SC/68B/CMP/23 Rev1

Assessing the body condition of the worlds only non-migratory humpback whale population, the endangered Arabian Sea humpback whale

Fredrik Christiansen, Robert Baldwin, Gianna Minton, Tim Collins, Kate R Sprogis, Jessica Rudd, Suaad Al Harthi, Mattthew Leslie, Darryl MacDonald, Andrew Willson

INTERNATIONAL WHALING COMMISSION

Assessing the body condition of the world's only non-migratory humpback whale population, the endangered Arabian Sea humpback whale

F. Christiansen[1,2,3*], R. Baldwin[4], G. Minton[5], T. Collins[6], K. Sprogis[2,3], J. Rudd[7], S. Al Harthi[8], M. Leslie[9], D. MacDonald[10], A. Willson[4,7]

[1]*Aarhus Institute of Advanced Studies, Høegh-Guldbergs Gade 6B, 8000 Aarhus C, Denmark*
[2]*Zoophysiology, Department of Biology, Aarhus University, C.F. Møllers Allé 3, 8000 Aarhus C, Denmark*
[3]*Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, Murdoch, 6150 Western Australia*
[4]*Five Oceans Environmental Services, PO Box 660, PC131, Ruwi, Sultanate of Oman*
[5]*Megaptera Marine Conservation, the Hague, the Netherlands*
[6]*Wildlife Conservation Society, Bronx, New York, 10460, USA*
[7]*Environment and Sustainability Institute, University of Exeter, Penryn Campus, Cornwall, UK*
[8] *Environment Society of Oman, P. O. Box 3955, Ruwi 112, Sultanate of Oman*
[9] *Biology Department, Swarthmore College, 500 College Ave., Swarthmore PA, 19081 USA*
10 Clear Blue Photo, 2435 32 ave SW, Calgary, Alberta, T2T1X4, Canada

*email f.christiansen@aias.au.dk

ABSTRACT

The Arabian Sea humpback whale (ASHW, *Megaptera novaeangliae*) is the only non-migratory humpback whale population in the world. This small and genetically isolated population is Endangered and extremely vulnerable to anthropogenic threats. While fisheries and shipping have been identified as possible direct threats to the population, non-lethal effects resulting from potential fishing gear entanglement, low prey availability and disease, have the likelihood to negatively affect survival and reproduction by reducing the body condition of whales. We assessed the body condition (residual of body volume against body length) of Oman's ASHW population by comparing it to a healthy (growing) population of humpback whales of Western Australia (breeding stock D). Unmanned aerial vehicle (UAV or drone) photogrammetry methods were used to measure the body condition of ASHWs (n=9) in November 2019, and breeding stock D humpback whales of South-western Australia early (June, n=56) and late (October, n=111) in the 2017 breeding season. The body lengths of the sampled ASHWs ranged from 11.8 to 14.2 m, which means that all the sampled whales were adults. The body condition of ASHWs (mean=7.2%, SE=3.28, n=9) were similar to that of similarly-sized (11.2-15.3 m body length) breeding stock D adults at the beginning of the breeding season (mean=8.6%, SE=3.98, n=19), but significantly higher than stock D humpback whales at the end of the season (mean=-3.4%, SE=3.57, n=48). This suggests that whales sampled in the study were not nutritionally supressed. Three of the ASHWs were identified as females, with their body condition (mean=12.5%, SE=6.10, n=3) being similar to that of early lactating females (mean=5.5%, SE=6.39, n=31) from the migratory stock D population. However, to determine the link between body condition and reproduction, additional sampling of ASHWs is needed to determine inter- and intra-seasonal variations in body condition. Continued research into the health of the ASHW population, together with continued monitoring of population demographics and assessment of fisheries interactions is therefore needed.

INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a cosmopolitan species known for its long annual migrations between high latitude feeding grounds and low latitude breeding grounds (Lockyer 1984). However, a small (82 animals, CI 95% 60-111) population of humpback whales in the Arabian Sea does not migrate, but instead spends the whole year feeding and breeding in the Northern Indian Ocean (Mikhalev 1997, Minton et al. 2011). The Arabian Sea humpback whale (ASHW) is the most threatened and genetically isolated population of humpback whales in the world (Pomilla, Amaral et al. 2014). Like most humpback whale populations, the ASHWs were targeted by commercial whaling, specifically illegal Soviet whaling in the 1960s (Mikhalev 1997). While other humpback populations have recovered strongly following the cessation of whaling (Hedley et al. 2011), the ASHW is still listed as Endangered under the International Union for the Conservation of Nature (IUCN) (Minton et al. 2008) and the U.S. Endangered Species List (Bettridge et al. 2015). Given its small population size and limited distribution, the ASHW population is extremely vulnerable to anthropogenic stressors. Ship strikes and fishing gear entanglements pose potential direct threats and non-lethal effects resulting from human disturbance are also likely to negatively affect the population.

Non-lethal human stressors are those that do not directly kill the animal, but which can alter its behaviour, energetics and body condition to such an extent that it compromises its survival and reproductive success (Beale & Monaghan 2004). The long-term consequences of these disruptions can severely hamper a population's recovery rate, as evidenced in the North Atlantic right whale (*Eubalaena glacialis*), where frequent and prolonged entanglements in fishing gear (van der Hoop et al. 2017), stress from ship noise (Rolland et al. 2012), and a reduction in prey has resulted in a significant decline in their body condition and consequently their reproduction rate (Rolland et al. 2016, Christiansen et al. 2020a). The ASHW population is likely to suffer from a range of non-lethal impacts, including underwater noise and disruptions to feeding and breeding. Their distribution overlaps with high levels of vessel traffic, much of it linked to oil exploration, production and transportation. Areas of critical habitat, evidenced by habitat utilisation mapping, shows that ASHW co-occur with artisanal gillnet fishing fleets (Willson et al. 2016); recent work has revealed that two thirds of individuals within the Oman photo-ID catalogue (66.6%: 95% CI 52-80%) have scarring assumed to be associated with entanglement in fishing gear (IWC/68B/CMP16). Non-lethal fishing gear entanglements can have major energetic costs. There are also potential reductions in prey availability associated with fisheries and climate change. Additionally, there has been a significant increase in the prevalence of tattoo-like skin disease (caused by cetacean poxvirus) in this population (from 24.1% between 2000-2011 to 51.7% between 2012-2018, IWC/68B/CMP16), which could carry energetic costs. Further study of body condition in conjunction with other measures of health and anthropogenic pressures is required to understand what is driving the population's apparent failure to recover.

