



Determination of growth, mass, and body mass index of harbour porpoises (*Phocoena phocoena*): Implications for conservational status assessment of populations

Emilie Nicoline Stepien^{a,b,c,*}, Jacob Nabe-Nielsen^c, Kirstin Anderson Hansen^{a,d}, Jakob Højer Kristensen^d, Marie-Anne Blanchet^{d,e,f}, Sabrina Brando^{d,g}, Geneviève Desportes^{d,h}, Christina Lockyer^{i,j}, Lauro Marcenaro^k, Paulien Bunskoek^k, José Kemper^l, Ursula Siebert^m, Morten Tange Olsen^b, Magnus Wahlberg^{a,d,*}

^a Marine Biological Research Centre, University of Southern Denmark, Denmark

^b Evolutionary Genomics, Globe Institute, University of Copenhagen, Denmark

^c Section of Marine Mammal Science, Department of Ecoscience, Aarhus University, Denmark

^d Fjord&Bælt, Margrethes Pl. 1, 5300 Kerteminde, Denmark

^e Norwegian College of Fishery Science, The Arctic University of Norway, Tromsø, Norway

^f Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway

^g World Association of Zoos and Aquariums, Spain

^h NAMMCO – North Atlantic Marine Mammal Commission, Norway

ⁱ Age Dynamics, Huldbergs Alle 42, 2800 Søborg, Denmark

^j Danish Institute for Fisheries Research, Charlottenlund, Denmark

^k Dolfinarium Harderwijk, Zuiderzeeboulevard 22, 3841 WB Harderwijk, the Netherlands

^l Ecomare, Ruijslaan 92, 1796 AZ De Koog, the Netherlands

^m Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Germany

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ABSTRACT

Longitudinal data on individual growth and seasonal changes in body mass, girth, and blubber thickness are rarely available for cetaceans, making it difficult to assess their population composition and individual nutritional condition. During different time intervals from 1997 to 2020, we collected longitudinal data on length, body mass, girth, and blubber thickness from seventeen harbour porpoises (*Phocoena phocoena*) in human care. We compared Gompertz and von Bertalanffy growth curves to collected length data at age 0–4 years for five individuals with known dates of birth. Von Bertalanffy had the lowest AICc value and was used to predict the birth year of twelve animals which age had previously been estimated based on tooth ring analysis and ossification of flipper bones. The growth curve was accurate within 1 yr. of age estimates. Within the first year, the calves grew 66%, attaining 84% of their adult length, and reached asymptotic length at age 3–4. For adults, there were large seasonal variations in body mass, body mass index, girth, and blubber thickness, with up to 28% of variation in body mass between seasons. We predicted individual body mass within ± 2 kg using measurements of length and girth, allowing estimation of body mass index of individuals with unknown mass. Our findings enable monitoring

* Corresponding authors at: Marine Biological Research Centre, University of Southern Denmark, Denmark.

E-mail addresses: emilie.stepien@gmail.com (E.N. Stepien), magnus@biology.sdu.dk (M. Wahlberg).

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and assessments of population composition as well as nutritional condition of individual harbour porpoises, which is crucial for assessing conservational status and guiding management.

1. Introduction

Although the harbour porpoise (*Phocoena phocoena*) has been studied intensely in the northern hemisphere for the last decades, its conservational status remains unclear due to lack of data on population composition and nutritional condition. Such data provide important information on habitat quality and are crucial for guiding management and may be used as indicators of the impact by anthropogenic stressors (fisheries, contaminants, ship traffic, construction work, etc., (Council, 2005; Stone and Tasker, 2006; Desforges et al., 2016; van Beest et al., 2017; Nabe-Nielsen et al., 2018; van den Heuvel-Greve et al., 2021; Joy et al., 2022)). Data on growth, body mass, and age distribution can be used in bioenergetic models to predict how vulnerable populations are to changes in individual animals' body reserves and life expectancy when external conditions change (Council, 2005; van Beest et al., 2017; Nabe-Nielsen et al., 2018; New et al., 2014; Gallagher et al., 2018, 2021a; Hin et al., 2019, 2021b; Keen et al., 2021; Siebert et al., 2022)). Traditionally, population composition and nutritional status of animals have been derived from bycaught or stranded individuals (Møhl, 1954; Yasui and Gaskin, 1986; Worthy and Edwards, 1990; Lockyer, 1995a, 1995b; Kock and Benke, 1996; Koopman et al., 2002; McLellan et al., 2002), which can result in biased estimates. More recently, photogrammetry (the science of measuring objects from images) from e.g., drone images have been used to determine morphometrics of large whales and infer their age and nutritional status (Christiansen et al., 2016, 2018, 2019; Russell et al., 2022; Christie et al., 2022; Hirtle et al., 2022)). Until now, photogrammetric methods have not been validated for smaller cetaceans such as porpoises.

The harbour porpoise is the smallest cetacean in North Pacific and North Atlantic waters (Read, 1999). Due to their small size, porpoises have elevated heat loss per unit mass compared to larger cetaceans, as the amount of energy lost as heat is proportional to the ratio between body surface and volume (McLellan et al., 2002). To compensate for the small body size, porpoises rely on a relatively thick layer of blubber; a multifunctional tissue that prevents extensive heat loss, while it also supports locomotion, adjusts buoyancy, streamlines the body and works as an efficient energy storage (Gallagher et al., 2021a; Worthy and Edwards, 1990; Koopman et al., 2002, 1996; McLellan et al., 2002; Parry, 1949; Ryg et al., 1988, 1993; Koopman, 1998; Hamilton et al., 2004; Castellini, 2018; Pabst et al., 1999). The total body mass of porpoises consists of 27% blubber (Lockyer, 1995a, 1995b), of which 82% is attributed to lipids (Worthy and Edwards, 1990). Blubber anabolism or catabolism are activated during growth, reproduction, lactation, and in response to seasonal water temperature changes (Lockyer et al., 2003a, 2003b; Rojano-Doñate et al., 2018).

