Laser photogrammetry reveals variation in growth and early survival in free-ranging bottlenose dolphins

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Abstract

Growth and body condition can be used as indices of health and fitness, but are difficult to collect for populations of conservation concern where individuals cannot be captured. We incorporated a laser photogrammetry system into boat-based photo-identification surveys that underpin individual-based studies of cetacean populations. These data were integrated with >25 years of observations from a temperate bottlenose dolphin population in Scotland to investigate the influence of sex on growth patterns, effects of birth order on calf size and the longer term consequences of variation in early growth. Field measurements of the distance from the blowhole to the dorsal fin were made in multiple years from 87 dolphins that had been followed from birth, ranging in age from newborn to 26 years. These estimates were validated against direct measurements of 12 individuals that had previously been captured and released in Florida and two study individuals that subsequently stranded. Using relationships derived from other stranded individuals, age-specific body lengths were used to produce growth curves that were based entirely on remote observations. Multilevel regression growth curve analyses suggested males and females showed similar patterns of growth, unlike bottlenose dolphins in sub-tropical areas, and growth was best described by a Richards' growth curve. Newborn length was unrelated to sex; however, females' first calves were shorter than subsequent calves. Sample sizes remain small, yet there was evidence of fitness consequences of variation in calf length; calves that died in their first winter were significantly shorter than those that survived. The incorporation of this simple-to-use and inexpensive method into individual-based photo-identification studies provides new opportunities to non-invasively investigate drivers of variation in growth and the demographic consequences of variation in early growth in cetaceans from protected populations.

Introduction

Conservation managers typically focus on monitoring changes in wildlife population abundance, survival and fecundity. However, significant changes in population processes can be difficult to detect (Maxwell & Jennings, 2005; Taylor *et al.*, 2007; Tyne *et al.*, 2016), potentially resulting in delayed implementation of conservation initiatives (Thompson *et al.*, 2000; Turvey *et al.*, 2007). Additionally, identifying the drivers underlying these changes can be challenging (Estes *et al.*, 2009; Currey *et al.*, 2011). To complement these monitoring methods, data are therefore required on shorter term responses of individuals to environmental change and anthropogenic affects. One approach is to measure variation in body size, growth and individual condition. For example, changes in population size structure may inform understanding of the effects of by-catch or hunting

(Holmes & York, 2003), while information on individual condition is critical for exploring population consequences of non-lethal disturbance (Pirotta *et al.*, 2015; McHuron *et al.*, 2017).

When collected during individual-based studies, morphometric data can help link the effects of anthropogenic or environmental changes to events at multiple life-history stages (Clutton-Brock & Sheldon, 2010). Individual-based studies can provide opportunities for direct morphometric measurements during capture-release programmes (e.g. Wells *et al.*, 2004; Ozgul *et al.*, 2010; Coulson *et al.*, 2011). However, captures within populations of conservation concern, particularly for some species such as cetaceans, may be impractical or unsafe. To overcome this, many individual-based studies use photographic observations of natural marks to recognize individuals (Würsig & Würsig, 1977; Hammond, Mizroch & Donovan, 1990; Wells & Scott,

1990). The disadvantage is that opportunities to simultaneously obtain a time series of individual morphometric data are rare (Altmann & Alberts, 2005).

Recent developments in photogrammetry highlight the potential for collecting morphological data from free-ranging terrestrial (Bergeron, 2007; Rothman *et al.*, 2008) and marine (Deakos, 2010; Rohner *et al.*, 2011) vertebrates. In particular, laser photogrammetry, where two parallel lasers provide a known-length scale in photographs, can be integrated into the photo-identification techniques underpinning cetacean studies (Durban & Parsons, 2006; Rowe & Dawson, 2008; Rowe *et al.*, 2010).

Here, we developed and tested a laser photogrammetry technique to remotely measure body length and model the growth of individuals from a protected population of wild bottlenose dolphins on the east coast of Scotland (Wilson *et al.*, 2004; Cheney *et al.*, 2013). We integrated these measurements with long-term demographic data to characterize growth (i.e. change in body length with age) in our study population, assess the influence of sex and birth order on growth and explore whether variation in early growth influenced subsequent survival.