Migratory humpback whale populations build up fat reserves on their feeding grounds during summer, which they then utilize as their main source of energy on their breeding grounds during winter (Christiansen et al. 2016). On the breeding grounds, lactating females experience the highest energy demand, and might lose up to 25% of their body mass (Lockyer 1984, Christiansen et al. 2018). Optimal body condition is therefore critical to their reproductive success, and will dictate the probability of females becoming pregnant (Lockyer 1984, Williams et al. 2013), as well as foetal growth rates (Christiansen et al. 2014), calf growth rates (Christiansen et al. 2018) and consequent survival (McMahon et al. 2000). Further, the body condition of adults will determine their ability to survive prolonged periods of time without food, and hence their survival (Le Boeuf et al. 2000). There is currently very limited knowledge about the body condition and reproductive potential of ASHWs. With a small population size, their rate of reproduction is likely to be low, which one would expect to be reflected in their body condition. A comparison of the body condition of the non-migratory ASHW population with migratory humpback whale populations, should provide a good understanding of the survival and reproductive potential of the ASHW population, and its vulnerability to human activities. Furthermore, comparison of body condition at different times of year in a population that does not perform annual migrations between feeding and breeding grounds, may yield insight into the mechanisms that drive migration in other humpback whale populations.

This study provides an initial assessment of the body condition of the ASHW population off Oman. The aim is to better understand their reproductive potential and resilience to anthropogenic disturbance. Our overarching hypothesis is that poor body condition is hampering the reproductive rate of this population, and is contributing significantly to its small population size. To test this hypothesis we used unmanned aerial vehicle (UAV) photogrammetry methods to measure the body condition of ASHWs, and compare this to existing body condition data from a healthy migratory population of humpback whales of Western Australia (WA), which is growing at a rapid pace (>10%, Hedley et al. 2011).

MATERIALS AND METHODS

Data collection and processing

UAVs were used to record aerial videos of humpback whales in the Gulf of Masirah (19.67ºN, 58.19ºE), Oman, in November 2019. The study area, which constitutes a hotspot for ASHW (Corkeron et al. 2011, Minton et al. 2011, Willson et al. 2016), was systematically surveyed using a small (~6m) research vessel with dedicated observers and a hydrophone (to detect singing males). UAV video recordings were also made of IWC breeding stock D (BS D) humpback whales off south-west Australia during the beginning (June) and end (October) of the 2017 breeding season. Sampling was conducted from a small (~6m) research vessel operated within two nautical miles of the coast in Flinders Bay and Geographe Bay, in WA, respectively (for details see Christiansen et al. 2020b). South-west Australia represents the area of both entry and exit for the majority of BS D that feeds in the Eastern section of feeding Area

IV, Antarctica (Chittleborough 1965, Gill & Burton 1995, Jenner et al. 2001) and hence represent whales in their best and poorest body condition on the breeding grounds, respectively.

During sampling, a DJI Inspire 1 Pro UAV with a Zenmuse X5 camera and a 25mm lens was flown above the whale at altitudes ranging from 20 to 65 m, and recorded videos of the whales as they surfaced to breathe. During post-processing, a still frame photograph of each whale was extracted from the videos. An ideal photograph represented a whale lying flat at the surface with its dorsal side visible with its body non-arching and the body contour (both length and width) clearly visible (Christiansen et al. 2016, 2018) (Fig. 1). Each photograph was quality graded (based on posture, clarity and contrast) following the protocol of Christiansen et al. (2018), and only photographs of adequate quality were included in analyses. Each whale was individually identified using the unique shape and pattern of the whale's fluke and/or dorsal fin, which was photographed by one of the researchers on board the research vessel. In Oman, skin biopsy samples were also obtained using a crossbow to determine the sex of each individual (Lambertsen 1987) and many photo identified individuals in the Oman catalogue have been sampled and sexed during past work.

Body morphometrics and condition

A custom-programmed Graphical User Interface developed by Dawson et al. (2017) was used to measure body lengths and widths from best aerial photographs (video still frames) at 5% increments along the entire body axis of the whale according to the method developed for the comparative dataset (Christiansen et al. 2016, 2020b). All measurements were scaled (converted from pixels to meters) using the known altitude of the UAV (measured using a LightWare SF11/C laser range finder), the camera sensor size, focal length and image resolution (for details, see Christiansen et al., 2018). Each whale was classified into a specific reproductive class: calf, juvenile, adult and lactating. Calves and lactating females were classified based on their relative size (calves are <2/3 the length of their mothers, Christiansen et al., 2016) and close association with each other. Juveniles and adults (sexually mature animals that were not pregnant or lactating) were separated based on a body length threshold of 11.2 m (Chittleborough 1955a b, Christiansen et al. 2016), although it is possible the ASHWs reach sexual maturity at a larger (>11.6m) body size (Mikhalev 2000). Body condition metrics for each individual were only retained for further comparative analysis from the processed images that scored over a threshold (following the quality assessment protocol of Christiansen et al. 2018) and were the highest in quality assessment (for a given whale) to ensure accurate representation of their morphological attributes within the comparative dataset.

