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No evidence for recovery in the population of sperm whale bulls off Western Australia, 30 years post-whaling

Gemma Carroll[1,*], Sharon Hedley[2], John Bannister[3], Paul Ensor[4], Rob Harcourt[1]

[1]Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia
[2]Centre for Research into Ecological and Environmental Modelling, Buchanan Gardens, University of St Andrews, St Andrews, Fife KY16 9LZ, UK
[3]The Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia
[4]33 Governors Bay-Teddington Road, Ohinetahi Valley, Governors Bay, RD1 Lyttelton 8971, New Zealand

ABSTRACT: The global sperm whale *Physeter macrocephalus* population has been protected from large-scale commercial whaling for >25 yr, yet there is no clear evidence of recovery in any heavily exploited stock. This may indicate that whaling has long-term demographic effects on this species or that other endogenous or exogenous processes are inhibiting population growth. This study investigates the status of mature sperm bulls off Albany, Western Australia, a population reduced through whaling by 74% between 1955 and 1978. We conducted an aerial survey designed as far as possible to provide an index of abundance comparable with that derived from the whale 'spotter' planes employed by the Albany whaling company from 1968 to 1978, using the number of sperm bulls seen on each morning flight as a comparative index between bulls seen historically and in 2009. The mean number of sperm bulls seen on transect in 2009 was 2.43 (95% percentile interval [0.96, 6.08]); this increased to 3.38 (95% percentile interval [1.30, 7.60]) when sightings off transect were included. Both 2009 point estimates were lower than the mean (±SE) number seen in any of the years between 1968 and 1978, which ranged from 6.30 (±1.18) in 1976 to 12.45 (±1.83) in 1968. The lack of recovery in the population of bull sperm whales off Albany, despite full protection, is of concern and adds weight to the growing body of evidence that suggests that sperm whales may not be recovering effectively from past exploitation.

KEY WORDS: *Physeter* · Comparative abundance · Aerial survey · Population decline

INTRODUCTION

Monitoring the recovery of historically exploited great whale stocks can enable us to recognise and overcome impediments to population growth (Baker & Clapham 2004). This is particularly important in light of the failure of some whale populations to show recovery despite the fact that others of the same species have increased rapidly, often at their theoretical maximum rate (e.g. western vs. eastern Pacific grey whales, Bradford et al. 2008; southwest vs. southeast Australian right whales, Carroll et al. 2011; East Australian [E1] vs. oceanic [E2 & E3] humpback whales, Olavarría et al. 2007, Noad et al. 2011). Although the causes of such differential population recovery are often poorly understood, factors such as a loss of genetic diversity (Reed & Frankham 2003) and the level of exposure to ongoing threats (Lotze et al. 2011) influence the capacity of a population to recover. It is therefore of concern to conservation scientists and management agencies to address data deficiency in regards to depleted whale populations and adopt a case-by-case approach to population recovery efforts (Clapham et al. 1999).

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*Corresponding author: gemma.carroll@mq.edu.au

In the 25+ yr since sperm whaling *Physeter macrocephalus* operations became uneconomical or were closed down following the 1986 moratorium, exploited sperm whale stocks can be expected to have shown a trend towards recovery at their theoretical growth rate of 1 to 1.1% (Whitehead 2003, Chiquet et al. 2013). Due to their wide distribution (Rice 1989) and relatively large global population size (Whitehead 2002), it is often assumed by management agencies that sperm whale populations are likely to be recovering in lieu of data to suggest otherwise. Indeed some populations that were not heavily whaled appear to be healthy and growing slowly (Gordon et al. 1998, Gero et al. 2007). There has, however, been little clear evidence for recovery in any heavily exploited population, notably the southeastern Pacific (Whitehead et al. 1997), Southern Ocean south of 60° S (Magera et al. 2013) and Mediterranean (Reeves & Notarbartolo Di Sciara 2006) stocks. This indicates that whaling may have effects on sperm whale demography that are felt for decades (Whitehead et al. 1997) or that other endogenous or exogenous processes have hampered population growth.

Sperm whales were hunted off Albany, Western Australia, where the continental shelf is narrow and drops sharply to 5000 m (Fig. 1). Modern industrial whaling took place here from 1955 until 1978, with annual catches exceeding 400 individuals from 1961 onwards (Bannister 1968). This contributed to the 3000 to 5000 individuals caught per year in the southern Australian region (Bannister 1974), an area thought to contain a single stock of sperm whales in terms of the demographic effect of exploitation (Bannister 1969, Brown 1981). This catch resulted in substantial declines in the number of animals in the Albany region, particularly mature sperm bulls (35 ft and over [~11 m], age 17 to 20+ yr), which constituted the primary target class. In 1979, the population of females had been reduced by 9% and males by 74% from their pre-exploitation abundance (Kirkwood et al. 1980).

