



Poor body condition associated with an unusual mortality event in gray whales

Fredrik Christiansen^{1,2,3,*}, Fabian Rodríguez-González⁴, Sergio Martínez-Aguilar^{4,5}, Jorge Urbán^{4,5}, Steven Swartz⁵, Hunter Warick³, Fabien Vivier⁶, Lars Bejder^{2,3,6}

¹Aarhus Institute of Advanced Studies, Høegh-Guldbergs Gade 6B, 8000 Aarhus C, Denmark

²Zoophysiology, Department of Biology, Aarhus University, C.F. Møllers Allé 3, 8000 Aarhus C, Denmark

³Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, Murdoch, 6150 Western Australia, Australia

⁴Departamento de Ciencias Marinas y Costeras, Universidad Autónoma de Baja California Sur, La Paz, BCS 23081, Mexico

⁵Laguna San Ignacio Ecosystem Science Program (LSIESP), Darnestown, MD 20874, USA

⁶Marine Mammal Research Program, Hawaii Institute of Marine Biology, University of Hawaii at Manoa, Kaneohe, HI 96744, USA

ABSTRACT: The eastern North Pacific gray whale *Eschrichtius robustus* experienced an unusual mortality event (UME) in 2019–2020, with 384 whales found dead along the Pacific coasts of Mexico, USA and Canada. A similar UME in 1999–2000 was speculated to have been caused by starvation, but body condition data were not available to test this hypothesis. Between 2017 and 2019, we used unmanned aerial vehicles (drones) and photogrammetry methods to measure the body condition of gray whales in San Ignacio Lagoon, Baja California Sur, Mexico. Body condition was calculated from the residual of the relationship between body volume and length. The body condition of gray whales was significantly lower in 2018 (–11.1%, SE = 1.74, n = 531) and 2019 (–9.7%, SE = 1.76, n = 628) compared to 2017 (n = 59) for all reproductive classes (calves, juveniles, adults and lactating females). Overall, lactating females were in good body condition. The reduction in body condition of whales in 2018–2019 is unlikely to have affected their survival, but could have reduced their reproductive rate by prolonging the post-weaning recovery time. This could explain the low number of mother–calf pairs observed in the San Ignacio Lagoon in 2018 and 2019. For juveniles and adults that arrived in the lagoons with less energy reserves, their reduced body condition may have been close to their survival threshold. This could explain the high proportion of juveniles and adults among the stranded dead whales in 2019–2020. Although the underlying cause of the reduction in gray whale body condition is unknown, starvation likely contributed to the 2019–2020 UME.

KEY WORDS: Baleen whales · Bioenergetics · Reproduction · Starvation · Survival · Unmanned aerial vehicles

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

In 2019–2020, a total of 384 eastern North Pacific gray whales *Eschrichtius robustus* were found dead along the west coast of Mexico, USA and Canada, in what has been described as an unusual mortality event (UME) (NOAA 2020). Under the US Marine Mammal Protection Act (www.fisheries.noaa.gov), a

UME is defined as ‘a stranding that is unexpected; involves a significant die-off of any marine mammal population; and demands immediate response’. A similar UME occurred in 1999–2000, when 651 whales were recorded dead along the west coast of North America, which was approximately 8 times the annual mean stranding rate of 41 animals between 1995–1998 (Gulland et al. 2005). During the 10 yr fol-

*Corresponding author: f.christiansen@aias.au.dk

lowing that event, elevated numbers of dead whales were found along the Pacific coast (Gulland et al. 2005). During the 1999–2000 UME, the gray whale population declined from ~21 000 animals in 1998 to ~16 000 in 2002, which is equivalent to a loss of nearly 25% of the population (Laake et al. 2012).

Gray whales undertake annual migrations between feeding grounds in the Bering, Chukchi and Arctic Seas, and breeding grounds from the Southern California Bight to lagoons along the Pacific coast of Baja California, Mexico (Rice & Wolman 1971, Sumich 1983, Berzin 1984, Moore et al. 1986, 2000, Swartz 1986). The feeding season takes place between May and October, during which time gray whales develop large energy reserves, mainly in the form of blubber (but also muscle, visceral fats and lipids stored in other tissues, Lockyer et al. 1985, Lockyer 1987, Næss et al. 1998), to support the energetic costs of migration and while residing on the breeding grounds where they do not feed extensively or at all (Swartz 1986, Highsmith & Coyle 1992). The migration of gray whales is among the longest known for any mammal, covering 15 000–20 000 km (round trip) (Rice & Wolman 1971, Sumich 1983, Berzin 1984, Moore et al. 1986, 2000, Swartz 1986). The southbound migration begins in October (Rugh et al. 2001), with near-term pregnant females being the first to leave the feeding grounds, followed by breeding adult males and females, then juveniles and later on yearlings (Rice & Wolman 1971, Perryman & Lynn 2002). Mating occurs during the southbound migration, with first ovulation usually occurring in late November and December, with a second oestrus possible about 40 d later for females that fail to conceive (Rice & Wolman 1971). Gray whales are present on their Mexican breeding aggregation grounds between December and April (hereafter referred to as the 'winter breeding season'), where mothers with calves may reside for several months, while other reproductive classes (juveniles, females without calves and adult males) may spend considerable less (<10 d) time (Jones & Swartz 1984, Swartz 1986, Highsmith & Coyle 1992, Mate et al. 2003, Urbán et al. 2003b). Following a gestation period of roughly 13 mo (Rice & Wolman 1971, Swartz & Jones 1983), females generally give birth to a single calf between December and February, with a peak of births in mid- to late January (Swartz & Jones 1983, Perryman & Lynn 2002). The northbound migration starts around February and ends in May, and is initiated by breeding whales without calves (February–March), followed by mother-calf pairs (March–April) (Rice & Wolman 1971, Jones & Swartz 1984, Poole 1984, Perryman & Lynn 2002).

During the 1999–2000 gray whale UME, the majority of stranded whales were juveniles (37.6 and 38.0% in 1999 and 2000, respectively) and adults (33.8 and 49.3% in 1999 and 2000, respectively), and most (85.8%) strandings occurred towards the end of the winter breeding season (February–March) and during the northbound migration (April–July) back to the feeding grounds (Le Boeuf et al. 2000, Gulland et al. 2005). The event was also characterized by record low numbers of mother-calf pair sightings, suggesting low recruitment in both years (Le Boeuf et al. 2000, Perryman et al. 2002, Urbán et al. 2003a,b, 2011, Gulland et al. 2005). The 2019–2020 UME showed similar patterns, with low numbers of mother-calf pairs on the Mexican breeding grounds between 2018 and 2020, and with juveniles and adults comprising the majority of the dead whales (Martínez-Aguilar et al. 2019, 2020, Urbán et al. 2019, 2020). During the first year of both events, the majority of stranded animals were females (Le Boeuf et al. 2000, Gulland et al. 2005, Martínez-Aguilar et al. 2019).

Although the underlying cause of the 1999–2000 UME could not be identified (only 3 of the 651 stranded animals were necropsied), many of the stranded whales appeared to be emaciated, suggesting that starvation could have contributed to the elevated mortalities (Le Boeuf et al. 2000, Moore et al. 2001, Gulland et al. 2005). Unfortunately, the advanced decomposition of many of the stranded whales in 2019–2020 prevented the cause of death being identified (Martínez-Aguilar et al. 2019, 2020). However, a visual qualitative scoring assessment of body condition from boat-based photographs of the lateral sides (post-cranial area, scapular region and flanks) of living gray whales in the San Ignacio breeding lagoon in 2008–2011 (following the 1999–2000 UME) and in 2018–2020 showed an increase in the proportion of 'skinny' single whales (juveniles and adults) in 2018, 2019 and 2020 and an increase in the proportion of lactating females that were in 'fair' condition in 2018 and 2019 (Ronzón-Contreras et al. 2019, 2020). While this decrease in apparent body condition is of significance, it is important to quantify the magnitude of this decline relative to energetic costs for survival and reproduction. Being capital breeders (Stephens et al. 2009), good body condition is crucial for both the survival and reproductive success of gray whales, which already lose between 11 and 29% of their body weight between the southbound and northbound migration (Rice & Wolman 1971). Studies of other baleen whale species show that maternal body condition strongly influences fecundity (Lockyer 2007, Williams et al. 2013), foetal growth (Christiansen et

al. 2014b), calf growth (Christiansen et al. 2018) and calf body condition (Christiansen et al. 2016).

This study aimed to evaluate whether poor body condition was associated with the 2019–2020 gray whale UME, and to quantify the magnitude of this difference for different reproductive classes. To do this, we used unmanned aerial vehicle (UAV, or drone) photogrammetry data, collected as part of an ongoing body condition monitoring program, to compare the body condition of gray whales in San Ignacio lagoon in 2017, 2018 and 2019.

2. MATERIALS AND METHODS

2.1. Data collection

Aerial videos of gray whales were recorded by UAVs in San Ignacio Lagoon (Laguna San Ignacio, LSI), Baja California Sur, Mexico, in 2017 (5–9 March: 4 d of sampling), 2018 (16 January–6 April: 48 d of sampling) and 2019 (20 January–23 March: 43 d of sampling). Sampling was conducted both from land (up to 2 km distance), from fixed locations at the southern end of the lagoon near or at Punta Piedra, and from the sea, using a 7 m research vessel that surveyed the lagoon in an opportunistic way. A DJI Inspire 1 Pro UAV with a Zenmuse X5 camera and a 25 mm lens was flown above the whales and recorded 4K (3840 × 2160 pixels) videos of the whales from altitudes between 12.7 and 59.3 m (mean ± SD = 30.7 ± 3.99 m) as they surfaced to breathe. During post-processing, a still-frame photograph of each whale was extracted from the video recordings. 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). If the whale rolled over during video recording, we also extracted photographs of the lateral side of the animal (Christiansen et al. 2019). Following the protocol of Christiansen et al. (2018), each photograph was quality-graded (based on body posture, image clarity and contrast), and only photographs of adequate quality were included in analyses. Still frames of the bodies of the whales were also extracted for photo-ID purposes. When operating from the research vessel, photo-ID data of the measured whales were also collected by photographing the flanks of each whale (Jones & Swartz 1984). The aerial and flank photographs made it possible to identify individual gray whales and also to re-measure animals within seasons.