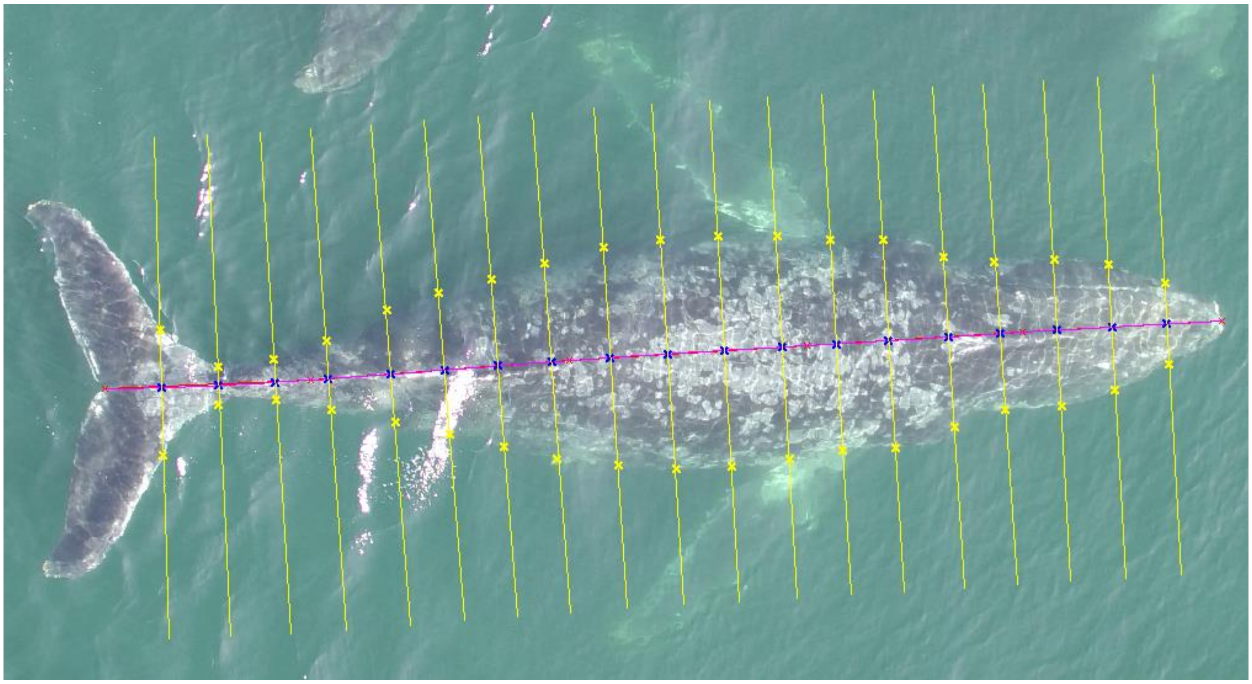

Figure 1. Aerial photograph (video still frame) of an adult ASHW, showing the location of the body length (purple line) and body width (yellow lines) measurement sites. The picture was extracted from the custom-programmed Graphical User Interface developed by Dawson et al. (2017).

The body condition of individual humpback whales was calculated from the residual of the relationship between body volume and body length (Christiansen et al. 2018). First, we used the body length and width data to estimate the body volume of the whales. To account for the elliptical cross-sectional body shape of the whales (Lockyer et al. 1985, Christiansen et al. 2019, 2020b), we first calculated the corresponding height (dorso-ventral distance) of the whales at each width measurement site, using the known height-width (HW) ratios of humpback whales provided by Christiansen et al. (2020b). The total body volume (V_{Total}) of each whale (i) was then estimated from the sum of the volumes of all body segments (s), the section of the body between two adjacent width/height measurement sites, S=20 in total):

$$V_{Total,i} = \sum_{s=1}^{20} V_{s,i} \qquad (1)$$

where the volume of each segment (V_s) was modelled as a series of infinitesimal ellipses, following the methods of Christiansen et al. (2019):

$$V_{S,i} = BL_i \times 0.05 \times \int_0^1 \pi \times \frac{W_{A,s,i} + (W_{P,s,i} - W_{A,s,i}) \times x}{2} \times \frac{H_{A,s,i} + (H_{P,s,i} - H_{A,s,i}) \times x}{2} dx \qquad (2)$$

where BL_i is the body length of whale i, $W_{A,s,i}$ and $H_{A,s,i}$ are the anterior width and height measurements of body segment s for individual i, and $W_{P,s,i}$ and $H_{P,s,i}$ are the posterior width and height measurements of segment s for individual i, respectively. To account for the gradual decrease in height and width towards the end points of the animal, the segments closest to the rostrum (0-5% BL from the rostrum) and the end of the tail region (85-100%BL from rostrum) were modelled as elliptical cones (Christiansen et al. 2019).

From the body volume estimates, a morphometric body condition index (*BCI*) was calculated following the methods of Christiansen et al. (2018):

$$BCI_i = \frac{BV_{obs,i} - BV_{exp,i}}{BV_{exp,i}} \qquad (3)$$

where $BV_{obs,i}$ is the observed body volume of whale i, in m^3, and $BV_{exp,i}$ is the expected (or predicted) body volume of whale i, in m^3, from the linear relationship between body volume and length on the log-log scale. Rather than calculating this relationship for the two humpback whale populations together, we used the published relationship between body volume (BV_i) and body length (BL_i) for BS D humpback whales (i), which was based on 167 whales (24 calves, 55 juveniles, 67 adults and 21 lactating females), ranging in body length from 5.4 to 15.3 m ($F_{1,165}$=3586, P<0.001, R^2=0.96, Christiansen et al. 2020b):

$$\log(BV_{exp,i}) = -3.70 + 2.77 \times \log(BL_i) \qquad (4)$$

The body condition of ASHWs was compared to that of BS D humpback whales, using linear models in *R* v.3.5.3 (R Core Team 2019). Separate models were fitted for each reproductive class. For each model, model validation tests were performed to test for homogeneity and normality of residuals, as well as influential data points and outliers. All model assumptions were fulfilled.

RESULTS

During the 25th and 26th of November 2019, 11 individual ASHWs were measured from a total of 15 encounters where aerial video was obtained. A sample size of nine individuals remained after data filtering of images that did not meet measurement criteria. Previous biopsy sampling and genetic analysis of known individuals from the Oman humpback whale photo-identification catalogue confirmed that measured individuals included three females, three males and three animals of unknown sex (biopsy samples collected in 2017 or 2019 will allow sexing of two these individuals). All the measured ASHWs were adults, ranging in body length from 11.8 to 14.2 m (mean=12.8 m, SD=0.78, n=9) (Fig. 2A).

From a total of 167 whales (56 in June and 111 in October) measured from BS D, 67 were adults (non-pregnant/non-lactating) of unknown sex, which ranged in body length from 11.2 to 15.3 m (mean=12.3 m, SD=0.69, n=67) (Fig. 2A). For information about the other reproductive classes from stock D (24 calves, 55 juveniles and 21 lactating females), see Christiansen et al. (2020b). The altitude of the drone during measurements was similar between Oman (mean=38.4 m, SD=4.73, min=30.6, max=47.4) and WA (mean=34.6 m, SD=5.16, min=26.5, max=53.1). The estimated body volume of the measured ASHWs ranged from 24.2 to 47.9 m^3 (mean=31.4 m^3, SD=7.02, n=9) (Fig. 2A). The body volume of adult humpback whales from stock D ranged from 18.1 to 41.4 m^3 (mean=26.1 m^3, SD=4.27, n=67) (Fig. 2A).