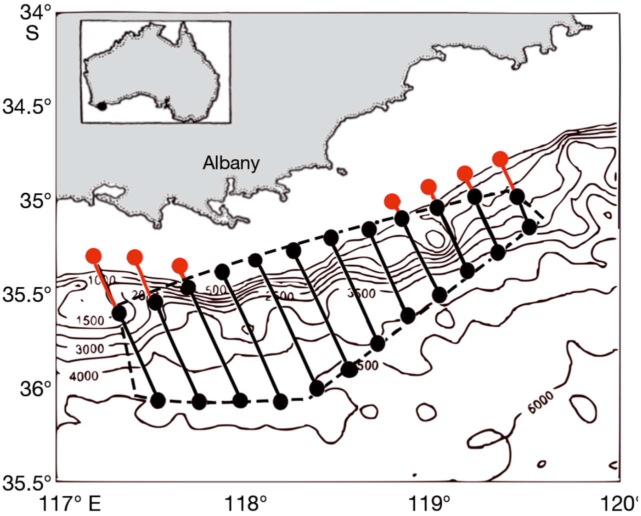

Fig. 1. Waypoints, trackline design and survey region for the 2009 survey, near Albany, Australia, with bathymetry detailed (in m). Dashed line represents the approximate area searched by the twin-engined aircraft from 1967 to 1978, as determined from Kirkwood & Bannister (1980). Survey track lines used prior to 20 October 2009 are shown in black. From this date onwards, easternmost and westernmost transects were extended northwards (red waypoints and lines)

The availability of long-term historical data from Albany sperm whaling operations provides an important opportunity to assess the recovery of this population. The aim of this study is to provide an index of sperm bull abundance in the waters off Albany, Western Australia, that is directly comparable to estimates derived from the number of 'catchable' bulls seen by spotter planes in the period from 1968 to 1978. This should allow us to assess the status of the Albany sperm whale population and identify whether the population has shown evidence of recovery in the period since whaling operations ceased.

MATERIALS AND METHODS

Historical data selected for comparison with 2009

Sperm whales *Physeter macrocephalus* were caught at Albany from April through the end of November each year from 1955 to 1978. Aerial spotters were employed to assist the catch after 1962, first using a single-engined float plane (1962 to 1966), and then with a faster and more efficient twin-engined aircraft from 1967 on.

The aircraft were flown along a standard grid pattern by a pilot who spotted whales and informed the catcher boats of the locations of sperm whale groups. Flights were conducted at an altitude of approximately 1500 ft (~457 m) during searching (G. P. Kirkwood unpubl.). The plane sometimes remained with a pod of sperm whales to assist the boats with locating and catching whales, during which time the altitudes differed from the searching altitude. The daily logs from these flights recorded departure time, survey time, wind speed and direction, sea state (Beaufort 0 to 12) and visibility (exceptional = 0, good = 1, fair = 2, poor = 3, very poor = 4, nil = 5) (G. P. Kirkwood unpubl.). Data were chosen for comparison where both the Beaufort sea state and the visibility score were 2 or less, based on a preliminary analysis of the frequency distribution of sperm bulls by G. P. Kirkwood (unpubl.), which showed a decline in detectability when visibility was 'poor'. The spotters recorded the number and location of cetaceans sighted — in particular the number of 'catchable' sperm whales, i.e. mature sperm bulls >35 ft (~11 m). The number of 'catchable' bulls recorded during these flights provided a reliable index, as the whaling boats were directed to and often subsequently caught sighted bulls, providing continual and immediate feedback on the accuracy of a sighting (G. P. Kirkwood unpubl.).

We used data on sperm bull sightings from 1968 to 1978 as an index from the whaling era. Although it is difficult to match indices such as catch per unit effort (CPUE) between historic and contemporary studies (particularly as there was unfortunately no period of overlap to calibrate indices), the use of the twin-engined aircraft during this period made the surveys undertaken by the spotter planes replicable using aircraft still available for charter. We selected data from September to November for comparison, following the recommendation of G. P. Kirkwood (unpubl.) that the abundance of sperm bulls in the area during this period was higher than at other times of the year and, furthermore, that the weather during these months was (historically at least) more likely to be favourable for aerial surveys. We then digitally encoded the historical data, and anomalies resulting from transcription errors between the original log sheets and a paper database were rectified. The mean number of bulls seen on the first morning flight was used as a relative index for comparison with data collected in 2009. This was believed to be the most appropriate index on the following basis:

(1) The number of hours flown skews the index: as the spotter aircraft often spent time assisting the whaling ships to locate and catch whales, flights with longer survey times tended to occur when few, if any, whales were seen, and shorter flights resulted from flights that encountered whales or when weather was poor. Using a traditional CPUE index would therefore be inappropriate, as flight duration was often not a true measure of search effort (G. P. Kirkwood unpubl.).

(2) During the whaling operation, the aircraft covered the same area multiple times per day (during either 1 or 2 morning flights and an afternoon flight). Whales that were thought to have already been recorded due to their location and pod size were not re-recorded, even if they were seen several times. The first morning flight was therefore the survey that was most likely to accurately portray the true abundance of whales in the area.