Materials and methods

Study population

This study was conducted on bottlenose dolphins using the Moray Firth Special Area of Conservation (SAC) (92/43/ EEC) on the east coast of Scotland (Cheney *et al.*, 2014*b*) (Supporting Information Fig. S1). Since 1989 individual-based demographic studies have been conducted using standardized photo-identification survey procedures (for full details, see Cheney *et al.*, 2014*a*; Wilson, Hammond & Thompson, 1999; Wilson, Thompson & Hammond, 1997). The population of <200 individuals is estimated to be stable or increasing (Cheney *et al.*, 2014*a*).

Laser photogrammetry

We adapted the laser photogrammetry technique used by Durban & Parsons (2006). Two Beamshot <5mW laser sights (Quarton USA Inc, CA, USA) were fixed horizontally, 10 cm apart, in a machined aluminium block and attached to a camera lens tripod mount (Fig. 1a and Supporting Information Fig. S2). Laser sights were adjusted using internal adjustment screws and controlled via an electronic control switch attached to the camera remote release (Supporting Information Fig. S3). When the shutter was fired, lasers were projected onto the subject, providing a 10-cm scale on the photograph. Before and after each survey, calibration photographs were taken at five distances between 5 and 25 metres to ensure the lasers remained parallel and 10 cm apart (Fig. 1b).

From 2007 onwards, we applied this technique during annual photo-identification surveys (Cheney *et al.*, 2014*a*). Only photographs, where the dolphin was parallel to the photographic plane, both lasers were clear, and the individual

dolphin was identifiable, were used (Fig. 2). We aimed to estimate body length (tip of rostrum to tail notch) of each dolphin, but the dolphins' entire body was rarely above the water. Therefore, calibrated photographs were first used to estimate the distance from the blowhole to the anterior insertion point of the dorsal fin (BH-DF), features that were often visible in photographs (Fig. 2). Individual dolphin's BH-DF measurements were averaged for each month and year. Each dolphin's length was then estimated using the relationship between the BH-DF and body length derived from measurements of stranded individuals (Supporting Information Fig. S4). The height of each dolphin's dorsal fin (anterior insertion point to fin tip) was also measured (Fig. 2). When there were photographs of the BH-DF but no lasers visible, we used these contemporary data on the average height of an individuals' dorsal fin as an alternative scale for measuring the BH-DF. All measurements were made by BC using Image J (http://rsbweb.nih.gov/ij/). Measurement error was estimated using five repeat blind measurements of five different photographs. Statistical analyses were carried out in R version 3.3.0 (R Core Team, 2016).

This study focussed on a subset of laser photogrammetry photographs from known-age individuals. Year of birth was estimated from field observations and archive photographs, based on a newborn's colour, size, foetal folds and behaviour (Grellier *et al.*, 2003). Where possible, birth month was estimated using repeated observations of the mother without and with a calf (ensuring observations were within 3 months). To increase our sample of adult dolphins, we also measured 23 dolphins that were first identified as adults or sub-adults between 1989 and 1996 (Supporting Information Table S1). As their age was estimated, these adults were not used in the growth curve analyses. Instead, these measurements were used to investigate variation in length measurements of the same individual in different photographs. Sex was determined using genital photographs or repeat associations with a calf.

Growth curve

Annual length measurements from each known-aged individual were first used in a multilevel regression growth curve (MRGC) analysis (Mirman, Dixon & Magnuson, 2008; Mirman, 2014) to explore sex differences in length and growth. MRGC is ideal for longitudinal data where quantifying individual differences and group level effects are required (Mirman *et al.*, 2008; Mirman, 2014). This method was chosen as it explicitly models time as a continuous variable and captures the non-linearity of growth (Mirman, 2014). Finally, it deals with repeated measurements from individuals that are not independent and describes the group level patterns and individual variability in one analysis (Mirman, 2014). This analysis used a subset of data from known sex individuals, where length estimates were available for all year classes from newborn (≤3 months) to 13 years old. Growth curves were modelled using the lme4 package (Bates *et al.*, 2014) with third-order orthogonal polynomials, to account for age-specific changes in growth over this period
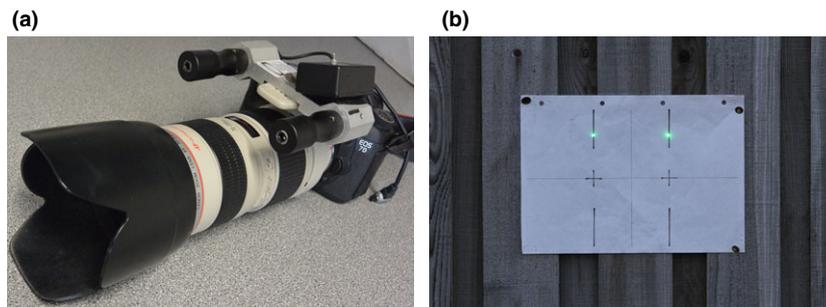
Figure 1 Laser photogrammetry equipment showing (a) two Beamshot laser sights attached to the lens tripod mount and (b) a calibration sheet with laser dots 10 cm apart.
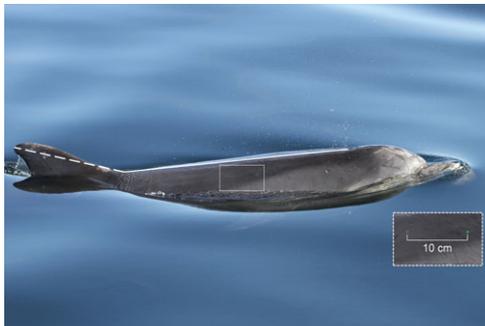