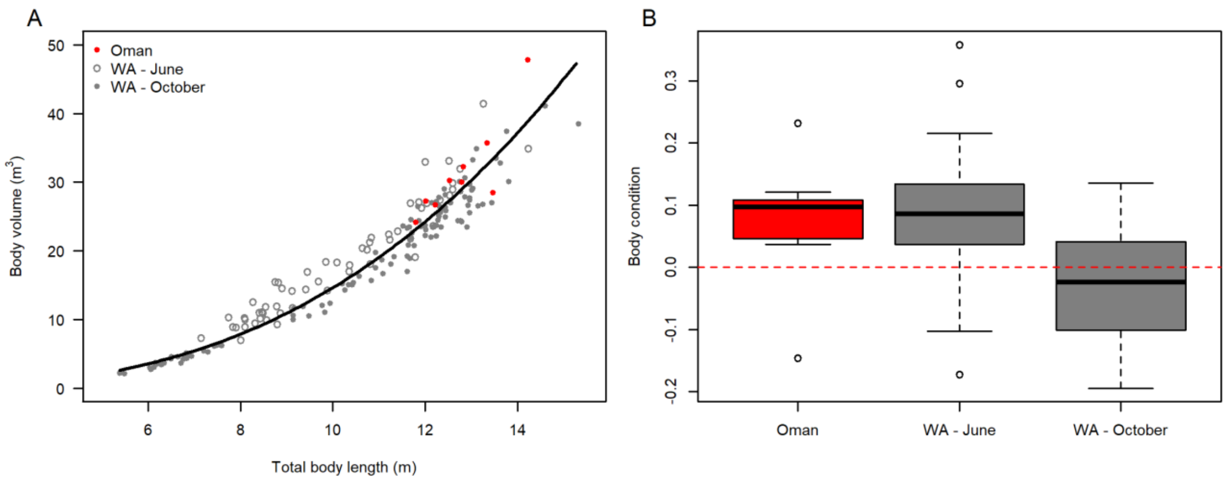

Figure 2. (A) Body volume as a function of body length for ASHWs (red points, n=9) and BS D humpback whales at the beginning (June, open circles, n=56) and end (October, filled circles, n=111) of the breeding season. The fitted line represents the predicted body volume from body length (equation 4) estimated for BS D humpback whales (Christiansen et al. 2020b). (B) Boxplots of body condition of humpback whale adults from Oman (n=9) and Western Australia during the beginning (June, n=19) and end (October, n=48) of the breeding season. The dashed red horizontal line represents a BS D humpback whale of average body condition (BC=0).

The body condition (based on the formula derived for BS D humpback whales, Christiansen et al. 2020b) of the measured ASHWs ranged from -14.7 and 23.2% (mean=7.2%, SD=10.09). The body condition of the adult whales from BS D ranged from -19.4 to 35.7% (mean=0.0%, SD=11.13, n=67). ASHW adults were in similar (t-value=0.346, P=0.730) body condition (mean=7.2%, SE=3.28, n=9) as adult BS D humpback whales at the beginning of the breeding season (mean=8.6%, SE=3.98, n=19), but in significantly better condition (t-value=-2.968, P=0.004) compared to BS D adults measured at the end of the season (mean=-3.4%, SE=3.57, n=48) (Fig. 2B). The linear model explained 25.1% (R^2) of the variance in the body condition data.

Although female ASHWs appeared to have a higher body condition index (mean=12.5%, SE=6.04, n=3) compared to males (mean=6.9%, SE=8.54, n=3) (Fig. 3A), this difference was not statistically significant (t-value=-0.660, P=0.534) and the sample size was small. The body condition of the confirmed ASHW females (mean=12.5%, SE=6.10, n=3) were similar (t-value=-1.091, P=0.280) to that of lactating females from BS D when measured on their breeding/nursing grounds in Exmouth Gulf (mean=5.5%, SE=6.39, n=31, data obtained from Christiansen et al. 2016), but significantly higher (t-value=-2.817, P=0.007) than that of lactating females measured off the south-western corner of WA (mean=-5.9%, SE=6.52, n=21) just before departing to their feeding grounds (Fig. 3B). The linear model explained 25.7% (R^2) of the variance in the female body condition data.

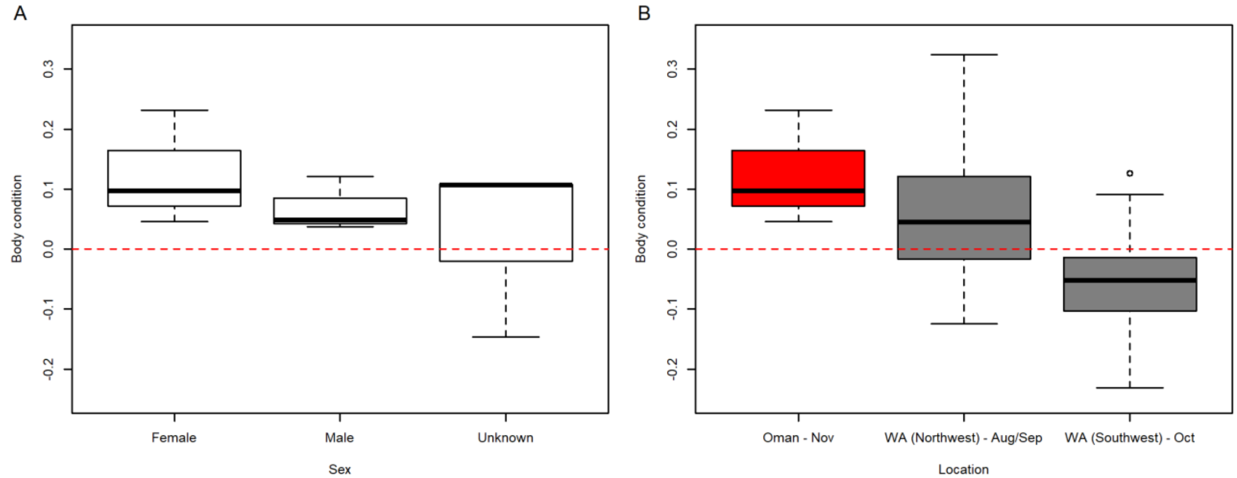

Figure 3. (A) Boxplots of body condition of ASHWs divided into females (n=3), males (n=3) and adults of unknown sex (n=3). (B) Boxplots of body condition of ASHW females (n=3) and BS D lactating females measured in North-western (Exmouth Gulf, n=31) and South-western (Geographe Bay, n=21) Western Australia. The dashed red horizontal lines represent a stock D humpback whale of average body condition (BC=0).