Survey area and design 2009

We followed a dedicated survey programme specifically designed by G. P. Kirkwood (unpubl.) to enable monitoring of the Albany population post-whaling. The area denoted by the dashed lines in Fig. 1 estimates the area searched by the twin-engined aircraft from 1967 to 1978. Coordinates were determined manually by referencing nautical charts against the map presented as Fig. 1 in Kirkwood & Bannister (1980). This area was then searched using a standard grid of parallel transects. Trackline design was undertaken in *Distance* v5.0 Release 2 (Thomas et al. 2010), with parallel transects oriented perpendicular to the major axis of the survey region. The final design resulted in 12 transects approximately 10.5 nautical miles (n miles) apart, covering 386 n miles on transect and 630 n miles in total, including transits to and from the airport and connecting legs between transects.

During the course of the survey, the 5 easternmost and 3 westernmost transects were extended northwards. It was considered unlikely that the whaling operations would have regularly surveyed the extended transect area; however, this modification was deemed necessary in order to cover more shelf area (Fig. 1) and to increase the sample size. The sum of the extensions was 76 n miles, and this increased the total transect length to 462 n miles and the total flight length to 696 n miles.

Data collection 2009

We scheduled our 2009 survey from 10 September to 30 November, following Kirkwood's recommendation that this was the period with fairest weather and highest numbers of sperm whales. The aerial survey commenced on 25 September 2009 (due to poor weather in the earlier part of September) and was completed on 5 December 2009. In order to maintain consistency with the whaling era data, we undertook survey flights only when the sea state was Beaufort 2 or less and the visibility was deemed 'fair,' with a score of 2 or less on a scale of 0 to 5. Data were collected using a single-platform configuration consisting of 2 observers experienced with modern aerial survey techniques, 1 on each side of the aircraft. The aircraft, a twin-engined Cessna 337, flew at 1500 ft (~457 m) at a speed of 120 knots (222 km h^{-1}). Sightings of animals were recorded and time-stamped on Microtrack digital voice recorders (M-Audio Microtrack 24/96) using Dick Clark aviation headsets and Aviall (Avix A4000) portable intercom systems. For each cetacean sighting, the declination angle of its abeam location was measured using a hand-held Suunto clinometer (Suunto PM-5/360 PC); species, group size and behaviour were also recorded. Times of sightings were taken as the times when the declination angle was recorded. Microtrack voice recorders were synchronized with the time from a GPS to match sightings with location. Sightings recorded on the Microtrack were transcribed into Excel spreadsheets after the flight. Digital single-lens-reflex cameras were used to photograph sperm whales and other cetaceans to verify observer sightings and facilitate classification of sperm bulls into the >35 ft (~11 m) target class based on the known height of the aircraft, the fixed focal length of the camera lens and the number of pixels in the image.

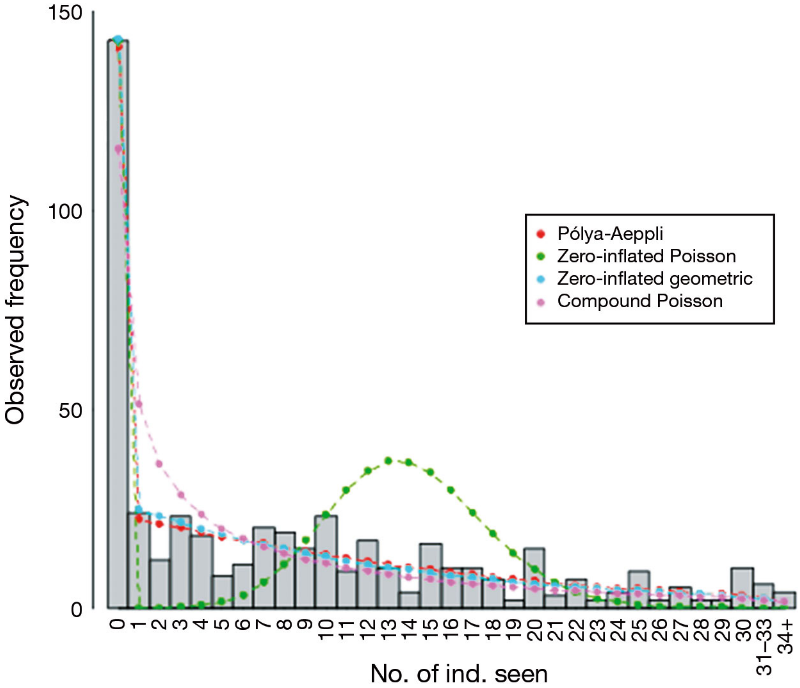

Fig. 2. *Physeter macrocephalus*. Distribution of number of sperm whale bulls seen on the first morning flight in September to November from 1968 to 1978. Conditions were restricted to at least ‘fair’ visibility (visibility of 0 to 2 on a scale of 0 to 5) and sea state up to Beaufort 2. Fitted distributions shown as indicated in the key

RESULTS

Historical data

A frequency distribution for the data from 1968 to 1978 is shown in bar plots in Fig. 2, for sea states up to 2 and visibility at least ‘fair’ (0 to 2). The distribution showed a high frequency of zero sightings (143) and a long tail, suggesting that when sperm whale *Physeter macrocephalus* bulls were seen they were usually in relatively small groups.