Figure 2 A good-quality photograph, with the dolphin parallel, both lasers visible. The two green laser dots (dotted line and insert) are the scale (10 cm), the white line measures the distance between the middle of blowhole and anterior insertion point of dorsal fin (BH-DF), and the diagonal white dashed line measures the height of the dorsal fin from anterior insertion point to tip.

(i.e. initial change from flat, increase and finally plateau) and to allow parameter estimates to be evaluated independently (Mirman *et al.*, 2008; Mirman, 2014). Males were treated as the baseline and parameters estimated for females. Models included random effects of individual identity on all time terms (i.e. linear, quadratic and cubic orthogonal polynomials) to account for repeated measures in different years and capture individual variability in length at birth and/or growth. Random effects were specified separately for each time term for model convergence (Mirman, 2014). The fixed effect of sex on all time terms based on age was added individually. Improvements in model fit were evaluated using two times the change in log-likelihood, which is distributed as χ^2 with degrees of freedom equal to the number of parameters added (for full details of MRGC analyses, see Mirman *et al.*, 2008; Mirman, 2014).

This MRGC analysis was valuable for including repeat measures and assessing sex differences. However, these polynomial functions are less suitable for fitting asymptotic data (Mirman, 2014) and could not incorporate the sparser data from older individuals. Marine mammal growth curve analyses have generally used the Gompertz (Gompertz, 1825; Read *et al.*, 1993; Stolen, Odell & Barros, 2002; Mattson

et al., 2006; Webster, Dawson & Slooten, 2010), von Bertalanffy (Von Bertalanffy, 1938; Stolen *et al.*, 2002; Mattson *et al.*, 2006) and/or Richards growth curves (Richards, 1959; Webster *et al.*, 2010; Fearnbach *et al.*, 2011). However, the Richards curve has increased flexibility as the point of inflection depends on the parameter M (Fearnbach *et al.*, 2011). Model selection in the drc (Ritz & Streibig, 2005) and fish-methods packages (Nelson, 2017) in R showed the Richards growth curve had the better fit for all our data (Supporting Information Table S2). Therefore, we fit a generalized logistic (Richards) growth curve (Richards, 1959), $L_t = A$ $[1-b \times \exp(-ct)]^M$, where L_t is the expected length at age t (years), A is the asymptotic adult length, b and c are free parameters that adjust the slope and inflection point of the curve and M describes the relative position of the inflection point relative to the asymptote. Unlike the MRGC analysis, this method cannot account for repeat measurements of individuals at different ages. Therefore, we randomly selected one annual length estimate for each individual dolphin (newborn to 26 years old), maximizing the number of individuals of each age while ensuring a spread of data across ages. Our full dataset is provided to allow exploration using other growth models (Supporting Information Table S6).

In addition, MRGC analysis detected no significant differences in length or growth between the sexes (see Results), so we combined data from both sexes in this analysis. Nevertheless, given that sex differences in growth have been found in other bottlenose dolphin populations (Read *et al.*, 1993; McFee *et al.*, 2012), we also fitted the Richards' growth curve to males and females separately using the drc package (Ritz & Streibig, 2005).