DISCUSSION

Based on their body lengths (11.8 to 14.2 m), the sampled ASHWs were most likely adults. This is supported by earlier findings from illegal Soviet whaling operations, which showed that all females over 11.5 m were sexually mature (Mikhalev 1997). The proportional size of their heads (mean=25.9% of body length, SD=1.35) also corresponds to that of adult humpback whales of WA (~25% of body length, Christiansen et al. 2016). Contrary to our expectations, we found ASHWs to be in similar body condition to migratory humpback whales that had just arrived on their breeding grounds. At that stage in the migratory cycle, humpback whales are in good condition, following recent completion of their feeding season in the Southern Ocean (Irvine et al. 2017, Christiansen et al. 2020b), where they replenished fat reserves for migration and breeding. While some of these reserves will have been spent during the migration to the breeding ground, the whales should still have most of their energy reserves remaining. Through the breeding season, adults from BS D humpback whales declined significantly in body condition (Christiansen et al. 2016, 2020b). Consequently, at the time of departure from their breeding grounds, BS D humpback whales were in significantly poorer body condition compared to ASHWs. If this is reflective of the ASHW population then nutritional stress is unlikely to compromise adult survival. However, this is a hypothesis that needs further testing. It should also be noted that the sampling location in Oman is believed to be one of the population's most important feeding grounds (Corkeron et al. 2011, Minton et al. 2011, Willson et al. 2017), and the timing of the sampling also coincides with the end of a season of peak productivity following on from monsoon-driven upwelling along the Arabian Sea coast of Oman (Brock & McClain 1992, Brock et al. 1992, Minton et al. 2011). Schools of fish and feeding birds were observed during the November 2019 Oman sampling period, and one whale was observed to defecate during sampling, indicating that whales were actively feeding within the timeframe of our survey.

Previous photographic and biopsy sampling in Oman allowed us to identify and sex the majority of individuals sampled in this study, and hence compare the body condition of ASHW females and males. Although the small sample size prevented any statistically robust comparison, our exploratory plots suggest that females might be in overall better body condition than males. ASHW females, demonstrated similar body condition to lactating females from BS D that had recently given birth to their calves at the northern extreme (i.e. Exmouth Gulf) of their breeding grounds. In migratory baleen whale populations, late pregnant/early lactating females are in their best body condition state compared to other reproductive classes (Miller et al. 2012, Christiansen et al. 2016, 2020a, Soledade Lemos et al. 2020), since they need to carry sufficient fat reserves to grow their calf for the first 3-4 months while fasting. Based on foetal lengths obtained from pregnant females caught in Soviet whaling operations, ASHWs should begin calving in December, with a peak in February (Mikhalev 1997). It is thus possible that the females measured in this study could be pregnant (Mikhalev 1997 reported foetuses measured in November to be 340-375 cm in length), or at least in sufficiently good condition to reproduce. In the future we aim to determine the pregnancy rate of adult females by combining UAV photogrammetry with hormone (androstenedione and testosterone) sampling (Dalle Luche et al. 2020).

Caution is required when interpreting the preliminary results of this body condition sample from Oman, as it only constitutes a snapshot in time of a small number of animals. While the relatively good body condition suggests that the animals were not nutritionally stressed (i.e. starving), without knowledge of the inter- and intra-seasonal (if any) variation in body condition of this population, it is hard to link our findings to reproductive rates and population dynamics. Baleen whale females need considerable energy to support the cost of gestation and lactation (Lockyer 1981, 1984, Christiansen et al. 2018). The toll this takes on female body condition is clearly visible for the lactating humpback females sampled from BS D, which declined significantly in body condition from the time they gave birth to the time they left their Australian breeding ground. For capital breeding baleen whales, this loss in energy is compensated for by the rapid accumulation of fat reserves on the feeding grounds (Lockyer 1987, Vikingsson 1990, Næss et al. 1998, Christiansen et al. 2013). For the non-migratory ASHW population however, which are presumed to have access to food throughout the year (Mikhalev 1997, Minton et al. 2011), it is hypothesised that such seasonal fluctuations in body condition are unlikely to occur to such an extent for two reasons: First, with lactating females having access to food while they are nursing their calf, the rate of decline in body condition should be mitigated, at least in part, by the concurrent energy intake. Second, the rate at which post-weaning females build up their energy reserves should also be considerably lower than for migratory humpback whales since the Arabian Sea is far less productive than the Southern Ocean where southern hemisphere humpbacks are feeding. These assumptions require further testing, particularly with respect to food availability, which may be negatively affected by other processes, including disturbance (for instance from suitable habitats) fisheries and climate change.