Body lengths and widths (at 5% increments along the entire body axis, Fig. 1) of the whales were measured from the dorsal photographs (Christiansen et al. 2016), using the custom-programmed Graphical User Interface developed by Dawson et al. (2017). Similarly, from the lateral photographs, we measured the body height (dorso-ventral distance) at the same measurement sites (Fig. 1) (Christiansen et al. 2019). All measurements were scaled (converted from pixels to metres) 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 or lactating female. Calves and lactating females were classified based on their relative size (calves are <2/3 the length of their mothers; Rice & Wolman 1971, Sanchez Pacheco 1998) and close association with each other. Juveniles and adults (sexually mature animals that were not late-pregnant or lactating) were separated based on a body length threshold of 11.2 m (Rice & Wolman 1971, Blokhin 1984, Yablokov & Bogoslovskaya 1984, Brandon et al. 2005). Unfortunately, not enough late-pregnant females (adults with a body width similar to early-lactating females) were photographed to accurately estimate variation in body condition between years and hence this reproductive class was excluded from analyses.

2.2. Body shape, volume and condition

Intra-seasonal changes in body condition of baleen whales are not exhibited homogeneously across the body of the animals, and the pattern of variability appears to be species-specific (Vikingsson 1990, Folkow & Blix 1992, Næss et al. 1998, Miller et al. 2012, Christiansen et al. 2013, 2016, 2018). To assess which width measurements best capture intra-seasonal changes in the body condition of gray whales, we developed linear models (LMs) in R 3.6.2 (R Core Team 2019) to test the effect of day of year on each width measurement site (Fig. 1). Year was included as a variable in the model. Separate models were developed for each reproductive class to explore if variation in body width varied between reproductive classes.

The body length, width and height data were used to estimate the body volume of the whales. To account for the elliptical cross-sectional body shape of baleen whales (Lockyer et al. 1985, Christiansen et

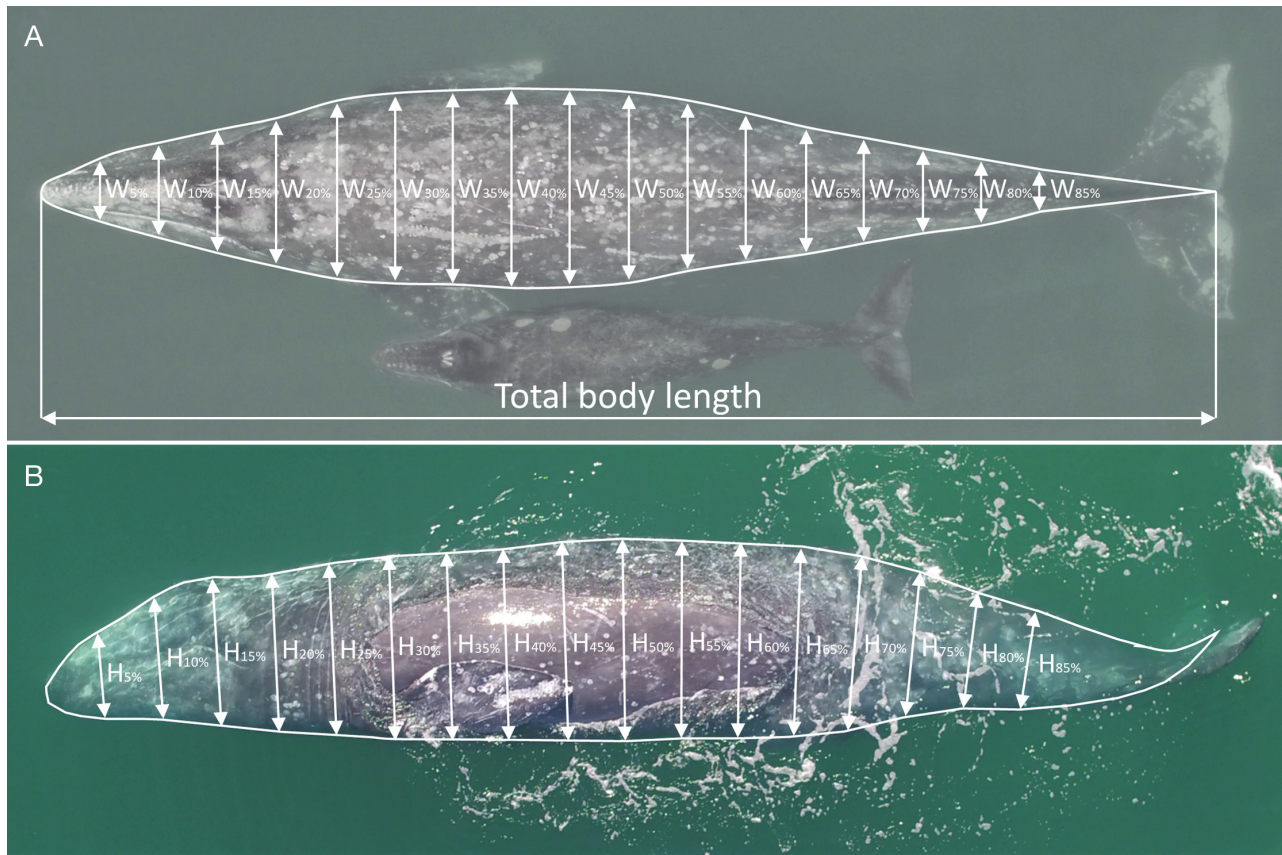


Fig. 1. Example aerial photographs of (A) the dorsal surface of a gray whale, used to measure body length and width (W) at 5% increments along the body axis from 5 to 85% body length from the rostrum (white arrows), and (B) the lateral side of another gray whale, used to extract body height (H , dorso-ventral distance) along the same measurement sites

al. 2019, 2020b), we first calculated the height:width (HW) ratio across the bodies of the whales (Christiansen et al. 2019), using individuals for which both dorsal width and lateral height measurements had been obtained. The HW ratio was calculated for each measurement site and separately for each reproductive class. We then estimated the total body volume (V_{Total}) of each whale (i) from the sum of the volumes of all body segments (s , the section of the body between 2 adjacent width/height measurement sites, $S = 20$ in total; Fig. 1):

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

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

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

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. The equations within the 2 sets of brackets of Eq. (2) assure that the width and height measurements are gradually interpolated from $W_{A,s,i}$ and $H_{A,s,i}$ when x is 0 to $W_{P,s,i}$ and $H_{P,s,i}$ when x is 1. For whales that lacked height measurements (lateral photographs), $H_{A,s,i}$ and $H_{P,s,i}$ were calculated from the corresponding $W_{A,s,i}$ and $W_{P,s,i}$ using the estimated HW ratios for the specific measurement sites. 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 [hereafter just '% BL']) and the end of the tail region (85–100% BL) were modelled as elliptical cones (Christiansen et al. 2019).

The body condition (BC_i) of gray whales was calculated from the residual of the relationship between body volume and body length (Christiansen et al. 2020a,b):

$$BC_i = \frac{BV_{obs,i} - BV_{exp,i}}{BV_{exp,i}} \quad (3)$$

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 , given by the log–log relationship between body volume and body length. A positive body condition means that an individual was in relatively better condition (had a relatively wider girth) than an average individual of the same body length, whereas a negative body condition means that the individual was in relatively poorer condition (had a relatively narrower girth).

2.3. Yearly variations in body condition

Linear mixed effect models (LMMs) were developed in R, using the ‘nlme’ package, to investigate and compare yearly variation in gray whale body condition in 2017, 2018 and 2019. Day of year and reproductive class were also included as explanatory variables to account for intra-seasonal variation in body condition and differences between reproductive classes. To avoid pseudo-replication, individual IDs were included as a random effect in the model. Comparison of model fit was made using Akaike’s information criterion (AIC). To determine the amount of variance explained by the models, the marginal R^2 (R^2_m , the variance explained by the fixed effects) and conditional R^2 (R^2_c , the variance explained by both the fixed and random effects) were obtained (Nakagawa & Schielzeth 2013), using the ‘MuMin’ package. Predicted values and confidence intervals were calculated using the ‘emmeans’ package. Model validation test included scatter plots of residuals versus fitted values and against each explanatory variable (to determine homogeneity of variance), histograms of residuals (to determine normality of variance) and estimates of leverage and Cook’s distance (to determine influential points and outliers, respectively). No violation of the assumptions of the LMMs were found.

In addition to accounting for individual variation through the random effect in the LMMs, we also ran a bootstrapping simulation where only a single value for each individual was randomly selected for each iteration. A LM (without random effect since there were no repeated measurements) was then fitted to the data, and the parameter values were extracted. We repeated this process 1000 times to obtain a density distribution around each model parameter, and compared these to the parameter values obtained from the best-fitting LMM.

