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Inferring dolphin population status: using unoccupied aerial systems to quantify age-structure

F. Vivier[1], C. Andrés[2], J. Gonzalvo[2], K. Fertitta[1], M. van Aswegen[1], V. Foroughirad[3], J. Mann[3,4], M. McEntee[3], R. S. Wells[5] & L. Bejder[1,6]

1 Marine Mammal Research Program, Hawai‘i Institute of Marine Biology, University of Hawai‘i at Mānoa, Kaneohe, Hawai‘i, USA
2 Tethys Research Institute, Milan, Italy
3 Department of Biology, Georgetown University, Washington, DC, USA
4 Department of Psychology, Georgetown University, Washington, DC, USA
5 Chicago Zoological Society’s Sarasota Dolphin Research Program, c/o Mote Marine Laboratory, Sarasota, FL, USA
6 Zoophysiology, Department of Bioscience, Aarhus University, Aarhus, Denmark

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Correspondence
Fabien Vivier, Marine Mammal Research Program, Hawai‘i Institute of Marine Biology, University of Hawai‘i at Mānoa, MMRP/HIMB 46-007 Lilipuna Rd, Kaneohe, HI 96744, USA.
Email: fabienvivier79@yahoo.fr

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Abstract

Assessing trends in population abundance and demographics is crucial for managing long-lived and slow-reproducing species. Obtaining demographic data, and age-structure information, is challenging, notably for cetaceans. To address this, we combined Unoccupied Aerial System (UAS; drone) photogrammetry data with long-term (>20 years) photo identification data to assess the age-structure of the critically endangered sub-population of common bottlenose dolphins (*Tursiops truncatus*) of the Gulf of Ambracia, Greece. We compared our findings with two extensively studied non-endangered bottlenose dolphin populations (*T. aduncus* in Shark Bay, Australia, and *T. truncatus* in Sarasota Bay, USA). Using a log-linear model, we estimated the total body lengths (TL) of 160 known-aged dolphins between 2021 and 2023 from blowhole-to-dorsal-fin distance (BHDF) measurements collected during surfacing. Subsequently, we tested four growth models to establish an age-length growth curve. We assessed the sub-population’s age-structure using three methods: (1) UAS-derived TL estimates, (2) age-length growth curve and (3) long-term monitoring data (i.e. actual age-structure). UAS-measured TL (247.6 ± 32.2 cm) and UAS-estimated TL (246.0 ± 34.7 cm) of the Greek sub-population showed no differences. The Richards Growth model suggested an asymptotic length of 258.5 cm. In Greece, resulting age-structure estimates across the three methods revealed no significant differences ($P > 0.1$). The Gulf of Ambracia and Shark Bay populations shared similar age-structures, while Sarasota had higher proportions of 2–10 year-olds and lower proportions of 10+ year-olds. All populations had a comparable proportion of 0–2 year-olds (∼14%), indicating a similar reproductive rate. Our findings suggest stability in the Greek sub-population; however, additional monitoring of reproductive parameters is essential before concluding its status. We demonstrated the effectiveness of UAS-photogrammetry in rapidly quantifying population age-structure, including scenarios with limited or no demographic data. This technique shows promise for enhancing precision, timeliness, cost-effectiveness and efficiency in population monitoring and informing timely conservation management decisions.

Introduction

Globally, cetaceans face significant threats including habitat degradation (Bearzi *et al.*, 2004), climate change (Van Weelden, Towers, & Bosker, 2021; Gulland *et al.*, 2022; Lettrich *et al.*, 2023), prey depletion through overfishing (Bearzi *et al.*, 2006; Bearzi *et al.*, 2008b), mortality due to fisheries bycatch (Read, Drinker, & Northridge, 2006; Brownell *et al.*, 2019) and chemical (Tanabe, Iwata, & Tatsukawa, 1994; Law *et al.*, 2012; Weijs & Zaccaroni, 2016) and noise pollution (Weilgart, 2007; Thompson *et al.*, 2010). Coastal cetaceans, especially in semi-closed habitats, are particularly vulnerable to various anthropogenic threats due to their restricted geographic ranges, disjunct distributions, and limited movements (Reeves *et al.*, 2003). Approximately one-quarter of the 92 recognized cetacean species are currently listed as at risk of extinction, falling into categories such as critically endangered, endangered or vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Braulik *et al.*, 2023). Additionally, 11% are considered near-threatened. Hence, there is a clear and urgent need to implement effective conservation strategies to address the increasing pressures many cetacean species or populations face.

Eleven cetacean species are commonly found in the Mediterranean Sea, with an additional 13 recorded as occasional (ACCOBAMS, 2021). Of these, eight are commonly found in Greek waters, demonstrating a high level of diversity compared to the rest of the Mediterranean (Frantzis, 2010). Yet, this diversity is declining due to the general degradation of the marine habitat (Notarbartolo di Sciara & Bearzi, 2010). Bottlenose dolphins are the most commonly found cetacean species in Greek coastal waters and the second most abundant after the striped dolphin (*Stenella coeruleoalba*) (Frantzis *et al.*, 2023). Bottlenose dolphins are the only cetacean species found in the Gulf of Ambracia, western Greece, and the population has relatively high density compared to the rest of the Mediterranean (Bearzi *et al.*, 2008a). Population estimates produced between 2006 and 2015 for this sub-population were between 130 and 170, with an estimated 137 ± 21.12 individuals in 2015 (Gonzalvo *et al.*, 2016).

Species with limited ranges are more likely to be threatened than those with broader ranges (Braulik *et al.*, 2023). Ambracian dolphins are vulnerable due to their reproductive isolation, limited population size and small geographic range (Gonzalvo *et al.*, 2016). The only connection to the Ionian Sea, and therefore access to conspecifics, is a narrow channel (3 km wide) at one end of the Gulf of Ambracia (Gonzalvo, Giovos, & Mazzariol, 2015). By definition, with fewer than 250 mature individuals and an inferred ongoing decline, the Gulf of Ambracia bottlenose dolphin sub-population was listed as Critically Endangered under the IUCN Red List in 2021 (Gonzalvo & Notarbartolo-DI-Sciara, 2021). Ambracian dolphins are also particularly vulnerable to inbreeding depression, as suggested by their elevated kinship levels together with limited gene flow, indicating their high-risk status and potential for local extinction (Gaspari *et al.*, 2023).

