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Southern right whales (*Eubalaena australis*) return to a former wintering calving ground: Fowlers Bay, South Australia

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Abstract

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Southern right whales (SRW), Eubalaena australis, have reoccupied historically important winter habitat ranges (calving grounds) in recent years along the southern Australian coast. Here we present findings of increased abundance of SRW at Fowlers Bay, South Australia, a previous shore-based whaling station. This study investigates: SRW inter- and intraseasonal trends in relative abundance; changes to the relative proportion of the southwestern subpopulation represented by SRW at Fowlers Bay; distribution, and occupancy. Sighting and photo identification data were collected during annual aerial (1993-2016) and vessel surveys (2014-2016). The total number of female and calf pairs was three during 1993-2003 and 63 during 2004-2014. Despite high variability in annual relative abundance (SE = 29.7), the rate of mean increase (38.8%/yr) exceeded the maximum biological rate for the species (6%-7%/yr). Peak relative abundance was recorded in July and August. SRW at Fowlers Bay represent an increasing proportion of the southwestern subpopulation (range = 0.9%-7.4%). Mean occupancy was 23 d (range = 1-75) for female and calf pairs and 2 d (range

= 1-15) for unaccompanied adults. Reduced sightings in 2015 and 2016 demonstrate plasticity in SRW abundance at Fowlers Bay. Research into the movement and connectivity of SRW is needed to understand drivers of habitat dispersal in Australia. Key words: southern right whale, Eubalaena australis, Australia, calving, photo identification, abundance, distribution, conservation.

Southern right whales (SRW), Eubalaena australis, were heavily exploited and reached near global extinction owing to commercial whaling in the 19th and 20th centuries (Dawbin 1986, Tormosov et al. 1998, Carroll et al. 2014b, Harcourt et al. 2019). An estimated 55,000-70,000 whales were present in the Southern Hemisphere in the late 1700s. By the 1920s there may have been fewer than 300 individuals remaining (IWC 2001). Prewhaling abundance of SRW in eastern Australia and New Zealand (NZ), was estimated between 53,000 and 58,000 individuals (Carroll et al. 2014b). In Australia, whaling of SRW took place from approximately 1805 to the early 1900s (Dawbin 1986, Carroll et al. 2014b). Two main types of whaling activity occurred last century on and off the Australian coast: "bay" and "shore station" whaling by locals and "pelagic" whaling by vessels from several countries including the United States, France, Great Britain, and Australia (Dakin 1938, Dawbin 1986). Shore- and ship-based whaling was heavily concentrated in south eastern Australia and NZ, where most SRW were caught between 1830 and 1849 (Carroll et al. 2014b). There were approximately 115 Australian shore-based whaling stations in 50 locations along

the southern coast of Australia (Pirzl 2008).

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Fowlers Bay was the site of a shore-based whaling station in the far west of South Australia (SA) where the only available record of the number of whales taken in a single year is from the log of the American ship Amazon which took 33 SRW and 8 humpback whales, Megaptera novaeangliae, in 1840 (Bannister 1986). Kemper and Samson (1999) reported that at least 65 SRW were taken by bay whalers during 1840-1844 from the Fowlers Bay region, including those taken by the Amazon. During the same period (1840-1844), Dawbin (1986) reported 193 taken off SA, and Carroll *et al.* (2014*b*) reported additional catches of 91 off Victoria, 1,568 off Tasmania and 1,007 off New South Wales.

Despite almost a century of protection since 1935, SRW long term, annual monitoring has been restricted to areas where the largest remnant populations exist (Burnell 2001, Charlton *et al.* 2019, Rowntree *et al.* 2001, Bannister *et al.* 2011). At these locations signs of population increase at or near the maximum plausible rate of around 7%/yr have been recorded (Best *et al.* 2001, Cooke *et al.* 2003, Carroll *et al.* 2013, Bannister 2017, Charlton 2017). Conspecific attraction and historic whaling

effort combined with philopatry appear to be the main drivers of SRW calving ground occupation (Payne 1986, Best et al. 2001, Burnell 2001, Rowntree et al. 2001, Pirzl 2008). These factors are considered key drivers for the differences in mitochondrial and microsatellite DNA haplotype frequencies between the southwestern and southeastern subpopulations in Australia, and the New Zealand, Argentinian/Chilean, and South African populations (Baker et al. 1999; Patenaude et al. 2007; Carroll et al. 2011, 2015, 2018; Harcourt et al. 2019). In contrast to the typically strong fidelity to calving grounds, there is also evidence that SRW can shift selected calving habitat and display flexibility in how philopatric they are (Best 1993, Groch et al. 2005, Carroll et al. 2014a). As SRW abundance increases it is important to understand distribution shifts and characteristics of whales in emerging areas to inform species conservation management and recovery assessments (Harcourt et al. 2019).

In Australia, SRW are divided into two subpopulations, in the south east and southwest of Australia based on genetic and geographical diversity and contrasting rates of population increase (Bannister *et al.* 2011; Carroll *et al.* 2015, 2018). The

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current population estimate for SRW in Australia is around 2,500 individuals including 2,200 individuals in the southwestern subpopulation and less than a few hundred individuals in the south eastern subpopulation (Bannister 2017). SRW have expanded their habitat range with increased abundance along the southern Australian coast in recent years. There are now 13 recognized aggregation areas along the southern coastline of Australia (Fig. 1). Large established aggregation areas where SRW calve, nurse, rest, mate, and socialize include: Doubtful Island Bay and Israelite Bay in Western Australia (WA) and Head of Bight in SA. Small established aggregation areas include: Yokinup Bay in WA, Fowlers Bay in SA, and the Warrnambool region in Victoria. Other aggregation areas that are sporadically occupied include Flinders Bay, Hassell Beach, Cheyne/Wray Bays, Twilight Cove in WA, and Encounter Bay in SA (DSEWPaC 2012). SRW are mainly concentrated along the southwest coast of Australia (representing the southwestern subpopulation off WA and SA).