2.4. Effect of maternal body condition on calf growth

The effect of maternal body condition on calf growth (i.e. body length) was investigated using LMMs. Year was included as an explanatory variable in the model to test if there was an overall difference in the body length of calves between years. To account for the growth of calves through the winter breeding season, day of year was included as a covariate in the model. The effect of maternal size (i.e. body length) was also assessed, as calf body length is positively related to maternal body length in gray whales (Perryman & Lynn 2002), humpback whales *Megaptera novaeangliae* (Christiansen et al. 2016) and right whales *Eubalaena* spp. (Christiansen et al. 2020a). Repeated measurements from the same whales were again accounted for by adding individual ID as a random effect in the model. The same model selection process and validation tests were performed (see Section 2.3).

2.5. Identifying lower body condition emaciation threshold

To identify the lower body condition threshold for gray whales at which emaciation (and possibly death by starvation) occurs, we used morphometric data from stranded gray whales recorded between 1997 and 2019 by The Marine Mammal Center, Sausalito, CA, USA, and the California Academy of Sciences, San Francisco, CA, USA. Only freshly stranded animals were used to minimize distortion in morphometric measurements resulting from bloating or deflation of the carcass (Moore et al. 2004). Further, only measurements from animals which had been classified as ‘emaciated’ were used, since the cause of death in these instances was linked to starvation. From the records that fulfilled these criteria, the body volume was estimated from the body length and girth measurements, following the methods of Christiansen et al. (2019), who demonstrated that morphometric data (i.e. length and girth) from lethally caught North Pacific right whales *E. japonica* could be used to accurately estimate body volume, and hence condition. In the current study, the number of girth measurements that were taken differed between individual gray whales, but were taken across 1 or more of the following 5 measurement sites: girth at eyes (G1, located at 17% BL), girth at axilla (G2, located at 30% BL), maximum girth (G3, located at 40% BL), girth at anus (G4, located at 72%

BL) and girth midway between the anus and the fluke notch (G5, located at 86% BL). The body volume of the stranded whales was calculated (predicted) from LMs that we developed using the data from our free-ranging gray whales, for which body girths at the same 5 girth measurements sites were calculated (for details, see Christiansen et al. 2019). The body condition of the stranded whales was then estimated using the same equation (Eq. 3) as for the free-living whales. We also opportunistically measured the body condition of a free-ranging, but visibly emaciated, gray whale in Cabo Pulmo, Mexico, on 2 March 2019, using a DJI Phantom 4 UAV (video courtesy of Kathryn Ayres). Although we did not have altimeter data to accurately measure its body length, it was visually determined to be a juvenile with a body length of approximately 10 m.

3. RESULTS

3.1. Sample size and effort

A total of 1245 measurements of gray whales were obtained, representing 322 measurements from calves, 231 from juveniles, 426 from adults (males and females without calves) and 266 from lactating females. After quality filtering and removing measurements of unidentified individuals (to avoid potential pseudo-replication), 1218 measurements (2017 = 59, 2018 = 531, 2019 = 628) remained of 742 individuals (2017 = 54, 2018 = 305, 2019 = 383) (Table 1). Measurements included 310 calves (mean \pm SD, BL = 5.38 \pm 0.77, min. = 3.74, max. = 7.20), 226 juveniles (10.52 \pm 0.73 m, 7.59, 11.20), 422 adults (11.90 \pm 0.57 m, 11.20, 14.23) and 260 lactating females (12.14 \pm 0.53 m, 10.73, 13.78) (Table 1). Single measurements

Table 1. Number of measurements (N) and number of gray whales measured (IDs) by unmanned aerial vehicle photography by year and reproductive class

Reproductive class	2017		2018		2019	
	N	IDs	N	IDs	N	IDs
Calves (3.74–7.20 m)	25	24	163	60	122	37
Juveniles (7.59–11.20 m)	2	2	72	60	152	126
Adults (11.20–14.23 m)	8	7	167	134	247	185
Lactating (10.73–13.78 m)	24	21	129	51	107	35
Total	59	54	531	305	628	383

were obtained from 501 (67.5%) whales, while 145 (19.6%) individuals were measured twice, and 96 (12.9%) whales were measured between 2 and 18 times.

3.2. Body shape, volume and condition

The body morphometric data showed that the bodies of individual gray whales were widest at approximately 40% BL for all 4 reproductive classes (Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m658p237_supp.pdf). The intra-seasonal change in body width during the winter breeding season in LSI varied between measurement sites and reproductive classes (Fig. 2). Calves increased in relative body width all across the body, from 20–75% BL, with the most significant increase at the mid region of the body, from 40–60% BL (Fig. 2). Juveniles, adults and lactating females all decreased in body width from behind the eyes (~17% BL) all the way to the peduncle (>85% BL). For the 3 reproductive classes, most of the change occurred between 40 and 70% BL; however, the rate of decline in body width was nearly twice as high for adults and lactating females compared to juveniles (Fig. 2).

The cross-sectional body shape of gray whales was slightly flattened in the lateral plane around the head region (0–20% BL), almost circular in the mid region (20–50% BL) and significantly flattened in the lateral plane across the posterior half of the body (50–85% BL) (Fig. 3; Table S1). There was no difference in the cross-sectional body shape between calves (N = 21), juveniles (N = 5) and adults (N = 9). No lateral photographs were obtained of lactating females.

The estimated body volume of gray whales ranged between 0.58 and 4.35 m³ (mean \pm SD, 2.01 \pm 0.90 m³) for calves, between 4.14 and 21.52 m³ (11.56 \pm 2.63 m³) for juveniles, between 10.36 and 29.60 m³ (16.82 \pm 3.39 m³) for adults and between 11.85 and 30.34 m³ (20.23 \pm 3.35 m³) for lactating females (Fig. 4A). There was a strong linear relationship between body volume and body length on the log–log scale ($F_{1,1243} = 65428$, $p < 0.001$, $R^2 = 0.98$, Fig. 4B):

$$\log(BV_j) = -4.31 + 2.81 \times \log(BL_j) \quad (4)$$

3.3. Yearly variations in body condition

The LMM that best explained the body condition of gray whales included reproductive class ($F_{3,736} = 76.4$,

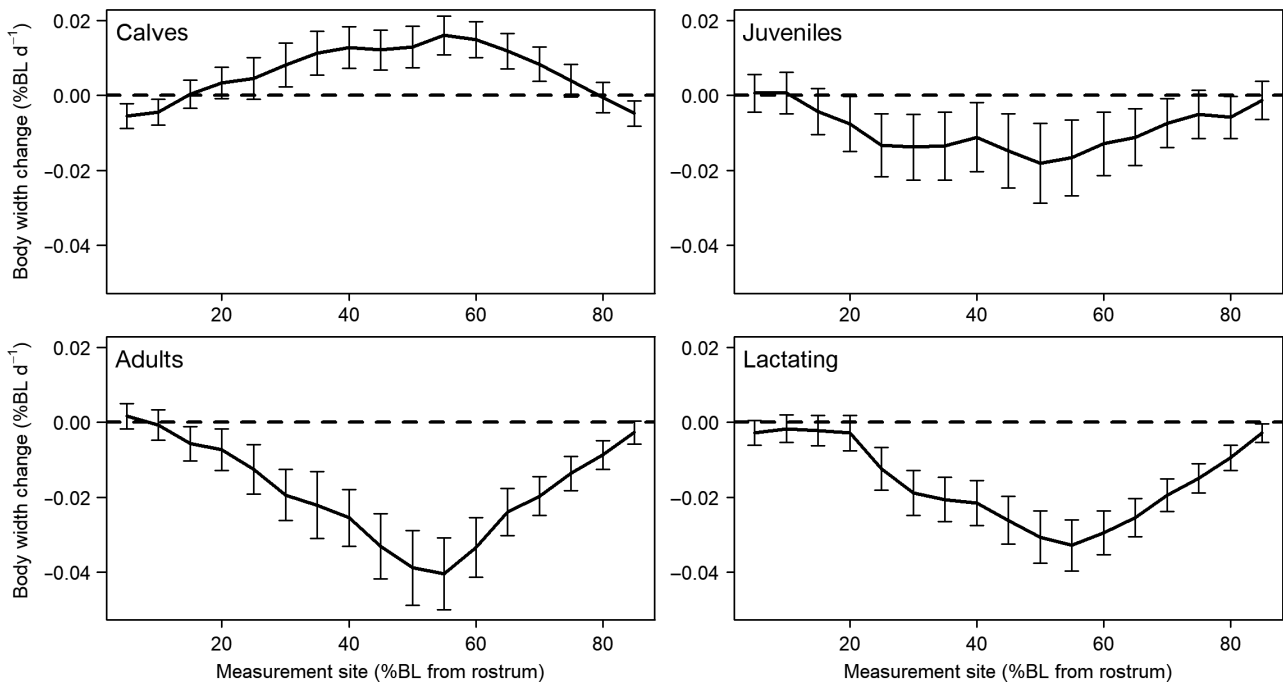


Fig. 2. Rate of change in relative body width (W, % of body length, % BL) of gray whale calves (N = 322), juveniles (N = 231), adults (N = 426) and lactating females (N = 266), at different measurement sites (Fig. 1). The solid black line represents the day effect (i.e. slope parameter (β) values of the day effect, based on the linear model: $W/BL = \alpha + \beta \times \text{day} + \text{year}$). Error bars represent the lower and upper 95% CIs. The dashed lines represent the level where relative body width remains constant ($\beta = 0$) throughout the winter breeding season