Four distributions for these data were considered: the Pólya-Aeppli distribution (with Poisson number of groups and geometric group sizes); zero-inflated Poisson and geometric distributions, and a compound Poisson distribution (with Gamma group sizes). Goodness-of-fit of these distributions were compared visually and using χ^2 goodness-of-fit tests. Test statistics are shown in Table 1. As can be seen in Fig. 2, the results in Table 1 indicate that either the Pólya-Aeppli distribution or the zero-inflated geometric distribution fit the data reasonably; the former is marginally better according to its goodness-of-fit. We therefore base our comparisons on this distribution.

The probability density function (pdf) of the Pólya-Aeppli distribution is given by:

$$\Pr(N{=}x)=\begin{cases} e^{-\theta} & x=0\\ e^{-\theta}p^{x}\sum_{j=1}^{x}\binom{x-1}{j-1}\dfrac{[\theta(1-p)/p]^{j}}{j!} & x=1,2,\ldots \end{cases} \qquad (1)$$

for $\theta > 0$ and $0 < p < 1$ where Pr = probability; N = random of variable (sperm bull counts); θ and p = shape parameters; x = a set of natural numbers including 0; j is an index of x in Eq. (1); i is an index of x in Eq. (2). The mean of the response is $\theta/(1 - p)$ and variance is $\theta\ (1 + p)/(1 - p)^2$. The log-likelihood function (l) is given by:

$$l(\theta,p)=\sum_{i=1}^{n} l(x_i=0)(-\theta)+l(x_i>0)$$

$$\left\{-\theta+x\log(p)+\log\left[\sum_{j=1}^{x_i}\binom{x_i-1}{j-1}\frac{(\theta(1-p)/p)^{j}}{j!}\right]\right\} \qquad (2)$$

The negative log-likelihood was minimized using the function ‘optim’ in R (R Development Core Team 2009), and estimates of the mean number of bulls seen were calculated using the above formula. Percentile confidence intervals were calculated by simu-

Table 1. *Physeter macrocephalus*. χ^2 goodness-of-fit statistics from fitting Pólya-Aeppli, zero-inflated Poisson, zero-inflated geometric and compound Poisson distributions of sperm bull sightings

Distribution	Total seen
Pólya-Aeppli	94.4
Zero-inflated Poisson	158 854.5
Zero-inflated geometric	107.3
Compound Poisson	179.0

lation from the posterior distribution of the parameters (see, for example, Wood 2006, p. 246–247) and were compared with analytical confidence intervals calculated using the expression for variance above. For the whaling data (with 488 morning flights), either method of interval calculation should suffice, and standard errors were chosen for their greater precision; for the survey data (with only 21 samples), the percentile method is preferable.

2009 survey

Flights and data included in the analyses

A total of 61 flights were flown in 2009. Four flights were classified as training or video camera testing flights. Eighteen flights were aborted with either no or very little survey effort (due to poor weather). Fifteen flights surveyed all transects once; 12 flights surveyed half the transects, with the other half of the transects surveyed during a later flight on the same day (2 half surveys were considered a full survey for the remainder of the analysis); and 12 flights were incomplete surveys that were discarded from the analysis. This came to a total of 21 surveys of the transect area that were used in our analysis. During these 21 surveys, 40 sperm whale pods (160 individuals, including females and immature animals) were seen on-effort; an additional 8 pods (118 whales) were sighted off-effort, in areas outside the transect area, or on transit to the airport.

The Pólya-Aeppli distribution was also fitted to the relatively sparse 2009 data. These data were derived from the 21 completed surveys. The data and fitted distributions are shown in Fig. 3 (using the same frequency bins as for the whaling data).

Comparison of historical abundance with 2009

A trend of decreasing relative abundance of sperm bulls exists from 1968 to 1978 (Fig. 4). In 2009, using all sightings, including sightings made off-effort or beyond the designated search area, the mean number of bulls seen per flight was 3.38 (95% percentile interval [1.30, 7.60]); this declined to 2.43 (95% percentile interval [0.96, 6.08]) when only on-effort sightings were included. Although both point estimates for 2009 are lower than in any of the whaling years, the percentile intervals for the 'all sightings'