Annual aerial surveys conducted through the Western Australian Museum (WAM) since 1976 provide information on longterm trends in abundance of the southwestern subpopulation of

SRW in Australia (Bannister 2001, 2010, 2017; Bannister et al. 2011). The annual aerial survey program began following increasing reports of SRW off the south coast of WA in the early 1970s (Bannister 1990). From 1976 to 1992 surveys were flown between Cape Leeuwin, WA, and Israelite Bay, and occasionally to Twilight Cove, WA. From 1993 to 2016 aerial surveys were undertaken annually between Cape Leeuwin, WA, and Ceduna, SA. While there is knowledge of the broad scale distribution and abundance trends (Bannister 2001, 2010, 2017; Bannister et al. 2011), spatial ecology (Pirzl 2008), and fine scale demographics and population trends at the primary aggregation area at Head of Bight (Burnell and Bryden 1997, Burnell 2001, Charlton 2017; Charlton et al. 2019), understanding the characteristics of SRW in small established and emerging aggregation areas is prioritized in the Commonwealth SRW Conservation Management Plan to (DSEWPaC 2012). Such knowledge is required for species conservation management and for setting of population recovery targets.

Fowlers Bay is a small established aggregation area at the eastern range of the southwestern subpopulation of SRW.

Increased sightings of SRW at Fowlers Bay have occurred since the mid 2000s based on aerial surveys (Bannister *et al.* 2011)

and anecdotal reports by tourism operators since 2010.

This study investigates SRW inter- and intraseasonal trends in relative abundance, changes to the relative proportion of the overall southwestern subpopulation that SRW at Fowlers Bay represent, distribution and occupancy at Fowlers Bay.

Methods

Study Site

Fowlers Bay (32°0'S, 132°30'E) is the eastern range of the southwestern subpopulation, located approximately 160 km south east of the most important SRW Australian aggregation area at Head of Bight, SA (31°29'S, 131°08'E) in the Great Australian Bight Commonwealth Marine Reserve. The bay is located within the Great Australian Bight that extends from Cape Arid, WA, to Port Lincoln, SA (Fig. 2). Fowlers Bay is approximately 95 km² in area and is in a habitat protection zone within the Nuyts Archipelago Marine Park (Fig. 3). The area is open to fishing and no access or fishing restrictions apply in the Marine Protected Area. Fowlers Bay provides sheltered sandy habitat,

protected from the prevailing southwesterly weather conditions, and has water depths ranging from 0 to 20 m within 5 km of the shore, making it an ideal habitat for SRW in winter when they occupy shallow gently sloping sandy bays in water depths of less than 10 m and within 2 km of the coast (Pirzl 2008). Data Collection

To fulfill study objectives, sightings and photo ID data were collected using a combination of aerial (1993-2016) and vessel based surveys (2014-2016).

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Aerial survey-Aerial surveys of the southwestern subpopulation of SRW were undertaken annually from 1993 to 2016 between Cape Leeuwin, WA (34°22'S, 115°08'E) and Ceduna, SA (Fig. 2) to collect SRW count data and photo identification (ID) in Fowlers Bay (Bannister 2017). Surveys were completed using a high wing, single engine aircraft (Cessna 172). The aircraft was crewed by a pilot/observer and photographer/observer who searched, counted, and photographed whales while on transect. Surveys consisted of a single transect running parallel to the coast between approximately 0 and 1.85 km (*ca*. 0-1 nautical miles) off the coast as SRW are known to aggregate in shallow

waters close to shore on breeding grounds along the southern Australian coast. Observers searched for whales on both sides of the aircraft, and once a whale was sighted, it was circled by the aircraft to collect photo ID images and record count data and location, after which the aircraft returned to the fixed transect line. In SA waters surveys were flown at 304 m (1,000 ft) and a speed of 185 km/h (100 kn) while on transect and 148 km/h (80 kn) when circling whales for counting/photography. Within Fowlers Bay, the aerial survey transect covered approximately 10 km of coastline. A large portion of the SRW that utilize Fowlers Bay can be observed from near-shore surveys, and from these data population demographics and life history parameters can be estimated. A single transect was completed from west to east on an "outward" leg (from WA to SA), followed by a second count on an "inward" (return) leg from east to west, weather permitting. The higher count of the two flights on each leg was taken as the minimum estimated abundance of whales in the area. Flights were undertaken only in wind speed conditions of <8 km/h (15 kn) for comparability of counts. When a group of whales was sighted, the individuals were circled to

verify and record group size and composition and to obtain photo ID images (Bannister 2017). Group composition was recorded either as a female and calf pair or an "unaccompanied" animal (juveniles or adults not unaccompanied by a calf of the year. The method for photo ID is described below. The GPS location of whales was recorded in degrees and decimal minutes. Most animals, particularly female and calf pairs, are easily observed in the relatively clear and shallow waters of the south coast of Australia and the probability of sighting close to the aircraft, g(0), was assumed to be 1 (Bannister 2017). Observer bias was reduced as much as possible by using the same survey design methods and pilot and observer/photographer throughout the duration of the surveys (1993-2016).