Calf length and growth

To investigate whether newborn length or growth differed between sexes, we used the subset of individuals with a known sex and month of birth and with at least two measurements in the first 2 years of life (*n* = 17). MRGC and Richards growth curve analyses suggested early growth was linear (Fig. 3 and Supporting Information Fig. S7), so we used a linear mixed-effects model with ID as a random effect, allowing for a separate intercept and slope for each individual. We also considered models with uncorrelated

random effects (e.g. independent intercept and slope) and comparison with an ANOVA suggested that these were the more parsimonious. Due to our small sample size, we used the second-order Akaike Information Criterion (AIC_c) (Burnham & Anderson, 2002) for model selection using the AICcmodavg package (Mazerolle, 2015).

To investigate individual variability in growth during this same period, we used individuals with a known month of birth that had been measured both as a newborn and 1 year old ($n = 17$). We used linear mixed-effects models with age as our explanatory variable, and ID as a random effect (to account for non-independence of repeat measurements) and a fixed effect (to capture individual differences and investigate individual growth). We also included whether a dolphin was a female's first calf to determine if this influenced newborn length or growth. The fixed effects of ID and first calf were modelled separately due to the limited amount of data available and model comparison was carried out using AIC_c (Burnham & Anderson, 2002).

First-year survival

To investigate whether length or birth order influenced first-year survival, we compared first-year data from calves that were seen in their second summer with calves that were assumed to have died (based on repeated observations of their mothers without a calf in the year after birth). Using a generalized linear model (GLM) with binomial error distribution and logit link, we also included the age when the latest laser measurement was made (L_age) to account for the fact that calves could have been first measured anywhere from <1 month to 3 months old. We dropped the least significant explanatory variable, in turn, and refitted the model until only the significant variables remained. Model selection was again carried out using AIC_c (Burnham & Anderson, 2002).
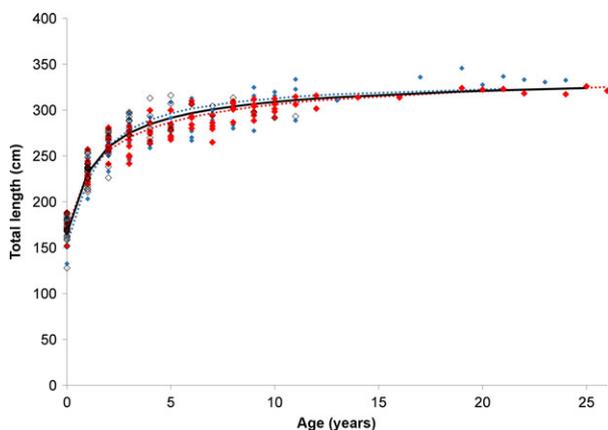

Figure 3 Annual estimates of length at age for female (red, $n = 22$), male (blue, $n = 18$) and unknown sex (white, $n = 47$) known-age bottlenose dolphins from the east coast of Scotland (Supporting Information Table S3). The solid line represents the Richards growth curve for all individuals, females (red dotted line) and males (blue dotted line), all fitted using only one measurement per individual.

Accuracy and precision of laser photogrammetry

To confirm the accuracy and test the precision of our laser photogrammetry method, we used this same technique during six photo-identification surveys in December 2011 with bottlenose dolphins in Sarasota Bay, Florida (Wells & Scott, 1990). In this population, BH-DF and length measurements have been measured directly during capture release for health assessments (Read *et al.*, 1993; Wells *et al.*, 2004). Only photographs of dolphins >11 years old were used to minimize growth between the dates of the health assessment measurements and laser photogrammetry photographs. Again all photographs were graded for quality and only the best photographs chosen for analysis. Laser BH-DF measurements were compared with health assessment measurements using a paired *t*-test, and the coefficient of variation (CV) was estimated from repeated measurements of the same individuals in different photographs. We compared estimated lengths to direct measurements made during the health assessments with a paired t-test.

In addition, two known individuals stranded on the east coast of Scotland in 2010 and 2011 (SRUC, 2017), permitting comparison of direct BH-DF and length measurements made after death with laser photogrammetry measurements made when alive.