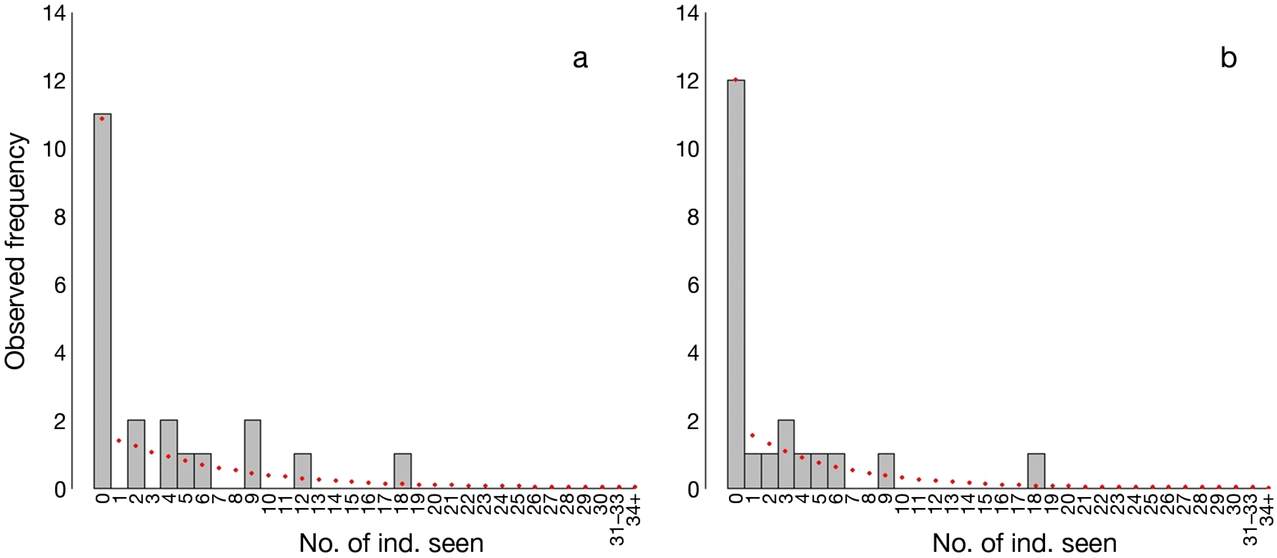

Fig. 3. *Physeter macrocephalus*. Distribution of the number of sperm whale bulls seen on each completed survey during the 2009 survey (n = 21). Conditions were restricted to at least 'fair' visibility (visibility of 0 to 2 on a scale of 0 to 5) and sea state up to Beaufort 2. Red dots show the fitted Pólya-Aeppli distribution. (a) All sightings, including those made beyond the transect area and on transit to the airport. (b) On-effort data only

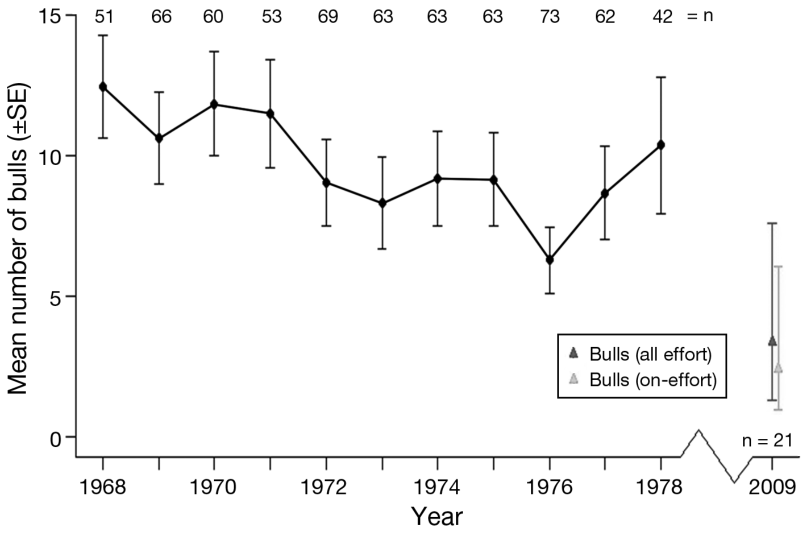

Fig. 4. *Physeter macrocephalus*. Comparison of the mean number (±SE) of bulls seen on the first morning flights from the September to November whaling data, and the mean number seen during the 2009 survey. Total numbers (solid line) are comparable with those plotted in Fig. 2 in G. P. Kirkwood (unpubl.), and sample sizes above point estimates refer to the number of flights. The dark grey triangle is the mean number of bulls seen during surveys undertaken in 2009, including animals seen off transect and on transit to the airport; the light grey triangle is the mean number seen 'on-effort' during these surveys (percentile intervals shown)

2009 survey data overlap with the point estimate for 1976 (mean ± SE, 6.30 ± 1.18) and the standard errors of the estimates for the years 1972 to 1978. The wide confidence intervals for the 2009 data caused by flying relatively few surveys, therefore, make it difficult to interpret this result as a true decline in sperm whale abundance in the area. A more conservative interpretation of these results is that the population of sperm whale bulls off Albany has apparently failed to recover since the cessation of whaling in the area.