Surveys each year (WA to SA return) were completed within a five day weather window between 15 August and 15 September, which allowed for comparability of minimum numbers of SRW occupying the Australian coast among yrs. At Fowlers Bay, the aerial transect was undertaken as part of the longer leg of the aerial surveys from Head of Bight to Ceduna. Because mean calving SRW occupancy periods between 40 and 71 d were recorded

at Head of Bight (Burnell 2001, Charlton 2017), and whales are known to depart Head of Bight in September/October (Charlton *et al.* 2019), female and calf pair sightings during the aerial surveys in this study were assumed to have selected Fowlers Bay as their calving or nursing habitat for the season. Unaccompanied adults are highly transient within season, so the aerial surveys captured a snapshot of information on habitats

used by unaccompanied adults.

Vessel Surveys

Vessel-based surveys were undertaken onboard one of three Fowlers Bay Eco Whale Tours charter vessels between July and September from 2014 to 2016 (Table 1). The vessel used by the tourism operator depended upon availability. The vessels included: a 13.58 m (45 ft), aluminum Cathedral hull vessel (*Asheera*) with 600 hp Yanmar inboard engines and a 4.5 m vantage height; a 6 m (20 ft), a Fibreglass Tri Hull vessel (Jaguar) with 2 × 70 hp Yamaha outboard engines and a 1.5 m vantage height; and a 15 m (50 ft) fibreglass catamaran (Tuna Explorer) with 395 kW Volvo Penta inboard engine and a 5 m vantage height. Surveys were conducted opportunistically in Beaufort Sea State

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conditions of three or less. The operational area extended to approximately 12 km in the SW to NE directions and 6 km from shore in the NE to SE direction; covering an approximate area of 35 km². Tracks were haphazard in their spatial coverage because they were determined by the tourism operation. Vessel tracks were recorded using a Holux M-1000C GPS data logger that recorded the date and time, latitude and longitude of the vessel every second.

During vessel surveys, two observers searched for whales using a combination of the naked eye and Nikon 10 × 50 marine grade binoculars from the foredeck. This vantage point allowed unrestricted, 180° views forward of the vessel. When searching, one observer scanned from 0° forward to 90° on the port side, while the second observer scanned from 0° forward to 90° on the starboard side. Scanning for whales was undertaken by continuously searching the entire visible area of the ocean from the horizon down to the vessel, or from shore to the vessel. The detection range was limited to approximately 4 km by the relatively low vantage point.

When an individual or group of SRW was sighted, the vessel

changed from search mode to closing mode with a minimum approach distance of 150 m (as required by the licence conditions). The location of the whale was calculated using range, height and trigonometry. Once the group of whales was approached, the following data were recorded at the closest distance reached to the whale: GPS location of the vessel in latitude and longitude; range (if possible) using Bushnell Elite 1600 ARC laser rangefinders; bearing from the vessel to whale using a compass; group size and group composition (female accompanied by a calf, unaccompanied adult, or unknown); time and date. To ensure that error in the compass was not introduced by nearby ferromagnetic metal, observers did not stand near nonaluminum metal and ensured they did not have any metal objects on them. The following weather conditions were recorded qualitatively at the start and end of each survey, and as conditions changed: wind speed, wind direction, Beaufort Sea State, swell height (meters), and percentage of cloud cover. In addition, water and air temperature were recorded at the start of the survey from instruments on the vessel. Photographs of individual whales were collected when possible for identification. Once data were

obtained from the group and the whale watch interaction terminated, the vessel departed the group and continued its search.

Photo Identification

Photographs of individual whales were obtained for comparing and matching individuals photographed previously. Photographs of the dorsal surface of the head allow callosity patterns, unique to each individual, to be documented. Callosity patterns are keratinized skin patches colonized by cyamids that provide individually unique patterns on the dorsal surface of the rostrum, the lip line of the lower jaw, and just posterior to the blowhole. They remain recognizable for life (Payne *et al.* 1983). In addition to callosity patterns, dorsal blazes on the body and notable scars were also used as identifiable features when present.

Boat-based images for photo ID were obtained using a Nikon 5200 Camera fitted with a Nikon 300 mm lens. Photos of the left, right and front of the head including perspectives from the left and right posterior and anterior of each animal were obtained when possible. Digital photo ID images were sorted daily in the

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field, including within season cross matching of individuals to document the total number of individuals identified in that year. Quality of images was dealt with by following an image quality protocol and grading images into categories (excellent, high, average, poor, very poor quality). Only average or above images were selected for future matching and all images were stored. Distinctiveness was not accounted for, however, with a small population like Fowlers Bay, where images were available for most individuals from vessels and aircraft, the error associated with distinctiveness is considered low. Images collected during aerial surveys were accrued directly after the survey so that vessel based images could be compared with aerial images in the field. For between year comparisons, photo ID resights were identified through matching photographs with the photo ID catalog developed in Big Fish v6 Microsoft Access database (Pirzl et al. 2007).