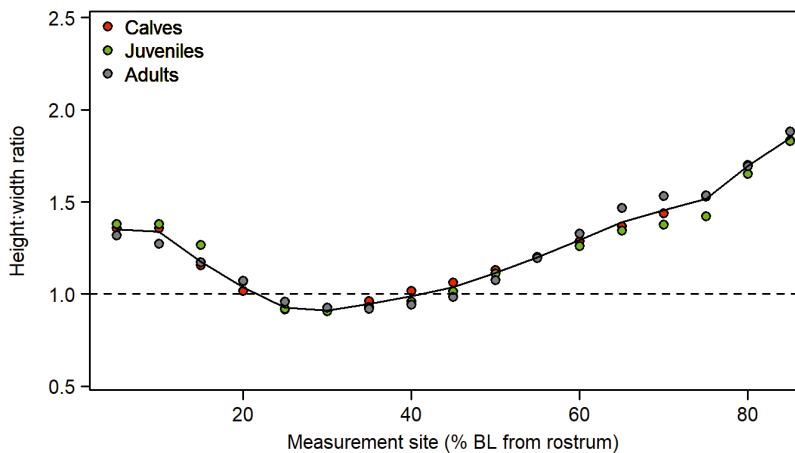


Fig. 3. Body height to width (HW) ratio of gray whale calves (N = 21), juveniles (N = 5) and adults (N = 9) across the body from 5 to 85% BL from the rostrum (see Fig. 1 for location of measurement sites). The solid black line represents the average HW ratio of all reproductive classes. The dashed black line indicates a ratio of 1:1, equivalent to a circular cross-sectional body shape

$p < 0.001$), year ($F_{2,736} = 15.7$, $p < 0.001$) and day of year conditional on reproductive class ($F_{4,472} = 66.7$, $p < 0.001$) as covariates (Model 9 in Table 2, Fig. S3). The fixed effects explained 35.1% (R^2_m) of the variance in body condition, whereas the fixed and random effects together explained 75.8% (R^2_c) of the variance.

For all 3 years, lactating females had the highest body condition (mean \pm SE: $34.2 \pm 2.23\%$, using 2017 as a reference year) at the beginning of the winter breeding season (16 January = the earliest day of sampling), followed by adults ($17.8 \pm 2.45\%$), juveniles ($10.7 \pm 2.83\%$) and newborn calves ($1.9 \pm 2.06\%$) (Fig. 5). The body condition of calves increased through the winter breeding season, at a rate of $0.24 \pm 0.026\% \text{ d}^{-1}$ (Fig. 5). Juveniles, adults and lactating females all decreased in body condition through the winter breeding season, at a rate of (mean \pm SE) -0.22 ± 0.063 , -0.34 ± 0.048 and $-0.33 \pm 0.031\% \text{ d}^{-1}$, respectively (Fig. 5). Consequently, at the end of the winter breeding season (6 April = the last day of sampling), adults were

in poorest body condition ($-9.5 \pm 2.76\%$, using 2017 as a reference year), followed by juveniles ($-6.6 \pm 3.47\%$), lactating females ($7.9 \pm 2.03\%$) and older (2–3 mo) calves ($21.4 \pm 1.93\%$) (Fig. 5). The body condition of all reproductive classes was significantly lower in 2018 ($-11.1 \pm 1.74\%$) and 2019 (-9.7

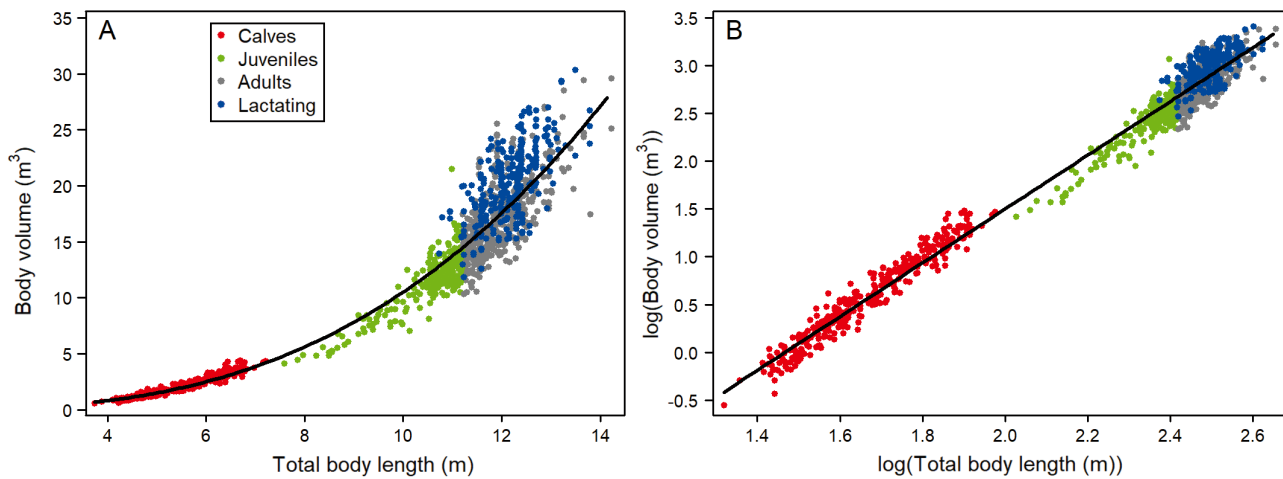


Fig. 4. (A) Gray whale body volume (BV) as a function of body length (BL) for different reproductive classes. The solid black line represents the back-transformed fitted values of the linear model. (B) Log–log relationship between BV and BL for the same data set, with the solid black line representing the fitted values of the linear model: $\log(\text{BV}) = -4.13 + 2.81 \times \log(\text{BL})$, $R^2 = 0.98$; $N = 1245$ measurements

Table 2. Results of the linear mixed effect model selection for gray whale body condition (BC) based on minimization of Akaike's information criterion (AIC). Rep: reproductive class (calf, juvenile, adult, lactating female); Animal.ID: number of individual whales (Groups); k : number of model parameters; N : sample size; R^2_m : marginal R-square (variance explained by fixed effects); R^2_c : conditional R-square (variance explained by fixed and random effects)

Model	Fixed effects	Random effects	k	N	Groups	R^2_m	R^2_c	AIC	ΔAIC
1	BC~1 (null)	~Animal.ID	1	1218	742	0.00	0.65	-1655.9	331.0
2	BC~Year	~Animal.ID	3	1218	742	0.06	0.65	-1704.7	282.2
3	BC~Day	~Animal.ID	2	1218	742	0.00	0.65	-1638.8	348.1
4	BC~Rep	~Animal.ID	4	1218	742	0.21	0.67	-1803.4	183.5
5	BC~Rep+Year	~Animal.ID	6	1218	742	0.21	0.66	-1812.6	174.3
6	BC~Rep+Rep×Year	~Animal.ID	12	1218	742	0.25	0.67	-1797.5	189.4
7	BC~Rep+Day	~Animal.ID	5	1218	742	0.22	0.66	-1793.1	193.8
8	BC~Rep+Rep×Day	~Animal.ID	8	1218	742	0.34	0.76	-1965.4	21.5
9	BC~Rep+Year+Rep×Day	~Animal.ID	10	1218	742	0.35	0.76	-1986.9	0.0

$\pm 1.76\%$) compared to 2017 (Fig. 5). The intra-seasonal change in body condition of whales did not differ between years.

The bootstrapping simulation showed a good fit between the model parameters derived from the LMM (where individual variation was accounted for by a random effect) and the density distribution of model parameters resulting from the simulated LMs (where only a single measurement of each individual was included per model iteration) (Fig. S4). The density distributions of the LMs overlapped with the LMM parameter values for 7 of the 10 model parameters, whereas the remaining 3 parameters were still showing the same general trend, and did not deviate far from the range of the corresponding density distribution (Fig. S4). This shows that our results were not biased by the inclusion of repeated measurements from some individuals.

3.4. Effect of maternal body condition on calf growth

We obtained 225 dual measurements of 91 mother–calf pairs. Most pairs were measured in 2018 ($N = 117$) and 2019 ($N = 98$), with only 10 mother–calf pairs being sampled in 2017. There was no effect of year or maternal body condition on the growth rate (i.e. body length) of gray whale calves (Table 3). Instead, the best-fitting model included day of year ($F_{1,133} = 466.8$, $p < 0.001$) and maternal body length ($F_{1,89} = 7.8$, $p = 0.007$) as covariates (Model 6 in Table 3). The fixed effects of the LMM explained 60.7% (R^2_m) of the data, whereas the fixed and random effects together explained 88.4% (R^2_c) of the variance. We found a positive relationship between calf body length and maternal body length, with calves increasing in length at a rate of (mean \pm SE) 0.249 ± 0.089 m

