RESEARCH ARTICLE

Global Change Biology **WILEY**

Modeling individual growth reveals decreasing gray whale body length and correlations with ocean climate indices at multiple scales

Enrico Pirotta[1] ![ORCID] | K. C. Bierlich[2] | Leslie New[3] | Lisa Hildebrand[2] | Clara N. Bird[2] ![ORCID] | Alejandro Fernandez Ajó[2] | Leigh G. Torres[2]

[1]Centre for Research into Ecological and Environmental Modelling, University of St Andrews, St Andrews, Scotland, UK

[2]Geospatial Ecology of Marine Megafauna Laboratory, Marine Mammal Institute, Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Newport, Oregon, USA

[3]Department of Mathematics, Computer Science and Statistics, Ursinus College, Collegeville, Pennsylvania, USA

Correspondence
Enrico Pirotta, Centre for Research into Ecological and Environmental Modelling, University of St Andrews, The Observatory, Buchanan Gardens, KY16 9LZ St Andrews, Fife, Scotland, UK.
Email: ep343@st-andrews.ac.uk

Abstract

Changes in body size have been documented across taxa in response to human activities and climate change. Body size influences many aspects of an individual's physiology, behavior, and ecology, ultimately affecting life history performance and resilience to stressors. In this study, we developed an analytical approach to model individual growth patterns using aerial imagery collected via drones, which can be used to investigate shifts in body size in a population and the associated drivers. We applied the method to a large morphological dataset of gray whales (*Eschrichtius robustus*) using a distinct foraging ground along the NE Pacific coast, and found that the asymptotic length of these whales has declined since around the year 2000 at an average rate of 0.05–0.12 m/y. The decline has been stronger in females, which are estimated to be now comparable in size to males, minimizing sexual dimorphism. We show that the decline in asymptotic length is correlated with two oceanographic metrics acting as proxies of habitat quality at different scales: the mean Pacific Decadal Oscillation index, and the mean ratio between upwelling intensity in a season and the number of relaxation events. These results suggest that the decline in gray whale body size may represent a plastic response to changing environmental conditions. Decreasing body size could have cascading effects on the population's demography, ability to adjust to environmental changes, and ecological influence on the structure of their community. This finding adds to the mounting evidence that body size is shrinking in several marine populations in association with climate change and other anthropogenic stressors. Our modeling approach is broadly applicable across multiple systems where morphological data on megafauna are collected using drones.

KEYWORDS
baleen whales, Bayesian modeling, drones, morphology, Pacific Decadal Oscillation, photogrammetry, shrinking size, upwelling and relaxation

Enrico Pirotta and K. C. Bierlich should be considered joint first author.

1 | INTRODUCTION

The distribution of body sizes within a population can vary as a plastic response to changing environmental conditions, and on an evolutionary scale due to selective pressures on smaller or larger individuals (Gardner et al., 2011; West-Eberhard, 2003). In recent decades, studies across ectotherms and endotherms have documented declines in body size in association with anthropogenic changes in the global climate, for example, rising temperatures, ocean acidification, and altered precipitation patterns (Gardner et al., 2011; Isaac, 2009; Sheridan & Bickford, 2011). Among the many examples spanning taxa and time scales, body size has been varying alongside climate in multiple species of birds (Weeks et al., 2020; Yom-Tov, 2001), fish and other aquatic organisms (Avaria-Llautureo et al., 2021; Daufresne et al., 2009), amphibians (Reading, 2007), and mammals (Hoy et al., 2018; Ozgul et al., 2009; Post et al., 1997; Smith et al., 1995). This evidence has led to the suggestion that decreasing size constitutes a common response to climate change (Sheridan & Bickford, 2011), although this hypothesis and the underlying mechanisms are still debated (Gardner et al., 2011). Proximately, changes in body size are generally driven by variation in the quality and availability of food resources, which affect nutrition and thus can promote or limit individual growth (Gardner et al., 2011; Yom-Tov & Geffen, 2011). For example, fluctuations in body weight and allometry of cohorts of red deer (*Cervus elaphus*) were associated with the North Atlantic Oscillation, which influences temperature and precipitation patterns with cascading effects on the growth of plant resources (Post et al., 1997).

The body size of an individual affects many physiological, behavioral, and ecological processes, including metabolic rates, thermoregulation, feeding success, the ability to store energy reserves, competition, and predation (Calder, 1984; Schmidt-Nielsen, 1984). As such, it exerts immense influence on most life history parameters. For example, body size is a key driver of survival and lifespan across taxa (Metcalfe & Monaghan, 2003). It is also related to the time of sexual maturity, and the rate and success of reproductive attempts thereafter (Blueweiss et al., 1978). Therefore, the distribution of body sizes in a population has consequences on its demography (Sauer & Slade, 1987) and, ultimately, its resilience to stressors (Isaac, 2009). If global climate change is associated with reductions in body size, smaller sizes could aggravate a population's ability to adjust to these changing conditions (Isaac, 2009; Sheridan & Bickford, 2011). In support of this theory, Cerini et al. (2023) and Clements and Ozgul (2016) proposed that changes in body size may be early signals of population decline. For example, the body size of equids rapidly decreased before their extinction in North America in the Pleistocene (Guthrie, 2003). In harvested populations, a dramatic decline in body size in baleen whales caught during commercial whaling operations preceded the global collapse of stocks by up to 40 years (Clements et al., 2017), while the collapse in biomass

in Atlantic cod (*Gadus morhua*) followed on from similar size shifts (Olsen et al., 2005).

Among marine mammals, changes in body size have been associated with density dependence in sperm whales (*Physeter macrocephalus*) (Kasuya, 1991), increased prey availability to harbor porpoises (*Phocoena phocoena*) (Read & Gaskin, 1990), nutritional stress in killer whales (*Orcinus orca*) (Groskreutz et al., 2019), and reduction in sea ice for polar bears (*Ursus maritimus*) (Rode et al., 2010). In critically endangered North Atlantic right whales (*Eubalaena glacialis*), exposure to multiple stressors is hypothesized as the cause of a multidecadal decrease in length (Stewart et al., 2021). In general, understanding how growth patterns vary as a function of habitat quality was identified as a key knowledge gap in a recent review of marine mammal growth (Adamczak et al., 2023), requiring extensive datasets on individual size and morphology.

The use of unoccupied aircraft systems (hereafter "drones") has revolutionized the collection of morphological data in free-ranging megafauna (Johnston, 2019). Photogrammetry methods can be applied to the aerial images collected from drones to derive unprecedented information on individual length and girth (e.g., Bierlich et al., 2021; Christiansen et al., 2019; Dawson et al., 2017; Durban et al., 2015). Some of the resulting datasets for cetaceans are now sufficiently large to contain repeated measurements of individuals over extended periods of time. Such datasets provide the unique opportunity to investigate individual growth patterns and address some of the knowledge gaps regarding growth, environmental conditions, and vital rates. However, aerial photogrammetry is associated with uncertainty that arises from different aspects of the observation process. Analytical methods have been developed to incorporate such measurement error in single observations (Bierlich et al., 2021), but these methods have not taken into account that observations form a time series of individuals' growth and consequently have not explicitly ensured that there is consistency in individual size over time (e.g., that an individual is not estimated to shrink between consecutive time points). Building mechanistic information on growth into these models is therefore required to improve size estimation and to correctly investigate growth patterns of animals within a population. Moreover, drone technology and photogrammetry methods have improved rapidly over recent years. An explicit model for growth could therefore help leverage the greater accuracy of recent measurements of an individual to reduce the uncertainty around data collected using older technology.

The Eastern North Pacific (ENP) population of gray whales (*Eschrichtius robustus*; population size: 14,526 individuals; Eguchi et al., 2023) spend the summer months in foraging grounds in the Bering, Chukchi, and Beaufort Seas feeding on benthic amphipods (Hildebrand et al., 2021), after migration from wintering lagoons along Baja California Peninsula. In contrast, the Pacific Coast Feeding Group (PCFG) is a small subgroup of ~212 gray whales (Harris et al., 2022) that forage in shallow (<20 m) coastal waters between northern California (USA) and Vancouver Island (Canada) often targeting pelagic zooplankton prey (Hildebrand et al., 2021)

with distinct foraging tactics (Torres et al., 2018). It is unclear when PCFG whales started using this coastline and why, but the first available records in the northern part of their range date back to the late 1960s and early 1970s, whereas presumed PCFG whales have been reported along the coast of northern California as early as 1920 (Bierlich et al., 2023; Rice & Wolman, 1971). Recent studies indicate that individuals in the PCFG are in worse body condition (Torres et al., 2022) and overall shorter (Bierlich et al., 2023) than their ENP counterparts. These findings have led to a hypothesis that the habitat of the PCFG provides an ecological opportunity for smaller whales targeting alternative prey types in shallow habitat and migrating over shorter distances. Alternatively, the PCFG range could represent an ecological trap, where individuals gain less energy due to different, lower-density prey or more costly foraging tactics (Torres et al., 2022).