Based on the assumption that ASHWs are following a reproductive strategy more similar to an income breeder, where prey is availability throughout the reproductive cycle (although at a relatively lower density), the body condition of an animal at any point in time would reflect their foraging success over an unknown period. Measuring the body condition of ASHWs, in particular the same individuals, throughout the year for successive years would help determine over what period the animals are building up their fat reserves. A lack of seasonal variation in body condition would indicate that ASHWs are acquiring just enough energy throughout the year to sustain their own metabolic needs (their energy intake is balanced by their energy expenditure), which means that even if animals appear to be in good body condition, they do not have much energy reserves to allocate to reproduction. Judging from the small population size and limited distribution (Minton et al. 2011), it is likely that ASHW females would need several years to build up sufficient energy reserves to reproduce. It is further possible that the lactation period lasts longer compared to migratory humpback whales, since ASHW females are not under the same energetic "pressure" to feed their calf quickly. Sea surface temperatures in the Arabian Sea generally range from $16^{o\ C}$ during the southwest monsoon to $30^{o\ C}$ at other times of year, with high interannual variability in the strength of monsoon-driven upwelling, and other less predictable local upwelling events associated with bathymetric features (Lee et al. 2000, Piontkovski & Al Jufaili 2013). However, variability in temperature is mild compared to the differences between most Southern Hemisphere humpback whales' low-latitude breeding grounds and their feeding grounds in Antarctica. As such, there are no obvious heat loss benefits for calves to grow quickly, or to deposit fat to thicken their blubber layer. There is also no immediate need for them to migrate long distances, which calves would do more efficiently if they were larger with more muscle mass. Killer whales (*Orcinus orca*) do however exist in the Arabian Sea (NIOKWA 2018) which means that it might still be beneficial for ASHW females to grow their calves quickly to reduce the risk of predation. While more data is needed to address these questions, the comparison between the non-migratory ASHW population and the migratory BS D population will help answer the broader ecological question of why humpback whales (and other baleen whale species) migrate, and how much energy (i.e. prey) is required to sustain these two different reproductive strategies (income versus capital breeding).

While this study provides the first assessment of the body condition of ASHWs, further sampling is needed to better understand inter- and intra-seasonal changes (if any) in body condition of this population. Ocean productivity and the association with nutritional status that controls thresholds of reproductive success also need further study. Sardines are known prey items of ASHWs (Mikhalev 2000) and the strength of the summer monsoon is considered to influence annual landings that are known to vary by as much as 39% in the Arabian Sea (George et al. 2012). Basin scale declines in the sardine fishery were reported off the coast of Oman between 2001 and 2011 (Piontkovski et al. 2014). An on-going or long-term survey approach using body condition as a tracked metric would enable the influences of such large scale and long cycle events to be considered within evaluation of future population trends. The method presented here should be considered for adoption within the set of Key Ecological Attributes adopted by the Convention on Migratory Species Concerted Action for ASHWs (Convention on Migratory Species, 2017).

Further, our sample was exclusively made up of adults, which would be expected in a population with low recruitment. Information on the body condition of mother-calf pairs would be extremely valuable, as it would help determine the minimum body condition needed for females to reproduce in this non-migratory population. Data on the size (i.e. length) and body condition of juveniles would help quantify the cost of growth in this population, and at what age ASHWs reach sexual maturity, which in baleen whales is determined more by length than age (Sigurjónsson et al. 1990). Future sampling of body condition would further benefit from concurrent biopsy sampling to determine pregnancy rates (from hormone levels, Dalle Luche et al. 2020) and age (Polanowski et al. 2014), with the long-term goal of determining the reproductive potential of the ASHW population and its resilience to non-lethal anthropogenic impacts (WWF 2012).

Being a small and slow breeding population, the ASHW is extremely vulnerable to anthropogenic factors. The Arabian Sea is home to a large fishing fleet assumed to be associated with high rates of entanglement and bycatch of a range of species, although further evidence is needed to confirm this (IWC 2019, Anderson et al. 2020), and 66% of ASHWs carry scars assumed to be from fishing gear entanglements (Minton et al. 2011, IWC/SC68B/CMP16). The Ministry of Agriculture and Fisheries Wealth in Oman is working on mitigating the impact of fisheries on the marine environment, and is in the progress of introducing a new law on banning catch use of cetaceans, and regulations on the use of drift nets. Aside from the potential direct threat of fishing gear entanglements (i.e. drownings), the energetic costs resulting from the additional drag, buoyancy and impeded foraging capacity, can be very high for baleen whales (Cassoff et al. 2011, van der Hoop et al. 2017), and further impede the reproductive rate of this population. With the fishing effort in Oman and the wider Arabian Sea being estimated to increase rapidly (Ministry of National Economy 2009; FAO 2007), it is possible that both lethal and non-lethal impacts could increase further. In addition, industrial ports, fast-ferry terminals and coastal resorts are under construction in Oman, with consequences for disturbance in inshore ASHW habitats, including favoured breeding and feeding sites (Minton et al. 2011). In addition, more than 25% of ASHWs are infected by a poxvirus called tattoo-like skin disease (Van Bressem et al. 2015, IWC/SC68B/CMP16), which could carry energetic costs. Continued research into the health of the ASHW population, together with continued monitoring of population demographics and assessment of fisheries interactions (Minton et al. 2011), is hence highly recommended.

ACKNOWLEDGEMENTS

This work was conducted under Ministry of Defence National Survey Authority permit ESO/GOV/MODEF/19-118 and Ministry of Environment and Climate and Climate Affairs permit ESO/GOV/MOECA/19-15. FC received funding from the AIAS-COFUND II fellowship programme that is supported by the Marie Skłodowska-Curie actions under the European Union's Horizon 2020 (Grant agreement no. 754513) and the Aarhus University Research Foundation. We are grateful to the Ministry of Environment and Climate Affairs, Oman, for issuing of permits to conduct field research, sampling and analysis. We thank partners at the Environment Society of Oman (www.eso.org.om) whom have supported applications for permits, the vessel for fieldwork, collaboration on data resources, encouragement to keep the project active and institutional support made possible through the Renaissance Whale and Dolphin Project in Oman. Appreciation is expressed for the board and staff at Five Oceans Environmental Services for provision of resources, expertise, time and equipment in support of Arabian Sea humpback whale, and other cetacean research in Oman over the past 18 years. The Wildlife Conservation Society is thanked for supporting the on-going participation of team members in support of field activities, data analysis and reporting. Thanks are also extended to Sean Nelson of Nelson Expeditions, Tom Kenyon and Dianna Long for supporting field research.

LITERATURE CITED

Anderson RC, Herrera M, Ilangakoon AD, Koya K, Moazzam M, Mustika PL, Sutaria DN (2020) Cetacean bycatch in Indian Ocean tuna gillnet fisheries. Endanger Species Res 41:39–53.

Beale CM, Monaghan P (2004) Human disturbance: people as predation-free predators? J Appl Ecol 41:335–343.