Population management and conservation often rely on population abundance and demographic data. In fisheries sciences, age-structure information is crucial for setting appropriate harvest limits, preventing overexploitation and promoting sustainable fishing practices (Aubone, 2004). For cetaceans, collecting such data can be labour-intensive and costly (Pryor & Norris, 1992; Mann & Karniski, 2017; Symons, Sprogis, & Bejder, 2018) and often provides limited statistical power to estimate population trends promptly (Taylor *et al.*, 2007; Authier *et al.*, 2020). Therefore, there is a pressing need to develop alternative approaches to improve population status assessment.

Photogrammetry is widely used to evaluate individual/population status, biological parameters and demography in a wide range of taxa, including fish (e.g. Pauly *et al.*, 2002; Marrable *et al.*, 2023), birds (Trathan, 2004; Fudala & Bialik, 2022; Mattern *et al.*, 2023; Qian *et al.*, 2023) and terrestrial (Shrader, Ferreira, & van Aarde, 2006; Postma *et al.*, 2015; Galbany *et al.*, 2016; Rahman *et al.*, 2023) and aquatic mammals (Miller *et al.*, 2012; Alvarado *et al.*, 2020; Christiansen *et al.*, 2021; Shero *et al.*, 2021). Aerial photogrammetry, facilitated by UAS, has emerged as a valuable and non-invasive tool, overcoming traditional challenges in data collection for cetaceans (Booth & Heinis, 2018). UAS-derived body morphometrics have been used to study growth rates, health, and bioenergetics of large baleen whales (Christiansen *et al.*, 2018; Bierlich *et al.*, 2023; Russell *et al.*, 2023). UAS-photogrammetry is also accurate for measuring and estimating the body length (Vivier *et al.*, 2023) and volume of small cetaceans (e.g. Currie *et al.*, 2021). Additionally, this technique shows promising potential to efficiently assess the age-structure of free-ranging delphinid communities (Vivier *et al.*, 2023). Stable and healthy populations typically exhibit a relatively consistent (stable) proportion of calves, juveniles, and adults (Gamelon *et al.*, 2016), deviation from which may indicate population growth or decline (Coulson, Gaillard, & Festa-Bianchet, 2005; Jones *et al.*, 2018; Jackson *et al.*, 2020). Assigning individuals to age-classes enables the quantification of changes in survival and other parameters within and between age groups over time (Holmes & York, 2003). Studies that aim at quantifying population age-structure consequently hold the potential to provide insights into future abundance changes in cetacean populations (Holmes & York, 2003; Booth, Sinclair, & Harwood, 2020).

This study aimed to assess and compare the age-structure of the critically endangered sub-population of bottlenose dolphins in the Gulf of Ambracia, Greece, using three methods derived from two sources of information: (a) two decades of demographic data derived from regular monitoring and photo-identification effort, and (b) UAS-photogrammetry data collected over three field seasons. This allowed us to also evaluate the viability of employing UAS-photogrammetry to infer the age-structure in dolphin populations lacking long-term demographic records. Lastly, we compared our findings to two of the most well-studied non-endangered bottlenose dolphin populations: Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, and common bottlenose dolphins (*Tursiops truncatus*) in Sarasota, Florida. Our study offers insights into the use of UAS-photogrammetry for rapid assessments of age-structure in small delphinid populations to identify possible implications for their conservation and inform timely management decisions.

Materials and methods

Study site

The Gulf of Ambracia, identified as an IUCN Important Marine Mammal Area (IMMA) for bottlenose dolphins (IUCN-MMPATF, 2017), is a shallow (average depth ∼30 m) and semi-enclosed bay of about 405 km^2 (Gonzalvo, Giovos,

& Mazzariol, 2015). In 2008, it was designated as a 'National Park' following Greek national legislation (11989/08 KYA), and it was included in the network of Natura 2000 and Ramsar sites. Despite being protected by national, European and international legislation, the health of this increasingly fragile ecosystem, characterized as the only Mediterranean fjord-type system due to its water circulation and morphology (Ferentinos *et al.*, 2010), is strongly affected by habitat degradation and pollution (Georgiou *et al.*, 2021; Kordella *et al.*, 2021). Although banned in 2001 by the Stockholm Convention, high levels of dichlorodiphenyltrichloroethane (DDTs), polychlorinated biphenyls (PCBs), hexachlorobenzene (HCB) and other pesticides contaminated this environment and were detected in various forms of marine life inhabiting the Gulf (Albanis, Hela, & Hatzilakos, 1995; Gonzalvo *et al.*, 2016). Furthermore, increasing anthropogenic activities such as fish farming, agriculture, and sewage discharges from coastal areas accelerate the eutrophication process of the Gulf (Gonzalvo, Giovos, & Mazzariol, 2015; Piroddi *et al.*, 2016). Both anthropogenic and environmental stressors can impact individual vital rates (i.e. fertility and survival), ultimately affecting population demographics (Caughley, 1994; Benton, Plaistow, & Coulson, 2006; Pirotta *et al.*, 2018).

Long-term database

Boat-based dolphin surveys were conducted during 2001 through 2023 (Gonzalvo *et al.*, 2016). Surveys used a transect line design to uniformly cover the Gulf under Beaufort Sea State conditions ≤3. At least two observers scanned the sea surface for dolphins simultaneously. When dolphins were spotted, a slow approach was made to assess group size and composition (i.e. number of newborns, calves, juveniles and adults). In this study, groups are defined as individuals within a 100-m radius, moving together in the same direction and often engaged in similar activities (Wells, Irvine, & Scott, 1980). For each encounter, dorsal fins were photographed to allow individual photo identification based on dorsal fin features (i.e. notches and nicks), and other body marks (i.e. scars and stains). Two trained analysts independently matched the individuals and identification was confirmed upon agreement. Upon sighting, calves (up to 2 years old) and juveniles (up to 4 years old) were categorized based on their relative size compared to adults, and newborns were also identified based on their dark, lead-grey coloration with visible fetal creases and their immature swimming style with stereotyped surfacing pattern when breathing (Bearzi, Notarbartolo-DI-Sciara, & Politi, 1997). Calf and juvenile identities were confirmed when sighted in association with their mother on two or more subsequent and independent encounters during a season.