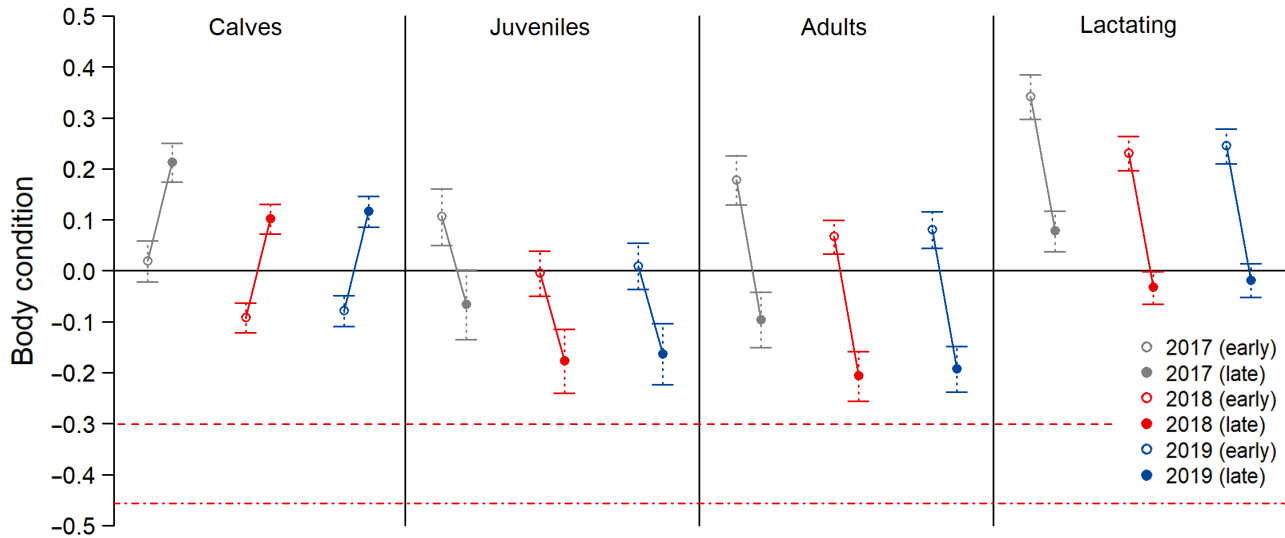


Fig. 5. Predicted (from Model 9 in Table 2) body condition of gray whale calves, juveniles, adults and lactating females early (16 January, open circles) and late (6 April, filled circles) in the winter breeding season, as a function of year. Error bars represent 95% confidence intervals. The sample size for different reproductive classes and years is given in Table 1. The red dashed line represents the body condition (-30.1%) of a visibly emaciated gray whale in Cabo Pulmo on 2 March 2019. The red dash-dotted line represents the mean body condition (-45.7%) of 3 emaciated stranded gray whales (see Table 4)

Table 3. Results of the linear mixed effect model selection for gray whale calf body length (CL) based on minimization of Akaike's information criterion (AIC). ML: maternal body length; MBC: maternal body condition; other abbreviations as in Table 2

Model	Fixed effects	Random effects	k	N	Groups	R^2_m	R^2_c	AIC	Δ AIC
1	CL~1 (null)	~Animal.ID	1	225	91	0.00	0.44	482.6	222.3
2	CL~Year	~Animal.ID	3	225	91	0.04	0.44	481.8	221.5
3	CL~ML	~Animal.ID	2	225	91	0.08	0.44	474.9	214.6
4	CL~MBC	~Animal.ID	2	225	91	0.27	0.69	420.7	160.4
5	CL~Day	~Animal.ID	2	225	91	0.57	0.88	262.9	2.6
6	CL~Day+ML	~Animal.ID	3	225	91	0.61	0.88	260.3	0.0
7	CL~Day×ML	~Animal.ID	4	225	91	0.61	0.88	272.2	11.9
8	CL~Day+ML+Year	~Animal.ID	5	225	91	0.61	0.88	265.2	4.9
9	CL~Day×ML×Year	~Animal.ID	12	225	91	0.60	0.89	306.7	46.4

per m increase in maternal length (Fig. 6A). The body length of calves increased through the winter breeding season at a rate of (mean \pm SE) $0.029 \pm 0.001 \text{ m d}^{-1}$ (Fig. 6B).

3.5. Lower body condition emaciation threshold

Only 3 of the stranded whales fulfilled our selection criteria of being both emaciated and in fresh condition. The selected animals were all juveniles (i.e. yearlings) (Table 4). The LMs used to predict body volume from the body length and girth measurements of the stranded animals explained between 99.49 and 99.91% of the variance (R^2) in body vol-

ume (Text S1). The estimated body condition of the emaciated gray whales ranged from -33.6 to -54.7% , with a mean of -45.7% (Table 4). The live emaciated juvenile gray whale measured in Cabo Pulmo in 2019 had a body volume of 7.35 m^3 and a body condition of -30.1% .

4. DISCUSSION

The aim of this study was to evaluate whether poor body condition of gray whales on their winter breeding grounds was associated with, or may have contributed to, the UME of 2019–2020. We found that the body condition of all reproductive classes in both

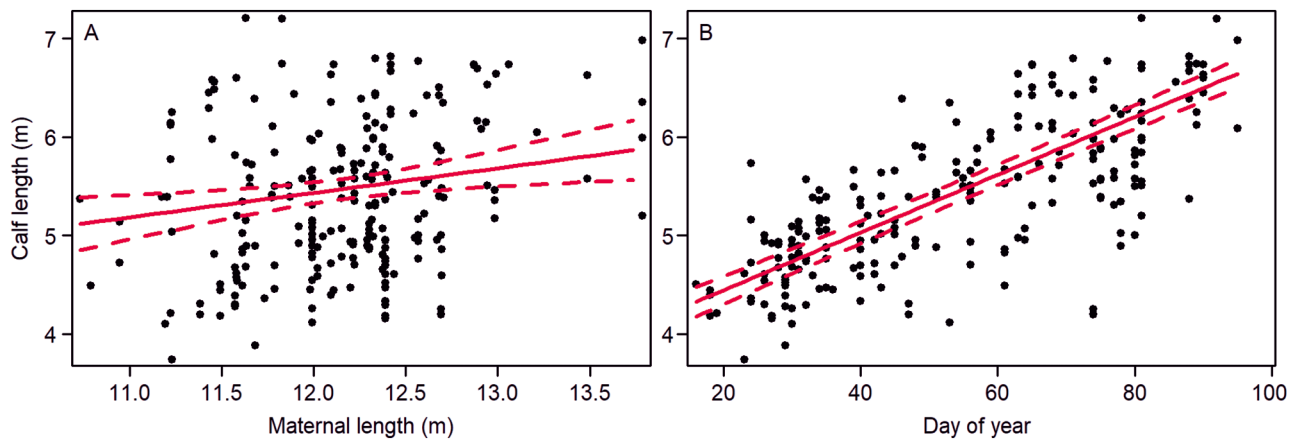


Fig. 6. Partial effect plots of gray whale calf body length as a function of (A) maternal body length and (B) day of year. The solid red lines represent the fitted values of the best-fitting linear mixed effect model (Model 6 in Table 3). The dashed red lines represent 95% confidence intervals. In (A), day of year was fixed at 55 (24 February), which is the middle of the gray whale winter breeding season. In (B), maternal body length was fixed at 12.15 m, which represents the average body length of a lactating female in the dataset. $N = 225$ measurements from 91 mother–calf pairs

Table 4. Body morphometric and condition data of stranded emaciated gray whales. Rep: reproductive class; BL: body length; G: girth at different points along the body (see Section 2.5 for details); BV: body volume; BC: body condition; M: male; F: female; Juv: juvenile; –: missing data points. Dates are given as yr-mo-d

ID	Date	Sex	Rep	BL (m)	G1 (m)	G2 (m)	G3 (m)	G4 (m)	G5 (m)	BV (m ³)	BC (%)
C-105	2000-04-08	M	Juv	8.24	2.42	2.64	3.20	–	–	3.13	–48.7
C-479	2015-10-22	F	Juv	8.14	2.80	–	–	1.80	1.46	3.91	–33.6
C-593	2019-03-10	F	Juv	8.16	–	–	2.80	–	–	2.69	–54.7

2018 and 2019 were significantly lower compared to 2017. Although elevated stranding numbers were not documented in 2018, the numbers of mother–calf pairs in LSI (and in other winter aggregation and lagoon areas in Baja California) were lower than expected in both 2018 (86 pairs) and 2019 (41 pairs) compared to 2017 (218 pairs) and before (Urbán et al. 2018, 2019). Our findings are in agreement with those of Ronzón-Contreras et al. (2019, 2020), who used visual qualitative scoring methods (Bradford et al. 2012) to classify the body condition of gray whales into ‘good’, ‘fair’ or ‘poor’ condition. They found a higher proportion (23.6 and 30.0%) of single (juvenile/adult) whales in ‘poor’ body condition in 2019 and 2020, compared to previous years (4.9–8.2%) and a higher proportion of lactating females in ‘fair’ condition in 2018 and 2019.

Taken together, our findings suggest that poor body condition and starvation contributed to the 2019–2020 gray whale UME. Between 2012 and 2018, the majority of stranded whales in Mexico were calves, whereas during the 2019–2020 UME, juveniles and adults made up the majority of deaths (Martínez-Aguilar et al. 2019, 2020). Our body condition data

support this pattern, with juveniles and adults being in significantly poorer condition (~0–10 and ~10–20% BC, respectively) compared to lactating females (~25–35% BC) when arriving on the Mexican breeding grounds (Fig. 5). Although juveniles spent relatively less energy than adults while on the breeding grounds, as would be expected since juveniles do not carry the added energetic costs of reproduction (Christiansen et al. 2013, 2016), both reproductive classes were in similarly poor condition (ca. –20% BC) at the end of winter breeding seasons of 2018 and 2019 (and seemed to be metabolising fat from the same body region). This was only slightly above the estimated body condition of the visibly emaciated gray whale juvenile (–30.1%) measured alive in Cabo Pulmo. With the body condition of juveniles and adults expected to decrease even further during the northbound migration, it is possible that some individuals in 2018 and 2019 would have fallen below the lower body condition threshold derived from the stranded emaciated whales (–45.7). This could explain the high proportion of stranded adults and juveniles during the 2019–2020 UME, and also the fact that most strandings occurred towards the

end of the winter breeding season and during the northern migration, when the animals had depleted their energy reserves (Martínez-Aguilar et al. 2019, 2020). In contrast, despite the high cost of lactation in baleen whales (Lockyer 1981, Christiansen et al. 2016, 2018), gray whale mothers were still in relatively good condition (14.4 and 17.4 percentage points higher than juveniles and adults, respectively) at the end of the 2018 and 2019 winter breeding season. This suggests that most lactating females would have survived the northbound migration back to the feeding grounds in those years. The facts that food resources of calves are ensured as long as their mothers live, that mothers were in relatively good condition at the end of the winter breeding seasons, and that dead calves are less likely to strand and may be discovered, could explain the relatively low number of dead calves during the 2019–2020 UME.