Due to the high heat loss and large blubber thickness variations between summer and winter (Yasui and Gaskin, 1986; Kock and Benke, 1996; Lowry and Teilmann, 1994), harbour porpoises have a high energetic demand (Lockyer et al., 2003b). Several studies have raised concerns that the porpoises may be particularly sensitive to natural as well as anthropogenic-induced environmental changes (Millar and Hickling, 1990; Hanks and Siniff, 1992; Beineke et al., 2005; Carstensen et al., 2006; Das et al., 2006; Tougaard et al., 2006, 2015; Fontaine et al., 2007; MacLeod et al., 2007; Brandt et al., 2011; Andreasen et al., 2017; Kesselring et al., 2017; Wisniewska et al., 2018; Kastelein et al., 2019a, 2019b; Booth, 2020; Carlén et al., 2021). The animals' ability to efficiently find prey, and hence maintain their energetic status may be affected by increased pressure e.g., from fisheries, chemical pollutants, offshore construction, underwater noise and changes in water temperature, all of which have the potential to heavily affect behaviour, energy reserves as well as prey availability (Gallagher et al., 2021b; Beineke et al., 2005; Das et al., 2006; MacLeod et al., 2007; Wisniewska et al., 2018; Reyes, 1991; Clark et al., 2009; Reeves et al., 2013; Jepson et al., 2016).

Individuals' energy reserves can be assessed with physiological indices (Keys et al., 1972; Read, 1990), such as the Body Mass Index (BMI), which is linked to survival, reproductive success and fitness (Peig and Green, 2010; Kershaw et al., 2017). For large cetaceans, BMI has been assessed from data collected using unmanned aerial vehicles (UAVs; drones), but without the possibility to physically measure the whales to validate the estimates (Christiansen et al., 2016, 2018, 2019; Russell et al., 2022). For porpoises, BMI can be calculated for individuals kept in human care, where animal size and weight can be measured repeatedly across seasons and life stages (Lockyer et al., 2003a; Kastelein et al., 1997a, 1997b, 2018). Similar longitudinal data cannot be obtained for wild porpoises, as individuals are hard to identify (Elliser et al., 2018; Keener et al., 2011; Koopman and Gaskin, 1994). Future data from UAV-based measures of wild individuals' energy reserves can be validated and more accurately interpreted by using data on captive animals. Furthermore, the age of wild animals can hopefully be derived from length measurements using growth curves established from animals of known ages.

Our goal in this study was to determine whether it is possible to determine age, body mass, body mass index, and blubber thickness from parameters available from photogrammetry, that is length and sometimes also girth. In pursuing this aim, we evaluated the growth rate and seasonal responses from longitudinal data on 17 harbour porpoises kept in human care from 1997 to 2020 and compared it with data from wild populations. This study thereby provides models applicable for non-invasive methods to determine the age and nutritional status for wild harbour porpoises.

2. Materials and methods

2.1. Description of animals and facilities

In Denmark, data from five harbour porpoises (C1, F1–F3 and M1 in Table 1) were collected from March 1997 to November 2010,

Table 1

Age of animals during periods of data collection (1997–2020). Years with data collection at facilities; FB: Fjord&Bælt, DH: Dolfinarium Harderwijk, EC: Ecomare, SD: SOS Dolfijn. Comparing age of harbour porpoises derived from the von Bertalanffy growth curve (VBGC) with the age derived from dental layers and flipper bone ossification. Estimated error between VBGC and additional aging method (in years).

ID	Age	Years (w. data)	Year of birth from VBGC or known*	Additional aging method and at age	Est. year of birth from additional aging method	Est. error (± yrs.)	No. data points
C1 ♀	0–3 years	2007–2010, 2013 (FB)	2007 *	Dental	2007	0	14
C2 ♀	0–4 years	2012–2016 (DH)	2012 *	Ossification	2012	0	53
C3 ♀	0–2 years	2009–2011 (DH)	2009 *			0	31
C4 ♀	0–6 years	2012–2019 (DH)	2012 *	Ossification	2012	0	34
C5 ♂	0–5 months	2012 (DH)	2012 *			0	5
F1 ♀	2–24 years	1997–2006, 2017–2019 (FB)	1995				304
F2 ♀	9–12 months	1999–2000 (FB)	1998	Dental	1998	< 1	33
F3 ♀	4 months – 13 years	2004–2017 (FB)	2004	Dental	2004	< 1	64
F4 ♀	3–6 months	2008 (SD)	2008				4
F5 ♀	0–11 years	2007–2019 (DH)	2007	Ossification	2007	< 1	86
F6 ♀	1–5 years	2011 (SD), 2012 (EC), 2013–2015 (DH)	2011	Ossification	2010	1	16
F7 ♀	12–16 years	2015–2019 (DH)	2002	Ossification	≤ 2003	< 1	17
F8 ♀	9–11 years	2015–2016 (DH)	2005	Ossification	2005	< 1	10
M1 ♂	2–12 years	1997–2010, 2016 (FB)	1995	Dental	1996	1	374
M2 ♂	8 months – 2 years	2014–2015 (SD), 2015 (DH)	2013	Ossification	2013	< 1	19
M3 ♂	8 months – 4 years	2013 (SD), 2014 (DH), 2015–2019 (EC)	2013	Ossification	2012/2013	< 1	65
M4 ♂	0–9 years	2009 (SD), 2010–2011 (DH), 2012–2019 (EC)	2009				58

and continued from October 2017 to August 2020, at the marine outreach and research centre Fjord&Bælt (FB) in Kerteminde. The semi-enclosed facility measures 30 × 18 × 3.5 m (length × width × depth) and is situated within a small harbour, allowing for natural water flow and seasonal variations in salinity and water temperature. Water is well-mixed with no stratification, with salinity of 15–21 ppt. and a water temperature rarely lower than 2 °C in the winter and not higher than 18 °C in the summer (Riisgård et al., 2008). The FB porpoises had access to wild fish, such as gobies and sometimes herring entering the enclosure, however the major caloric intake came from the fish fed during training sessions (Rojano-Doñate et al., 2018).