Determining birthing seasonality of the bottlenose dolphins in the Gulf of Ambracia

To determine the birth seasonality of this sub-population, only mothers observed with a calf within 6 months of their last sighting without a calf were used ($n = 26$). A calf's date of birth (DOB) was set as the midpoint date between their first sighting and the last sighting of their mothers without a calf. For full details on methods of determining birthing seasonality, see Mann *et al.* (2000) and Symons, Sprogis, & Bejder (2018).

Body morphometric data

A DJI Inspire 2 multi-rotor drone was used to capture aerial videos of bottlenose dolphins during three separate survey periods: August 7–10, 2021; July 17–22, 2022; and May 25–29, 2023. A DJI Zenmuse X5s digital camera (20.8-megapixel, Micro Four Thirds format) mounted with an Olympus M.Zuiko 25 mm f/1.8 lens was used to collect videos of surfacing dolphins. To ensure precise altitude readings, a LightWare SF11/C laser altimeter (accuracy of 0.1 m and resolution of 1 cm, Christiansen *et al.*, 2018) was attached to the UAS. Additionally, a custom-made smoother was applied to the original altitude data to correct any erroneous altitude readings resulting from environmental condition and/or system misfunction (Vivier *et al.*, 2023). Individual dolphins in each UAS video were identified via synchronous boat-based photo identification. Video stills were extracted using VLC MediaPlayer Software (VideoLAN) under two scenarios: (1) when dolphins displayed a fully extended body – with the tip of the rostrum and the notch in the flukes fully visible, and (2) while surfacing with the blowhole and dorsal fin exposed above the water. Only images of identified individuals were extracted and included in the analyses. When possible, up to three video stills were extracted per individual and scenario. Images were then processed (Dawson *et al.*, 2017) by measuring total body length (TL) and the blowhole-to-dorsal-fin distance (BHDF) on the fully extended dolphins and measuring BHDF for surfacing animals. BHDF is a reliable proxy for TL in bottlenose dolphins (Cheney *et al.*, 2018; van Aswegen *et al.*, 2019). For dolphins fully extended at the surface, TL and BHDF measurements were adjusted to account for UAS overestimation (Vivier *et al.*, 2023). Initially, a linear model was fit to explore the relationship between TL and BHDF. Subsequently, coefficients from a log-linear model were used to estimate TL based on BHDF for surfacing animals (Vivier *et al.*, 2023). Finally, UAS-derived TL measurements were corrected for UAS overestimation (3.3% ± 3.1; Vivier *et al.*, 2023). A paired Wilcoxon test was used to test the difference between UAS-measured TL and UAS-estimated TL from BHDF.

Data filtering and sensitivity analysis

The quality of all extracted images from UAS videos was graded following Christiansen *et al.* (2018). Images of poor quality in length measurability were removed from the analyses (Fig. 1). To align with the typical average length estimates (<300 cm) for coastal bottlenose dolphins, TL measurements greater than 290 cm were removed (2 Standard

Figure 1 Example images of common bottlenose dolphins collected by Unoccupied Aerial System in the Gulf of Ambracia, Greece, included or removed from the analyses. Top row depicts examples of images included in the analyses, with yellow arrows and dotted lines indicating measurement placements. Bottom row depicts examples of images of poor quality in length measurability. These images were removed from the analyses, either due to strong body pitch (i.e. the body axis is angled in the water), body leap out of the water (i.e. the body axis is both pitched and not at water level), obstruction of body parts (i.e. blowhole not visible) and camera focus (i.e. strong camera motion blurriness).

Deviations, SD, from the calculated median, $n = 14$ or 3.9%; Leys *et al.*, 2013; Shimizu, 2022). Similarly, all estimated TLs from BHDF measurements greater than 290 cm were considered erroneous and were removed from all the analyses ($n = 22$ or 2.7%). Measurement precision of unique individuals was assessed by extracting multiple independent images of each individual (i.e. different times in a video, different videos or different flights), and subsequently calculating the coefficient of variation (CV) in length estimates (see Appendix S1). All analyses were conducted using custom-written scripts in R version 4.3.1 (R Core Team, 2023).

Age estimation of individual dolphins

Using long-term photo-identification records from the Ionian Dolphin Project (IDP; Andrés, Cardona, & Gonzalvo, 2021; Bearzi *et al.*, 2008a; Gonzalvo, Giovos, & Mazzariol, 2015; Gonzalvo *et al.*, 2016), UAS-measured dolphins were categorized into age-classes (e.g. calf, juvenile, or adult; Herrman *et al.*, 2020) based on various indicators such as body size ratios, dorsal fin characteristics and distinctive marks. Adults were identified with a minimum age of 10 years from their initial sighting. To avoid age bias, the age of juveniles ($n = 10$) without maternal association was randomly assigned between 3 and 9 years to align with their typical independence age of around 3–5 years for *T. aduncus* (Karniski, Krzyszczyk, & Mann, 2018; van Aswegen *et al.*, 2019) and 3–6 years for *T. truncatus* (Wells, 2003). Individuals first sighted over a year from their mother's last sighting alone had their year of birth set as their first sighting year. Among the 160 unique UAS-measured dolphins, 62 were initially identified as calves by the IDP during 2006–2023. We refined their age estimates using the mother's previous sighting information. For calves sighted within 6 months of their mother's last sighting alone ($n = 6$), the midpoint of this gap was used as their date of birth (DOB). For those seen more than 6 months after their mother's last sighting alone ($n = 56$), we calculated probabilities to estimate their DOB based on the birth seasonality distribution. To do so, we calculated the probability of being born during each month of the season, assigning an equal probability to each day of a given month. Then, we calculated the probability of birth between March 1st (the beginning of the season) and the estimated date of the first sighting. Finally, we referenced the ages of these individuals to the midpoint dates of the UAS sampling seasons (i.e. 2021/08/10, 2022/07/20 and 2023/05/27).