DISCUSSION

The aerial survey that we conducted in 2009 compared the modern abundance of sperm bulls *Physeter macrocephalus* off Albany with the number seen on each morning flight from the whaling fleet's 'spotter' planes between 1968 and 1978. The mean number of sperm bulls seen in 2009 was lower than the mean number calculated from any of the years from 1968 to 1978. Although the 95% percentile indices from the 2009 data overlapped with standard errors of the estimates in several of the whaling years, there was no evidence of population recovery despite 31 yr of complete protection in the region. This lack of recovery in the population of sperm whale bulls off Albany is of concern and suggests that sperm whales may not be recovering effectively from past exploitation.

An inherent assumption that is made in comparative abundance studies such as this is that the method of data collection is equivalent between the 2 survey periods. This can be particularly problematic when comparing modern and historical datasets (Brown et al. 2011). In this study, we faithfully followed the recommendations for survey design set out in the whaling era report (G. P. Kirkwood unpubl.). Unfortunately, the recommendation that sampling over the latter part of the whaling season was most likely to provide fair weather for the survey did not hold true for September to November 2009. The number of morning flights was reduced to fewer than that in any of the years between 1968 and 1978 (21 in 2009 cf. 42 to 74 in the whaling era). This also raises concerns regarding the potential for a bias due to an uneven distribution of sperm bull attendance off Albany during September to November 2009, such that we might have missed flights at times when sperm bull abundance was higher. However, examination of the 2009 data shows that the sighting rate on successful flights was consistently low across the 70 d survey period, with no obvious temporal clustering of sperm whale attendance. In fact, across the entire 10 yr of historical data no specific trends in sighting variability by month appear for September to November. Despite the relatively small sample size obtained in 2009, there is no information to suggest that missed survey time biased our results in any further way.

In the replication of any historic survey, there will undoubtedly be some minor disparities in sighting efficiency between the 2 periods. Changes in technology and differences in equipment and technique may have had a measurable effect in this study, as information regarding survey method in the whaling era was in some cases sparse. For example, while we know that the spotter planes generally flew in a standard grid pattern across the search area (G. P. Kirkwood unpubl.), and we attempted to replicate this method using modern survey planning, specific details of these transects (besides the location of the search area and the approximate speed and height flown by the spotter aircraft; G. P. Kirkwood unpubl.) were unavailable. Given the time that had passed since the whaling era, we were unable to employ any pilots with experience spotting for the whaling fleet, which would have optimised comparative power (G. P. Kirkwood unpubl.). However, one of the authors (J.B.) was the whaling scientist at the time of the original surveys, ensuring that we matched effort and study design as closely as possible to the original flights. Further, we employed a team of 2 experienced observers in the aircraft on each survey flight to minimise inter-observer bias between eras.

The purpose of the whaling era flights to act as a tool for hunting whales differs from the rationale behind the flights conducted in the current study, which simply aimed to survey the number of sperm bulls in the designated search area. This will undoubtedly have implications for the comparability of the 2 datasets. During the whaling era, the afternoon flight probably often returned to areas where whales had already been seen that morning, rather than flying strict survey transects (P. Best, pers. comm.). We have largely controlled for this effect by using the first morning flight as an index of sperm bull abundance for the whaling era. Although it is possible that in the morning pilots went to places where whales were seen the previous afternoon, they were more likely to be surveying the area to determine the number and location of whales while the whaling ship steamed out from the port. Our inclusion of an 'all sightings' estimate of abundance including whales seen outside the transect area and en route between the airport and the study site also maximised our potential to capture the presence of whales in the same opportunistic fashion that the spotter pilots almost certainly would have, while still enabling us to undertake a survey using a standardised method that enables the application of modern analytical techniques.

With the above caveats, we are confident that the survey that we undertook in 2009 provides a reasonable comparative index for assessment of the status and potential recovery of the sperm bull stock at Albany. It therefore follows that the most parsimonious conclusion is that the lack of recovery seen in our results is real. The absence of demonstrable recovery is surprising given the complete cessation of commercial whaling, the sole factor attributed to the initial population decline (Taylor et al. 2008). We explore some factors that may have led to reduced sighting of sperm bulls off Albany in 2009 below.

Demographic analysis has shown that sperm whale populations are potentially so fragile that they could experience decline with even a slight decrease in adult survivorship and could face extinction with the occurrence of a major stochastic event (Chiquet et al. 2013). Female sperm whales usually have their first calf at age 10 (Rice 1989) and then reproduce every 4 to 6 yr (Best et al. 1984). Sperm whale bulls reach physical maturity at age 17 to 20; however, they do not appear to effectively participate in reproduction until they are in their late twenties, when they begin to attend breeding grounds (Best 1979). These life history traits underpin the fragility of sperm whale populations and are responsible for their low intrinsic rate of increase (Whitehead 2003, Chiquet et al. 2013). Additionally, it appears that populations of sperm whales and other odontocetes may be inherently less resilient to exploitation than mysticetes with similar life history characteristics, due to behavioural and social traits (Wade et al. 2012), and that this has been compounded by sex-biased hunting (Whitehead et al. 1997).