In the Netherlands, body measurements from twelve harbour porpoises were included in this study from August 2007 to April 2019. The animals were kept in three different facilities (Dolfinarium Harderwijk (DH), Rehabilitation Facility SOS Dolfijn (SD) and Ecomare (EC)) of different pool sizes and types of water. Eight animals (F4–F8, and M2–4 in Table 1) arrived as stranded wild harbour porpoises at SD and were later transferred to DH, and four animals (C2–5, Table 1) were born at DH. One animal (F4, Table 1) was kept at SD during the entire period it was measured for this study. Two of the animals at DH (M3 and M4, Table 1) were later transferred and housed at EC. Another animal from DH (F8, Table 1) spent one year at EC before it was returned to DH.

The rehabilitation facility, SOS Dolfijn, consisted of two separate pools that were oval in shape and measured 6 × 8 × 1.6 m. The pools were located indoors, filled with artificial saltwater filtered using sand filters and changed regularly and tempered to maintain proper water quality, with salinity of 20–23 ppt. and water temperature of 12–25 °C. The SD facility was used to rehabilitate stranded porpoises during the first period after arrival in human care; after their condition stabilised, they were either transferred to DH or released into the wild.

Dolfinarium Harderwijk has an outdoor porpoise facility with artificial saltwater consisting of two pools connected by one small pool with a total volume of 470 m³ and a maximum depth of 2.6 m. The pool water salinity was 21–29 ppt. Water temperature followed the seasonal fluctuations, from a winter minimum of 2°C and a summer maximum of 25°C, but most often restricted between 10 and 18 °C (Fig. 3).

The porpoise facility at the natural history museum Ecomare consists of two connected pools, with a total volume of 284 m³ and a maximum depth of 3 m, containing chlorinated seawater. Water temperatures ranged between 4 and 21 °C in both pools, slowly fluctuating due to seasonal changes and most often staying within 10–18 °C, with a salinity of 29–31 ppt.

Except for a single animal kept at the rehabilitation facility, SOS Dolfijn, throughout the time where data were included in this study (F8, Table 1), the environmental conditions (such as water and air temperature, water salinity and diel photoperiod) in this study were kept equal to the environmental conditions in North European coastal waters.

2.2. Individual harbour porpoise measurements

The animals were trained using operant conditioning and positive reinforcement methods (Pryor, 1999) to participate in voluntary husbandry procedures (i.e. handling, weighing, blubber thickness, and medical sampling), public presentations and scientific experiments. Individual measurements of weight (kg), length (cm), girth (cm) and blubber thickness (mm) were conducted on four females and one male at FB (C1, F1–3, and M1), as well as eight females and four males (C2–C5, F4–8 and M2–M4) at SD, DH and EC. Measurements were made either during training sessions during feeding, or while the animal was brought on land for medical checks. Typically, measurements were made every month, but additional measurements were made as well as longer breaks due to change in staff or management procedures at the facilities.

Each measurement session included some or all of the following measurements (see Fig. 1): i) Standard length (measured in a direct line from the tip of the rostrum to the notch in the tail fluke); ii) Girths (G1: right in front of pectoral fins, G2: right behind pectoral fins, G3: right in front of the dorsal fin, G4: right behind the dorsal fin, G5: at anal opening, and G6: halfway between anal opening and the tail); and iii) blubber thickness at multiple locations on the body (D2–D4, L2–L4, V2–V4); all measurements *sensu* Lockyer (Lockyer et al., 2003a) (see Fig. 1). Length and girths were measured with a string and a measurement rod, and body mass with a large scale on which the animal was located, either by voluntarily beaching itself on a pontoon or by lifting the animal out of the water in a sling. Blubber thickness was measured with an ultrasonic scanner (Esaote MyLab 30 Vet Gold with a PA230E 2 –3.5 MHz phased array transducer, Genoa, Italy) in the Netherlands, and an ultrasound estimator (Renco LEAN-MEATER®, Minnesota, USA, in Denmark).

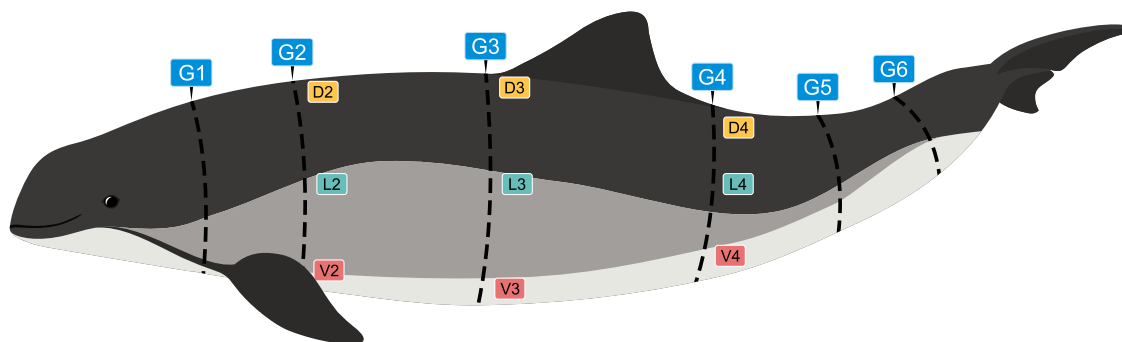


Fig. 1. Measurements of girth (G1–G6), blubber thickness (D2–D4, L2–L4, V2–V4), and length collected monthly from five harbour porpoises at Fjord&Bælt (Denmark), and at Dolfinarium Harderwijk, Ecomare, and SOS Dolfijn (the Netherlands). Illustration by Cara Gallagher.