Age-length growth curve analysis

We developed an age-length growth curve for the Greek dolphin sub-population using four non-linear growth functions that were fitted to the length-at-age data derived from UAS estimates of TL and improved age estimates. We developed an overall growth curve, as we were not able to develop sex-specific growth curves as we had limited information on the sex of individual dolphins. The four functions tested were the original (equation 1) and typical (equation 2) von Bertalanffy functions (von Bertalanffy, 1938), the Richards growth model (RGM; Richards (1959); equation 3) and the Gompertz function (GOM; Gompertz (1833); equation 4). The respective equations are as follows:

$$\text{Original von Bertalanffy}: L_t = L_\infty - (L_\infty - L_0) \times e^{-Kt} \qquad (1)$$

$$\text{Typical von Bertalanffy}: L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \qquad (2)$$

$$\text{Richards}: L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right)^p \qquad (3)$$

$$\text{Gompertz}: L_t = L_\infty \times e^{-e^{g_i(t-t_0)}} \qquad (4)$$

where L_t represents the length-at-age t, L_∞ is the asymptotic average length, K is the Brody growth rate coefficient, t_0 is an artificial time when the average length is zero, t is a theoretical function of time and age, L_0 is the mean length at time zero (birth), g_i is the instantaneous growth rate at the inflection point; and p is a dimensionless parameter determining the shape of the curve.

All models were fitted using the '*nlstools*' (version 2.0–0, Baty *et al.*, 2015) and '*FSA*' (version 0.9.4, Ogle *et al.*, 2023) packages. The four models were compared using Akaike Information Criterion (AIC). Using corrected delta AIC values (AIC_c; '*AICcmodavg*' version 2.3–2; Mazerolle, 2023) in R, all models were ranked and compared relative to the best-fitting model. The best model was determined based on the Akaike model weights ($\text{AIC}_\text{c}\text{W}_\text{t}$).

Long-term database and age designation of dolphins in Shark Bay and Sarasota Bay

Shark Bay, Australia

The Shark Bay Dolphin Research Project focuses on a resident population of Indo-Pacific bottlenose dolphins in the eastern gulf of Shark Bay, Western Australia. The project has monitored over 1800 individual dolphins since 1984 using boat-based surveys and focal follows (Karniski *et al.*, 2015) and biopsies for genetic data (e.g. Foroughirad *et al.*, 2022). Total population size is estimated to be around 3000 dolphins (Preen *et al.*, 1997) with a subset of about 400 being sighted annually in the main study area. Birth dates for dolphins born after the start of the study (>1984) were estimated based on consecutive observations of the mother before and after birth, calf size, and the presence of fetal lines (Mann *et al.*, 2000; McEntee *et al.*, 2023). For individuals who were first observed after weaning (mean weaning age is 4; Karniski, Krzyszczyk, & Mann, 2018; Mann *et al.*, 2000) ages were estimated based on body size and the presence and degree of ventral and dorsal fin speckling (Krzyszczyk & Mann, 2012). Median lifespan is ~30 years and maximum lifespan in the low 50s (McEntee *et al.*, 2023).

Sarasota Bay, USA

The Sarasota Dolphin Research Program (SDRP) has been studying the long-term, year-round resident community of common bottlenose dolphins of Sarasota Bay, Florida, USA, and vicinity since 1970 (Wells, 2020) through systematic photographic identification surveys since 1992 (Wells, 2009). Periodic catch-and-release health assessments (Wells *et al.*, 2004) were conducted to supplement sighting data with background life history, morphometric, and health information (Wells, 2013). The community is composed of around 170 individuals, observed across six generations, spanning up to five concurrent generations within a given maternal lineage, including members up to 67 years old. The ages of most individuals are known because they have been observed from the year of their birth to identifiable mothers. Ages of other individuals were estimated from growth layer groups in a tooth extracted under local anaesthesia (Hohn *et al.*, 1989), from epigenetic analyses (Beal *et al.*, 2019; Barratclough *et al.*, 2021), or from radiographic examination of fusion of flipper bones (Barratclough *et al.*, 2019).

Determining age-structure of the three dolphin populations

Between 2021 and 2023, the annual age-structure of the Greek sub-population was determined using three methods. We assumed equal detectability of all age classes, as we surveyed most of the study area daily (randomly choosing starting points) and the Ionian Dolphin Project has not detected any evidence that different age or sex classes of dolphins use the habitat differently. First, we followed the frequentist approach used by Vivier *et al.* (2023) to infer age-class via UAS estimates of TL based on BHDF of surfacing dolphins in which animals were assigned to one of three age-classes 0–2 (calves, strictly lower than 2 years), 2–10 (juveniles, greater or equal to 2 years, but strictly lower than 10), and 10+ years (adults, any individual greater or equal to 10 years) (age categories defined in Herrman *et al.*, 2020). We calculated the mean (±SD), minimum, and maximum values of UAS-measured BHDF and TL for each age-class using age and UAS-measured TL data from the Gulf of Ambracia. We then calculated the probabilities of assigning individuals to each age-class based on their UAS estimates of TL from BHDF and calculated the proportion of individuals in each age-class to establish the age-structure of the sub-population. Secondly, the lower confidence intervals in TL at 2 and 10 years old resulting from our age-length growth curve were used to identify age-class using UAS-estimated TL from BHDF. For example, all individuals falling under the lower interval threshold at 2 years old were considered calves. Lastly, we utilized long-term photo-identification data to establish the accurate age-class for each individual, revealing the true age-structure within the sub-population. The UAS method was adapted from Vivier *et al.* (2023) while the age-length growth curve and the long-term photo-identification data approaches were developed specifically for this study. Age-structures estimated with the three different methods were compared using a chi-square test. Using the same age-classes, the age-structure in Shark Bay and Sarasota was derived from photo-identification yearly between 2008–2010 and 2017–2019, respectively, based on age estimates. These periods represented the most recent years for which data were readily available and formatted for this analysis. Both the Shark Bay (Manlik *et al.*, 2016) and Sarasota Bay (Lacy *et al.*, 2021) dolphin populations were deemed stable during these times. In Shark Bay, the age-class was assigned based on the age of the individual for most of the calendar year. In Sarasota, dolphins born at any time during a given year were designated as age-class 0 and were calves from birth through all of the next calendar year (i.e. age-class 1). In both locations, dolphins observed in the area for at least 10 years, but with an undetermined age, were categorized as adults. The combined age-structure for all three populations was derived as the average across the 3 years.