In baleen whales, mature females generally build up large body fat reserves during pregnancy to compensate for the additional energetic costs of gestation and lactation (Lockyer 1987, 2007, Vikingsson 1990, Christiansen et al. 2013). Our data show that for gray whale females, most of the fat reserves are stored around the mid-region of the body, between 40 and 70 % BL. The time it takes a female to build up these reserves will depend on the life history of the species (Lockyer 1984) and the amount of food available during the feeding season (Perryman et al. 2004, Leaper et al. 2006). The typical inter-calving interval of the eastern North Pacific gray whale is 2 yr, but can be 3 or more years (Rice & Wolman 1971, Blokhin 1984, Jones 1990). Hence, if a female does not have sufficient energy reserves to reproduce in a given year, she may simply postpone breeding for another year, during which time she may accumulate additional fat reserves (Rolland et al. 2016, Villegas-Amtmann et al. 2017). Consequently, late pregnant and early lactating females on the breeding grounds are generally in considerably better body condition compared to other reproductive classes (Christiansen et al. 2016, 2020a), as supported by our data. The overall higher body condition of lactating females could explain why few mother–calf pairs were found among the dead whales associated with the UME in 2019–2020, despite their relatively lower condition compared to 2017. However, if a mother and calf died during the migration, it is unlikely that the 2 carcasses would wash up on the same beach, and without a necropsy (most stranded whales were too decomposed, Gulland et al. 2005), it would be impossible to know if a stranded female had been lactating or not. Thus, it is possible that at least a proportion of the high number

of adult females that stranded during the first year of the 1999–2000 and the 2019–2020 UMEs (Le Boeuf et al. 2000, Gulland et al. 2005, Martínez-Aguilar et al. 2019) were in fact lactating females.

Although poor maternal body condition is known to suppress calf growth rates (Christiansen et al. 2018) and body condition (Christiansen et al. 2016) in baleen whales, we found no effect of maternal body condition on calf body length in gray whales. This suggests that the mothers were still investing the same amount of energy into their calves, irrespective of their own body condition at the beginning of the winter breeding season, and consequently their body condition may decline to a low level. The long-term consequence of this strategy would be that post-weaning females will need more time to build up the necessary fat reserves to breed again, which will reduce calving rates rather than calf survival (Rolland et al. 2016). This would help explain the low calving rates of gray whales in LSI between 2018 and 2020. However, it is also important to note that our body condition index is based on the estimated body volume of the whales (relative to body length), which does not account for potential variations in tissue composition, or within body variation in lipid content of various tissues through the winter breeding season (Lockyer 1981, Gunnlaugsson 2020). By combining aerial photogrammetry (to measure body volume) with hydrodynamic glide models applied to animal-borne tag data (to estimate tissue density, Narazaki et al. 2018), a more accurate estimate of energy content, and hence body condition, could be obtained in future studies.

While our study indicates that the suppressed survival and reproductive rates of gray whales during the UMEs of 2019–2020 and 1999–2000 were, at least partly, caused by starvation, the underlying factors that caused this reduction in body condition has not yet been determined. The lower body condition of gray whales on their Mexican breeding grounds in 2018 and 2019 could have been caused by (1) an increase in energy expenditure during the winter breeding season in Mexico, (2) an increase in energy expenditure and/or a reduction in feeding opportunities during the southbound migration or (3) a reduction in foraging success and/or an increase in energy expenditure during the previous feeding season.

An increase in energy expenditure of gray whales on their winter breeding grounds in Mexico could result from external factors, such as water temperature and anthropogenic factors (e.g. stress). The number of boats (including whale-watching vessels) operating in LSI were similar across the study period,

so the exposure of noise on individual whales should also have been similar between years. During both UMEs, water temperatures at the Mexican breeding grounds were lower than average, resulting in a southward shift in gray whale winter distribution (Le Boeuf et al. 2000, Gulland et al. 2005, Urbán et al. 2018, 2019, Martínez-Aguilar et al. 2019), as the animals generally seek optimal temperatures during the winter breeding season (Gardner & Chávez-Rosales 2000, Salvadeo et al. 2015). This change in water temperature and distribution did not seem to affect the energy expenditure of gray whales in LSI during the winter breeding seasons of 2018 and 2019, since the intra-seasonal rate of body condition decline was the same as in 2017. Further, the poorer body condition of gray whales in 2018 and 2019 was already visible by the time the whales arrived on their Mexican breeding grounds. Aerial photogrammetry research of southbound gray whales in 1999 found the same pattern, with whales already arriving at their breeding grounds in poorer body condition (Perryman et al. 1999). This suggests that the underlying cause of the 2018 and 2019 decline in gray whale condition began either on the feeding grounds or during the southbound migration.

The long-distance migration of gray whales undoubtedly carries significant energetic costs, which might vary between years due to variation in feeding opportunities (and location of foraging habitat) along the way and/or environmental or anthropogenic factors (Villegas-Amtmann et al. 2017). Gray whales feed opportunistically in several locations along their migratory route (Pike 1962, Sund 1975, Moore et al. 2007, Lagerquist et al. 2019, Soledade Lemos et al. 2020), and annual variations in the relative prey productivity of different foraging habitats could influence their body condition before they arrive at their Mexican breeding grounds. Human activities (e.g. shipping, naval activities, fisheries, oil and gas exploration and whale watching) along the migratory route could result in gray whales deviating from their optimal migration path (and hence extending the distance travelled, Frankel & Stein 2020, Sprogis et al. 2020) and/or increasing their metabolic rate (due to stress or increased swim speed) to avoid the stressors (Sumich 1983, Christiansen et al. 2014a). If the individual exposure to such stressors is sufficiently high, it could reduce the body condition of the whales before they arrive at their Mexican breeding grounds.

The poorer body condition of gray whales in 2018 and 2019 could also be due to a decline in prey on their feeding grounds. Benthic amphipods are of

great importance to gray whales in the Bering and Chukchi Seas, with 2 species comprising 90% of their food intake (Nerini 1984, Highsmith & Coyle 1992, Coyle & Highsmith 1994). Since the late 1980s, there has been a decline in the abundance and biomass of the amphipod community in the central Chirikov Basin, the main feeding area for gray whales in the Bering Sea, which in turn is believed to be caused by a change in the benthic community (Highsmith & Coyle 1992, Serenko & Koltun 1992, Coyle & Highsmith 1994, Grebmeier & Dunton 2000, Le Boeuf et al. 2000). In addition, Perryman et al. (2002, 2020) found a positive correlation between the length of time that primary feeding habitats in the Bering and Chukchi Seas were free of seasonal ice and the production of gray whale calves in the following year. This suggests a close relationship between prey availability and female body condition and reproduction. Soledade Lemos et al. (2020) found that gray whales on their foraging grounds along the Oregon coast, USA, were in significantly poorer condition in 2017 and 2018 (prior to the 2018 and 2019 winter breeding seasons, respectively), but not in 2016 (prior to the 2017 winter breeding season), which is in agreement with our findings. They explained the poorer condition of gray whales in 2017–2018 to be caused by lower upwelling, and consequently prey productivity, off the US west coast between 2016 and 2018 (Soledade Lemos et al. 2020).

Disease could also have contributed to the poor body condition of gray whales in 2018 and 2019. Infectious diseases, especially viral infections, are known to cause mass mortality events in cetaceans, and can affect all reproductive classes (Van Bressemer et al. 2009, 2014, Stephens et al. 2014, Morris et al. 2015). Infected animals often suffer a reduction in body condition, which in turn can increase the likelihood of further infection, which further reduces condition in a synergetic relationship (Beldomenico et al. 2008). Gulland et al. (2005) speculated that diseases, biotoxins and chemical contaminants could have contributed to the 1999–2000 gray whale UME; unfortunately, not enough data from stranded animals were available to test this hypothesis. While the same holds true for the 2019–2020 UME, it is still possible that diseases could have contributed to the observed reduction in gray whale body condition in 2018 and 2019. The whales could have attained the disease by feeding in certain areas or on certain prey species during those years.

Finally, density-dependent factors might be at play, with the eastern North Pacific gray whale population starting to reach the presumed current carry-

ing capacity of their environment (Moore et al. 2001, 2003). During the 1999–2000 gray whale UME, the population was believed to have been reduced by 25 % (Laake et al. 2012), after which the calving rate remained low for 3 yr (1999–2001), but started recovering again after 2002 (Perryman et al. 2004, 2020). In LSI, the number of mother–calf pairs was increasing from 2011 to 2017, after which it declined significantly in 2018, 2019 and 2020 (Urbán et al. 2019, 2020). If density-dependent factors are similarly influencing the gray whale calving rate, future surveys should detect a recovery of the calving rate following a reduction in the population size attributable to the 2019–2020 UME, and such surveys should be a future research priority.