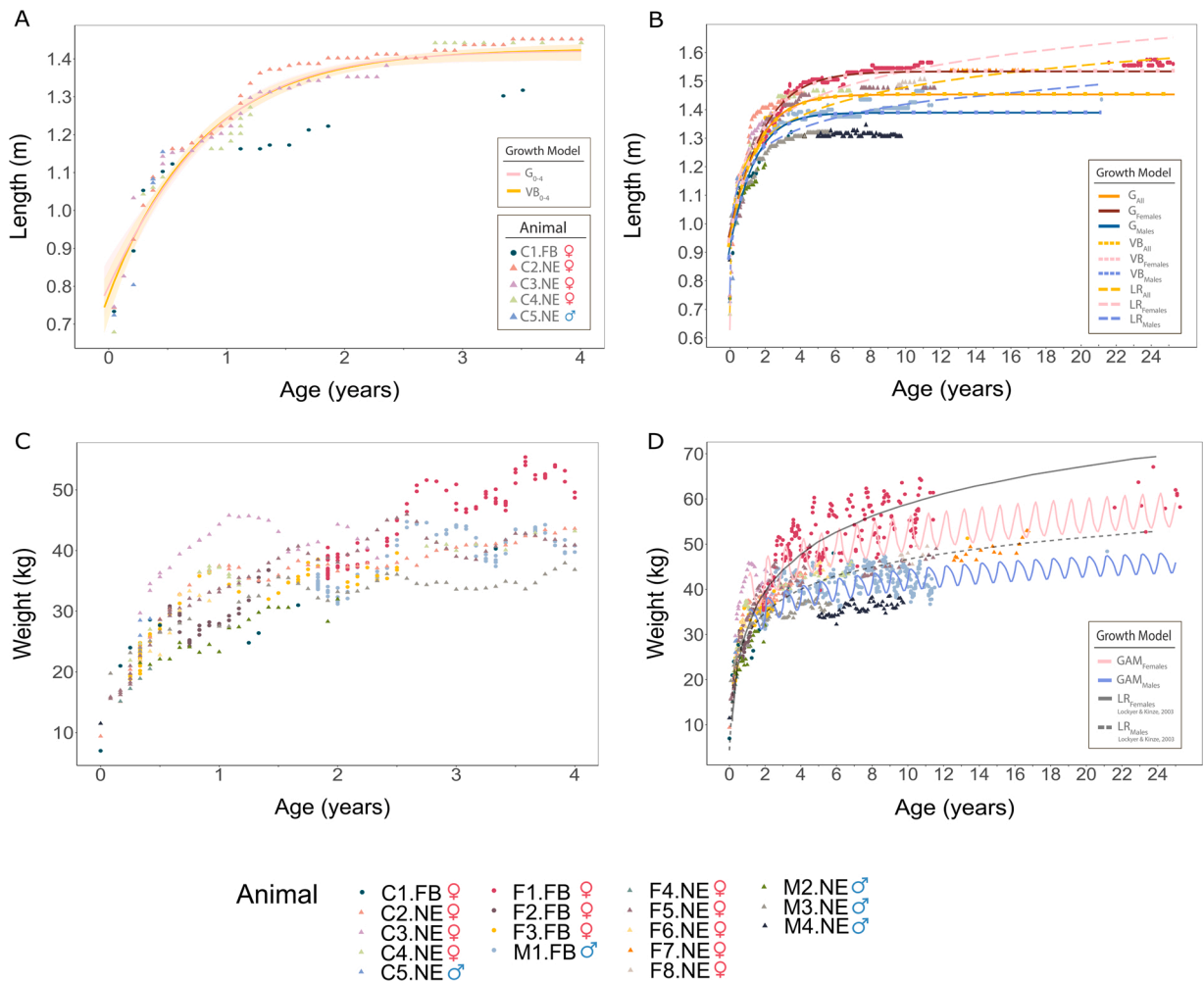


Fig. 2. Long-term growth of individual harbour porpoises for age-classes 0–4 years (A and C), and 0–25 years (B and D) for four females (C1, and F1–3) and one male (M1) harbour porpoise in the semi-enclosed natural environment at Fjord&Bælt (circles), as well as eight females (C2–3, and F4–8) and four males (C4, and M2–4) in temperature-regulated pools at Dolfinarium Harderwijk and Ecomare (triangles). **A**) Gompertz Growth Curve (G , $Length = 1.42 e^{-0.542 (e^{-0.119 AgeMonth})}$) and von Bertalanffy Growth Curve (VB, $Length = 1.42 (1 - e^{-0.104 (AgeMonth + 8.038)})$) fitted for four females (C1–4), and one male (C5) from 0 to 4 years, with known date of birth; **B**) Gompertz Growth Curve (G , solid lines, $Length = L_{\infty} e^{-K (e^{-t_0 \times AgeMonth})}$), von Bertalanffy Growth Curve (VB, dotted lines, $Length = L_{\infty} (1 - e^{-K (AgeMonth - t_0)})$) and linear regression (LG, dashed lines, $Length = a + b (\log_{10}(Age_{month} + 0.1))$), for all individuals from 0 to 25 years (yellow), as well as females (pink) and males (blue) separately; **C**) Shows the body mass from 0 to 4 years; **D**) The fit for females (pink line), males (blue line) based on *gam* (Body mass = $\log_{10}(Age_{year} + 0.1) + Month$). Inserted grey lines are growth curves based on bycaught, hunted or stranded harbour porpoise females (solid line) and males (dotted line) as reported in Lockyer & Kinze (Lockyer and Kinze, 2003).