Results

A summary of our fieldwork efforts and sample sizes is presented below (Table 1).

Applying birth seasonality for calibrating calf/juvenile biological parameters

Bottlenose dolphins in the Gulf of Ambracia exhibited birth seasonality spanning from March to August, with a notable peak in June accounting for 38.5% of the total births (Fig. 2).

Relationship between UAS-measured TL and BHDF

UAS measurements of TL and BHDF were obtained on 107 unique individuals in the Gulf of Ambracia during 2021–2023 for which a fully extended body was visible (65, 21, and 21 individuals in 2021, 2022 and 2023, respectively). A significant positive correlation between UAS-measured TL and BHDF was found (*F*-statistic: 794.1 on 1 and 105 DF, $P < 0.001$, $R^2 = 0.88$; Fig. 3). A log-linear model was then fit to estimate TL based on BHDF only for surfacing

Table 1 Summary of fieldwork effort and the number of dolphins measured in 2021, 2022 and 2023 in the Gulf of Ambracia, Greece

	2021	2022	2023
Number of survey days	4	5	5
Number of UAS flights	36	44	50
Number of UAS-operating hours	10.3	9.9	9.8
Number of unique dolphins measured	98	89	103
Number of unique dolphins included in the analyses after image quality grading	95	86	93
Number of calves after image quality grading	18	10	11
Number of juveniles after image quality grading	14	18	16
Number of adults after image quality grading	63	58	66

UAS, Unoccupied Aerial System.

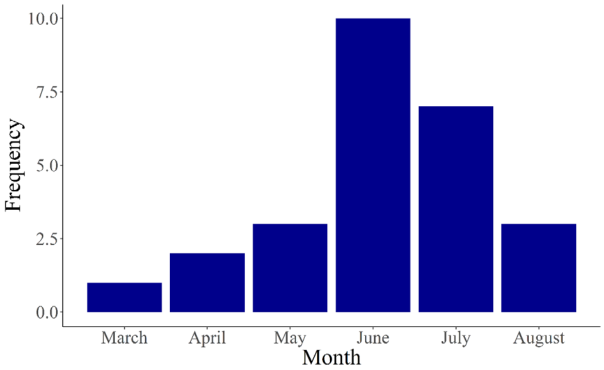

Figure 2 Estimated birthing seasonality for bottlenose dolphins in the Gulf of Ambracia, Greece, based on life history information. For this analysis, only mothers observed with a calf within 6 months of their last sighting without a calf were used ($n = 26$). The date of birth of each calf was set as the midpoint date between its first sighting and the last sighting of its non-accompanied mother (see: Mann *et al.*, 2000; Symons, Sprogis, & Bejder, 2018).

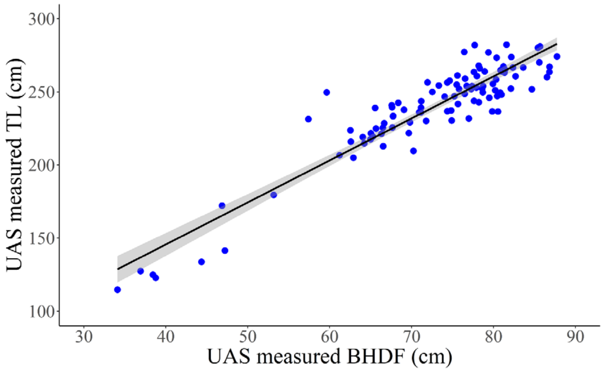

Figure 3 Relationship between the total body length (TL) and the blowhole-to-dorsal-fin distance (BHDF) collected by Unoccupied Aerial System for bottlenose dolphins in the Gulf of Ambracia, Greece, in 2021–2023. The black line depicts the smoothed BHDF to TL relationship, and the grey area represents the 95% confidence intervals ($n = 106$, $R^2 = 0.86$, $y = 30.436x + 2.878$).

individuals ($F_{1,105} = 912.9$ on 1 and 104 DF, $y = 1.56014x + 0.91437$, $P < 0.001$, $R^2 = 0.90$). Only TL estimates based on BHDF were used for the rest of the study.

UAS-measurements and estimates of dolphin morphometrics

There were no significant differences detected between median UAS-measured TL and median UAS-estimated TL from BHDF of dolphins in the Gulf of Ambracia ($P > 0.05$). Across all three seasons, median BHDF and TL measurements of dolphins lying extended at the surface were 76.5 ± 10.2 cm (median ± SD, 34.1–90.3, $n = 157$) and 247.6 ± 32.2 cm (114.8–290, $n = 165$), respectively. Median estimated TL using BHDF for surfacing dolphins averaged 246.0 ± 34.7 cm (100.6–287.1, $n = 274$). TL and BHDF measurements of fully extended dolphins were obtained at an average altitude of 35.7 ± 3.7 m while BHDF measurements of surfacing dolphins were obtained at an average altitude of 36.3 ± 4.0 m.

Best-fitting growth model and biologic parameters

The Richards Growth Model provided the best fit for bottlenose dolphins in the Gulf of Ambracia (AICcWt = 1, Table 2). The Typical von Bertalanffy, Original von Bertalanffy and Gompertz functions did not fit well for younger individuals (i.e. <2 years, Fig. 4) with a cumulative weight of 0 (Table 2). The RGM suggested fast calf growth in the first 2 years, especially during the first year of life (Fig. 4). The median TL for newborn calves was 126.13 cm (95% CI = 96.8–139.5). Predicted median TL at Years 1 and 2 were 188.9 cm (95% CI = 184.3–193.2) and 205.2 cm (95% CI = 201.8–208.8), respectively. The median TL for 3-year-old juveniles was 215.1 cm (95% CI = 212.0–218.6). The RGM estimated an asymptotic length of 258.5 cm (95% CI = 254.5–265.1) for this sub-population.