The PCFG foraging range is the nearshore habitat (within ~3 km of shore) of the Northern California Current system (NCCS), which is part of an eastern boundary current upwelling system where strong northerly winds in spring and summer bring cold, nutrient-rich waters into the photic zone (Bograd et al., 2009). Local retention of these nutrients is critical to promote primary productivity that supports the food web (Botsford et al., 2006; Wing et al., 1995). This retention is facilitated by relaxation events, when the dominant northerly winds cease and prevent nutrients from being advected offshore. The importance of this alternation between upwelling and relaxation for phytoplankton growth and zooplankton recruitment and aggregation is known as the Intermittent Upwelling Hypothesis (IUH; Menge & Menge, 2013). In line with this hypothesis, recent evidence shows that PCFG gray whale zooplankton prey, foraging effort, and density is maximal when moderate levels of upwelling are interspersed with relaxation events (Barlow et al., 2024). While the IUH may shape gray whale foraging opportunities within their foraging range, basin-wide oceanographic patterns, like the Pacific Decadal Oscillation (PDO; Mantua & Hare, 2002; Newman et al., 2016), potentially regulate these upwelling and relaxation processes at a broader scale (Bylhouwer et al., 2013; Macias et al., 2012). The PDO is known to oscillate at an approximately decadal scale and to correlate with various components of the ecosystem (e.g., Mantua et al., 1997; Pfister et al., 2018; Shimabukuro et al., 2023), including ENP gray whale calf production (Perryman et al., 2021). Both upwelling and PDO cycles and intensity may be changing with climate change (e.g., Bograd et al., 2023; Litzow et al., 2020; Sydeman et al., 2014; Wang et al., 2015), which may thus influence foraging conditions for PCFG gray whales in the NCCS.

In this study, we use a 7-year morphological dataset from 130 individual PCFG gray whales to develop a Bayesian hierarchical modeling approach for estimating individual growth patterns over time, while accounting for the uncertainty associated with length estimation from aerial imagery. We then apply the model to investigate the temporal trend in individual size within this group of whales and test its correlation with indices of ocean climate fluctuations (PDO and the balance between upwelling and relaxation) at multiple temporal scales.

2 | METHODS

2.1 | Data collection and processing

Data collection on PCFG gray whales was carried out from a small research vessel over seven foraging seasons (late May to mid-October 2016–2022) along the coast of central Oregon, USA (departing from Newport, OR, 44.6368° N 124.0535° W), as described in Lemos et al. (2022). Visual surveys concentrated in the coastal strip (<3 km from shore), aiming to maximize whale encounters (i.e., surveys did not follow standardized transect lines). Individual whales were photo-identified by comparing photographs taken in the field with catalogs for the PCFG held by the Marine Mammal Institute at Oregon State University and Cascadia Research Collective (Olympia, WA, USA). Sex was derived from existing information in the catalogs, previous genetic analyses (Lang et al., 2014), or genetic analyses of the fecal samples (Lemos et al., 2020). Age in years was estimated from the date of the first sighting, which provided either a known age (i.e., whales first sighted as calves) or a minimum estimate (the time elapsed from the first sighting, plus 1 because unknown-age individuals could not be <1 year old at first sighting). For some individuals, the identity of their mother was known from photo-identification records, as they were first encountered as calves in the study area in close association with an adult (see Data S1).

Aerial images of individual gray whales were collected using drones deployed from the survey vessel. Over the years, different drone models with improved technology were used (DJI Phantom 3 Pro, Phantom 4, Phantom 4 Pro, and two distinct Inspire 2 drones, referred to as Inspire 2-a and Inspire 2-b; see Table S1 for all model, camera, and altimeter specifications in different study periods). From the drone footage, we extracted snapshots using VLC media player (Version 3.16 VideoLAN), which were then processed and measured using software MorphoMetriX and CollatriX (Bird & Bierlich, 2020; Torres & Bierlich, 2020). All drones are susceptible to measurement uncertainty associated with the camera, focal length lens, altimeter, altitude, and pixel measurement (Bierlich et al., 2021). To account for photogrammetric uncertainty associated with each drone, we carried out calibration flights to collect training data of a known-sized object at various altitudes throughout each field season (Bierlich et al., 2021). Specifically, we collected videos of a 1.0 m board floating at the surface at altitudes between 13 and 62 m and extracted snapshots using VLC media player to measure in MorphoMetriX (W. Torres & Bierlich, 2020; Table S2).

2.2 | Environmental data

We accessed data on two environmental indices influencing the oceanography of the ENP at different spatiotemporal scales, to investigate their correlation with gray whale length. Monthly values of the PDO index were derived from NOAA National Centers for Environmental Information (https://www.ncei.noaa.gov/access/monitoring/pdo/) and summarized as annual means. Because PDO

is a decadal index, we tested its correlation with asymptotic length at two large temporal scales: (1) the mean annual PDO over the 10 years prior to the birth of an individual, representing the PDO regime experienced by the mother, and (2) the mean annual PDO in the 10 years after birth, representing the PDO regime an individual experienced during the growth phase.

As a more proximate metric of habitat quality in the PCFG range, we derived a second index from the daily values of the Coastal Upwelling Transport Index (CUTI) at 44°N, representative of vertical transport near the study area (Jacox et al., 2018), which were downloaded from https://mjacox.com/upwelling-indices/. We classified each day between the observed spring transition date and the observed end date of the upwelling season as either a relaxation day, when the daily CUTI was below the mean daily CUTI value during the upwelling season (across years) at 44°N, or an upwelling day otherwise. We then calculated two annual metrics: the Total Upwelling Magnitude Index (TUMI), that is, the cumulative sum of the CUTI index (Bograd et al., 2009) on upwelling days only, and the total number of relaxation days during the upwelling season. We took the ratio of these two metrics to represent the balance between upwelling and relaxation in the system. We tested the correlation of the resulting index with asymptotic length at three temporal scales, which represent three different biological hypotheses for how gray whales may achieve their asymptotic body size: (1) the mean index in the 2 years prior to birth was taken to represent the environmental conditions experienced by the mother during the year prior to pregnancy and during gestation; (2) the mean index in the 5 years after birth was assessed to capture the environmental conditions experienced by a young individual as it undergoes its phase of fastest growth; and (3) the mean index across both periods (from 2 years prior to birth until 5 years after birth) was investigated to assess the influence of environmental conditions experienced by the mother and by the calf.

2.3 | Statistical analysis

We developed an analytical approach that combines a process model for whale growth over time and an observation model to account for the uncertainty associated with length estimation from aerial imagery.

For the process component, we used a Putter growth curve, following Bierlich et al. (2023) and Agbayani et al. (2020), assuming that whale length did not change over one data collection season (May–October; but see treatment of calf measurements below). Specifically, the length of individual i on year t was formulated as:

$$L_{i,t} = A_i \cdot \left(1 - e^{-K \cdot (y_{i,t} - t_0)} \right) \quad (1)$$

where K is the growth rate, $y_{i,t}$ is the age of the individual in years (see Data S1 for a discussion of the age prior for unknown-age individuals; Figures S5 and S6), t_0 is the age at which size is 0, and A_i is the individual-specific asymptotic length.

We evaluated the occurrence of a temporal trend in the asymptote using a broken-stick formulation (model version v1; see Data S1 for discussion on the choice of this functional form and for exploration of a temporal trend in the growth rate parameter K; Figures S7 and S9). Specifically, we assumed the mean asymptotic length for the population, A, was constant up until a breakpoint, δ, after which A was assumed to change over time, according to the slope v:

$$A_i = b \cdot A + (1 - b) \cdot \left[A + v \cdot (B_i - \delta) \right] + \varepsilon_i \quad (2)$$

where b is an indicator variable taking value 1 if the birth year of that individual (B_i) is $\leq \delta$ and 0 otherwise. ε_i represents an individual-level random effect, with standard deviation σ_A:

$$\varepsilon_i \sim \text{Normal} \left(0, \sigma_A \right) \quad (3)$$

Separately, we investigated whether the temporal trend varied by sex (s_i; model v2), by fitting a distinct intercept and slope for the asymptote:

$$A_i = b \cdot A_{s_i} + (1 - b) \cdot \left[A_{s_i} + v_{s_i} \cdot (B_i - \delta) \right] + \varepsilon_i \quad (4)$$

In alternative to the temporal trend, we tested the correlation between PDO and the asymptote using:

$$A_i = A + \beta_1 \cdot E_i + \varepsilon_i \quad (5)$$

where E_i is the mean annual PDO index summarized either over the 10 years prior to the birth of individual i (model v3.1) or over the 10 years after birth (model v3.2), and β_1 is the corresponding coefficient. Finally, we tested the correlation between the mean ratio of TUMI on upwelling days to the number of relaxations (R_i) and the length asymptote, using the same formulation presented in Equation 5:

$$A_i = A + \beta_2 \cdot R_i + \varepsilon_i \quad (6)$$

As detailed above, the mean ratio R_i was calculated at three different scales (2 years prior to birth, model v4.1; 5 years after birth, model v4.2; from 2 years prior until 5 years after birth, model v4.3), representing three hypotheses for how environmental conditions may associate with gray whale growth. Note that the CUTI index (and thus the TUMI-derived covariate) is only available from 1988 onwards; therefore, we provided a uniform prior distribution (ranging between the minimum and the maximum values in the data) for the missing values of the ratio in earlier years, from which the mean R_i was then calculated. The three sets of covariates that were investigated in the model (i.e., year, PDO, and the ratio of TUMI to number of relaxations) are highly collinear (see Data S1). Therefore, their concurrent inclusion in the same model affects the stability of the estimation of model coefficients (Belsley et al., 1980; Dormann et al., 2013), as we demonstrate in the Data S1, and is not discussed further.