Data Analysis

Inter- and intraseasonal trends in relative abundance-Interseasonal trends in relative abundance at Fowlers Bay were assessed and the annual rate of change estimated using aerial

count data from 1993 to 2016. Generalized linear models (GLM) with Poisson distribution and log link functions for count data were used to determine the relationship between the number of SRW and year (1991-2016). Explanatory variables included years 1993-2016 (as a factor) and annual count data (maximum count recorded from two aerial surveys/year) as a variable. Variance inflation factors (VIF) were used to test for collinearity. All covariates showed VIFs <3, indicating no collinearity between covariates (Zuur et al. 2007, 2009). Model fit was tested by plotting observed vs. fitted values as well as plotting fitted values vs. scaled Pearson's residuals to assess the mean variance relationship. GLMs were undertaken using R Studio and loess smoothers applied. The mean rate of increase in relative abundance used a linear regression of the natural logarithm of the annual count data for "all animals" and for females with a calf and presented with 95% confidence intervals (CI). CIs were not calculated for years with zero abundance.

Intraseasonal trends in relative abundance were assessed using SRW count data collected between July and September during the years 2014-2016 (using vessel based counts). The highest

daily count was used on days when two vessel surveys were completed. The variation in relative abundance of each population class (females accompanied by a calf, unaccompanied adults) was assessed using highest maximum daily counts. Relative abundance counts were not corrected for effort and are considered the minimum number of whales present in the area on the day of survey. The proportion of the maximum count of the season in July, August, and September was calculated and displayed as a stacked bar chart using the R package ggplot2 (Wickham 2009) to assess the relative seasonal usage of the area.

Changes to the proportion of SRW that Fowlers Bay represents, compared to the overall southwestern population-The percentage of SRW documented in Fowlers Bay of the overall southwestern population was calculated by dividing the annual aerial survey count from Fowlers Bay by the southwestern population size estimate derived from aerial survey data each year (1993-2016). A chi-squared test for trend in proportions was undertaken using the function prop.trend.test in the R package *stats* to test whether there was a linear trend in the

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proportion of SRW in Fowlers Bay of the total southwestern population across years.

Distribution-Inter- and intraseasonal distribution was assessed during 3 yr of vessel-based sightings data (2014-2016). Spatial data processing used purpose built programs in MATLAB software (The Mathworks, Natick, MA) to generate whale locations for each sighting. Maps were generated in MATLAB from Australian Hydrographic Service charts under Seafarer GeoTIFF license No 2618SG (Curtin University). The GPS location of the vessel, the range between vessel and whale and the vertical angle from the observer height to the whale on the surface of the water were considered when calculating the whale location. Errors in location data were estimated to be within 100 m. Spatial data were normalized for effort to number of whales counted per unit effort (0.5 km^2) and displayed as kernel density distribution plots using ArcMap v10 (ESRI 2011). Data were presented as raw with tracks overlaid among years and pooled for 2014-2016 in kernel density plot. For relative abundance assessment, the maximum daily count represents the minimum number of individuals in the study area. All times were presented in Australian

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Central Standard Time (UTC + 9.5 h). Various handheld GPS units were used to log position, all using the WGS 84 chart datum

(equivalent to GDA 90). Bathymetry was retrieved from the Geoscience Australia ~250 m resolution grid (Whiteway 2009). To display intraseasonal distribution, kernel density plots were generated for each month of the field season (July to September) and data pooled for years 2014-2016. While behavior before and after vessel approach was recorded, disturbance from the vessel was not assessed in this study, resulting in a possible bias in whale distribution influenced by vessel presence.

Occupancy-Occupancy of females accompanied by a calf and unaccompanied adults was assessed using photo ID resights of individuals collected during vessel and aerial studies (2014-2016). Occupancy was considered the minimum period that an individual (or female accompanied by a calf) spent in Fowlers Bay. If no sightings were recorded for days between resights it is possible that the animal left the area and then returned or was outside of the vessel survey area. The interval between first and last sighting of SRW in Fowlers Bay was considered occupancy and animals were often resighted in the interim.

Sighting location of three female and calf pairs were displayed on a map for each day of sighting to provide example of variation in site use at Fowlers Bay. Female and calf pairs were selected because they had longer resident times and because the paper focuses on the importance of Fowlers Bay for female and calf pairs selecting the site for nursing.

Results

Inter- and Intraseasonal Trends in SRW Relative Abundance

Interseasonal—A total of 139 individual sightings of SRW adults were recorded during annual aerial surveys at Fowlers Bay between 1993 and 2016, of which 74 were unaccompanied adults and 65 were females accompanied by a calf of the year. SRW group compositions at Fowlers Bay included 53% unaccompanied adults and 47% females accompanied by a calf.

Over the 10 yr time period between 1993 and 2003, six SRW were sighted at Fowlers Bay. These six individuals included one female and calf pair in 1993 and two female and calf pairs in 1999 (Fig. 4). In comparison, over the following 10 yr of surveys between 2004 and 2014, a total of 216 different individuals were sighted, including 74 unaccompanied adults and

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62 females accompanied by a calf. No SRW were recorded during aerial surveys at Fowlers Bay in 2015 or 2016. However, SRW were present during vessel surveys in 2015 and 2016 (Table 2). The mean rate of increase in relative abundance for total individuals was 38.8%/yr (95% CI = 0.0, 97.0) and for female and calf pairs was 29.2%/yr (95% CI = 0.0, 93.0) between 2004 and 2014. The one-way ANOVA *post hoc* Tukey's HSD test in XLStat (XLSTAT 2017) with time period (1993-2003 and 2004-2014) as the independent variable and rate of increase in SRW relative abundance the dependent variable, indicating that the rate of increase between all years during 1993-2003 was significantly different from 2004 to 2016 (P < 0.05).