Table 2 Summary of corrected Akaike's information criterion (AICc) model selection output for the four candidate growth models: The Richards Growth Model (RGM), Original von Bertalanffy (OvB), Typical von Bertalanffy (TvB) and Gompertz function (GOM), used to describe the length-at-age data obtained for the bottlenose dolphins from the Gulf of Ambracia, Greece

	K	AIC_c	ΔAIC_c	AIC_cW_t	Log likelihood
RGM	**5**	**2249.2**	**0**	**1**	**−1119.5**
OvB	4	2290.4	41.1	0	−1141.1
TvB	4	2290.4	41.1	0	−1141.1
GOM	4	2298.1	48.9	0	−1145.0

The most parsimonious model is indicated in bold. Age estimates were obtained from life history data, and total length estimates were obtained via Unoccupied Aerial System photogrammetry.

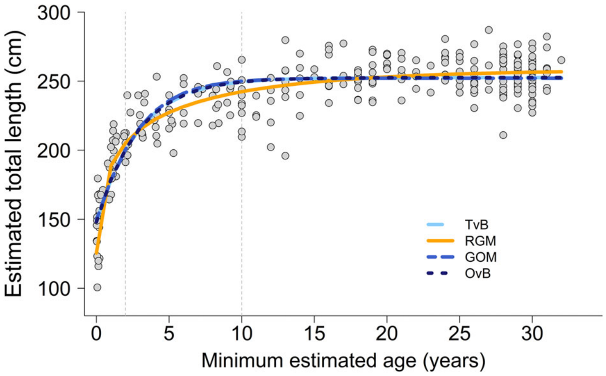

Figure 4 Visual representations of each of the four candidate growth models for the bottlenose dolphins from the Gulf of Ambracia, Greece. Age estimates were obtained from life history data, and total length estimates were obtained via Unoccupied Aerial System photogrammetry. The most parsimonious model was obtained with the Richards Growth Model (RGM). The same fit was provided by the three other candidate models: original von Bertalanffy (OvB), typical von Bertalanffy (TvB) and Gompertz (GOM).

Dolphin population age-structure in the Gulf of Ambracia, Sarasota Bay and Shark Bay

In the Gulf of Ambracia, yearly assessments of age-class structure based on UAS estimates of TL did not differ significantly from those derived from long-term life history data (Table 3). Estimates exhibited greater accuracy when forecasting the 0–2 age-class category, while there was more variability for the 2–10 and 10+ year age-class categories. Over the 3 years, an average of 91 (±4.7 SD) individuals were encountered and the true age-class distribution was 14.2% for 0–2 years, 17.5% for 2–10 years and 68.3% for 10+ years. Similarly, the average UAS-estimated age-class distribution was 13.1% for 0–2 years, 25.6% for 2–10 years and 61.3% for 10+ years. Age-structure comparisons between the study population and the two test populations showed similarities between the Gulf of Ambracia and Shark Bay, with a notable variation in the proportion of 2–10/10+ years observed in Sarasota Bay (Table 4).

Discussion

Age-structure serves as an important indicator of population status, yet gathering these metrics can be challenging especially for marine mammals. This study employed UAS-photogrammetry to measure body morphometrics and developed an age-length growth curve for a critically endangered sub-population of bottlenose dolphins. Through the integration of this method coupled with long-term life history data, we demonstrated the effectiveness of UAS-photogrammetry in readily quantifying population age-structure with a low level of field effort (~5 days/year). Despite caveats, this study highlights how UAS-photogrammetry can improve

Table 3 Chi-square analyses (χ^2, d.f., *P*-value) comparing three methods used to estimate the age-structure of the bottlenose dolphin sub-population in the Gulf of Ambracia, Greece: Total length estimates from Unoccupied Aerial System (UAS) photogrammetry, age-length growth curve (Growth curve) and long-term photo-identification data (Long-term data)

<table>
<tr><th></th><th colspan="6">Age-class (years)</th></tr>
<tr><th></th><th colspan="3">2021 (%|<i>n</i>)</th><th colspan="3">2022 (%|<i>n</i>)</th></tr>
<tr><th>Method</th><th>0–2</th><th>2–10</th><th>10+</th><th>0–2</th><th>2–10</th><th>10+</th></tr>
<tr><td>UAS</td><td>19|18</td><td>24.2|23</td><td>56.8|54</td><td>9.3|8</td><td>25.6|22</td><td>65.1|56</td></tr>
<tr><td>Growth curve</td><td>20|19</td><td>20|19</td><td>60|57</td><td>10.5|9</td><td>24.4|21</td><td>65.1|56</td></tr>
<tr><td>Long-term data</td><td>19|18</td><td>14.7|14</td><td>66.3|63</td><td>11.6|10</td><td>21|18</td><td>67.4|58</td></tr>
<tr><td>χ^2, d.f., <i>P</i>-value</td><td colspan="3">$\chi^2 = 2.94$, d.f. = 4, $P = 0.57$</td><td colspan="3">$\chi^2 = 0.7$, d.f. = 4, $P = 0.95$</td></tr>
<tr><th></th><th colspan="6">Age-class (years)</th></tr>
<tr><th></th><th colspan="3">2023 (%|<i>n</i>)</th><th colspan="3">Three-year average (%|<i>n</i>)</th></tr>
<tr><th>Method</th><th>0–2</th><th>2–10</th><th>10+</th><th>0–2</th><th>2–10</th><th>10+</th></tr>
<tr><td>UAS</td><td>10.8|10</td><td>26.8|25</td><td>62.4|58</td><td>13.1|12</td><td>25.6|23</td><td>61.3|56</td></tr>
<tr><td>Growth curve</td><td>14|13</td><td>23.6|22</td><td>62.4|58</td><td>15|14</td><td>22.6|21</td><td>62.4|57</td></tr>
<tr><td>Long-term data</td><td>11.8|11</td><td>17.2|16</td><td>71|58</td><td>14.2|13</td><td>17.5|16</td><td>68.3|62</td></tr>
<tr><td>χ^2, d.f., <i>P</i></td><td colspan="3">$\chi^2 = 3.12$, d.f. = 4, $P = 0.54$</td><td colspan="3">$\chi^2 = 1.81$, d.f. = 4, $P = 0.77$</td></tr>
</table>

Differences were tested per age class (years). In total, 95, 86, 93 and 91 individuals were included in the analysis in 2021, 2022, 2023 and 2021–2023, respectively. Results are expressed in percentages and respective numbers of individuals.