In the first year of life, calves have a faster growth rate, which is generally captured using a two-phase growth model (e.g., Agbayani et al., 2020). However, we did not have precise data on calf ages to inform the first growth phase. Therefore, we drew the length

of <1-year-old calves from a uniform distribution ranging between 3.5 m (approximately 1 m shorter than the reported average size at birth; Agbayani et al., 2020) and the estimated length of that individual at age 1 year, that is,

$$L_{i,0} \sim \text{Uniform}\left(3.5, L_{i,1}\right) \tag{6}$$

We retained this modification for consistency with previous work on baleen whales, but note that modeling calves' length using the same growth model as for non-calves had no effect on the results (Data S1).

The observation component was based on the Bayesian uncertainty model proposed by Bierlich et al. (2021). For simplicity, the subscripts indicating the measured individual, the measurement date and the corresponding images are omitted from the equations below. Following Bierlich et al. (2021), the expected length of an object in pixels (*P*) was thus modeled as:

$$P = L \cdot f \cdot I / (a \cdot S) \tag{7}$$

where *L* is the true length of the object (in m), *f* is the focal length of the camera (in mm), *I* is the image width (in pixels), *a* is the altitude (in m), and *S* is the sensor width of the camera (in mm). The true length in pixel is measured with error (σ_P), that is,

$$X \sim \text{Normal}\left(P, \sigma_P\right) \tag{8}$$

There is also uncertainty around the measured altitude (*v*), which depends on the methodology used for measurement ($m = 1, 2$; either a barometer or a laser altimeter respectively) and on the drone model ($d = 1, 2, \ldots 5$; note that the two Inspire 2 drones were treated separately; see Data S1):

$$v_{d,m} \sim \text{Normal}\left(a + c_{d,m}, \varphi_{d,m}\right) \tag{9}$$

where *a* is the true altitude, $c_{d,m}$ is a bias parameter specific to the barometer and/or laser altimeter of each drone type, and $\varphi_{d,m}$ is the associated standard deviation. Note that multiple aerial images of the same object could contribute to inform its true length (Bierlich et al., 2021). Length was known and equal to 1 m for the training data, which informed the parameters of the observation model.

Models were fitted in a Bayesian framework using Markov chain Monte Carlo (MCMC) algorithms implemented in package NIMBLE v1.0.0 (de Valpine et al., 2017) for R (R Core Team, 2023; see Tables S5–S11 for a list of the priors of all model parameters, and an exploration of the sensitivity of the results to the specification of the priors for the growth curve). Three chains were iterated in parallel for 1,000,000 iterations with a burn-in of 20,000 iterations. Chains were thinned to manageable object sizes by retaining 1 in 1000 iterations. Convergence and mixing were assessed by visually inspecting trace and density plots. Moreover, we ensured that the Brooks-Gelman-Rubin diagnostic fell below 1.1, that the Monte Carlo error was less than 5% of the sample standard deviation, and that the effective sample size was >400 for all parameters (Lunn et al., 2013).

3 | RESULTS

We measured 130 individual gray whales over the 7-year study period, amounting to a total of 827 images of 293 unique individual-year combinations. Specifically, 54 individuals were measured only in 1 year, 36 in two separate years, 19 in 3 years, 6 in 4 years, 6 in 5 years, 7 in 6 years, and 2 in 7 years. Age was known for 39 individuals (30%), while sex was known for 75% of individuals (54 females and 44 males). MCMC algorithms mixed and converged correctly, returning a satisfactory posterior effective sample size. The posterior estimates of all model parameters are reported in Data S1 for the four versions of the model (Tables S5–S11); here, we present the estimates (posterior medians and 95% credible intervals in square brackets) for version v1, except where otherwise stated.

The estimated curve indicates that PCFG gray whales undergo a period of rapid growth until an age of approximately 10–15 years, after which growth slows down, approaching the asymptote $A = 12.19$ m [11.96–12.48] at around 20–25 years of age, prior to the breakpoint (Figure 1a). However, we found large individual variation around this asymptotic length ($\sigma_A = 0.68$ [0.57–0.83]), with the largest individual estimated to reach 13.13 m [12.47–13.76], and the smallest only reaching 9.79 m [9.21–10.34]. The sex-specific analysis (model v2) indicates that males had a smaller asymptotic length than females prior to the breakpoint (males: 11.67 m [11.41–11.94]; females: 12.55 m [12.31–12.86]; Figure 1b).

The average length asymptote remained stable at *A* until around 2000 [1992–2005], after which it is estimated to have declined at a rate of −0.08 m/y [−0.12 to −0.05] (Figure 2a). The decline was stronger in females (−0.14 m/y [−0.20 to −0.09]) than in males, where the posterior distribution overlapped with 0 (−0.03 m/y [−0.08 to 0.01]; Figure 2b). Model v3.1 shows that declining asymptotic length was positively correlated with the mean of PDO over the 10 years prior to an individual's birth ($\beta_1 = 1.08$ [0.67–1.46]; Figure 3a), while there was no correlation with mean PDO over the 10 years after birth (model v3.2; $\beta_1 = 0.15$ [−0.35–0.66]; Figure 3b). The decline in asymptotic length was also negatively correlated with the mean ratio between TUMI on upwelling days and the number of relaxations summarized over 2 years prior to birth (model v4.1; $\beta_2 = −1.79$ [−2.67 to −0.86]; Figure 3c), 5 years after birth (model v4.2; $\beta_2 = −1.32$ [−2.22 to −0.40]; Figure 3d), and from 2 years prior until 5 years after birth (model v4.3; $\beta_2 = −1.65$ [−2.64 to −0.66]; Figure 3e).