Results

Laser photogrammetry

Photographs of sufficient quality for laser photogrammetry were available for 87 known-age individuals (88% of known-age dolphins photographed during this period and 45% of the estimated population). Ages ranged from <1 month to 26 years old with 18 males, 22 females and 47 individuals of unknown sex (Supporting Information Fig. S5). The month of birth was estimated for 55 of these individuals (10 males, 13 females and 32 unknown sex) (Supporting Information Fig. S6). An average of three ($SE = 0.02$) and maximum of 8 years of photogrammetry data were available for each dolphin, with an average of four ($SE = 0.26$) and maximum of 15 measurements for each individual in any 1 year. Length was estimated using the relationship between the BH-DF and body length derived from measurements of 11 Scottish bottlenose dolphin strandings (SRUC, 2017) ($F_{1,9} = 230.9$, $P < 0.0001$, $R^2 = 0.958$, $y = 3.1314x + 7.0626$). The average CV for length measurements of 20 adults (3 known age, 17 estimated age) with multiple photographs was 1.4% (ranging from 0.2 to 3.0%). CVs for repeat measurements of the same photographs were <0.6%.

Estimated lengths of known-age dolphins ranged from 128 cm for a <1 month old calf to 326 cm for a 25-year-old female and 346 cm for a 19-year-old male. The longest male dolphin was a 349 cm and longest female was 333 cm, both identified as adults in the early 1990s. Males over 15 years old were on average longer ($n = 13$, 335 cm, $SE = 2.8$ cm) than females ($n = 13$, 321 cm, $SE = 2.4$ cm) (Welch Two Sample *t*-test: $t = 3.8705$, d.f. $= 23.554$, $P < 0.001$).

Growth curve

The MRGC analysis indicated that, at least up to the age of 13 years, sex did not improve model fit on the intercept ($\chi^2(1) = 0.286$, $P = 0.593$), the linear ($\chi^2(1) = 1.315$, $P = 0.251$) nor all time terms ($\chi^2(1) = 0.567$, $P = 0.753$) (Supporting Information Tables S2 and S3 and Fig. S7). The Richards' growth curve for this study population levelled off, but did not reach a clear asymptote (Fig. 3). Separate models for males and females were similar to the growth curve for all individuals, and also showed no clear asymptote (Fig. 3).

Calf length and growth

Sex also did not appear to influence newborn length or growth (Table 1a). Measurements made during the first 2 years of each dolphin's life (<1–14 months old) indicate that first-born calves were slightly shorter (Fig. 4 and Table 1b). However, overall there was little individual variability in newborn length or growth (Table 1b).

First-year survival

Generalized linear modelling indicated that first-year survival was linked to body length (Table 1c). Sample sizes were small, but newborn bottlenose dolphins that died over their first winter were significantly shorter ($n = 7$, median = 159 cm) than those that survived ($n = 29$, median = 171 cm) (Mann–Whitney U test: $W = 165.5$, $P = 0.01$) (Fig. 5). In addition, there may be some influence of birth order on first-year calf survival ($\Delta AIC_c = 1.8$, Table 1c). Thirty-eight per cent of first calves died over their first winter, whereas only 14% of subsequent calves died.

Accuracy and precision of laser photogrammetry

Laser photogrammetric measurements were obtained from 78 photographs of 12 dolphins from Sarasota that had previously been captured, measured directly and released. There was no significant difference between the BH-DF measurements made during health assessments and laser photogrammetry (paired *t*-test, $t_{51} = -0.767$, $P = 0.447$). Differences between the BH-DF laser and health assessment measurements ranged from -7.5 to 8 cm (mean = 3 cm, SE = 0.3 cm). The mean CV from different photographs of the same individual was 1.7% (range 0.2–2.7%). For Sarasota dolphins, body length was estimated using the relationship between the BH-DF and length of a subset of 42

Table 1 Model selection and results of (a) linear mixed-effects model to investigate the influence of sex on newborn length and growth in male ($n = 6$) and female ($n = 11$) calves from newborn to 1 year old; (b) linear mixed-effects model to explore individual variability in newborn length and growth for all calves measured as a newborn and 1 year old ($n = 17$); and (c) generalized linear model with binomial error distribution to investigate the best predictor of calf over-winter survival ($n = 36$). The AIC_c values are shown for all models, the results are shown for the most parsimonious model with the lowest AIC_c (bold) and all models with some support ($\Delta AIC_c < 2$).