Interseasonal variation in abundance (SE = 29.7) was high during yrs when whales were present. Triennial peaks in SRW numbers were observed in 2005, 2008, 2011, and 2014 and an additional peak in 2009 (Fig. 4). Between 2004 and 2014, females accompanied by a calf were sighted annually, except for 2010 when no female and calf pairs were sighted. The mean daily maximum number of females accompanied by a calf recorded between 2004 and 2014 was 5.6 (range = 0-16, 95% CI 2.9, 8.3). A maximum

of 55 individuals were sighted during the 2011 aerial survey, including 16 females accompanied by a calf and 23 unaccompanied adults. Unaccompanied adults were observed annually during the aerial survey between 2004 and 2014 with a mean maximum of 6.7 individuals (range = 1-23, 95% CI = 2.6, 10.8). Triennial peaks in abundance were also observed for unaccompanied adults in the years 2005, 2008, and 2011 (Fig. 4).

Intraseasonal-A total of 147 h of observation was undertaken over 65 d during 73 vessel surveys between 4 July and 18 September 2014-2016 (Table 1). On 8 d, two surveys were completed on a single day, one in the morning and one in the afternoon. The vessel used and elevation of observers above sea level varied throughout the surveys (Table 1). While the observed distance to the horizon from different platforms ranged from 4.4 to 7.6 km, the maximum visual detection range for whales was considered ~4 km from all platforms (with different viewing heights), measured through a sighting frequency histogram. The average vessel speed was 11.5 km/h (6.2 kn, range = 0-24 kn). While the vessel tracks varied between years, the survey effort was primarily concentrated between 1 and 8 km northeast of the Fowlers Bay jetty, with effort expanding in 2016 out to the area around Fowlers Point and into the middle of the bay due to fewer SRW in the region and an increased search range by the tour operator (Fig. 5).

A total of 440 sightings of 436 individual whales (including calves) were recorded during the 73 vessel surveys at Fowlers Bay. Out of all surveys, 79% (n = 173) were females accompanied by a calf and 21% (n = 90) were unaccompanied adults. Intraseasonal relative abundance of SRW varied between 2014 and 2016 (Table 2, Fig 6). Relative abundance was not corrected for varying effort among years because absolute values were presented. The mean maximum relative abundance recorded for daily vessel surveys between 2014 and 2016 was six individuals and ranged from 0 to 22 individuals (95% CI = 4.77, 7.23; Table 2). Sightings of female and calf pairs varied between 0 and 10 during daily surveys, with a mean maximum daily count of two female and calf pairs during 2014 and 2016 (95% CI = 1.41, 2.59). Between zero and seven unaccompanied adults were sighted on daily surveys and the mean maximum daily count was one during 2014 and 2016 (95% CI = 0.59, 1.41). The maximum group size

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recorded on daily surveys for female and calf pairs was 11 (range = 2-11, \bar{x} = 2.5) and for unaccompanied adults was four (range = 1-4, \bar{x} = 2.3). The median group size for unaccompanied adults and females accompanied by a calf was two.

Peak SRW relative abundance was recorded between 20 July and 17 August (Fig. 6). A total of 60% of all whales sighted between 2014 and 2016 were observed in July, 39% in August and only 1% in September. Female and calf pairs occupied the site throughout the study period (July to September). Between 20% and 100% of females accompanied by a calf were present at Fowlers Bay at the start of the study period in mid-July and between 0% and 50% of females accompanied by a calf remained in the study area until the end of the study period in late September (in 2014 only). There were no sightings of any whales in September in 2015 and 2016. There was intraseasonal variation in relative abundance of SRW between 2014 and 2016 (Table 2; Fig. 6).

Unaccompanied adults were more transient and their relative abundance more variable than females accompanied by a calf. Unaccompanied adults occupied the site in the greatest abundance in July and August, with up to 57% of all unaccompanied adults

observed in mid-July and none sighted in Fowlers Bay in

September. While whales may have occupied areas outside of the study site and therefore been missed by observers, variation in daily count data indicates movement into and out of the study area throughout the season, particularly for unaccompanied adults (Table 2, Fig. 6).

Changes to the Proportion of SRW that Fowlers Bay Represents, Compared to the Overall Southwestern Population

SRW sighted at Fowlers Bay represent a small percentage of the southwestern subpopulation of approximately zero from 1993 to 2001, 0.9% in 2002, and 7.4% in 2009. There was a significant linear trend in the proportion of SRW in Fowlers Bay of the total population across years (χ^2 =55.016, df = 1, P = 1.195e-13), with an increase in the proportion with increasing year.

Distribution-There was little variation in distribution of female and calf pairs or unaccompanied adults when comparing between 2014 and 2015. However, in 2015 and 2016 whales were sighted around Point Fowler (Fig. 5). In comparison to 2014/2015, in 2016 females accompanied by a calf were recorded

very close to the shore and unaccompanied adults sighted were recorded further away from the shore and around Point Fowler.

SRW sightings at Fowlers Bay during vessel surveys (2014-2016) were predominantly within the 10 m depth contour within 1-2 km from shore, and most commonly within a few hundred meters of shore, between Point Fowler and 8 km south east of the Fowlers Bay jetty. They were most common 1-5 km north east of the jetty (Fig. 7). Whale sightings were overlaid with vessel tracks in Arc Maps v10 (ESRI 2011) to show the density distribution of whales compared to spatial effort (Fig. 5).