The blubber thickness measured was the total depth of blubber at a given location of the body (D2–D4, L2–L4, V2–V4). Muscle activity may influence blubber thickness measurements, and therefore data was only included if the animal did not move while the reading was performed.

To minimise stress, the calf born at FB (C1) was not handled during the first three months after birth. After that, length and weight could be obtained by similar methods as described above for adults. Likewise, the four calves (C2–5) born at DH were not handled within the first four months after birth. At DH, indirect measurements of their length were obtained from photographs taken from above of the calf swimming alongside its mother. The pictures were processed in Matlab, where coordinates from rostrum (R) to the notch in the tail (T) were used to calculate the length in pixels $L_p = \sqrt{(T_2 - R_2)^2 + (T_1 - R_1)}$ (Reyes, 1991), where R_1 and R_2 and T_1 and T_2 are the x and y pixel coordinates for the rostrum and tail, respectively. This measurement was made for both mother and calf from the same picture with a pixel resolution from 96–180 dpi. It was then possible to estimate the length of the calf by comparing its pixel length to the mother’s known length, measured while handled on land. When the calves at DH reached four months of age, their length, body mass and girths were obtained from direct measurements by the trainers.

The age of three porpoises from FB were determined from tooth growth layers using teeth extracted post-mortem (Bjørge et al., 1995; Lockyer, 1995b), and the age of nine animals from the Netherlands X-rays of pectoral fins were used to determine bone maturity.

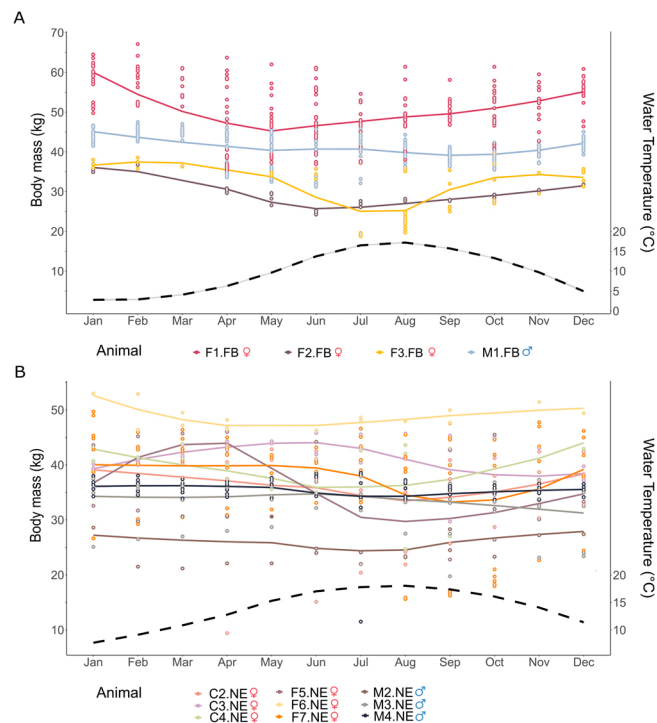


Fig. 3. Seasonal variations in body mass of individual harbour porpoises. Points of individual variations in body mass (kg) for March 1997 to August 2020 for A) one male (M1) and three female (F1–F3) harbour porpoises at Fjord&Bælt, and B) for six females (C2–4, and F5–7) and three males (M2–4) at Dolfinarium Harderwijk and Ecomare from August 2007 to April 2019. The black line illustrates the seasonal variations in ambient average monthly water temperature (°C) through the same period. Smoothed conditional means were applied for fitted lines using Local Polynomial Regression Fitting (*loess*) for each individual.

Development of ossification of epiphyses was compared to reported ossification patterns of harbour porpoises of known age of up to 15 years (Dawson, 2003; Galatius et al., 2006; Mellor et al., 2009). In addition, for newly arrived animals of young age, such as F1 and M1, we initially determined if they were less or more than one year old by assessing the presence of tongue papilla, known to be prominent in suckling calves (porpoises are weaned after about 10 months (Lockyer, 2003); Lockyer and Kinze, 2003).

The health of the animals was thoroughly monitored monthly by a veterinarian and daily by animal trainers. The animals were kept in good health condition by enriching their diet with vitamin supplements and by anthelmintic treatment. Two of the females at FB went through two gestations each; F1 giving birth in July 2006 and in August 2007 (included in the study as C1 in Table 1), and F3 giving birth in July 2013 and July 2014. Five porpoises went through gestation during the study period: F1 from October 2005 (she became pregnant in September) until September 2017, F7 had two pregnancies, giving birth in May 2009 and March 2012. F5 and F8 had one pregnancy each and gave birth in April 2012. For non-pregnant porpoises, no data were collected for F3 from November 2006 to September 2017, F5 were not measured from January 2012 until January 2015, and the data collection for F7 and F8 begun in February and January 2015, respectively. M2 was not sexually mature and F4 and F8 were not measured consistently (for more information of the animals, see Table 1).

The porpoises were fed 3–12 times a day by animal caretakers with 10–30 fish per feed. The species of fish varied throughout the years, but usually consisted of any of the following: herring (*Clupea harengus*), mackerel (*Scomber scombrus*), sprat (*Sprattus sprattus*), capelin (*Mallotus villosus*), and sand lance (*Ammodytes tobianus*). In addition, on rare occasions porpoises were fed cod (*Gadus morhua*), whiting (*Merlangius merlangius*), blue whiting (*Micromesistius poutassou*), trout (*Salmo trutta*) and squid (*Loligo sp.*). Fish was offered in roughly equal portions each day. The diet composition and energy content were continuously adjusted based on season, the animals' overall body appearance, and general motivation (regarding animals at FB, see (Rojano-Doñate et al., 2018; Blanchet et al., 2008) for details regarding seasonal diet).