Table 4 Age-structure for three populations of bottlenose dolphins (Gulf of Ambracia, GRE; Sarasota Bay, USA; and Shark Bay, AUS) derived from long-term life-history data

		Number of individuals				
Population	Age-class (years)	Year 1	Year 2	Year 3	Sum	Proportion (%)
Gulf of Ambracia	0–2	18	10	11	**39**	**14.2**
	2–10	14	18	16	**48**	**17.5**
	10+	63	58	66	**187**	**68.3**
	Sum	**95**	**86**	**93**	**274**	**100**
Sarasota Bay	0–2	29	25	23	**77**	**14.8**
	2–10	58	63	64	**185**	**35.6**
	10+	85	90	83	**258**	**49.6**
	Sum	**172**	**178**	**170**	**520**	**100**
Shark Bay	0–2	35	55	58	**148**	**12.4**
	2–10	67	81	92	**240**	**20.1**
	10+	224	298	284	**806**	**67.5**
	Sum	**326**	**434**	**434**	**1194**	**100**

Year numbers correspond to data collection periods: 2021–2023 for the Gulf of Ambracia, 2017–2019 for Sarasota and 2008–2010 for Shark Bay. Bold values indicates that they are the ones discussed in the manuscript.

population demographic monitoring, especially in scenarios lacking comprehensive demographic data. This study is one of the first to use UAS-estimated length measurements to develop a growth curve of a free-ranging dolphin population (see Kotik *et al.*, 2022), distinguishing itself from traditional photogrammetric approaches relying on stereo-laser photogrammetry (e.g. Cheney *et al.*, 2018; van Aswegen *et al.*, 2019; O'Callaghan, Daly, & Berrow, 2023) and 3D-photogrammetry (Morisaka *et al.*, 2022). UAS-photogrammetry offers an accurate, non-invasive way to collect morphometric data on free-ranging cetaceans, which can inform conservation strategies.

We estimated an asymptotic length (L_∞) of 258.5 cm for the critically endangered sub-population of common bottlenose dolphins in the Gulf of Ambracia, similar to that observed in other regions such as Mississippi Sound (255.4 cm for males, 249.7 cm for females; Mattson *et al.*, 2006) and Sarasota Bay, Florida (263.4 ± 4.2 cm for males, 250.1 ± 2.4 cm for females; Read *et al.*, 1993). Median measured TL and estimated TL did not differ significantly, highlighting the accuracy of UAS-photogrammetry in estimating TL based on BHDF of free-swimming dolphins. The median length of calves less than 1 year old was 151.0 ± 23.2 cm (100.6–190.4, $n = 24$), with those under 3 months at 149.0 ± 20.5 cm (100.6–179.6, $n = 19$). Similar lengths were measured in Moray Firth, Scotland (128–188 cm; Cheney *et al.*, 2018). This study is the first to measure and estimate the sizes of members of the Gulf of Ambracia sub-population.

Growth rates in young dolphins from Scotland and Greece are comparable and indicate rapid growth in their first year. This rapid growth enables young dolphins to better endure cold winters and dive and stay with their mothers as body thermoregulation costs decrease with larger body sizes (Harding *et al.*, 2005). In Moray Firth and the Gulf of Ambracia, Sea Surface Temperature (SST) typically ranges from ~7 to 13.5°C and ~15 to 26°C (winter–summer; World Sea Temperatures, 2023), respectively. Similar SSTs to the Gulf of Ambracia are found in Southwestern Australia where another species of bottlenose dolphins (*T. aduncus*) exhibits a similar and near-identical growth pattern (van Aswegen *et al.*, 2019). Dolphins in temperate regions are typically larger and more robust than those in warmer regions (McFee *et al.*, 2012; van Aswegen *et al.*, 2019), with a 20% length difference observed between geographically separated populations of Indo-Pacific bottlenose dolphins in Western Australia (van Aswegen *et al.*, 2019).

We determined the age-structure of the critically endangered sub-population of bottlenose dolphins in the Gulf of Ambracia using three approaches (a) UAS-derived TL estimates from BHDF measurements of surfacing dolphins, (b) age-length growth curves; and (c) long-term data (representing the true age distribution). Overall, age-structure estimates obtained from the three methods did not differ significantly, demonstrating the efficacy of UAS-photogrammetry in quantifying age-structure (Table 4). UAS-photogrammetry documented a higher proportion for 2- to 10-year-olds and a lower proportion of 10+ year-olds compared to the true age-class distribution, though statistically non-significant. Comparable results were obtained using the age-length growth curve method. Differences between the observed and true proportions are likely influenced by individual length variability within the same age group (Rahman *et al.*, 2023), particularly among 2–10 year-olds (Vivier *et al.*, 2023). Other factors such as unaccounted individuals during the surveys, mortality or emigration (although emigration is negligible in the Gulf; Gonzalvo *et al.*, 2016) might contribute to slight variations in age-structure across years. Our study supports the effectiveness of UAS-photogrammetry in accurately determining population age-structure and its potential for understanding demographics in data-limited populations.