Model		Coefficient	SE	t	P	Random effects	Variance	SD	AIC_c	ΔAIC_c
(a)										
Length ~ Age + Age|ID	**Intercept**	**160.644**	**3.149**	**51.02**	**<0.0001**	**ID**	**66.032**	**8.126**	**469.3**	**0**
	Age	**6.218**	**0.328**	**18.96**	**<0.0001**	**Age|ID**	**0.584**	**0.764**		
Length ~ Age + Sex + Age|ID									471.6	2.3
Length ~ Age × Sex + Age|ID									474.2	4.9
(b)										
Length ~ Age + First Calf + Age|ID	**Intercept**	**167.694**	**1.901**	**88.219**	**<0.0001**				**433.8**	**0**
	Age	**6.126**	**0.229**	**26.698**	**<0.0001**	**ID**	**0**	**0**		
	First Calf	**−8.253**	**3.022**	**−2.731**	**0.011**	**Age|ID**	**0.137**	**0.369**		
Length ~ Age × First Calf + Age|ID	Intercept	168.293	2.023	83.179	<0.0001				435.7	1.9
	Age	6.022	0.259	23.253	<0.0001					
	First Calf	−11.371	4.778	−2.380	0.023	ID	0	0		
	Age:First Calf	0.459	0.544	0.844	0.4033	Age|ID	0.129	0.360		
Length ~ Age + ID + Age|ID[a]									466.7	32.9
Length ~ Age × ID + Age|ID									565.1	131.3
(c)										
Survival ~ Length	**Intercept**	**10.999**	**5.771**	**1.906**	**0.057**				**34.1**	**0**
	Length	**−0.0751**	**0.352**	**−2.135**	**0.033**					
Survival ~ Length + First Calf	Intercept	9.860	6.001	1.643	0.100				35.9	1.8
	Length	−0.070	0.036	−1.920	0.055					
	First Calf	0.756	1.012	0.747	0.455					
Survival ~ Length + First Calf + L_Age									38.3	4.2

[a]The most parsimonious model was with correlated random effects.
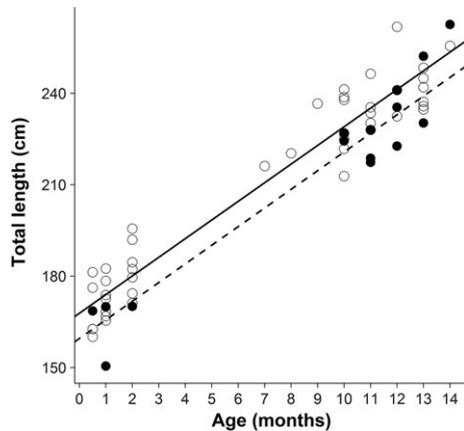
Figure 4 Length measurements of calves from <1 month to 14 months old with fitted lines from the most parsimonious linear mixed-effects model, showing estimated length of females' first calves (*n* = 3, black circle, dashed line) and subsequent calves (*n* = 14, white circle, solid line).
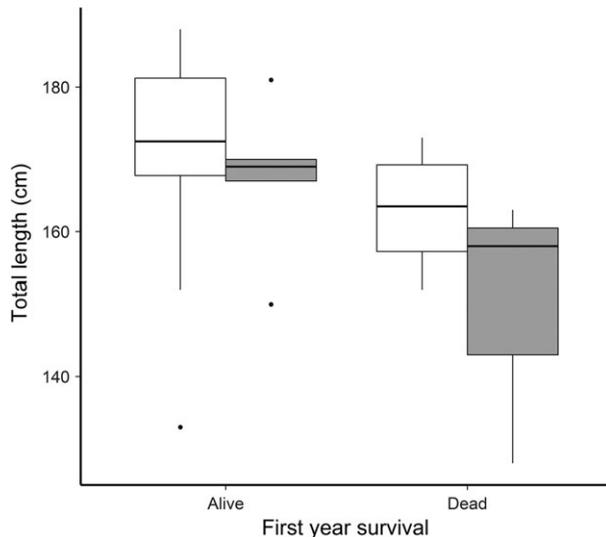

Figure 5 Length of newborn bottlenose dolphin calves during their first summer that either survived or died over their first winter, showing females' first (grey) or subsequent (white) calves.

Discussion

Growth and body condition can provide important indices of health and fitness, yet they can be difficult to collect alongside studies using remote observations of natural marks to monitor populations of conservation concern. Our findings illustrate how laser photogrammetry can be successfully integrated into boat-based photo-identification studies. Repeat measurements of free-ranging bottlenose dolphins were routinely made over 8 years, and the accuracy and precision of estimates characterized through comparison with direct measurements from free-living and stranded individuals. In combination with long-term observations that established the age of individuals, we developed a growth curve for individuals in this study population that was based entirely on measurements from remote observations. While sample sizes currently remain small, these data were used to explore the causes and consequences of variation in early growth. This highlights the potential for collecting data that can explore the energetic requirements and dynamics of protected cetacean populations.