2.3. Data analysis

2.3.1. Individual growth and seasonal variations

To determine the growth curve for 0–4 years old porpoises, we fitted Gompertz (Winsor, 1932) and von Bertalanffy growth curves (Beverton, 1954; Beverton and Holt, 1957) to allow for comparison with wild individuals from other studies. This was done using age and length data for five animals born in facilities (one male and four females, C1–5, Table 1), for the ages that could be determined with 1-day precision, from 0 to 4 years:

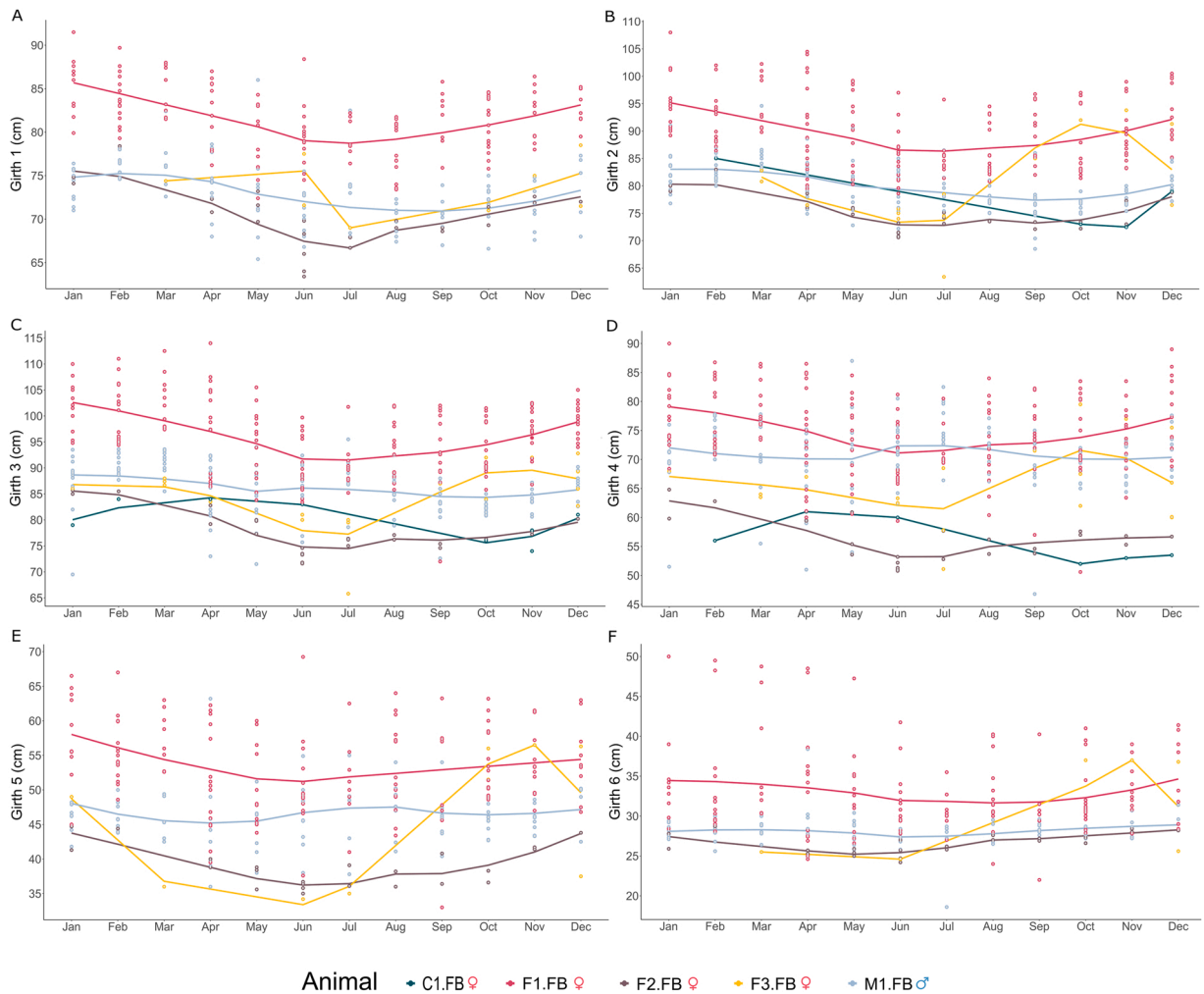


Fig. 4. Long-term seasonal variations in girths of individual harbour porpoises. Girths from one male (M1) and four females (C1 and F1–3) at FB measured at A) Girth 1 (n = 273); B) Girth 2 (n = 354); C) Girth 3 (n = 370); D) Girth 4 (n = 363); E) Girth 5 (n = 287); and F) Girth 6 (n = 267). Smoothed conditional means were applied for fitted lines using Local Polynomial Regression Fitting (*loess*). See Fig. 1 for body sites of measurement. C1 was only measured at G2, G3 and G4 and is therefore not included in A, E and F.

Gompertz Growth Curve:

$$nls(\text{Length} = L_{\infty} e^{-K(e^{-t_0 * \text{AgeMonth}})})$$

Von Bertalanffy Growth Curve:

$$nls(\text{Length} = L_{\infty} (1 - e^{-K(\text{AgeMonth} - t_0)})),$$

where L_{∞} is the asymptotic length at which growth is zero, K is the growth rate, and t_0 is defined as the age at which the animal would have zero size (von Bertalanffy, 1957). The year span 0–4 years was chosen to ensure higher accuracy when determining the age, and to obtain accurate age data during the most critical years in their lives (Kesselring et al., 2017). The best fitted growth curve was then used to estimate the age of the porpoises not born under human care by fitting their growth in length and body mass over time. Growth curves were fitted using least squares, *nls*, (*FSA* (Ogle et al., 2020) *car* (Fox and Weisberg, 2019), and *boot* (Canty and Ripley, 2020) packages) for R version 4.0 (Team, 2018).