With a low level of field effort, approximately 5 days per year, our UAS-photogrammetry method was able to assess the age-structure of the sub-population of bottlenose dolphins in the Gulf of Ambracia. We estimated that a minimum of 70 randomly selected individuals must be sampled (i.e. measured via UAS-photogrammetry) to accurately estimate the true proportion of individuals in each age-class, with a CV of 0.3 (Appendix S2, Figure S1). In this study, we measured, on average, 91 individual dolphins per year, which resulted in a CV of 0.25. This assumes that individuals were sampled randomly, that the number of individuals in each age-class follows a multinomial distribution, and that the UAS-measured individuals are a representative sample of this distribution with no sampling bias among age categories. This level of accuracy was possible only given the high density of dolphins inhabiting the Gulf. However, under different circumstances, more time and individuals may be needed to obtain representative estimates. In Shark Bay, for example, with an estimated population of around 3,000 individuals, sampling >110 individuals would be necessary to achieve a CV of 0.3 based on the current age-structure estimates (Table 4). However, it is critical for that sample to be representative of the true distribution. Given the vital role that juveniles play in population status (Booth, Sinclair, & Harwood, 2020; Lu *et al.*, 2023), timely monitoring and quantifying shifts in their demographics is essential. For example, an increase in the number of juveniles might suggest successful reproduction and a growing population (Owen-Smith & Mason, 2005), while a decline in adult numbers might signal breeding issues and/or increased adult mortality (Lehman *et al.*, 2024). These efforts may aid conservation, provide demographic insights, and improve our understanding of population sustainability.

The Gulf of Ambracia and Shark Bay exhibited similar age-structures (Table 4), whereas Sarasota Bay showed a higher proportion of juveniles (35.6% as opposed to 17.5% and 20.1%, respectively). Despite these differences, all three populations shared a similar proportion of calves (~14%), indicating comparable reproductive rates despite being of different species with different weaning ages. Although a lower proportion of juveniles might suggest potential juvenile survivability issues, both Shark Bay and Sarasota Bay populations are stable and healthy (Manlik *et al.*, 2016; Lacy *et al.*, 2021). This suggests potential stability for the Gulf of Ambracia's sub-population, despite its current critically endangered status and an estimated non-significant decline of 1.6% over a decade (Gonzalvo *et al.*, 2016). However, it may also indicate that population status relies on unique adaptations to local habitats (Chivers *et al.*, 2016). Between and among species, variations in body lengths and reproductive parameters, such as age at first reproduction, inter-birth intervals and age at weaning, can be observed (Mcmahon, Burton, & Bester, 2003; Larese & Chivers, 2009; Wittemyer, Daballen, & Douglas-Hamilton, 2013; Chivers *et al.*, 2016; van Aswegen *et al.*, 2019). In Western Australia, two geographically distinct populations of Indo-Pacific bottlenose dolphins showed two significantly different status trajectories, where reproductive rates and adult survival rates differed (Manlik *et al.*, 2016). Similarly, blue whale (*Balaenoptera musculus* spp.) morphology varied with environment, with larger/longer whales found in year-round productive waters compared to those in seasonally productive areas (Barlow *et al.*, 2023) potentially indicating different levels of fitness, vital rates and age-structures. Careful consideration is necessary to minimize bias when generalizing parameters from one population to another, especially when assessing age-structure based on length estimates.

An understanding of both population age-structure and population threats is required to assess changes to population dynamics. Short-term disruptions in demographic structure, including alterations in age-structure and sex ratios can strongly influence population dynamics and pose sustainability concerns, especially for endangered populations (Jackson *et al.*, 2020). For example, overfishing, poaching, and by-catch can significantly alter population age-structure, as described in Atlantic cods (*Gadus morhua*; Hutchings, 2005), brown bears (*Ursus arctos*; Bischof *et al.*, 2017), African elephants (*Loxodonta Africana*; Jones *et al.*, 2018) and spinner dolphins (*Stenella longirostris*; Larese & Chivers, 2009), respectively. In the Gulf of Ambracia, anthropogenic activities have caused seasonal anoxia in the eastern region (Kountoura & Zacharias, 2011), affecting 43% of the seafloor and 36% of the total water volume (Georgiou *et al.*, 2021). Hypoxic conditions peak at 70% (in September) and 62% (in July), leading to habitat degradation that might disrupt both prey and predator population dynamics both in the short and long term (Georgiou *et al.*, 2021). Further research is needed to monitor and understand environmental dynamics and their effects on the demographics of the Gulf of Ambracia's dolphin sub-population. These efforts may aid in predicting the population's future trajectory and informing timely management decisions.

Conclusion

Our study highlights the accuracy of UAS-photogrammetry as a rapid and reliable tool for quantifying and monitoring demographic parameters of free-ranging delphinids. Specifically, for a critically endangered population of common bottlenose dolphins, we documented similar age-structure estimates derived from (a) long-term life history data and (b) UAS-photogrammetry obtained during five annual field days. Our method shows promise for quantifying demographic parameters for populations with limited or no existing data which, in turn, optimizes efficiency in population monitoring and for informing timely conservation management decisions.

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Author contributions

F.V., L.B. and J.G conceived the study. J.G. and L.B. secured funding. F.V., C.A., L.B. and J.G. collected the UAS data in the Gulf of Ambracia, Greece. F.V. and K.F. processed the data. R.W. provided the data for Sarasota Bay, USA, and J.M., M.M. and V.F. for Shark Bay, Australia. F.V. designed the statistical analyses. F.V. conducted the statistical analysis with contribution from M.v.A. on age-length growth curves. F.V. wrote the manuscript with input from L.B. All authors reviewed and commented on the manuscript.

Conflict of interest

The authors declare no competing interests.

Data availability statement

The data that support this study will be shared upon reasonable request to the corresponding author.

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Supporting information

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

Appendix S1. Sensitivity analysis for UAS data collected in the Gulf of Ambracia.

Table S1. Mean coefficients of variation (CV) in the measured distance between the center of the blowhole and the anterior insertion of the dorsal fin (BHDF), and the estimated Total Length (TL) from BHDF measurements for surfacing dolphins in the Gulf of Ambracia, Greece.

Appendix S2. Determining the minimal number of individuals required to be measured using UAS-photogrammetry to accurately reflect the true population age-structure.

Figure S1. The minimal number of individuals required to be measured via Unoccupied Aerial System photogrammetry as a function of the coefficient of variation (CV) to accurately represent the true proportion of individuals in each age-class in the population of bottlenose dolphins in the Gulf of Ambracia, Greece.