While, in general, SRW at Fowlers Bay displayed little within seasonal variation in distribution, there was some evidence (although sample size is low) that individual distribution patterns within the study site varied within season (Fig. 8). For example, a female and calf pair sighted 20 times in 2015 across 33 d displayed a small distribution range during the first 12 d (sightings #1-9) and then expanded its range on days 15-33 (sightings #10-20) before departing the site (Fig. 8).

Occupancy-Occupancy was assessed using photo ID resight

data for the 46 individual adults (of which photo ID images of sufficient quality for matching existed), collected during 2014-2016. The percentage of unaccompanied adults and females accompanied by a calf photo ID'd at the site exceeded the maximum daily count each year, thus resulting in a value over 100%. This result indicated movement of individuals into and out of the area within a season. When comparing the maximum annual daily count to the number of individuals photo ID'd, rates were 0.87 (or 87% n = 14) of females accompanied by a calf and 1.76 (or 176%, n = 32) of unaccompanied adults (Table 3).

Within season resights were recorded for 72% of all individuals photo ID'd during vessel surveys, including 100% of females accompanied by a calf and 44% of unaccompanied adults (Table 3). The number of resights for each individual ranged from 0 to 20 between 2014 and 2016, including a maximum of 20 resights for a female accompanied by a calf in a single year (0 = 6), and six resights ($\bar{x} = 1.2$) for unaccompanied adults (Table 3).

Females accompanied by a calf displayed longer occupancy periods than unaccompanied adults. Occupancy periods for females

accompanied by a calf ranged from 1 to 75 d, \bar{x} = 23 d) and from 1 d to 15 d (\bar{x} = 2 d) for unaccompanied adults (2014-2016). In 2015 a female and calf pair was already in the bay when the surveys began on 26 July 2015 and they remained there for 25 d after the survey finished on 29 August 2015 (the minimum total occupancy was thus 59 d for this pair). Occupancy periods varied across years at Fowlers Bay, with whales displaying longer occupancy periods in years of higher relative abundance (Tables 2, 3). One calving female in 2014 was first sighted as a pregnant female and sighted 22 d later with a calf. In 2015, there were two female and calf pairs sighted at Fowlers Bay (CC1 and CC2) with residence periods of 35 d and 11 d, respectively. Both female and calf pairs displayed westerly movement and were later sighted that season during the annual cliff based SRW population monitoring at Head of Bight, 160 km to the west of Fowlers Bay. CC1 was sighted three times at Head of Bight between 8 and 17 September, and CC2 was sighted once at Head of Bight on 15 August (Charlton 2017).

DISCUSSION

SRW numbers in Fowlers Bay have increased since 2004, with

the area representing an important habitat for females accompanied by a calf. The abundance of SRW at Fowlers Bay was highly variable across years but showed a marked increase after 2003. The estimated rate of increase in SRW abundance recorded at Fowlers Bay between 2004 and 2014 of 38.8%/yr. (95% CI = 0.0, 97.0) for total individuals exceeds the biological maximum for the species of 6%-7%/yr (IWC 2013). The rate of increase estimated for the southwestern subpopulation of SRW in Australia of 5.55%/yr (95% CI 3.78, 7.36; Bannister 2017). The accelerated rate of increase in abundance of SRW at Fowlers Bay since 2004 suggests that there is movement into the site, because it is not biologically possible for a population increase at that rate. SRW sighted at Fowlers Bay represent a small but increasing percentage of the southwestern subpopulation, from 0% between 1993 and 2001, to a maximum of 7.4% in 2009. The percentage of SRW that Fowlers Bay represents of the overall southwestern subpopulation provides information on how the site was used over time and the growing importance of the area for SRW. At the same time that there was an increase in the percentage of the southwestern subpopulation of SRW sighted in Fowlers Bay, the

relative proportion sighted at nearby Head of Bight decreased (Charlton 2017). For example, in the early 1990s, SRW at Head of Bight represented up to 48% of the total southwestern subpopulation, while by 2016 the SRW at Head of Bight represented only 25% of the overall southwestern subpopulation (Charlton 2017). Distributional shifts in relative abundance at aggregation areas are evident for the southwestern subpopulation of SRW in Australia. When vessel based surveys undertaken throughout the season (July to September 2014-2016) were compared with overlapping aerial surveys they not surprisingly indicated that a greater number of individuals occupied Fowlers Bay throughout the season were sighted during an aerial survey on a single day. For example, no SRW were recorded during aerial surveys in 2015 and 2016, but 27 adults and three calves were photo ID'd from vessel-based surveys suggesting that whales had departed the area prior to the aerial survey. Aerial surveys

provide a snapshot of the SRW distribution on the day of the survey and represent a minimum number of individuals occupying the area in a season.