In summary, our study shows that the 2019–2020 gray whale UME was associated with poor body condition of whales on the Mexican breeding grounds. Starvation could hence have played an important role in the UME, although other factors (e.g. disease or human disturbance) cannot be ruled out. Gray whales arrived at their Mexican breeding grounds in significantly poorer body condition in 2018 and 2019, suggesting that this decline in body condition must have occurred either during the previous feeding season and/or during the southbound migration. Measuring the body condition of gray whales early in the southbound migration should therefore be a future research priority. The reduction in body condition of gray whales in 2018 and 2019 suggests that some individuals did not have sufficient energy reserves to sustain themselves throughout the winter breeding season. That the whales still undertook the full migration to their Mexican breeding grounds indicates that gray whales are obligate migrators (Sumich 2014). For juveniles and adults, the effect might have been cumulative, with negative consequences on survival manifesting themselves towards the end of the 2019 breeding season. For lactating females, this reduction in body condition did not seem to have led to death by starvation, but would instead have prolonged the post-weaning recovery period of females, which could have caused the reduction in calving rates in both 2018 and 2019. Photo-ID data of known breeding females in LSI will help determine this in coming years. Finally, it is possible that some of the dead adults in 2019 were post-weaning females, which were still trying to recover their energy reserves from the previous breeding season. This reproductive class would have been particularly susceptible to further reductions in body condition and could explain the high proportion of adult females found among the stranded dead whales

during the first year of both gray whale UMEs (Le Boeuf et al. 2000, Gulland et al. 2005, Martínez-Aguilar et al. 2019). Although the full extent of the current gray whale UME is yet to be determined, the latest field season in LSI in 2020 still showed an increase in the number of stranded dead whales, low numbers of mother–calf pairs, and observations of whales trying to feed in the shallow areas of the breeding lagoon (Martínez-Aguilar et al. 2020).

Acknowledgements. This study was funded by Murdoch University, the Universidad Autónoma de Baja California Sur and The Laguna San Ignacio Ecosystem Science Program, a Project of The Ocean Foundation. F.C. received funding from the AIAS-COFUND II fellowship program 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. All field research was carried out under scientific research permits from the Secretaría del Medio Ambiente y Recursos Naturales, Subsecretaría de Gestión Para La Protección Ambiental, Dirección General De Vida Silvestre, de México (SGPA/DGVS/013210/18, SGPA/DGVS/000531/18, SGPA/DGVS/01822/17) and an animal ethics permit from Murdoch University (R3012/18), Australia. We thank the necropsy team of The Marine Mammal Center, Sausalito, CA, and the California Academy of Sciences, San Francisco, CA, for collecting and providing their data subsets. We thank Kathryn Ayres for providing the aerial video data from the emaciated gray whale in Cabo Pulmo, Mexico. We thank C. Cabrera, T. Chapman, J. Hoffman, M. Preble and C. Wood for help with data processing. This paper represents HIMB and SOEST contribution nos. 1789 and 10920, respectively. Finally, we thank R. Suryan, P. J. O. Miller and 2 anonymous reviewers for their constructive comments which helped to improve the manuscript. F.C. and L.B. conceived the study in consultation with J.U. and S.S. J.U., S.S., F.C. and L.B. secured funding. F.R., S.M.A., F.V., H.W., F.C. and L.B. collected the field data. F.C., F.R., F.V. and H.W. processed the data. F.C. designed and conducted the statistical analysis. F.C. wrote the manuscript, with input from all other authors.

LITERATURE CITED

- ✦ Beldomenico PM, Telfer S, Gebert S, Lukomski L, Bennett M, Begon M (2008) Poor condition and infection: a vicious circle in natural populations. *Proc R Soc B* 275: 1753–1759
- Berzin AA (1984) Soviet studies on the distribution and numbers of the gray whale in the Bering and Chukchi Seas from 1968 to 1982. In: Jones ML, Swartz SL, Leatherwood S (eds) *The gray whale, *Eschrichtius robustus**. Academic Press, Orlando, FL, p 409–419
- Blokhin SA (1984) Investigations of gray whales taken in the Chukotka coastal waters, USSR. In: Jones ML, Swartz SL, Leatherwood S (eds) *The gray whale, *Eschrichtius robustus**. Academic Press, Orlando, FL, p 487–509
- ✦ Bradford AL, Weller DW, Punt AE, Ivashchenko YV, Burdin AM, VanBlaricom GR, Brownell RL (2012) Leaner leviathans: body condition variation in a critically endangered whale population. *J Mammal* 93:251–266

- Brandon JR, Blokhin SA, Brownell RL, Punt AE (2005) Preliminary summary of catch data for the Soviet aboriginal fishery for the eastern Pacific gray whale: 1980–1991. Rep Int Whal Comm Doc SC/57/BRG6
- ✦ 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, Rasmussen MH, Lusseau D (2014a) Inferring energy expenditure from respiration rates in minke whales to measure the effects of whale watching boat interactions. *J Exp Mar Biol Ecol* 459:96–104
- ✦ Christiansen F, Vikingsson GA, Rasmussen MH, Lusseau D (2014b) Female body condition affects foetal growth in a capital breeding mysticete. *Funct Ecol* 28:579–588
- ✦ 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, 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
- ✦ Christiansen F, Sironi M, Moore MJ, Di Martino M and others (2019) Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. *Methods Ecol Evol* 10:2034–2044
- ✦ Christiansen F, Dawson SM, Durban JW, Fearnbach H and others (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, 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
- ✦ Coyle KO, Highsmith RC (1994) Benthic amphipod community in the northern Bering Sea—analysis of potential structuring mechanisms. *Mar Ecol Prog Ser* 107:233–244
- ✦ Dawson SM, Bowman MH, Leunissen E, Sirguy P (2017) Inexpensive aerial photogrammetry for studies of whales and large marine animals. *Front Mar Sci* 4:366
- ✦ Folkow LP, Blix AS (1992) Metabolic rates of minke whales (*Balaenoptera acutorostrata*) in cold water. *Acta Physiol Scand* 146:141–150
- ✦ Frankel AS, Stein PJ (2020) Gray whales hear and respond to signals from a 21–25 kHz active sonar. *Mar Mamm Sci* 36:1111–1125
- ✦ Gardner SC, Chávez-Rosales S (2000) Changes in the relative abundance and distribution of gray whales (*Eschrichtius robustus*) in Magdalena Bay, Mexico during an El Niño event. *Mar Mamm Sci* 16:728–738
- Grebmeier JM, Dunton KH (2000) Benthic processes in the Northern Bering/Chukchi Seas: status and global change. In: Huntington HP (ed) Impacts of changes in sea ice and other environmental parameters in the Arctic. Final report of the Marine Mammal Commission workshop, Girdwood, Alaska, 15–17 February, p 80–93
- Gulland FMD, Pérez-Cortés H, Urbán JR, Rojas-Bracho L and others (2005) Eastern North Pacific gray whale (*Eschrichtius robustus*) unusual mortality event, 1999–2000. US Dep Commer NOAA Tech Memo NMFS-AFSC-150:33
- ✦ Gunnlaugsson T (2020) Spatial and temporal variation in body mass and the blubber, muscle and visceral fat content of North Atlantic common minke whales. *J Cetacean Res Manag* 21:59–70
- ✦ Highsmith RC, Coyle KO (1992) Productivity of arctic amphipods relative to gray whale energy requirements. *Mar Ecol Prog Ser* 83:141–150
- Jones ML (1990) The reproductive cycle in gray whales based on photographic resightings of females on the breeding grounds from 1977–82. Rep Int Whal Comm Spec Issue 12:177–182
- Jones ML, Swartz SL (1984) Demography and phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. In: Jones ML, Swartz SL, Leatherwood S (eds) The gray whale, *Eschrichtius robustus*. Academic Press, Orlando, FL, p 309–374
- Laake JL, Punt AE, Hobbs R, Ferguson M, Rugh D, Breiwick J (2012) Gray whale southbound migration surveys 1967–2006: an integrated re-analysis. *J Cetacean Res Manag* 12:287–306
- ✦ Lagerquist BA, Palacios DM, Winsor MH, Irvine LM, Follett TM, Mate BR (2019) Feeding home ranges of Pacific Coast Feeding Group gray whales. *J Wildl Manag* 83: 925–937
- Le Boeuf BJ, Pérez-Cortés MH, Urbán JR, Mate BR, Oller-vides UF (2000) High gray whale mortality and low recruitment in 1999: potential causes and implications. *J Cetacean Res Manag* 2:85–99
- ✦ Leaper R, Cooke J, Trathan P, Reid K, Rowntree V, Payne R (2006) Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biol Lett* 2: 289–292
- Lockyer C (1981) Estimation of the energy costs of growth, maintenance and reproduction in the female minke whale, (*Balaenoptera acutorostrata*), from the Southern hemisphere. Document SC/32/Mi19. The Scientific Committee of the International Whaling Commission, Cambridge
- Lockyer C (1984) Review of baleen whale (Mysticeti) reproduction and implications for management. Rep Int Whal Comm 6:27–50
- Lockyer C (1987) Evaluation of the role of fat reserves in relation to the ecology of North Atlantic fin and sei whales. In: Huntley AC, Costa DP, Worthy GAJ, Castellini MA (eds) Approaches to marine mammal energetics. Special Publication No 1. Society for Marine Mammalogy, Lawrence, KS, p 183–203
- ✦ Lockyer C (2007) All creatures great and smaller: a study in cetacean life history energetics. *J Mar Biol Assoc UK* 87: 1035–1045
- ✦ 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
- Martínez-Aguilar S, Mariano-Meléndez E, López-Paz N, Castillo-Romero F and others (2019) Gray whale (*Eschrichtius robustus*) stranding records in Mexico during the winter breeding season in 2019. Rep Int Whal Comm Doc SC/68A/CMP/14
- Martínez-Aguilar S, Casanovas-Gamba P, Farriols-García M, González-Cisneros A and others (2020) Gray whale stranding records in Mexico during the 2020 winter breeding season. Rep Int Whal Comm Doc Change to SC/68B/CMP/13
- Mate BR, Lagerquist BA, Urbán JR (2003) A note on using satellite telemetry to document the use of San Ignacio Lagoon by gray whales (*Eschrichtius robustus*) during their reproductive season. *J Cetacean Res Manag* 5: 149–154

