and this promotes dispersal into alternative habitat and the establishment of small and emerging aggregation areas along the Australian coast. To assess the within and across seasonal movements of whales between aggregation areas and to understand the mixing between the south-western (including HoB) and the eastern populations and NZ, a comparison of SRW photo-ID catalogues from Australia and NZ is required.

Life histories

Apparent mean calving interval

The mean apparent calving interval shows significant difference across the duration of this study, with an overall mean calving interval of 3.3 years (SD = 0.78, ± 0.14, 95% CI), and an increase in calving intervals to 4.2 and 4.1 years for 2015 and 2016, respectively (Figure 7). There is no difference in the apparent mean calving interval compared to 3.4 years for 1991–2007 recorded by Burnell (2008). The mean observed calving interval for the HoB is greater than estimates for the SRW population in South Africa of 3.16 years (95% CI, 3.13–3.19) (Brandão, Best & Butterworth, 2011), and is comparable to the mean calving interval recorded for SRW in south-eastern Australia of 3.5 years (± 0.2 SE, 1980-2018) (Watson et al., 2021), Argentina of 3.42 years (SE = 0.11) (Cooke, Rowntree & Payne, 2003) and NZ of 3.31 years (95% CI = 3.06–3.57) (Davidson et al., 2018).

The prior calving intervals were studied for individuals recorded with a four years calving interval in 2015 and 2016 to see if a shift in calving cohort had occurred and influenced the reduced number of observed three-year intervals. On two occasions, a single reproductive female shifted its calving interval from three to four years. One female had a prior calving interval of two years, followed by a four years interval. Other females either had a previous four years interval or were identified for the first time with a calf at the site. Although a low occurrence of shifts in calving intervals was recorded in 2015 and 2016, this does not explain the increased mean observed calving interval from three years to four years recorded in 2015 and 2016. Further investigation into the connectivity of whales from HoB to other Australian aggregation areas is underway through a collaborative project with the Australian Department of Environment National Environmental Science Programme.

The increased spread in data observed since 2014 may be influenced by increased survey effort in these years. The extended field seasons at HoB during 2014–2016 (3–4 months field season) meant that females in the area were captured through photo-ID and may have fidelity to other areas for calving/nursing and were transiting HoB towards the end of the season, thus possibly leading to increased recordings of five years intervals. For example, the mean percentage of individuals with greater than five years intervals in 2015 of 25.8% and 2016 of 25.3%, significantly exceeded the overall mean of 9.8%. It is also possible that calving events were undetected or that calving occurred outside of HoB. However, the variation in survey effort did not bias the increase in four-year intervals and reduction in three-year intervals, therefore the mean observed calving intervals are not compromised by variation in survey effort.

Fluctuations in calving intervals have also been observed in recent years in South Africa and south-eastern Australia (Brandão et al., 2018; Vermeulen et al., 2018; Watson et al., 2021). In South Africa, an increase in four years calving intervals and decrease in three years intervals was observed since 2015 and the estimated rate of population increase has declined slightly (Brandão et al., 2018). In south-eastern Australia, the mean apparent calving interval increased from of 3.5 years (± 0.2 SE, 1980-2018) to 3.9 years ((± 0.2) between 2007 and 2018 (Watson et al., 2021). A calving interval of two years is considered a calving failure (Knowlton, Kraus & Kenney, 1994) due to foetal loss late in gestation or the loss of a newborn (no lactating investment). A five-year interval can also represent a calf/newborn missed by observers, calved somewhere else or calving failure. These calving interval data provide crucial input to the IWC Southern Ocean Research Partnership funded project underway to develop a common model for a global assessment of SRW demographic parameters and links to climate variates.

Variation in calving rate (not due to measurement error or loss of calves) may have been influenced by climate factors impacting changes to calving intervals (Pirzl et al., 2009). Links between sea surface temperature in feeding areas and the calving success of SRW in Argentina have been documented (Leaper et al., 2006). Inter-annual variability observed in the Australian SRW population were related to Southern Ocean climate factors (Pirzl et al., 2009). SRW reproductive success was linked to krill density and climate for SRW in Brazil (Seyboth et al., 2016). Climate associated changes in prey availability were linked to a depression in calving intervals and population growth of the North Atlantic right whales, *Eubalaena glacialis,* (NARW) (Meyer-Gutbrod et al., 2015). Reproductive success was linked to body condition for western gray whales, *Eschrichtius robustus* (Bradford et al., 2008) and NARW (Miller, 2011). Foraging and distribution patterns of SRW in their Southern Ocean feeding grounds are poorly understood, causing difficulty in making a correlation between prey abundance, climate factors and demographic parameters. At HoB, there is a high year to year variability in numbers of calves observed. The increase in four years calving intervals since 2015 requires further assessment. International collaboration and assessment of potential links between southern right whale demographics, foraging ecology, health and climate is required to assess drivers of observed changes in calving intervals.