Methodological considerations

A number of studies have developed approaches for the remote measurement of cetaceans using boat-based stereo-photogrammetry (Growcott, Sirguey & Dawson, 2012), aerial surveys (Perryman & Lynn, 1993; Sweeney *et al.*, 2014) or unmanned aerial vehicles (UAVs) (Christiansen *et al.*, 2016; Durban *et al.*, 2016). However, when using small boats, stereo-cameras generally require dedicated survey effort limiting their integration into monitoring programmes. Aerial data can only be linked to long-term individual-based data for larger species with distinct marks (Best & Rüther, 1992; Fearnbach *et al.*, 2011), with financial and safety considerations limiting this approach. Finally, UAVs can present technical and permitting challenges for many populations. Laser photogrammetry provides a simpler approach, which requires less investment in equipment, and can be fully integrated into the camera systems used for photo identification.

Working with known-length bottlenose dolphins in Sarasota (Wells *et al.*, 2004), we demonstrated that laser photogrammetry can provide robust estimates of body length. Laser photogrammetric measurements of BH-DF and the resulting estimates of length both compared well with existing direct measurements from health assessments. Errors around BH-DF measurements were comparable to results using laser photogrammetry to measure primate tail length (mean difference of 1.7%) (Rothman *et al.*, 2008) and aerial photogrammetry (mean difference of 1.2%, based on measurements of known-length boats) (Fearnbach *et al.*, 2011). Estimates of length showed greater differences, as these incorporated uncertainty in the relationship between BH-DF and length. Laser photogrammetry and physical measurements of stranded dolphins from our Scottish study population were also similar and closest for the individual where the length estimate was based on an average of two photogrammetric measurements. Blackwell, Basse & Dickman

individuals measured during health assessments ($F_{1,40}$ = 438.4, *P* < 0.0001, R^2 = 0.916, *y* = 2.9846*x* + 17.9155). There was also no significant difference between the length measured during health assessments and estimated by laser photogrammetry (paired *t*-test: t_{11} = 0.052, *P* = 0.9597). Differences ranged from −23 to 17 cm (mean = 5.9 cm, SE = 2.0 cm) which equated to −8.5 to 6.9% (mean = 2.3%) of the health assessment length.

The direct BH-DF measurements of the two adult male dolphins stranded in Scotland were both within 3 cm of mean laser photogrammetry estimates. The estimated length of each male was 9 cm (2.7%) shorter and 18 cm (5.2%) longer than the directly measured length.

(2006) highlight that at least two repeats should ideally be made, even with direct physical measurements. This is a reminder that some errors could result from variation in direct measurements, as significant differences in inter-researcher length measurements can occur (e.g. Waite & Mellish, 2009). CVs of repeat measurements were comparable to other laser photogrammetry studies (1.5–3.7%) (Rowe & Dawson, 2008; Deakos, 2010; Webster *et al.*, 2010) but were slightly higher than CVs for repeat physical measurements of adult dolphins (0.705%) (Read *et al.*, 1993). One possible reason for the slightly higher CVs in this study is that these incorporate horizontal axis error (i.e. when the dolphin is not parallel to the camera). Similar to Webster *et al.* (2010), who found deviations of <20° resulted in laser photogrammetry measurements within 2% of actual values, we minimized this error by discarding all photographs where the dolphin was considered to be non-parallel. Given the level of body size variation in these populations, measurements with this level of error and repeatability should provide valuable additional information on study individuals. Nevertheless, estimates should wherever possible be based on multiple measurements.

Growth curve

Measurements of stranded and bycaught bottlenose dolphins highlight that this species exhibits marked variation in adult body size, with the largest individuals occurring in colder environments at the extremes of their global range. However, datasets of sufficient size to generate growth curves are rare, and previously restricted to populations inhabiting warmer waters (Read *et al.*, 1993; Fernandez & Hohn, 1998; Stolen *et al.*, 2002). Our remote estimates of length at age were used to provide the first growth curve for a bottlenose dolphin population inhabiting temperate waters. The mean length of males and females over 15 years old was *c.* 30% longer than estimates of adult size for populations in sub-tropical waters (Read *et al.*, 1993; Fernandez & Hohn, 1998; Stolen *et al.*, 2002).