- ✦ 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
- Moore MJ, Knowlton AR, Kraus SD, McLellan WA, Bonde RK (2004) Morphometry, gross morphology and available histopathology in North Atlantic right whale (*Eubalaena glacialis*) mortalities (1970–2002). *J Cetacean Res Manag* 6:199–214
- Moore SE, Ljungblad DK, Van Schoik DR (1986) Annual patterns of gray whale (*Eschrichtius robustus*) distribution, abundance and behavior in the northern Bering and eastern Chukchi Seas, July 1980–83. *Rep Int Whal Comm Spec Issue* 8:231–242
- Moore SE, DeMaster DP, Dayton PK (2000) Cetacean habitat selection in the Alaskan Arctic during summer and autumn. *Arctic* 53:432–447
- ✦ Moore SE, Urbán J, Perryman WL, Gulland F and others (2001) Are gray whales hitting 'K' hard? *Mar Mamm Sci* 17:954–958
- ✦ Moore SE, Grebmeier JM, Davies JR (2003) Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. *Can J Zool* 81:734–742
- ✦ Moore SE, Wynne KM, Kinney JC, Grebmeier JM (2007) Gray whale occurrence and forage southeast of Kodiak, Island, Alaska. *Mar Mamm Sci* 23:419–428
- ✦ Morris SE, Zelner JL, Fauquier DA, Rowles TK, Rosel PE, Gulland F, Grenfell BT (2015) Partially observed epidemics in wildlife hosts: modelling an outbreak of dolphin morbillivirus in the northwestern Atlantic, June 2013–2014. *J R Soc Interface* 12:20150676
- ✦ 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
- ✦ Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- ✦ Narazaki T, Isojunno S, Nowacek DP, Swift R and others (2018) Body density of humpback whales (*Megaptera novaengliae*) [sic] in feeding aggregations estimated from hydrodynamic gliding performance. *PLOS ONE* 13: e0200287
- Nerini M (1984) A review of gray whale feeding ecology. In: Jones ML, Swartz SL, Leatherwood S (eds) *The gray whale, Eschrichtius robustus*. Academic Press, Orlando, FL, p 423–450
- ✦ NOAA (2020) 2019–2020 Gray whale unusual mortality event along the west coast and Alaska. www.fisheries.noaa.gov/national/marine-life-distress/2019-2020-gray-whale-unusual-mortality-event-along-west-coast-and-gray-whale-strandings (accessed 9 October 2020)
- Perryman WL, Lynn MS (2002) Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. *J Cetacean Res Manag* 4:155–164
- Perryman WL, Donahue MA, Reilly SB (1999) Eastern Pacific gray whale calf production in 1999 is the lowest in six years. 13th Bienn Conf Biol Mar Mammals 28 November to 3 December, 1999, Wailea, Maui, Hawaii, p 47
- ✦ Perryman WL, Donahue MA, Perkins PC, Reilly SB (2002) Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? *Mar Mamm Sci* 18:121–144
- Perryman WL, Watters GM, Swartz LK, Rowlett RA (2004) Preliminary results from shore-based surveys of northbound gray whale calves in 2003 and 2004, with a comparison to predicted numbers based on the distribution of seasonal ice. SC/56/BRG43 Presented to IWC Sci Committee, June 2004, Sorrento
- ✦ Perryman W, Joyce T, Weller D, Durban J (2020) Environmental factors influencing eastern north Pacific Gray whale calf production 1994–2016. *Mar Mamm Sci*, doi: 10.1111/mms.12755
- ✦ Pike GC (1962) Migration and feeding of the gray whale (*Eschrichtius gibbosus*). *J Fish Res Board Can* 19:815–838
- Poole MM (1984) Migration corridors of gray whales along the central California coast, 1980–1982. In: Jones ML, Swartz SL, Leatherwood S (eds) *The gray whale, Eschrichtius robustus*. Academic Press, Orlando, FL, p 389–407
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rice DW, Wolman AA (1971) The life history and ecology of the gray whale (*Eschrichtius robustus*). *Spec Publ* 3. American Society of Mammalogists, Stillwater, OK
- ✦ 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
- Ronzón-Contreras F, Martínez-Aguilar S, Swartz S, Calderon-Yañez E, Urbán JR (2019) Gray whales' body condition in Laguna San Ignacio, BCS, Mexico during 2019 winter breeding season. *Rep Int Whal Comm Doc SC/68A/CMP/13*
- Ronzón-Contreras F, Martínez-Aguilar S, Swartz S, Huerta-Patino R, Vilorio-Gomora L, Urban JR (2020) Gray whale's body condition in Laguna San Ignacio, BCS, Mexico, during 2020 breeding season. *Rep Int Whal Comm Doc SC/68B/CMP/14*
- Rugh DJ, Shelden KEW, Schulman-Janiger A (2001) Timing of the gray whale southbound migration. *J Cetacean Res Manag* 3:31–39
- ✦ Salvadeo CJ, Gómez Gallardo UA, Nájera-Caballero M, Urbán JR, Lluch-Belda D (2015) The effect of climate variability on gray whales (*Eschrichtius robustus*) within their wintering areas. *PLOS ONE* 10:e0134655
- ✦ Sanchez Pacheco JA (1998) Gray whale mortality at Ojo de Liebre and Guerrero Negro Lagoons, Baja California Sur, Mexico: 1984–1995. *Mar Mamm Sci* 14:149–155
- Serenko BI, Koltun VM (1992) Characteristics of benthic biocenoses of the Chukchi and Bering Seas. In: Nagel PA (ed) *Results of the third US-USSR Bering and Chukchi Seas expedition (BERPAC), Summer 1988*. US Fisheries and Wildlife Service, Washington, DC
- ✦ 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
- ✦ Sprogis KR, Bejder L, Hanf D, Christiansen F (2020) Behavioural responses of migrating humpback whales to swim-with-whale activities in the Ningaloo Marine Park, Western Australia. *J Exp Mar Biol Ecol* 522:151254
- ✦ Stephens PA, Boyd IL, McNamara JM, Houston AI (2009) Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology* 90:2057–2067

- Stephens N, Duignan PJ, Wang J, Bingham J and others (2014) Cetacean morbillivirus in coastal Indo-Pacific bottlenose dolphins, Western Australia. *Emerg Infect Dis* 20: 666–670
- Sumich JL (1983) Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. *Can J Zool* 61: 647–652
- Sumich JL (2014) *E. robustus*: the biology and human history of gray whales. Whale Cove Marine Education, Corvallis, OR
- Sund PN (1975) Evidence of feeding during migration and of an early birth of the California gray whale (*Eschrichtius robustus*). *J Mammal* 56:265–266
- Swartz SL (1986) Gray whale migratory, social and breeding behavior. *Rep Int Whal Comm Spec Issue* 8:207–229
- Swartz SL, Jones ML (1983) Gray whale (*Eschrichtius robustus*) calf production and mortality in the winter range. *Rep Int Whal Comm* 33:503–507
- Urbán JR, Gomez-Gallardo A, Ludwig S (2003a) Abundance and mortality of gray whales at Laguna San Ignacio, Mexico, during the 1997–98 El Niño and the 1998–99 La Niña. *Geofis Int* 42:439–446
- Urbán JR, Rojas-Bracho L, Perez-Cortes H, Gomez-Gallardo A, Swartz SL, Ludwig S, Brownell RL (2003b) A review of gray whales (*Eschrichtius robustus*) on their wintering grounds in Mexican waters. *J Cetacean Res Manag* 5: 281–295
- Urbán JR, Swartz SL, Gómez-Gallardo UA, Rojas-Bracho L (2011) Report of the gray whales' censuses in San Ignacio and Ojo de Liebre breeding lagoons, Mexico. *Rep Int Whal Comm Doc SC/62/BRG15*
- Urbán JR, Swartz SL, Martínez SA, Viloría LG, Gómez-Gallardo AU (2018) Gray whale abundance in Laguna San Ignacio and Bahía Magdalena, México. *Rep Int Whal Comm Doc SC/67B/CMP/09*
- Urbán JR, Swartz SL, Martínez AS, Viloría GL, Ronzón-Contreras F (2019) Gray whale abundance in Laguna San Ignacio and Bahía Magdalena, Baja California Sur, México. *Rep Int Whal Comm Doc SC/69a/CMP/12*
- Urbán JR, Swartz SL, Martínez-Aguilar S, Viloría GL (2020) 2020 Gray whale abundance in Laguna San Ignacio and Bahía Magdalena, Baja California Sur, México. *Rep Int Whal Comm Doc SC/69b/CMP*
- Van Bressem MF, Raga JA, Di Guardo G, Jepson PD and others (2009) Emerging infectious diseases in cetaceans worldwide and the possible role of environmental stressors. *Dis Aquat Org* 86:143–157
- Van Bressem MF, Duignan PJ, Banyard A, Barbieri M and others (2014) Cetacean morbillivirus: current knowledge and future directions. *Viruses* 6:5145–5181
- Vikingsson GA (1990) Energetic studies on fin and sei whales caught off Iceland. *Rep Int Whal Comm* 40: 365–373
- Villegas-Amtmann S, Schwarz LK, Gailey G, Sychenko O, Costa DP (2017) East or west: the energetic cost of being a gray whale and the consequence of losing energy to disturbance. *Endang Species Res* 34:167–183
- 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
- Yablokov AV, Bogoslovskaya LS (1984) A review of Russian research on the biology and commercial whaling of the gray whale. In: Jones ML, Swartz SL, Leatherwood S (eds) *The gray whale, Eschrichtius robustus*. Academic Press, Orlando, FL, p 465–485

*Editorial responsibility: Robert M. Suryan,
Juneau, Alaska, USA*

Reviewed by: 3 anonymous referees

Submitted: April 28, 2020

Accepted: November 13, 2020

Proofs received from author(s): December 28, 2020