Given the 31 yr between the end of sperm whaling at Albany and the 2009 survey, the number of sperm bulls should have shown a significant increase from the levels observed in 1978, at the end of the whaling era. Preliminary demographic analysis of the Division 5 stock suggested that the population should have increased by 40% in 1983 and by 60 to 70% in 1988 (G. P. Kirkwood unpubl.). However, the pregnancy rates in the total population of female sperm whales at Albany (including animals that were not caught) were calculated to have decreased from 0.201 in 1966 to 0.067 in 1977 (Kirkwood et al. 1980). As sperm bulls recruit into the >35 ft (~11 m) size class at around age 17 to 20 yr, this decline in pregnancy rates was predicted to begin affecting recruitment of these sperm bulls by 1988, significantly reducing the rate of increase for this stock (G. P. Kirkwood unpubl.). It can therefore be expected that this depression of pregnancy rates will have affected recruitment of sperm bulls to the >35 foot size class for at least 17 to 20 yr after whaling ended, and probably longer. Therefore, while a substantial increase in the population of sperm bulls might have been expected, the rate of increase would then have been tempered by the lingering effects of whaling on sperm whale demographics.

The depression of reproductive rates may, in part, be the result of a demographic Allee effect caused by females having difficulty finding a suitable mate (Whitehead et al. 1997). In other mammalian societies, when large males are removed from a population, subordinate or foreign males are able to 'step in' and mate with females in their place (e.g. flying foxes, Ortega & Arita 2002; fish, Burmeister et al.

2005; lions, Loveridge et al. 2007). There is some indication, however, that this may not be the case in the sperm whale mating system. In the Galapagos, where the proportion of breeding males in the population was estimated at 2 to 3% in the 1990s, a quarter of their expected numbers (Whitehead 1990, 1993), mature males were still observed attending aggregations of females on 75% of days during the breeding season, yet pregnancy rates remained low (Whitehead 1993). This may indicate that females are highly selective in mate choice and require a large pool of males from which to choose a mate. Alternatively, male sperm whales may be limited in their absolute ability to inseminate females at low densities (see Ginsberg & Milner-Gulland 1994, Rankin & Kokko 2007), or, similar to African elephants (Slotow et al. 2000), there may be some mechanism of male sociality that is necessary for breeding success (such as a dominance hierarchy) that is dysfunctional with a substantially reduced number of males in the population (Whitehead 2003). Without an understanding of where the Albany stock of sperm whales breeds, it is difficult to examine the extent to which mating has been disrupted in this population, and the cessation of whaling has made it more difficult to determine whether pregnancy rates have returned to their pre-whaling equilibrium. However, based on a combination of life history characteristics and social traits, it seems likely that the sex-biased hunting that sperm whales were subjected to may have played a part in their subsequent lack of recovery.

Although significantly fewer female sperm whales than bulls were caught at Albany, depressed pregnancy rates were predicted to cause a decline in the number of mature females in the population until they reached 65% of their initial abundance in 1989 (Kirkwood et al. 1980). Female sperm whales aggregate into units of both related and unrelated individuals (e.g. Ortega-Ortiz et al. 2012) of different age classes, forming long-term multilevel associations (Whitehead 2003, Whitehead et al. 2012). As in elephants, which have a similar social structure, a loss of older females from these units may have fragmented these associations and caused a loss of cultural knowledge such as predator evasion tactics and the location of occasional feeding grounds (Whitehead 2003, McComb et al. 2011). Removal of matriarchs from social groups may serve to reduce female fitness and affect the population more broadly, as the demography of sperm whales is most sensitive to mortality of adult females (Chiquet et al. 2013).

In addition to the potential long-term effects of whaling on demography, there remain a number of extraneous threats that could also inhibit the ability of sperm whale populations to recover. High levels of organochlorines were found in the tissues of mass-stranded sperm whales in southern Australia in the late 1990s (Evans et al. 2004). The concentrations of these marine pollutants are expected to increase at higher latitudes due to their circulation from source points via long-range atmospheric or marine transportation (Wania 2003). These contaminants may have deleterious effects on the normal enzymatic activity of long-lived predators such as marine mammals, leading to reproductive impairment (Roos et al. 2012) and reduced immune function (de Swart et al. 1996).

Environmental noise in the form of seismic explorations is known to be audible to sperm whales (Madsen et al. 2006); however, there are conflicting reports on the extent to which this noise may trigger behavioural responses (Mate et al. 1994, but see Madsen et al. 2002) or interfere with the complex vocalisations that sperm whales employ for hunting and socialization (Bowles et al. 1994, but see Madsen et al. 2002). Although there has been long-term seismic exploration in relation to a petroleum deposit between Albany and Esperance along Australia's southern coast, the infrequency of this activity and the distance from the study site (>1000 km from Albany) probably preclude this from being a major source of concern, as it may be for example in the Gulf of Mexico (Mate et al. 1994).