The observation model estimates that pixel measurements had a median standard deviation of 4 pixels [3–5]. Additional uncertainty surrounding length estimation was associated with the measurement of altitude using different altimeters and drone types. The best-performing configuration was the Inspire 2-a drone equipped with a laser altimeter (bias = −0.36 m [−0.54 to −0.17]; standard deviation = 0.91 m [0.80–1.05]), while the worst performing was the Phantom 4 drone with altitude measured using a barometer (bias = 2.98 m [2.12–3.82]; standard deviation = 3.48 m [2.98–4.16]; see Data S1 for posterior results for all drone specifications). However, when recent measurements of an individual using an Inspire 2 with a
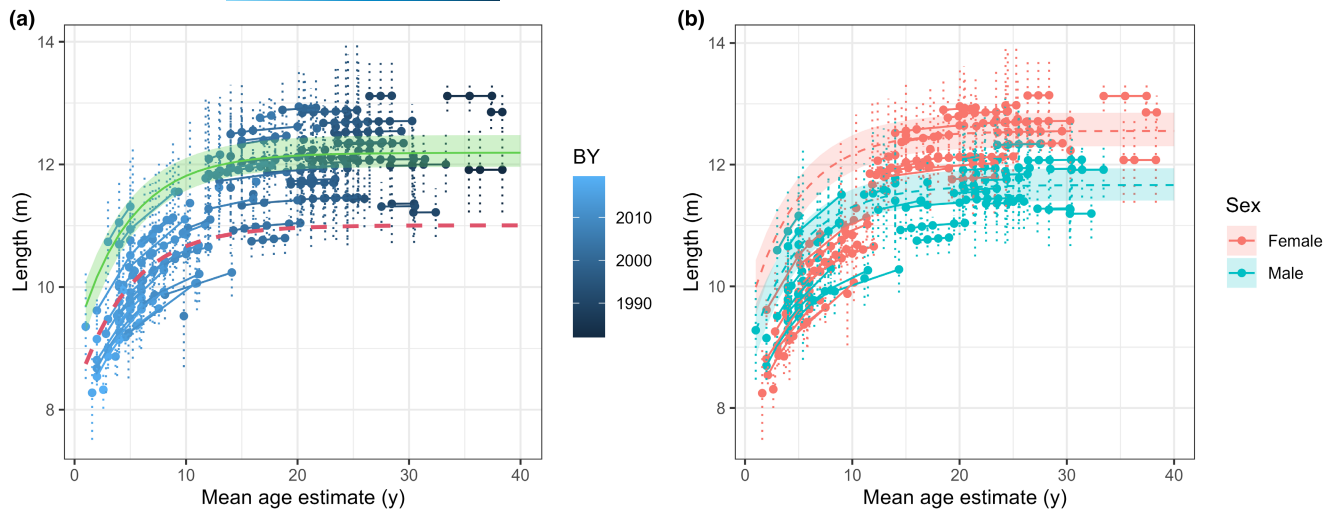
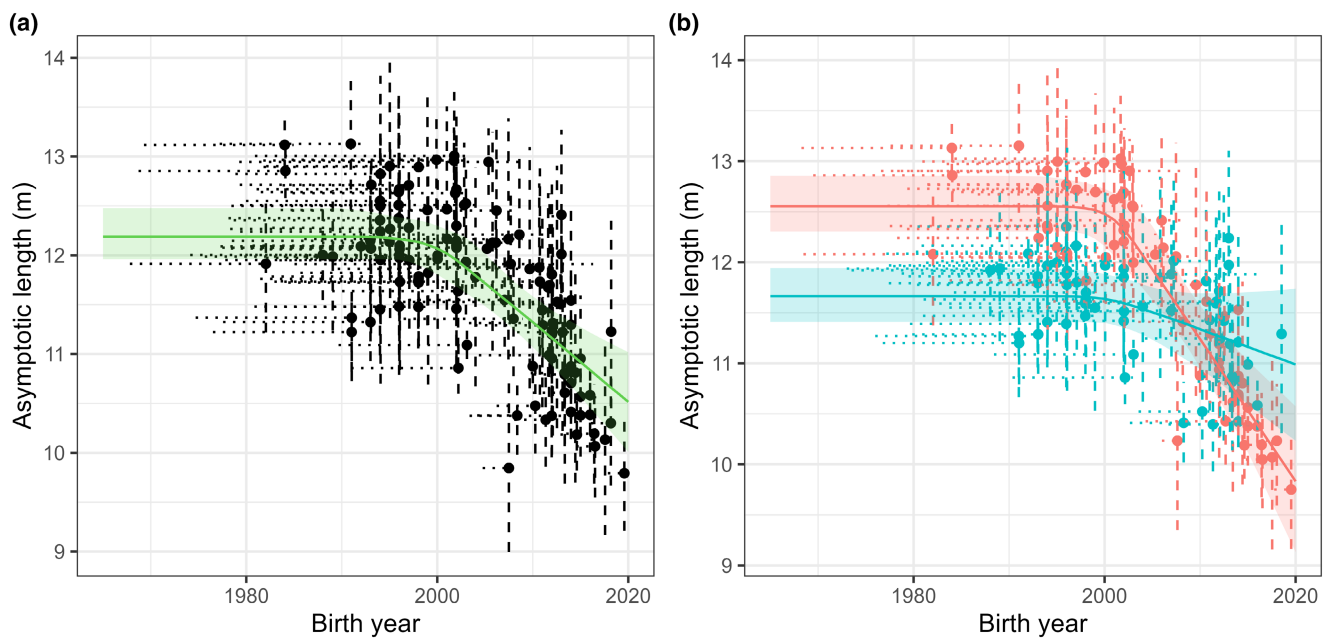**FIGURE 1** Posterior medians (points) and 95% credible intervals (dotted segments) of the estimated length of individual gray whales. Measurements from the same individual are connected by lines. In (a), results of model v1, colored by individual birth year, with the green line and ribbon visualizing the average growth curve for animals prior to breakpoint δ (i.e., the year after which the population asymptote is estimated to vary), and the red dashed line reporting the median expected growth curve for an animal born in 2015 (after the breakpoint). In (b), results of model v2 with sex-specific asymptote and temporal trend, where the colored dashed lines and ribbons represent the average growth curves for females and males prior to breakpoint δ.

FIGURE 2 Posterior medians (points) and 95% credible intervals (dashed vertical segments) of the estimated length asymptote of individual gray whales, plotted against the estimated birth year (95% credible intervals represented as dotted horizontal segments). In (a), results of model v1, with the green line and ribbon representing the estimated temporal trend in length asymptote. In (b), results of model v2, where a separate temporal trend was estimated for males (light blue line and ribbon) and females (red line and ribbon).

laser altimeter were available, the process model for growth allows for a substantial reduction in the uncertainty around older measurements with Phantom drones equipped with a barometer (e.g., Figure 4), which becomes particularly relevant for the 60 (out of 130) individuals that were only measured using Phantom drones. In the Data S1 we show that, despite the high bias and low precision estimated for the Phantom measurements, the inclusion of these data does not bias the median estimates and contributes to reduce the uncertainty.

4 | DISCUSSION

Using an analytical approach that models individual growth while accounting for measurement uncertainty in aerial photogrammetry, we found that the asymptotic length of a subgroup of gray whales feeding along the northeastern Pacific coast has decreased. The temporal trend in the asymptote of length followed a broken-stick form, with the decline starting around 2000 [1992–2005]. Remarkably, an
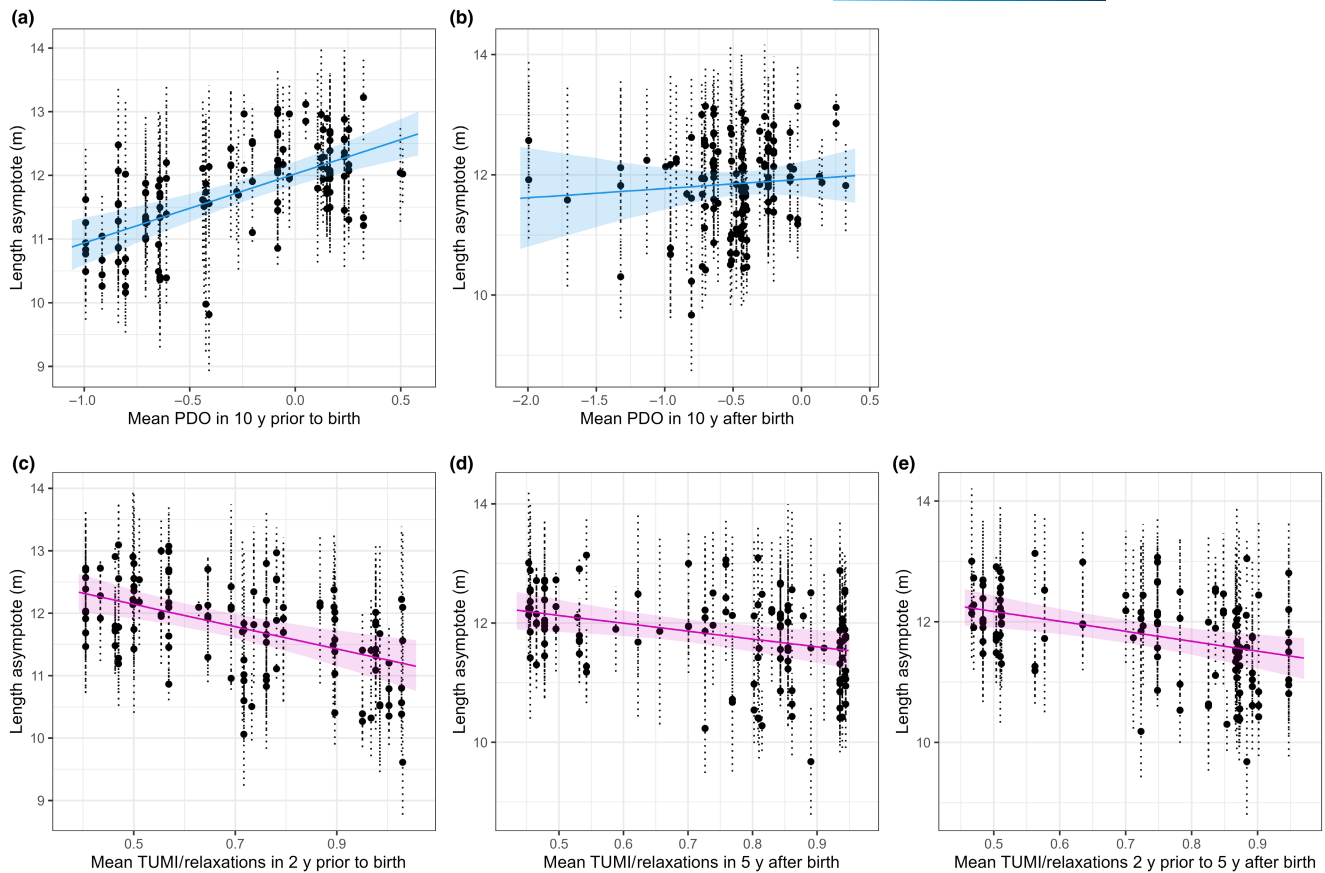
FIGURE 3 Estimated relationships between the environmental metrics and the asymptote of length. In (a, b), relationship with the mean PDO in the 10 years before and after an individual's birth, respectively. In (c–e), relationship with the mean ratio between TUMI on upwelling days and the number of relaxations in the 2 years before, 5 years after, and 2 years before to 5 years after an individual's birth, respectively. The points and segments are the medians and 95% credible intervals of the estimated asymptotes, while the line and ribbon represent the median and 95% credible interval of the relationship between the environmental metrics and the asymptote. See also Figure S2 for a comparison of the temporal trends of the length asymptote and the climate indices used in the model.

animal born in 2020 was estimated to reach a maximum length that was 1.65 m [1.38–1.96] shorter than that of an animal born in the 1980s. This decline in length was correlated with the trends in two climate indices that capture the productivity of the system at different scales, suggesting it could represent a plastic response to changing environmental conditions.