Bettridge S, Baker C, Barlow J, Clapham P, Ford M, Gouveia D, Mattila D, Pace III R, Rosel P, Silber G (2015) Status review of the humpback whale (*Megaptera novaeangliae*) under the Endangered Species Act. US Dep Commer NOAA Tech Memo NMFS-SWFSC 540:263.

Brock, J. C., C. R. McClain, and W. W. Hay. 1992. A southwest monsoon hydrographic climatology for the northwestern Arabian Sea. Journal of Geophysical Research 97(C6):9455-9465.

Corkeron, P. J., G. M. T. Collins, K. Findlay, A. Willson, and R. Baldwin. 2011. Spatial models of sparse data to inform cetacean conservation planning: an example from Oman. Endangered Species Research 15(1):39-52

FAO. The state of world fisheries and aquaculture 2006. 1-180 (Food and Agriculture Organisation of the United Nations, Rome, 2007).

Le Boeuf BJ, Pérez-Cortés M H, Urbán JR, Mate BR, Ollervides U F (2000) High gray whale mortality and low recruitment in 1999: potential causes and implications. J Cetacean Res Manag 2:85–99.

Van Bressem MF, Minton G, Collins T, Willson A, Baldwin R, Van Waerebeek K (2015) Tattoo-like skin disease in the endangered subpopulation of the Humpback Whale, *Megaptera novaeangliae*, in Oman (Cetacea: Balaenopteridae). Zool Middle East 61:1–8.

Brock JC, McClain CR (1992) Interannual variability in phytoplankton blooms observed in the northwestern Arabian Sea during the southwest monsoon. J Geophys Res 97:733–750.

Brock JC, McClain CR, Hay WW (1992) A southwest monsoon hydrographic climatology for the northwestern Arabian Sea. J Geophys Res 97:9455–9465.

Cassoff R, Moore K, McLellan W, Barco S, Rotstein D, Moore M (2011) Lethal entanglement in baleen whales. Dis Aquat Organ 96:175–185.

Chittleborough RG (1955a) Aspects of reproduction in the male humpback whale, *Megaptera nodosa* (Bonnaterre). Aust J Mar Freshw Res 6:1–29.

Chittleborough RG (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). Aust J Mar Freshw Res 16:33–128.

Chittleborough RG (1955b) Puberty, physical maturity, and relative growth of the female humpback whale, *Megaptera nodosa* (Bonnaterre), on the Western Australian coast. Aust J Mar Freshw Res 6:315–327.

Christiansen F, Dawson SM, Durban JW, Fearnbach H, Miller CA, Bejder L, Uhart M, Sironi M, Corkeron P, Rayment W, Leunissen E, Haria E, Ward R, Warick HA, Kerr I, Lynn MS, Pettis HM, Moore MJ (2020a) Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. Mar Ecol Prog Ser 640:1–16.

Christiansen F, Dujon AM, Sprogis KR, Arnould JPY, Bejder L (2016) Noninvasive unmanned aerial vehicle provides estimates of the energetic cost of reproduction in humpback whales. Ecosphere 7:e01468.

Christiansen F, Sironi M, Moore MJ, Di Martino M, Ricciardi M, Warick HA, Irschick DJ, Gutierrez R, Uhart MM (2019) Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. Methods Ecol Evol 10:2034–2044.

Christiansen F, Sprogis KR, Gross J, Castrillon J, Warick HA, Leunissen E, Bengtson Nash S (2020b) Variation in outer blubber lipid concentration does not reflect morphological body condition in humpback whales. J Exp Biol 223:jeb213769.

Christiansen F, Vikingsson GA, Rasmussen MH, Lusseau D (2013) Minke whales maximise energy storage on their feeding grounds. J Exp Biol 216:427–436.

Christiansen F, Víkingsson GA, Rasmussen MH, Lusseau D (2014) Female body condition affects foetal growth in a capital breeding mysticete. Funct Ecol 28:579–588.

Christiansen F, Vivier F, Charlton C, Ward R, Amerson A, Burnell S, Bejder L (2018) Maternal body size and condition determine calf growth rates in Southern right whales. Mar Ecol Prog Ser 592:267–282.

Convnetion on Migratory Species (2017) Proposal for a Concerted Action for Arabian Sea Humpback Whales. 12th Meeting of the conference of the parties. Manila, Philippines, October, 2017. UNEP/CMS/COP12/DOC/26.2.4

Corkeron PJ, Collins GMT, Findlay K, Willson A, Baldwin R (2011) Spatial models of sparse data to inform cetacean conservation planning: an example from Oman. Endanger Species Res 15:39–52.

Dalle Luche G, Boggs ASP, Kucklick JR, Groß J, Hawker DW, Bengtson Nash S (2020) Androstenedione and testosterone but not progesterone are potential biomarkers of pregnancy in Humpback Whales (*Megaptera novaeangliae*) approaching parturition. Sci Rep 10:2954.

Dawson SM, Bowman MH, Leunissen E, Sirguey P (2017) Inexpensive aerial photogrammetry for studies of whales and large marine animals. Front Mar Sci 4:366.

George G, Meenakumari B, Raman M, Kumar S, Vethamony P, Babu M, Verlecar X (2012) Remotely sensed chlorophyll: a putative trophic link for explaining variability in Indian oil sardine stocks. J Coast Res 28:105–113.

Gill PC, Burton CLK (1995) Photographic resight of a humpback whale between Western Australia and Antarctic Area IV. Mar Mammal Sci 11:96–100.

Hedley SL, Bannister JL, Dunlop RA (2011) Abundance estimates of Southern Hemisphere Breeding Stock 'D' humpback whales from aerial and land-based surveys off Shark Bay, Western Australia, 2008. J Cetacean Res Manag 3:209–221.

van der Hoop J, Corkeron P, Moore M (2017) Entanglement is a costly life-history stage in large whales. Ecol Evol 7:92–106.

Irvine LG, Thums M, Hanson CE, McMahon CR, Hindell MA (2017) Quantifying the energy stores of capital breeding humpback whales and income breeding sperm whales using historical whaling records. R Soc Open Sci 4:160290.

IWC (2019) Report of the IWC Workshop on Bycatch Mitigation Opportunities in the Western Indian Ocean and Arabian Sea. Int Whal Comm Cambridge, United Kingdom.

Jenner KCS, Jenner MN, McCabe KA (2001) Geographical and temporal movements of humpback whales in Western Australian waters. Appea J 38:692–707.