Variability in SRW abundance is generally driven by pulses

in calf production due to their average 3 yr calving cycles from different cohorts of females (Burnell 2001, Charlton 2017). Triennial peaks revealed in long term abundance trends at Fowlers Bay compare with peaks recorded for the southwestern subpopulation and Head of Bight (Bannister 2017, Charlton 2017). Peaks in abundance were recorded at Fowlers Bay and Head of Bight in 2005, 2008, 2011, and 2014. High years of abundance at Head of Bight typically correlated with high abundance at Fowlers Bay. For example, the maximum daily count of total individuals was recorded at Fowlers Bay in 2011 (n = 55) which was the second highest abundance recorded at Head of Bight (n =172) over the period 1991-2016 (Charlton 2017). The increased abundance of SRW at Fowlers Bay may be influenced by the adjacent habitat at Head of Bight reaching saturation capacity and individuals moving to alternate suitable habitat at Fowlers Bay (Charlton 2017). Alternatively, increased abundance at Fowlers Bay may be a result of females calving before reaching Head of Bight and selecting Fowlers Bay because it is the closest suitable habitat. Cross matching of individuals' photo ID'd at Fowlers Bay to other available photo ID catalogs is

required to assess where the individuals sighted at Fowlers Bay come from, or what proportion of the population represents a remnant population or first time breeders at the site.

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In contrast to the high abundance recorded at the adjacent aggregation ground at Head of Bight in 2016, no SRW were sighted during the aerial surveys and a single female and calf pair recorded residing in the Bay by vessel survey in 2016. SRW abundance at Fowlers Bay in 2016 was lower than expected; for the second consecutive year whale numbers were low in Fowlers Bay. The lower than expected number of females accompanied by a calf observed in 2015 and 2016 at Fowlers Bay together with the high annual variation in abundance, suggest that use of the area is not consistent between years. SRW show significant plasticity in habitat occupancy and individual variability, all effected by interactions of conspecific attraction, philopatry, and topography (Burnell 2001, Rowntree *et al.* 2001).

A key driver of variation in abundance of SRW in calving habitats is the cohort structured breeding cycles based on an average of 3 yr calving intervals (Burnell 2001, Charlton 2017). Lower than expected SRW abundance was observed for the

southwestern subpopulation between Cape Leeuwin, WA, and Ceduna, SA, in 2015 (Bannister 2017, Charlton 2017). High variability in trends in SRW abundance elsewhere in the Southern Hemisphere has also been observed in recent years (Harcourt *et al.* 2019). Variability in SRW abundance requires further investigation for possible correlation with drivers such as climate factors and prey availability (Leaper *et al.* 2006) or possible human disturbances (Harcourt *et al.* 2019).

SRW display within season variation in abundance at Fowlers Bay that can be explained in part by unaccompanied adult movement to and from the area within season. Mean occupancy periods are significantly lower for unaccompanied adults (2 d) than for female and calf pairs (23 d). Occupancy was recorded for up to four months for female and calf pairs in other areas in Australia and around the world (Thomas and Taber 1984, Burnell and Bryden 1997, Charlton 2017). Managers should consider this when promoting management decisions that support the establishment of SRW to an area.

Collection of photo ID resights may be biased towards female and calf pairs because they generally occupy the area

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over longer periods providing more opportunity to collect images and build profiles of left and right sides of the head. For vessel surveys, effort among surveys years at Fowlers Bay is an influencing factor, with survey effort lowest in 2016 and whale occupancy also lowest. However, anecdotal records from tourism operators who operate charters at Fowlers Bay between June and October suggest that the observer and effort bias is minimal.

Years of higher abundance resulted in longer occupancy periods, supporting the idea that conspecific attraction is a driver of habitat use. For example, in 2014, a maximum daily count of 10 female and calf pairs was recorded, and resident periods reached 75 d, whereas a maximum of two female and calf pairs recorded in 2016 had a resident period of only 12 d (Table 3).

The most frequently occupied habitat by SRW in Fowlers Bay was 1-5 km to the east along the coast from the jetty and within 1 km from shore inside the 10 m depth contour (Fig. 7). This supports the finding that wintering SRW generally occupy habitat with a shallow sandy bottom in a SE facing bay (Bannister 2017, Burnell 2001, Elwen and Best 2004, Payne 1986, Pirzl 2008,

Rayment et al. 2014).

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Range expansion and recolonization to new areas has been observed for other SRW populations, such as Brazil (Groch et al. 2005, Danilewicz et al. 2016), Argentina (Arias et al. 2017, Rowntree et al. 2001), Uruguay (Costa et al. 2005), South Africa (Best 1990, Barendse and Best 2014), and New Zealand (Carroll et al. 2011, 2014a) and Campbell Islands (Torres et al. 2016). These areas show evidence of recolonization into former areas around the main nursery area in association with population growth. Groch et al. (2005) reported rapid recolonization to Santa Catarina in southern Brazil at a rate greater than biologically plausible for the species, based on data collected between 1987 and 2003, suggesting dispersal from alternate habitat, such as Peninsula Valdes. Similarly, Carroll et al. (2014a) presented evidence of SRW recolonizing former wintering grounds on the mainland of NZ, nearly four decades postwhaling, presumably from a remnant population that persisted in the NZ subantarctic islands. As populations grow, resource pressures (space) at major SRW aggregation areas can be expected to result in increased abundance in small and emerging aggregation areas

and use of connective pathways. Investigation of the origin of breeding females sighted at Fowlers Bay is underway through photo ID matching with national databases (Charlton 2017). They could be first time young females "prospecting" for a calving ground; or whales shifting from other areas, with higher population densities.