The decreasing body size of these gray whales could have important consequences for the demography of the PCFG. A smaller size will likely affect several aspects of individuals' physiology, behavior, and ecology (Calder, 1984; Schmidt-Nielsen, 1984). These consequences are particularly true for a capital breeding species (Stephens et al., 2009) that relies on energy reserves stored during the feeding season to support migratory, maintenance, and reproductive costs throughout the winter months. Ultimately, smaller structural size is expected to limit the amount of reserve mass an individual is able to carry, which may impact their ability to survive and reproduce successfully (Adamczak et al., 2023; Pirotta, 2022). For example, decreasing body size was associated with declining calving probability in North Atlantic right whales (Pirotta et al., 2024; Stewart et al., 2022). We found that the decline in body size was especially marked in females, which were historically larger than

males (12.53 m [12.29–12.81] vs. 11.68 m [11.42–11.94]; Agbayani et al., 2020; Bierlich et al., 2023) but were estimated in our study to have shrunk to the same size or smaller in recent years. Isaac (2009) hypothesized that drivers of body size (e.g., environmental variation) may affect the growth of the two sexes disproportionately, with cascading consequences for sexual dimorphism, mating dynamics, and fecundity. The sharp decline in female size emerging from our analysis is particularly concerning, because females bear the entirety of the energetic costs of gestation and lactation (Villegas-Amtmann et al., 2015).

Recent abundance estimates for the PCFG indicate that the subgroup has been largely stable until 2015, after which a slight decline was inferred (Harris et al., 2022). Age at sexual maturity and calving rates are unknown, but it is possible that the worse body condition documented for this subgroup compared with the broader ENP population (L. G. Torres et al., 2022) impacts the time it takes individuals to grow to sexual maturity, which could cause them to be shorter (Bierlich et al., 2023) and thus less able to accumulate adequate reserves to support reproduction. These differences between PCFG and ENP whales may be increasing if the declining body size we detected is restricted to the PCFG. In general, our findings are relevant
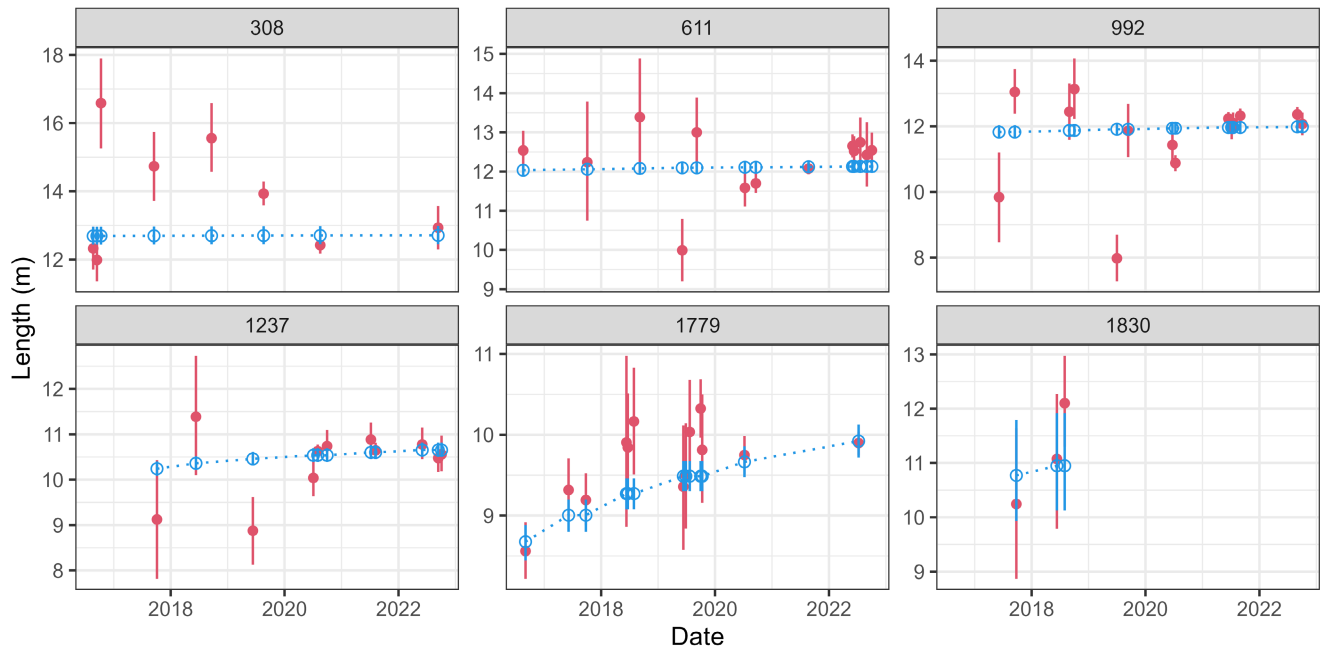
FIGURE 4 Posterior length estimates (median and 95% credible interval) for a sample of individual whales (identified using the individual code assigned by Cascadia Research Collective), obtained using the method presented here (blue) and compared with previous estimates from the Bayesian uncertainty model by Bierlich et al. (2021); the process model for growth helped reconcile some of the inconsistencies across measurements, and reduced the uncertainty around estimates obtained using earlier drones. Where recent measurements from improved drone technology were not available (e.g., individual #1830), uncertainty remained large. The method allowed estimating the growth of individuals that were followed through their juvenile years (e.g., individual #1779).

in the context of understanding why these individuals are using an alternative foraging ground, and why the usage continues if this habitat is associated with reduced growth. Differences in morphology and body condition between ENP and PCFG individuals have led to the contrasting hypotheses: (a) the PCFG habitat represents an ecological opportunity for animals to migrate over shorter distances and exploit a separate foraging niche, or (b) the PCFG range is an ecological trap, whereby smaller individuals, which may not be able to migrate as far as the Arctic or compete with larger individuals, are constrained to use a region of lower prey density of energetic gain (Bierlich et al., 2023; Torres et al., 2022). Future work should investigate growth patterns in the broader ENP population, which has undergone multiple large-scale mortality events associated with malnutrition in the past three decades (Christiansen et al., 2021; Gulland et al., 2005; Stewart et al., 2023), as other processes (e.g., density dependence) may also be causing a widespread size decline throughout the entire species.

There could be multiple mechanisms causing the observed decline in length, spanning from degrading habitat quality to increasing disturbance from human activities. We found a correlation between decreasing asymptotic length and two environmental metrics summarized over different temporal windows, suggesting that ocean climate conditions could be an underlying driver of whale length. Calf production in the broader ENP population has also been documented to positively correlate with PDO (Perryman et al., 2021), but at a shorter time scale (PDO conditions during early gestation). Moreover, this correlation was interpreted as an

effect of PDO on sea ice cover in northern feeding grounds, which would not apply to PCFG whales. Positive PDO phases are also correlated with increased gray whale abundance in breeding lagoons (Molina-Carrasco et al., 2024). In contrast, qualitative body condition estimates of PCFG whales determined from lateral photographs were found to be negatively associated with the 2-year running mean of PDO (Akmajian et al., 2021). Here, we investigated the potential relationship with mean PDO conditions at a temporal scale that is coherent with the scale at which the PDO regime varies. The correlation with the 10-year mean prior to an individual's birth could indicate that this long-term, multidecadal climatic oscillation influences the characteristics of the habitat experienced by females in a given year. Indeed, the mean PDO at this scale is negatively correlated with the second environmental metric assessed in our analysis: the mean of the ratio between total upwelling and number of relaxations (Figure S3; Bylhouwer et al., 2013; Macias et al., 2012). The correlations between whale length and summaries of this second metric aligns with oceanographic research showing that productivity in the coastal waters of Oregon is enhanced by the intermittency between upwelling and relaxation conditions, with extremes in either state being detrimental (Kudela et al., 2008; Menge & Menge, 2013). Recent work also indicates that PCFG gray whale density across their foraging range is related to the interactive effect of upwelling and relaxation, with high upwelling conditions associated with lower abundance (Barlow et al., 2024). Similarly, zooplankton prey of PCFG gray whales in coastal Oregon was found to be maximal at

moderate values of upwelling and relaxation (Dawn et al., Under review). We found a negative correlation between whale length and the ratio of upwelling and relaxation at multiple temporal scales, before and after the birth of an individual (Figure 3). Therefore, the asymptotic size of an individual might emerge from the integration of the conditions experienced by the mother as she prepares to reproduce and by the calf as it grows. The estimated relationships between individual body size and these indices of environmental quality remain purely correlative, and further exploration is warranted to determine the mechanistic drivers. As a result, it cannot be concluded that these variables drove the detected decrease in length in this population, which could also be the result of other stressors such as expanding human activities in the species' coastal habitat. Future studies should continue to monitor the trends in gray whale morphology in association with the PDO regime at a large scale, while further investigating the role of the balance between upwelling and relaxation conditions as a proxy of coastal habitat quality at a smaller time scale.