The other major threats identified for sperm whales include entanglement in fishing nets and environmental noise (Taylor et al. 2008). Entanglement in drift nets represents a major source of mortality for stocks of sperm whales in other regions (e.g. the Mediterranean; Reeves & Notarbartolo Di Sciara 2006), although the density of fishing activity is comparatively low in southwestern Australia. A shipping route with a relatively low volume of traffic does traverse the study area; however, to our knowledge there have been no reports of ships striking sperm whales in this area. To what extent pressures such as ship strike and entanglement may affect this sperm whale population is not known: however, the cumulative effect of multiple threatening processes could be highly significant in a vulnerable population that has low rates of recruitment and high sensitivity to individual mortality (Chiquet et al. 2013).

Finally, the apparent lack of recovery in sperm whale numbers at Albany may have occurred as a result of emigration from the area rather than increased mortality within the population. The southwestern region of Western Australia is generally oligotrophic due to the prevailing influence of the warm, nutrient poor Leeuwin current wrapping around the coast from the Indian Ocean (Cresswell & Golding 1980). However, a series of submarine canyons promote regions of localised high productivity caused by the interaction between surface and subsurface current systems and topography. This has been linked to aggregations of pygmy blue whales *Balaenoptera musculus brevicauda* in the Perth canyon north of Albany (Rennie et al. 2009), and it appears that the Albany canyon system along the southwest shelf was a productive feeding ground for sperm whales during the whaling era, with 70 to 80% of whales feeding recently prior to capture, primarily on squid (Bannister 1968).

Although there is little information on deep-sea squid in this region, as they are not directly exploited for human consumption, there are other data from Western Australia that suggest links between variations in the Leeuwin current system and food availability. The Leeuwin current has strengthened since the early 1990s, most likely as a result of natural decadal variability (Feng et al. 2010). This has been concomitant with an observed increase in the recruitment of tropical species (Pearce & Hutchins 2009) and changes in the distribution of pelagic fish. An analysis of southern bluefin tuna *Thunnus maccoyii* movements between Albany and Esperance found that increased temperatures associated with the Leeuwin current drove juvenile tuna to shift their foraging location even when temperature was not physiologically limiting, suggesting that food availability in the warm waters was insufficient to sustain the population (Fujioka et al. 2012). Increased strength and penetration of the Leeuwin current also appears to reduce recruitment success of pilchard *Sardinops sargax* in the Albany purse-seine fishery, potentially due to the current altering the distribution of the planktonic stages of this species (Caputi et al. 1996). It is unclear if or how the processes acting on other species may affect the mesopelagic squid fauna on which sperm whales primarily feed; however, the 'live-fast-die-young' life history strategies of most squid species make their populations particularly responsive to changes in food availability and environmental conditions (e.g. Jackson & Domeier 2003).

April 2008 to April 2009 was a La Niña event, characterized by a high southern oscillation index which correlates with stronger penetration of the unproductive Leeuwin current (Bureau of Meteorology 2012). Coupled with the multi-decadal increase in the strength of the Leeuwin current, this may have influenced the availability of prey in the waters off Albany in the period leading up to our 2009 survey. A particularly strong and lengthy La Niña event occurred between 1973 and 1976 (Bureau of Meteorology 2012), when sperm whale numbers were also low, although making meaningful inferences regarding the relationship between sperm whale abundance and environmental variability with the confounding influence of whaling on population size is impossible.

As sperm whales are highly mobile (e.g. Steiner et al. 2012), they almost certainly have the capacity to alter their distribution in response to environmental change and prey availability. Without any abundance estimates or monitoring programs for sperm whales in Australian waters, however, it is impossible to ascertain whether sperm whales that once attended Albany have moved elsewhere within the region. Intra- and inter-annual variability in many sperm whale abundance estimates was highlighted in a review of cetacean line transect surveys (Kaschner et al. 2012), and this variability is clearly problematic for studies conducted within a single season such as this one. Regardless, from 1955 to 1978, sperm whale bulls were regularly seen (and killed) at the same time each year off Albany (Kirkwood et al. 1980), suggesting that sperm whales were persistent in the region for more than 2 decades at that time. Irrespective of whether overall abundance is actually lower than expected or the animals have moved elsewhere, of concern is that there seems to be no evidence of local recovery in this population of sperm bulls despite over 30 yr of total protection.

Further surveys assessing the abundance and distribution of sperm whales at Albany and elsewhere in Australian waters are recommended, particularly those in relation to environmental covariates and anthropogenic pressures. This will enable us to address the data deficiency status of this stock of sperm whales and to understand and potentially mitigate any exogenous pressures that may be inhibiting the recovery of sperm whale populations.

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