Conclusion

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While Fowlers Bay was known historically as a location occupied by SRW for calving and nursing their young, aerial surveys conducted between 1993 and 2003 indicated infrequent use before 2003. The occurrence of SRW at Fowlers Bay since 2004 highlights the increasing significance of the area for females with calves and unaccompanied adults as a calving, nursing, mating and socializing ground. There is high variation in yearly abundance. Further investigation into population demographics, climate drivers, and human disturbances is needed to better understand the habitat use patterns of these whales. There is also a need to assess the connectivity and movement of SRW from Fowlers Bay with those from other aggregation areas in Australia and New Zealand to provide insight into the origin of the whales

at Fowlers Bay. New information provided by this paper addresses the objective in the Commonwealth SRW Conservation Management Plan of characterizing the SRW abundance, distribution, and occupancy at the small established aggregation area at Fowlers Bay. Ongoing monitoring of SRW abundance and distribution in Fowlers Bay can help inform management of potential local impediments to their recovery. Surveys will continue at Fowlers Bay and research is underway to assess distributional shifts and connectivity of SRW across Australia.

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Figure 1. Southern right whale (Eubalaena australis) distribution range in Australia (Source: DSEWPaC 2012).

Figure 2. Southern right whale (Eubalaena australis) aerial survey off southern Australia from 1993 to 2016 undertaken by the Western Australian Museum. Dashed line represents

approximate survey route but further offshore so that contour is visible (Source: Bannister 2017).

Figure 3. Southern right whale (Eubalaena australis) vessel survey study area at Fowlers Bay, South Australia.

Figure 4. Relative abundance of southern right whales (Eubalaena australis) at Fowlers Bay South Australia from Western Australian Museum aerial surveys 1993-2016 (fitted with loess smoother with 95% CI), (a) total individuals (All), (b) abundance of females accompanied by a calf (CC Pairs), and (c) abundance of unaccompanied adults.

Figure 5. Southern right whale (Eubalaena australis) sightings of female and calf pairs (open circles) and unaccompanied adults (x) recorded within the Fowlers Bay (South Australia) study site during vessel surveys between 4 July 2014 and 12 September 2014 (a); 26 July 2015 and 29 August 2015 (b); and 17 July 2016 and 18 September 2017 (c). Maps show vessel tracks and study area boundary.

Figure 6. Southern right whale (Eubalaena australis) maximum daily vessel based sightings of females accompanied by a calf of the year, calves and unaccompanied adults at Fowlers

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Bay, South Australia between 4 July and 12 September 2014, 26 July and 29 August 2015, and 17 July and 18 September 2016.

Figure 7. Kernel density distribution of southern right whales (Eubalaena australis) normalized for effort per km² using sightings data collected during vessel surveys at Fowlers Bay, South Australia between 2014 and 2016 (top).

Figure 8. Examples of the movement patterns of southern right whale (Eubalaena australis) females accompanied by a calf at Fowlers Bay, South Australia in 2015 and 2016; individual whale CC1 sighted 20 times between 26 July 2015 and 28 August 2015 (top left); CC2 sighted 9 times between 26 July 2015 and 5 August 2015 (top right), and CC3 sighted 13 times between 17 July 2016 and 22 August 2016 (bottom right). The sightings numbers are in chronological order and correspond to a date in the tables displayed at the bottom right of the figure. Multiple values represent more than one sighting in one day.

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Table 1. Vessel survey effort during 2014, 2015, and 2016 southern right whale (Eubalaena australis) surveys in Fowlers Bay, South Australia.

Year		Total effort (vessel hours)	Number of	Survey dates		
	# surveys		Tuna Explorer	Jaguar	Asheera	
2014	31	58	21	10	0	4 Jul-12 Sep
2015	27	49	0	2	25	26 Jul-29 Aug
2016	15	40	0	0	15	17 Jul-18 Sep
Total	73	147	21 (29%)	12 (16%)	40 (55%)	4 Jul-18 Sep

Table 2. Southern right whales (*Eubalaena australis*) sighted at Fowlers Bay, South Australia during vessel surveys in 2014, 2015, 2016, and pooled years, showing range in maximum daily counts across the season, and the mean maximum daily sighting of female and calf pairs, unaccompanied adults and total individuals for 2014, 2015, and 2016.

	2014		2015		2016		Pooled years		
	Daily range	x	Daily range	Ī	Da ra	ily nge	\bar{x}	Daily range	\bar{x}
Female calf pairs	0-10	9	1-2	1.2	0	-2	1	0-10	2
Unaccompanied adults	0-4	0.7	0-7	2.2	0	-5	0.9	0-7	1
Daily total	0-22	9	0-9	4.5	0	-7	2.9	0-22	6

Table 3. Number of southern right whales (*Eubalaena australis*) photo identified, number resighted, range in the number of times animals were resighted, and days of site occupancy (range and mean) for 2014, 2015, and 2016 at Fowlers Bay, South Australia (CC = female and calf pairs and UA = unaccompanied adult).

Year	Group type	<pre># SRW sighted during max daily count</pre>	# SRW Photo ID'd	# SRW resighted	Range in the # of times SRW were resighted	Range in site occupancy (d)	Mean (\bar{x} Error! Bookmark not defined.) site occupancy (d)
2014	CC	10	11	11	0-11	1-75	27
	UA	4	8	2	1-3	1-2	1
2015	CC	2	2	2	9-20	11-35	18
	UA	7	17	12	1-6	1-15	4
2016	CC	2	1	1	12	12	12
	UA	5	7	0	0	1-1	1
Total	CC	14	14	14	0-20	1-75	23
	UA	16	32	14	0-6	1-15	2







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