Albeit based on a small number of mother-calf pairs ($n = 9$), there is no indication that the smaller size of recently born calves was inherited from their mothers (Figure S14). This observation supports the hypothesis that the phenotypic decline in length emerges from a plastic response to changing environmental conditions, rather than being the result of selection (Gardner et al., 2011). A similar conclusion was reached when testing the contribution of ecological processes and adaptive evolution to the decreasing body size in Soay sheep (*Ovis aries*) (Ozgul et al., 2009). It should be noted that gray whales estimated to have shorter asymptotic lengths were also younger, that is, were further away from the asymptote. Moreover, the assumptions made regarding individuals of unknown age had some influence on the results (Figures S5 and S6). However, the decline in length was still detectable across a range of these assumptions, as well as when only using data on individuals with measurement from 2 or more years (Figure S9). Younger individuals that are currently smaller than expected may be able to "make up" for missed growth in the future (Metcalfe & Monaghan, 2001), although this contrasts with expected growth patterns in cetaceans (Stewart et al., 2021). In mammals, conditions in early life can lead to cohorts of individuals with distinct phenotypic traits and life history performance (Forchhammer et al., 2001; Metcalfe & Monaghan, 2001).

Our study has wide methodological implications beyond the system under analysis. We build on previous analyses (Bierlich et al., 2021, 2023) to develop an analytical approach that includes an explicit mechanistic model for individual growth and incorporates training data obtained from calibration flights, which are used to inform an observation component that accounts for various sources of uncertainty from different drone configurations. The proposed model thus expands on the model in Bierlich et al. (2023) by connecting measurements of a given individual at multiple time points and ensuring the consistency of an individual's size over time. Importantly, the direct inclusion of the observation model from Bierlich et al. (2021) also supports the appropriate propagation of

uncertainty across all steps of the analysis. In addition, the combination of the process and observation components allows refinement of the accuracy and precision of estimates derived using more error-prone configurations (as demonstrated in Figure 4). As such, the model makes use of improvements in technology so that older datasets can be retained in subsequent analyses. In contrast, previous studies have had to discard data points derived using earlier methods with high levels of uncertainty (Bierlich et al., 2023). The proposed approach is therefore directly applicable to the growing number of study systems where megafauna is regularly monitored using aerial imagery (Johnston, 2019). Building mechanistic information into the analysis of these photogrammetry data, and accounting for any measurement errors, are required for drawing robust inference about morphology, bioenergetics, and ecology.

In conclusion, our results contribute to the mounting evidence that the body size of some populations of large marine predators is shrinking (Groskreutz et al., 2019; Rode et al., 2010; Stewart et al., 2021). Reducing body size could result from increasing pressure from anthropogenic stressors, as well as represent a shared response to global climate change (Gardner et al., 2011; Sheridan & Bickford, 2011). The latter mechanism is supported by the correlations we found in this study between gray whale body size and indices of ocean climate conditions at different scales. It is imperative that this hypothesis and the underlying functional mechanisms are tested further with the expanding morphological datasets that are being collected using emerging technologies, such as drones, and the analytical approach presented here. Changes in the distribution of body sizes in a population could precede impending population declines and thus provide an early warning to trigger management and conservation interventions (Cerini et al., 2023; Clements et al., 2017; Clements & Ozgul, 2016). Moreover, the body size of predators can have cascading consequences on their prey, with implications for understanding and predicting changes across the trophic dynamics of communities (Shackell et al., 2010), although the potential for these trophic effects is unknown for gray whales in the PCFG.

AUTHOR CONTRIBUTIONS

Enrico Pirotta: Conceptualization; formal analysis; methodology; software; validation; visualization; writing – original draft; writing – review and editing. **K. C. Bierlich:** Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; writing – review and editing. **Leslie New:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Lisa Hildebrand:** Data curation; investigation; writing – review and editing. **Clara N. Bird:** Data curation; investigation; writing – review and editing. **Alejandro Fernandez Ajó:** Investigation; writing – review and editing. **Leigh G. Torres:** Conceptualization; funding acquisition; investigation; project administration; supervision; writing – review and editing.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code supporting this article are available from the Open Science Framework (https://osf.io/4xabg/; DOI: 10.17605/OSF.IO/4XABG).

ORCID

Enrico Pirotta https://orcid.org/0000-0003-3541-3676
Clara N. Bird https://orcid.org/0000-0001-7763-7761

REFERENCES

Adamczak, S. K., Mchuron, E. A., Christiansen, F., Dunkin, R., Mcmahon, C. R., Noren, S., Pirotta, E., Rosen, D., Sumich, J., & Costa, D. P. (2023). Growth in marine mammals: A review of growth patterns, composition and energy investment. *Conservation Physiology*, 11(1), coad035. https://doi.org/10.1093/conphys/coad035

Agbayani, S., Fortune, S. M. E., & Trites, A. W. (2020). Growth and development of North Pacific gray whales (*Eschrichtius robustus*). *Journal of Mammalogy*, 101(3), 742–754. https://doi.org/10.1093/jmammal/gyaa028

Akmajian, A. M., Scordino, J. J., Gearin, P., & Gosho, M. (2021). Body condition of gray whales (*Eschrichtius robustus*) feeding on the Pacific Coast reflects local and basinwide environmental drivers and biological parameters. *Journal of Cetacean Research and Management*, 22(1), 87–110. https://doi.org/10.47536/JCRM.V22I1.223

Avaria-Llautureo, J., Venditti, C., Rivadeneira, M. M., Inostroza-Michael, O., Rivera, R. J., Hernández, C. E., & Canales-Aguirre, C. B. (2021).

Historical warming consistently decreased size, dispersal and speciation rate of fish. *Nature Climate Change*, 11(9), 787–793. https://doi.org/10.1038/s41558-021-01123-5

Barlow, D. R., Strong, C. S., & Torres, L. G. (2024). Three decades of near-shore surveys reveal long-term patterns in gray whale habitat use, distribution, and abundance in the Northern California Current. *Scientific Reports*, 14(1), 9352.

Belsley, D. A., Kuh, E., & Welsch, R. E. (1980). *Regression diagnostics: Identifying influential data and sources of collinearity*. John Wiley & Sons. https://doi.org/10.1002/0471725153

Bierlich, K. C., Kane, A., Hildebrand, L., Bird, C. N., Fernandez Ajo, A., Stewart, J. D., Hewitt, J., Hildebrand, I., Sumich, J., & Torres, L. G. (2023). Downsized: Reliance on an alternative foraging ground is associated with smaller body size in gray whales. *Biology Letters*, 19(8), 20230043. https://doi.org/10.1098/rsbl.2023.0043

Bierlich, K. C., Schick, R. S., Hewitt, J., Dale, J., Goldbogen, J. A., Friedlaender, A. S., & Johnston, D. W. (2021). Bayesian approach for predicting photogrammetric uncertainty in morphometric measurements derived from drones. *Marine Ecology Progress Series*, 673, 193–210. https://doi.org/10.3354/meps13814

Bird, C., & Bierlich, K. (2020). CollatriX: A GUI to collate MorphoMetriX outputs. *Journal of Open Source Software*, 5(51), 2328. https://doi.org/10.21105/joss.02328

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., & Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologia*, 37(2), 257–272.

Bograd, S. J., Jacox, M. G., Hazen, E. L., Lovecchio, E., Montes, I., Pozo Buil, M., Shannon, L. J., Sydeman, W. J., & Rykaczewski, R. R. (2023). Climate change impacts on eastern boundary upwelling systems. *Annual Review of Marine Science*, 15, 303–328. https://doi.org/10.1146/annurev-marine-032122-021945

Bograd, S. J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W. J., & Schwing, F. B. (2009). Phenology of coastal upwelling in the California current. *Geophysical Research Letters*, 36(1), 1–5. https://doi.org/10.1029/2008GL035933

Botsford, L. W., Lawrence, C. A., Dever, E. P., Hastings, A., & Largier, J. (2006). Effects of variable winds on biological productivity on continental shelves in coastal upwelling systems. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 53(25–26), 3116–3140. https://doi.org/10.1016/j.dsr2.2006.07.011

Bylhouwer, B., Ianson, D., & Kohfeld, K. (2013). Changes in the onset and intensity of wind-driven upwelling and downwelling along the north American Pacific coast. *Journal of Geophysical Research: Oceans*, 118(5), 2565–2580. https://doi.org/10.1002/jgrc.20194

Calder, W. A. I. (1984). *Size, function and life history*. Harvard University Press.