In order to compare the fit of Gompertz and von Bertalanffy growth curves for our data with the linear regression method previously used to illustrate growth from bycaught harbour porpoises by Lockyer & Kinze (Lockyer and Kinze, 2003), we compared the fit of the growth curves with that of a linear regression of length as a function of age ($\ln(\text{Length} = \log_{10}(\text{AgeMonth} + 0.1))$) using Akaike Information Criterion corrected for small sample sizes (AICc).

To graphically demonstrate the seasonal variation in body mass, we used the *mgcv* package (Wood, 2011) for General Additive Model (GAM) to fit body mass as a function of age and month: $\text{gam}(\text{Body mass} = \log_{10}(\text{Age}_{\text{Year}} + 0.1) + \text{Month})$. When illustrating body

mass, girth and blubber thickness as a function of season, we used *geom_smooth* function from the *ggplot2* package (Wickham, 2016) to smooth conditional means for fitted lines using Local Polynomial Regression Fitting (*loess*).

The selection of variables and statistical model for body mass and blubber thickness determination was based on the *dredge* function in the *MuMIn* package (Barton, 2009), using the model with the lowest second-order corrected AICc values.

2.3.2. Predictors of harbour porpoise body mass, body condition index and blubber thickness

To determine the nutritional state of porpoises based on their length and girth, we used linear mixed-effects models with body mass being a function of length and each of the six girths measurements, and with animal ID as random factor (e.g., $Body\ Mass = Length + G1 + (1 | Animal)$). The reason for this was to determine how well each of the girth measurements explain the total body mass of an individual. Although the relationship between body mass and girth may vary among seasons, we did not include seasonal variation in the prediction models, as the impact of seasonality is likely to vary not only among seasons, but also between years and locations. A model including seasonality would thus only be suitable for predicting animal body mass in some years in areas with the same conditions as the facilities. Models were fitted using *lmer*, from the *lmerTest* package (Kuznetsova et al., 2017), and *lm.beta* (Behrendt, 2014) was used to determine the marginal and conditional R^2 -values, i.e. the proportion of total variance explained by fixed effects and by entire model, respectively. The Mean-Squared Deviation (MSD) was estimated from the mean of the model residuals.

To determine which girth measurements were needed to achieve the best prediction of each of the nine blubber thicknesses, the *dredge* function in the *MuMIn* package (Barton, 2009) was used for model selection to define the reduced *lm* models based on lowest AICc values.

3. Results

3.1. Growth of harbour porpoises

A total of five calves (females = 4, males = 1) with known date of birth were fitted to von Bertalanffy and Gompertz growth curves (Fig. 2A). Within the first year, the calves grew 60%, attaining 84% of their maximum adult length, and reached asymptotic size at age 3–4 (Fig. 2A–B). von Bertalanffy fitted better to the observed data (AICc = –359.6 for 0–4 years, –3017.7 for all individuals) than the Gompertz growth curve (AICc = –350.4 for 0–4 years, –3004.3 for all individuals). Although the linear regression model was best when including all seventeen individuals (AICc = –3077.4) it did not capture the overall trend in the observed data (Fig. 2B). When separating the growth into genders, the von Bertalanffy had the lowest AICc value for both females and males (Appendix Table 1). Asymptotic length was reached 1–2 years earlier for males than for females, and all but one of the females attained a larger length and body mass than the males. The formulas derived from the fitted growth curves of porpoises 0–4 years born in the facilities were:

Gompertz Growth Curve.

$$\text{Length} = 1.42(e^{-0.542 e^{-(0.119\text{AgeMonth})}}) \quad (1)$$

Von Bertalanffy Growth Curve.

$$\text{Length} = 1.42 (1 - e^{-0.104 (\text{AgeMonth} + 8.038)}) \quad (2)$$

The formulas for all of the fitted growth curves can be found in appendix.

3.2. Intra-seasonal variation in porpoise body condition

The two calves that were physically measured after birth (C1–C2) increased 288% in body mass from 0 to 1 year. This rapid increase

Table 2

lmer model for the prediction of body mass for harbour porpoises as a function of two explanatory variables; girth and length, for each of the six girth measurements. Animal ID was used as random effect in all models. Mean Squared Deviation (MSD in kg), Root-Mean Squared Error (RMSE in kg), Marginal R² (R²m, variance explained by fixed effects), conditional R² (R²c, variance explained by full model). All variables contributed significant to the models, with p-values < 0.001.

<i>lmer</i> Model	Parameter	MSD _{kg}	RMSE _{kg}	Obs.	R ² m	R ² c
Body mass ~ Length + G1	Length G1	5.6	2.4	396	88.7%	92.0%
Body mass ~ Length + G2	Length G2	4.0	2.0	466	90.5%	94.2%
Body mass ~ Length + G3	Length G3	3.9	2.0	529	93.6%	94.7%
Body mass ~ Length + G4	Length G4	8.9	3.0	314	77.9%	84.2%
Body mass ~ Length + G5	Length G5	7.9	2.8	380	80.7%	86.6%
Body mass ~ Length + G6	Length G6	10.7	3.3	258	72.3%	79.2%

Table 3

Reduced *lm* models for blubber thickness selected from the *dredge* function in the *MuMIn* package (Barton, 2009). Mean Squared Deviation (MSD in mm), Root-Mean Squared Error (RMSE in mm), Multiple R^2 (R_M^2) and Adjusted (R_A^2). All p-values were < 0.001.