Lambertsen, R. H. (1987). A biopsy system for large whales and its use for cytogenetics. Journal of Mammalogy, 443-445.

Lee CM, Jones BH, Brink KH, Fischer AS (2000) The upper-ocean response to monsoonal forcing in the Arabian Sea: seasonal and spatial variability. Deep Res Part II 47:1177–1226.

Lockyer C (1981) Estimation of the energy costs of growth, maintenance and reproduction in the female minke whale, (*Balaenoptera acutorostrata*), from the Southern hemisphere. The Scientific Committee of the International Whaling Commission, Cambridge, UK, p Document SC/32/Mi19

Lockyer C (1987) Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. In: *Approaches to Marine Mammal Energetics. Special Publication No 1*. Huntley AC, Costa DP, Worthy GAJ, Castellini MA (eds) Society for Marine Mammalogy, Lawrence, 183–203

Lockyer C (1984) Review of baleen whale (Mysticeti) reproduction and implications for management. Reports Int Whal Comm (special issue) 6:27–50.

Lockyer C, McConnell LC, Waters TD (1985) Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. Can J Zool 63:2328–2338.

McMahon C, Burton HR, Bester MN (2000) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. Antarct Sci 12:149–153.

Mikhalev YA (1997) Humpback whales Megaptera novaeangliae in the Arabian Sea. Mar Ecol Prog Ser 149:13–21.

Mikhalev YA (2000) Whaling in the Arabian Sea by the whaling fleets Slava and Sovetskaya Ukraina. Sov Whal data:141–181.

Miller CA, Best PB, Perryman WL, Baumgartner MF, Moore MJ (2012) Body shape changes associated with reproductive status, nutritive condition and growth in right whales *Eubalaena glacialis* and *E. australis*. Mar Ecol Prog Ser 459:135–156.

Minton G, Collins T, Findlay K, Ersts P, Rosenbaum H, Berggren P, Baldwin R (2011) Seasonal distribution, abundance, habitat use and population identity of humpback whales in Oman. J Cetacean Res Manag (Special Issue) 3:185–198.

Minton G, Collins T, Pomilla C, Findlay KP, Rosenbaum H, Baldwin R, Brownell RL (2008) *Megaptera novaeangliae* (Arabian Sea subpopulation). IUCN Red List Threat Species 2008 e.T132835A.

Næss A, Haug T, Nilssen EM (1998) Seasonal variation in body condition and muscular lipid contents in Northeast Atlantic minke whale *Balaenoptera acutorostrata*. Sarsia 83:211–218.

NIOKWA (2018) Killer Whales of the Northern Indian Ocean: a catalogue of photo-identified individuals. http://niokillerwhales.wixsite.com/niokw

(Oman) Ministry of the National Economy, *2009 statistical yearbook*. Vol. http://www.mone.gov.om/BOOK/syb2009/General/General_information.pdf (Ministry of National Economy, 2009).

Piontkovski SA, Al Jufaili S (2013) Coastal upwellings and mesoscale eddies of the Western Arabian Sea: some biological implications. Int J Ocean Oceanogr 7:93–115.

Piontkovski, S.A., Al-Oufi, H.S. and Al-Jufaili, S., (2014). Seasonal and Interannual Changes of Indian Oil Sardine, Sardinella longiceps, Landings in the Governorate of Muscat (the Sea of Oman). Marine Fisheries Review, 76(3), pp.50-60. Piontkovski, S.A. and Al-Oufi, H.S., 2014.

Polanowski AM, Robbins J, Chandler D, Jarman SN (2014) Epigenetic estimation of age in humpback whales. Mol Ecol Resour 14:976–987.

Pomilla C, Amaral AR, Collins T, Minton G, Findlay K, Leslie MS, Ponnampalam L, Baldwin R, Rosenbaum H (2014) The world's most isolated and distinct whale population? humpback whales of the Arabian sea. PLoS One 9:1–22.

R Core Team (2019) R: A language and environment for statistical computing.

Rolland RM, Parks SE, Hunt KE, Castellote M, Corkeron PJ, Nowacek DP, Wasser SK, Kraus SD (2012) Evidence that ship noise increases stress in right whales. Proc R Soc B 279:2363–2368.

Rolland RM, Schick RS, Pettis HM, Knowlton AR, Hamilton PK, Clark JS, Kraus SD (2016) Health of North Atlantic right whales *Eubalaena glacialis* over three decades: From individual health to demographic and population health trends. Mar Ecol Prog Ser 542:265–282.

Sigurjónsson J, Halldórsson SD, Konráðsson A (1990) New information on age and reproduction in minke whales

(*Balaenoptera acutorostrata*) in Icelandic waters. The Scientific Committee of the International Whaling Commission, Noordwijkerhout, Netherlands, Document SC/42/NHMi27

Soledade Lemos L, Burnett JD, Chandler TE, Sumich JL, Torres LG (2020) Intra- and inter-annual variation in gray whale body condition on a foraging ground. Ecosphere 11:e03094.

Vikingsson GA (1990) Energetic Studies on Fin and Sei whales caught off Iceland. Reports Int Whal Comm 40:365–373.

Williams R, Vikingsson GA, Gislason A, Lockyer C, New L, Thomas L, Hammond PS (2013) Evidence for density-dependent changes in body condition and pregnancy rate of North Atlantic fin whales over four decades of varying environmental conditions. ICES J Mar Sci 70:1273–1280.

Willson A, Baldwin R, Cerchio S, Collins T, Findlay K, Gray H, Godley B, Gray H, Al-Harthi S, Kennedy A, Minton AG, Sucunza F, Zerbini A, Witt M (2016) Research update on satellite tagging studies of the Arabian Sea humpback whale in the Sultanate of Oman. Rep Int Whal Comm Doc SC/66b/SH28.

Willson A, Baldwin R, Collins T, Godley BJ, Minton G, Al Harthi S, Pikesley SK, Witt. MJ (2017) Preliminary ensemble ecological niche modelling of Arabian Sea humpback whale vessel sightings and satellite telemetry data. Rep Int Whal Comm Doc SC/67A/CMP/15, Bled, Slov.

WWF (2012) WWF standards of conservation project and programme management. Unpublished document. World Wildl Fund:55.