We also found that males and females in our population showed similar patterns of growth, in contrast to studies in sub-tropical waters (Read *et al.*, 1993; Fernandez & Hohn, 1998; Stolen *et al.*, 2002; McFee *et al.*, 2010). This may be a result of only including individuals up to 13 years old in our MRGC analysis, as Read *et al.* (1993) found that male bottlenose dolphins from Sarasota continued to grow after females reach asymptotic length (~ age 10). However, Richards' growth curves for males and females were very similar, and there was overlap in lengths of all ages, although adult males were on average longer than females. Read *et al.* (1993) also found that females were longer and grew quicker than males at an early age, but this was not seen in our temperate population. Bottlenose dolphins in Scotland are at the northern extreme of the coastal range of this species, and colder water temperatures may require both sexes to maximize early growth as thermoregulation costs increase with decreasing body size (Harding *et al.*, 2005). Although our growth curves did not reach an asymptote,

they did level off and appeared close to asymptote. The absence of an asymptote may be a consequence of fewer known-age older individuals or continued somatic growth throughout life, as found in pinnipeds (Trites & Bigg, 1996). Alternatively, there may be cohort variation in growth due to trends in food availability (Fearnbach *et al.*, 2011). This technique provides opportunities to explore these questions through continued longitudinal studies of the size of known individuals in relation to intrinsic and extrinsic drivers.

Causes and consequences of variation in newborn size and early growth

Our results were consistent with previous studies of stranded and bycaught dolphins indicating that male and female newborn calves are a similar size (Hohn, 1980; Cockcroft & Ross, 1990). We also found that sex did not affect initial calf growth, and there was little individual variability in growth. Although the combined dataset from both sexes remained small, there was evidence that first-born calves were shorter than calves of experienced mothers, as previously reported for large whales (Best & Rüther, 1992). Size and growth can be affected by maternal characteristics in various species (Bowen *et al.*, 1994; Bernardo, 1996; Altmann & Alberts, 2005). Thus, first-born dolphin calves may be smaller because mothers were younger and less experienced and/or of smaller size.

Importantly, results indicate that observed variation in calf length has fitness consequences. Calves that died over their first winter were significantly shorter than those that survived. It seems likely that variation in calf length provides a proxy for maternal investment or measures of body mass and condition (Cockcroft & Ross, 1990; Reed & Plante, 1997). Individual-based studies in both terrestrial (Clutton-Brock *et al.*, 1987) and marine (Hall, McConnell & Barker, 2001; Harding *et al.*, 2005) species have illustrated how direct measures of early mass or condition may be related to subsequent survival. This is especially important in a conservation context, as the consequences of exposure to non-lethal stressors (e.g. noise, boat disturbance) are expected to act through changes in foraging energetics, and likely to be detected through variation in early growth and survival (Pirotta *et al.*, 2015). There is also some evidence that birth order affects early survival in other bottlenose dolphin populations (Mann *et al.*, 2000; Henderson *et al.*, 2014), but this may be confounded by variation in female size, small sample sizes and environmental contaminant concentrations (Wells *et al.*, 2005). Laser photogrammetry offers the potential to disentangle these effects by non-invasively integrating repeat measurements of recognizable individuals into routine monitoring of protected cetacean populations.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. The Moray Firth Special Area of Conservation.
Figure S2. Diagram of the laser photogrammetry machined aluminium block.
Figure S3. Diagram of the electronic control switch for the laser sights.
Figure S4. Relationship between the blowhole to dorsal fin distance and body length of bottlenose dolphins.
Figure S5. Number of dolphins by age and gender.
Figure S6. Number of dolphins of different estimated ages to the month.
Multilevel Regression Growth Curve Analyses.
Figure S7. Laser photogrammetry measurements of males and females from newborn to 13 years old with multilevel regression growth curve.
Table S1. Length (cm) of bottlenose dolphins first identified as adults or sub-adults between 1989 and 1996.
Table S2. Results of the multilevel regression growth curve analyses.
Table S3. Comparison of the multilevel regression growth curve models using ANOVA.
Table S4. Model selection results for Richards and Gompertz growth curves.
Table S5. Length (cm) of known-age bottlenose dolphins.
Table S6. Dataset.