Cerini, F., Childs, D. Z., & Clements, C. F. (2023). A predictive timeline of wildlife population collapse. *Nature Ecology & Evolution*, 7(3), 320–331. https://doi.org/10.1038/s41559-023-01985-2

Christiansen, F., Rodríguez-González, F., Martínez-Aguilar, S., Urbán, J., Swartz, S., Warick, H., Vivier, F., & Bejder, L. (2021). Poor body condition associated with an unusual mortality event in gray whales. *Marine Ecology Progress Series*, 658, 237–252. https://doi.org/10.3354/meps13585

Christiansen, F., Sironi, M., Moore, M. J., Di Martino, M., Ricciardi, M., Warick, H. A., Irschick, D. J., Gutierrez, R., & Uhart, M. M. (2019). Estimating body mass of free-living whales using aerial photogrammetry and 3D volumetrics. *Methods in Ecology and Evolution*, 10(12), 2034–2044. https://doi.org/10.1111/2041-210X.13298

Clements, C. F., Blanchard, J. L., Nash, K. L., Hindell, M. A., & Ozgul, A. (2017). Body size shifts and early warning signals precede the historic collapse of whale stocks. *Nature Ecology & Evolution*, 1(7), 0188. https://doi.org/10.1038/s41559-017-0188

Clements, C. F., & Ozgul, A. (2016). Including trait-based early warning signals helps predict population collapse. *Nature Communications*, 7, 10984. https://doi.org/10.1038/ncomms10984

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America, 106*(31), 12788–12793. https://doi.org/10.1073/pnas.0902080106

Dawn, A., Hildebrand, L., Sullivan, F. A., Barlow, D., & Torres, L. G. (Under review). Intermittent upwelling impacts zooplankton and their gray whale predators at multiple scales.

Dawson, S. M., Bowman, M. H., Leunissen, E., & Sirguey, P. (2017). Inexpensive aerial photogrammetry for studies of whales and large marine animals. *Frontiers in Marine Science, 4*, 366. https://doi.org/10.3389/fmars.2017.00366

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Temple Lang, D., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics, 26*, 403–413. https://doi.org/10.1080/10618600.2016.1172487

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography, 36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Durban, J. W., Fearnbach, H., Barrett-Lennard, L. G., Perryman, W. L., & Leroi, D. J. (2015). Photogrammetry of killer whales using a small hexacopter launched at sea. *Journal of Unmanned Vehicle Systems, 3*(3), 131–135. https://doi.org/10.1139/juvs-2015-0020

Eguchi, T., Lang, A. R., & Weller, D. W. (2023). *Abundance of Eastern North Pacific gray whales 2022/2023.* U.S. Department of Commerce, NOAA technical memorandum NMFS-SWFSC-680. (p. 10) https://doi.org/10.25923/n10e-bm23

Forchhammer, M. C., Clutton-Brock, T. H., Lindstrom, J., & Albon, S. D. (2001). Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology, 70*, 721–729.

Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution, 26*(6), 285–291. https://doi.org/10.1016/j.tree.2011.03.005

Groskreutz, M. J., Durban, J. W., Fearnbach, H., Barrett-Lennard, L. G., Towers, J. R., & Ford, J. K. B. (2019). Decadal changes in adult size of salmon-eating killer whales in the Eastern North Pacific. *Endangered Species Research, 40*, 183–188. https://doi.org/10.3354/ESR00993

Gulland, F. M. D., Perez-Cortes, H., Urban, R., Rojas-Bracho, L., Ylitalo, G., Weir, J., Norman, S. A., Muto, M. M., Rugh, D. J., Kreuder, C., & Rowles, T. (2005). *Eastern North Pacific gray whale (Eschrichtius robustus) unusual mortality event, 1999–2000 (NOAA technical memorandum NMFS-AFSC-150-150).* U.S. Department of Commerce.

Guthrie, R. D. (2003). Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature, 426*(6963), 169–171. https://doi.org/10.1038/nature02098

Harris, J. J., Calambokidis, J., Perez, A., & Mahoney, P. J. (2022). *Recent trends in the abundance of seasonal gray whales (Eschrichtius robustus) in the Pacific Northwest, 1996–2022.* AFSC Processed Report 2022-05. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, 7600 Sand Point Way NE, Sea. https://repository.library.noaa.gov/

Hildebrand, L., Bernard, K. S., & Torres, L. G. (2021). Do gray whales count calories? Comparing energetic values of gray whale prey across two different feeding grounds in the eastern North Pacific. *Frontiers in Marine Science, 8*, 1–13. https://doi.org/10.3389/fmars.2021.683634

Hoy, S. R., Peterson, R. O., & Vucetich, J. A. (2018). Climate warming is associated with smaller body size and shorter lifespans in moose near their southern range limit. *Global Change Biology, 24*(6), 2488–2497. https://doi.org/10.1111/gcb.14015

Isaac, J. L. (2009). Effects of climate change on life history: Implications for extinction risk in mammals. *Endangered Species Research, 7*(2), 115–123. https://doi.org/10.3354/esr00093

Jacox, M. G., Edwards, C. A., Hazen, E. L., & Bograd, S. J. (2018). Coastal upwelling revisited: Ekman, Bakun, and improved upwelling indices for the U.S. West coast. *Journal of Geophysical Research: Oceans, 123*(10), 7332–7350. https://doi.org/10.1029/2018JC014187

Johnston, D. W. (2019). Unoccupied aircraft systems in marine science and conservation. *Annual Review of Marine Science, 11*, 439–463. https://doi.org/10.1146/annurev-marine-010318-095323

Kasuya, T. (1991). Density dependent growth in North Pacific sperm whales. *Marine Mammal Science, 7*(3), 230–257. https://doi.org/10.1111/j.1748-7692.1991.tb00100.x

Kudela, R. M., Banas, N. S., Barth, J. A., Frame, E. R., Jay, D. A., Largier, J. L., Lessard, E. J., Peterson, T. D., & Vander Woude, A. J. (2008). New insights into the controls and mechanisms of plankton productivity in coastal upwelling waters of the northern California Current system. *Oceanography, 21*(4), 46–59. https://doi.org/10.5670/oceanog.2008.04

Lang, A. R., Calambokidis, J., Scordino, J., Pease, V. L., Klimek, A., Burkanov, V. N., Gearin, P., Litovka, D. I., Robertson, K. M., Mate, B. R., Jacobsen, J. K., & Taylor, B. L. (2014). Assessment of genetic structure among Eastern North Pacific gray whales on their feeding grounds. *Marine Mammal Science, 30*(4), 1473–1493. https://doi.org/10.1111/mms.12129

Lemos, L. S., Haxel, J. H., Olsen, A., Burnett, J. D., Smith, A., Chandler, T. E., Nieukirk, S. L., Larson, S. E., Hunt, K. E., & Torres, L. G. (2022). Effects of vessel traffic and ocean noise on gray whale stress hormones. *Scientific Reports, 12*(1), 18580. https://doi.org/10.1038/s41598-022-14510-5

Lemos, L. S., Olsen, A., Smith, A., Chandler, T. E., Larson, S., Hunt, K., & Torres, L. G. (2020). Assessment of fecal steroid and thyroid hormone metabolites in Eastern North Pacific gray whales. *Conservation Physiology, 8*(1), coaa110. https://doi.org/10.1093/conphys/coaa110

Litzow, M. A., Malick, M. J., Bond, N. A., Cunningham, C. J., Gosselin, J. L., & Ward, E. J. (2020). Quantifying a novel climate through changes in PDO-climate and PDO-salmon relationships. *Geophysical Research Letters, 47*(16), e2020GL087972. https://doi.org/10.1029/2020GL087972

Lunn, D., Jackson, C., Best, N., Thomas, A., & Spiegelhalter, D. (2013). *The BUGS book: A practical introduction to Bayesian analysis.* Chapman & Hall/CRC.

Macias, D., Landry, M. R., Gershunov, A., Miller, A. J., & Franks, P. J. S. (2012). Climatic control of upwelling variability along the Western North-American coast. *PLoS One, 7*(1), 20–23. https://doi.org/10.1371/journal.pone.0030436

Mantua, N. J., & Hare, S. R. (2002). The Pacific Decadal Oscillation. *Journal of Oceanography, 58*, 35–44.