Apparent age at first parturition

Apparent age at first parturition data indicate that sexual maturity can be reached by age five, at least in some individuals (Figure 9). The mean apparent age at first parturition of 9.0 years (± 0.33, 95% CI) is consistent with earlier calculation of 9.1 years (± 0.48, 95% CI) by Burnell (2008). A mean age at first parturition of 8.6 years was recorded off South Africa (Brandão, Best & Butterworth, 2011), and a mean age of 9.1 years was recorded off Argentina (Cooke, Rowntree & Payne, 2001) and more recently at 8.4 years (International Whaling Commission, 2013). To estimate age at first parturition of SRW in South Africa, only females that have a white dorsal blaze or partial grey coloration were included (Brandão, Best & Butterworth, 2011). Calves with visible white and grey blazes retain them through life and increase the probability of resighting these individuals into the future (Payne et al., 1983). The slightly lower mean age at first parturition recorded in South Africa may be attributed to increased sampling coverage of the whole population in South Africa compared to at HoB. It is possible that calving events may have occurred in areas outside the study area and thus reflected a different mean age at first parturition.

Longevity, reproductive age and maximum calving events

Southern right whales in Australian waters are still reproductively fit at 41 years of age. Senescence has not been reported in baleen whales. However, the oldest known Australian female (sex confirmed through observation and photograph of genitals) was first sighted in 1970 and based on size and body shape was assumed to be a mature adult at that time and would have already been approximately 9 years old, but was never sighted with a calf. The female was sighted 12 times at HoB, with the last sighting in 2010, which would make her at least 50 years. The oldest (northern or southern) right whale reported was a female NARW photographed with a calf in 1935 and authors estimated that she was at least 10 years at the time, but never again seen with a calf. Therefore, they used 69 years as her age and she was last seen in August 1995 with a large propeller wound (Hamilton et al., 1998). The lifespan of bowhead whales, *Balaena mysticetus* a close relative to the right whale is known to exceed 200 years (Keane et al., 2015). Whilst HoB is an open population and further assessment is needed of the complete Australian dataset, the results provide a useful documentation of on reproductive longevity and maximum calving events, which is currently limited in the scientific literature on SRW.

Conclusion

In this study, demographic parameters for SRW at a major wintering ground off Australia at HoB are presented using 26 consecutive years of photo ID data. The information presented directly addresses key priorities and objectives in the Australian Commonwealth SRW Conservation Management Plan to understand life history parameters and measure population growth. Baseline data are provided for assessment of potential before and after impacts associated with marine based activities in the broader area. The increase in calving intervals since 2015 is a cause for concern and there is a need to understand potential links between calving intervals, prey availability, health and climate. These data contribute significantly to the IWC-SORP theme 6: The Right Sentinel for Climate Change – assessing links between SRW demographics, foraging ecology, health and climate. Studies are underway to assess national abundance and connectivity of SRW and compare global demographic parameters among SRW wintering grounds. There is a need to collate all Australian photo ID datasets and assess the links between calving intervals and climate variates to assess the impact of climate change on the species. This paper highlights the imperative need to continue long-term count and photo-ID studies to detect changes to the SRW population over time and inform conservation management of the species.

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Tables

No tables in manuscript

Figure captions

Figure 1. Boundaries of the study site and location of observation stations for southern right whales, *Eubalaena australis*, at Head of Bight in the eastern Great Australian Bight, South Australia.

Figure 2. Linear regression of the natural logarithms of the maximum daily counts per year of southern right whales, *Eubalaena australis* at Head of Bight, South Australia between 1992 and 2016 for total adults (red squares) and female and calf pairs (black circles) with fits.

Figure 3. Southern right whale, *Eubalaena australis* maximum daily counts at Head of Bight, South Australia between 1992 and 2016.

Figure 4. Incremental growth rate using a natural logarithm regression analysis for southern right whales, *Eubalaena australis* at Head of Bight, South Australia between 2006 and 2016, for female and calf pairs (black) and total adults (red), with 95% CI error bars.

Figure 5. Southern right whale, *Eubalaena australis* female and calf pair relative abundance for the overall south-western Australian population and the Head of Bight aggregation area in South Australia between 1993 and 2016.

Figure 6. The number of new of southern right whale, *Eubalaena australis* females with a calf not previously sighted at Head of Bight, South Australia compared with females that were known to have previously been identified (1996 to 2016), presented with the proportion of new individuals (as black dots) and trendline with R^2 values.

Figure 7. Apparent calving intervals for southern right whales, *Eubalaena australis* identified in photographs between 1996 and 2016 at Head of Bight, South Australia, displayed as a box plot the

median (centre line), upper and lower quartiles (upper and lower limits of boxes), maxima and minima (lines on either end of boxes), and extremes (dots). Analysis completed for calving intervals 5 years or less, however, raw data displayed to show variation.

Figure 8. Frequency distribution of intervals between observed calving of individually identified southern right whales, *Eubalaena australis* at Head of Bight, South Australia between 1996 and 2016. Analysis completed for calving intervals 5 years or less, however, raw data displayed to show variation.

Figure 9. Frequency distribution of apparent age at first parturition of southern right whales, *Eubalaena australis* of known age at Head of Bight, South Australia (n = 20).