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society, 78*(6), 1069–1079. https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2

Menge, B. A., & Menge, D. N. L. (2013). Dynamics of coastal meta-ecosystems: The intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecological Monographs, 83*(3), 283–310. https://doi.org/10.1890/12-1706.1

Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: Grow now, pay later? *Trends in Ecology & Evolution, 16*(5), 254–260. https://doi.org/10.1016/S0169-5347(01)02124-3

Metcalfe, N. B., & Monaghan, P. (2003). Growth versus lifespan: Perspectives from evolutionary ecology. *Experimental Gerontology, 38*(9), 935–940. https://doi.org/10.1016/S0531-5565(03)00159-1

Molina-Carrasco, F. D., Ortega-Rubio, A., Acosta-Pachon, T. A., López-Paz, N., Mariano-Meléndez, E., Montes-García, C., & Martínez-Rincón, R. O. (2024). The role of the environment at the local and large-scale levels on the abundance of gray whales (*Eschrichtius robustus*) in Baja California. *Regional Studies in Marine Science*, 71, 103420. https://doi.org/10.1016/j.rsma.2024.103420

Newman, M., Alexander, M. A., Ault, T. R., Cobb, K. M., Deser, C., Di Lorenzo, E., Mantua, N. J., Miller, A. J., Minobe, S., Nakamura, H., Schneider, N., Vimont, D. J., Phillips, A. S., Scott, J. D., & Smith, C. A. (2016). The Pacific Decadal Oscillation, revisited. *Journal of Climate*, 29(12), 4399–4427. https://doi.org/10.1175/JCLI-D-15-0508.1

Olsen, E. M., Lilly, G. R., Heino, M., Morgan, M. J., Brattey, J., & Dieckmann, U. (2005). Assessing changes in age and size at maturation in collapsing populations of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62(4), 811–823. https://doi.org/10.1139/f05-065

Ozgul, A., Tuljapurkar, S., Benton, T. G., Pemberton, J. M., Clutton-Brock, T. H., & Coulson, T. (2009). The dynamics of phenotypic change and the shrinking sheep of St. Kilda. *Science*, 325, 464–467.

Perryman, W. L., Joyce, T., Weller, D. W., & Durban, J. W. (2021). Environmental factors influencing Eastern North Pacific gray whale calf production 1994–2016. *Marine Mammal Science*, 37(2), 448–462. https://doi.org/10.1111/mms.12755

Pfister, C. A., Berry, H. D., & Mumford, T. (2018). The dynamics of kelp forests in the Northeast Pacific Ocean and the relationship with environmental drivers. *Journal of Ecology*, 106(4), 1520–1533. https://doi.org/10.1111/1365-2745.12908

Pirotta, E. (2022). A review of bioenergetic modelling for marine mammal populations. *Conservation Physiology*, 10(1), coac036. https://doi.org/10.1093/conphys/coac036

Pirotta, E., Tyack, P. L., Durban, J. W., Fearnbach, H., Hamilton, P. K., Harris, C. M., Knowlton, A. R., Kraus, S. D., Miller, C. A., Moore, M. J., Pettis, H. M., Photopoulou, T., Rolland, R. M., Schick, R. S., & Thomas, L. (2024). Decreasing body size is associated with reduced calving probability in critically endangered North Atlantic right whales. *Royal Society Open Science*, 11(2), 240050.

Post, E., Stenseth, N. C., Langvatn, R., & Fromentin, J. M. (1997). Global climate change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society B: Biological Sciences*, 264(1386), 1317–1324. https://doi.org/10.1098/rspb.1997.0182

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org/

Read, A. J., & Gaskin, D. E. (1990). Changes in growth and reproduction of harbour porpoises, *Phocoena phocoena*, from the bay of Fundy. *Canadian Journal of Fisheries and Aquatic Sciences*, 47(11), 2158–2163. https://doi.org/10.1139/f90-240

Reading, C. J. (2007). Linking global warming to amphibian declines through its effects on female body condition and survivorship. *Oecologia*, 151(1), 125–131. https://doi.org/10.1007/s00442-006-0558-1

Rice, D., & Wolman, A. (1971). The life history and ecology of the gray whale: *Eschrichtius robustus*. In J. L. Layne, & J. K. Jones (Eds.), *American society of Mammalogists* Special Publication No. 3. American Society of Mammalogists.

Rode, K. D., Amstrup, S. C., & Regehr, E. V. (2010). Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications*, 20(3), 768–782. https://doi.org/10.1890/08-1036.1

Sauer, J. R., & Slade, N. A. (1987). Size-based demography of vertebrates. *Annual Review of Ecology and Systematics*, 18, 71–90. https://doi.org/10.1146/annurev.es.18.110187.000443

Schmidt-Nielsen, K. (1984). *Scaling: Why is animal size so important?* Cambridge University Press.

Shackell, N. L., Frank, K. T., Fisher, J. A. D., Petrie, B., & Leggett, W. C. (2010). Decline in top predator body size and changing climate alter trophic structure in an oceanic ecosystem. *Proceedings of the Royal Society B: Biological Sciences*, 277(1686), 1353–1360. https://doi.org/10.1098/rspb.2009.1020

Sheridan, J. A., & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1(8), 401–406. https://doi.org/10.1038/nclimate1259

Shimabukuro, U., Takahashi, A., Okado, J., Kokubun, N., Thiebot, J.-B., Will, A., Watanuki, Y., Addison, B., Hatch, S. A., Hipfner, J. M., Slater, L., Drummond, B. A., & Kitaysky, A. S. (2023). Across the North Pacific, dietary-induced stress of breeding rhinoceros auklets increases with high summer Pacific decadal oscillation index. *Marine Ecology Progress Series*, 708, 177–189.

Smith, F. A., Betancourt, J. L., & Brown, J. H. (1995). Evolution of body size in the woodrat over the past 25,000 years of climate change. *Science*, 270(5244), 2012–2014.

Stephens, P., Boyd, I., McNamara, J., & Houston, A. (2009). Capital breeding and income breeding: Their meaning, measurement, and worth. *Ecology*, 90(8), 2057–2067. https://doi.org/10.1890/08-1369.1

Stewart, J. D., Durban, J., Europe, H., Fearnbach, H., Hamilton, P., Knowlton, A., Lynn, M., Miller, C. A., Perryman, W. L., Tao, B., & Moore, M. (2022). Larger females have more calves: Influence of maternal body length on fecundity in North Atlantic right whales. *Marine Ecology Progress Series*, 689, 179–189. https://doi.org/10.3354/meps14040

Stewart, J. D., Durban, J. W., Knowlton, A. R., Lynn, M. S., Fearnbach, H., Barbaro, J., Perryman, W. L., Miller, C. A., & Moore, M. J. (2021). Decreasing body lengths in North Atlantic right whales. *Current Biology*, 31(14), 3174–3179. https://doi.org/10.1016/j.cub.2021.04.067

Stewart, J. D., Joyce, T. W., Durban, J. W., Calambokidis, J., Fauquier, D., Fearnbach, H., Grebmeier, J. M., Lynn, M., Manizza, M., Perryman, W. L., Tinker, M. T., & Weller, D. W. (2023). Boom-bust cycles in gray whales associated with dynamic and changing Arctic conditions. *Science*, 382, 207–211. https://doi.org/10.1126/science.adi1847

Sydeman, W. J., García-Reyes, M., Schoeman, D. S., Rykaczewski, R. R., Thompson, S. A., Black, B. A., & Bograd, S. J. (2014). Climate change and wind intensification in coastal upwelling ecosystems. *Science*, 345(6192), 77–80. https://doi.org/10.1126/science.1251635

Torres, L. G., Bird, C. N., Rodríguez-González, F., Christiansen, F., Bejder, L., Lemos, L., Urban, J. R., Swartz, S., Willoughby, A., Hewitt, J., & Bierlich, K. C. (2022). Range-wide comparison of gray whale body condition reveals contrasting sub-population health characteristics and vulnerability to environmental change. *Frontiers in Marine Science*, 9, 511. https://doi.org/10.3389/fmars.2022.867258

Torres, L. G., Nieukirk, S. L., Lemos, L., & Chandler, T. E. (2018). Drone up! Quantifying whale behavior from a new perspective improves observational capacity. *Frontiers in Marine Science*, 5, 319. https://doi.org/10.3389/fmars.2018.00319

Torres, W., & Bierlich, K. (2020). MorphoMetriX: A photogrammetric measurement GUI for morphometric analysis of megafauna. *Journal of Open Source Software*, 5(45), 1825. https://doi.org/10.21105/joss.01825

Villegas-Amtmann, S., Schwarz, L. K., Sumich, J. L., & Costa, D. P. (2015). A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. *Ecosphere*, 6(10), 1–19.

Wang, D., Gouhier, T. C., Menge, B. A., & Ganguly, A. R. (2015). Intensification and spatial homogenization of coastal upwelling under climate change. *Nature*, 518(7539), 390–394. https://doi.org/10.1038/nature14235

Weeks, B. C., Willard, D. E., Zimova, M., Ellis, A. A., Witynski, M. L., Hennen, M., & Winger, B. M. (2020). Shared morphological

consequences of global warming in north American migratory birds. *Ecology Letters*, 23(2), 316–325. https://doi.org/10.1111/ele.13434

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

Wing, S. R., Botsford, L. W., Largier, J. L., & Morgan, L. E. (1995). Spatial structure of relaxation events and crab settlement in the northern California upwelling system. *Marine Ecology Progress Series*, 128(1–3), 199–211. https://doi.org/10.3354/meps128199

Yom-Tov, Y. (2001). Global warming and body mass decline in Israeli passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, 268(1470), 947–952. https://doi.org/10.1098/rspb.2001.1592

Yom-Tov, Y., & Geffen, E. (2011). Recent spatial and temporal changes in body size of terrestrial vertebrates: Probable causes and pitfalls. *Biological Reviews*, 86(2), 531–541. https://doi.org/10.1111/j.1469-185X.2010.00168.x

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.