<i>lm</i> Model	MSD _{mm}	RMSE _{mm}	DF	R_M^2	R_A^2
D2 ~ Length + G1 + G2 + G3 + G4 + G6	10.4	3.3	200	64.5	63.4
D3 ~ Length + G1 + G2 + G3 + G6	13.2	4.5	191	61.6	60.4
D4 ~ Length + G1 + G2 + G3	7.8	4.1	176	67.6	66.9
L2 ~ Length + G1 + G2 + G3 + G4 + G6	20.0	4.5	202	46.2	44.6
L3 ~ Length + G1 + G2 + G3	15.7	4.0	204	56.1	55.3
L4 ~ Length + G1 + G2 + G3 + G6	6.2	2.5	199	68.4	67.6
V2 ~ Length + G1 + G2 + G3 + G6	13.8	3.7	159	56.9	55.5
V3 ~ Length + G2 + G3 + G5	9.1	3.0	163	44.3	43.0
V4 ~ Length + G2 + G5	5.7	2.4	71	55.8	54.0

Table 4

Derived formulas from Gompertz, von Bertalanffy and linear regression in Fig. 2B for all individuals, females and males separately. Lowest AICc value is in bold.

Growth Model	Formular	AICc
Linear Regression_{All}	Length = 0.937 + 0.257(log₁₀(Age_{Month}+0.1))	-3077.4
von Bertalanffy _{All}	Length = 1.46(1-e ^{(-0.1 (AgeMonth + 7.129))})	-3017.7
Gompertz _{All}	Length = 1.45 (e ^{(-0.419 e (-0.061 AgeMonth))})	-3004.3
von Bertalanffy_{Females}	Length = 1.53(1-e^{(-0.045 (AgeMonth + 21.664))})	-2416.5
Gompertz _{Females}	Length = 1.53 (e ^{(-0.458 e (-0.05AgeMonth))})	-2385.0
Linear Regression _{Females}	Length = 0.914 + 0.296(log ₁₀ (Age _{Month} +0.1))	-2097.3
von Bertalanffy_{Males}	Length = 1.38 (e^{(-0.42 e (-0.069 AgeMonth))})	-1788.0
Gompertz _{Males}	Length = 1.38(1-e ^{(-0.062 (AgeMonth + 16.745))})	-1783.9
Linear Regression _{Males}	Length = 0.963 + 0.217(log ₁₀ (Age _{Month} +0.1))	-1721.1

in the first year was evident in both sexes, and intra-seasonal variations began at the age of 1½–3 years, with a prominent increase in body mass, girths and blubber thicknesses during fall and winter (Fig. 2C–D & Appendix Figure A1).

All animals at FB followed a similar intra-seasonal pattern of changes in girth and blubber thickness; animals were larger and heavier in the winter compared to the summer. The body mass of F1–3 varied with 27–28% for different seasons (with maximum winter / summer differences being 15 kg for F1, 10 kg for F2, and 10 kg for F3), whereas for M1 it only varied by 12% (5 kg; Fig. 3A). The girths of F1–3 and M1 (with a total of 273 measurements of G1, 354 of G2, and 370 measurements of G3) decreased from late winter to summer minimum, before beginning to increase again in late summer (Fig. 4A–C). The largest seasonal variation in G1–3 ($n = 997$) was 5–10 cm, for both sexes. For the females, G4 ($n = 224$) and G5 ($n = 180$) decreased 5–15 cm from winter to summer, whereas G4 ($n = 139$) and G5 ($n = 107$) decreased 2.5 cm and 4 cm, respectively, in the male (Fig. 4D–E). For both sexes, G6 ($n = 267$) was close to constant throughout the year with a maximum variation of 2.5 cm for F2 (Fig. 4F). When G6 was initially measured in F3 she was 1–2 years, after which there was an interval of 11 years before measurements were resumed. Therefore, the 12 cm increase in length from summer to winter for F3 is due to the large age difference between data points from January–June. The blubber thickness of measured animals followed a similar intra-seasonal pattern: D2 ($n = 342$), D3 ($n = 339$), and D4 ($n = 311$) varied with 7–17 mm from winter to summer (see Supplemental material).

Porpoises kept at the Dutch facilities (DH, SD and ECM) exhibited less intra-seasonal variation in body mass than FB porpoises. The seasonal variation of females ranged from 6% to 14% (F5–6: 5 kg; F7: 6.7 kg; and C2: 4 kg; C3: 5 kg; C4 after the age of 3 years: 3.5 kg; Fig. 3B), and males M3–4 varied 5.7–14.1%, or 2–4 kg.

3.3. Comparing age derived by different methods

We used the growth curve to compare the age determined by dental layers (four animals) and the ones using bone ossification (seven animals). For porpoises born in a facility, the age determined by dental layers was within 1 year of known age. For two wild-born porpoises, the dental layer age differed by less than a year from the age derived by growth. The age of animals determined using bone ossification was also within one year of both known (in two animals) or growth-derived age (in seven animals; Table 1). The absence of tongue papillae in F1 and M1 upon arrival at FB in 1997 fitted very well with the growth-determined age of 2 years.

3.4. Predictors of harbour porpoise body condition

The *lmer* models showed that — when combined with length — all girth measures are strong predictors of body mass, with R_m^2 values from 72.3% to 93.6% (Table 2). The performance of the body mass prediction models had a high accuracy, with R_c^2 ranging from 79.2% to 94.7%. Of all girth measures, G3 was the most reliable for predicting the body mass of harbour porpoises, with a high $R_m^2 = 93.6%$ and a small MSD = 3.9 kg and RMSE = 2 kg.

Blubber thickness was predicted by linear models including length and girth measures with an R_m^2 ranging from 44.3% to 68.4%

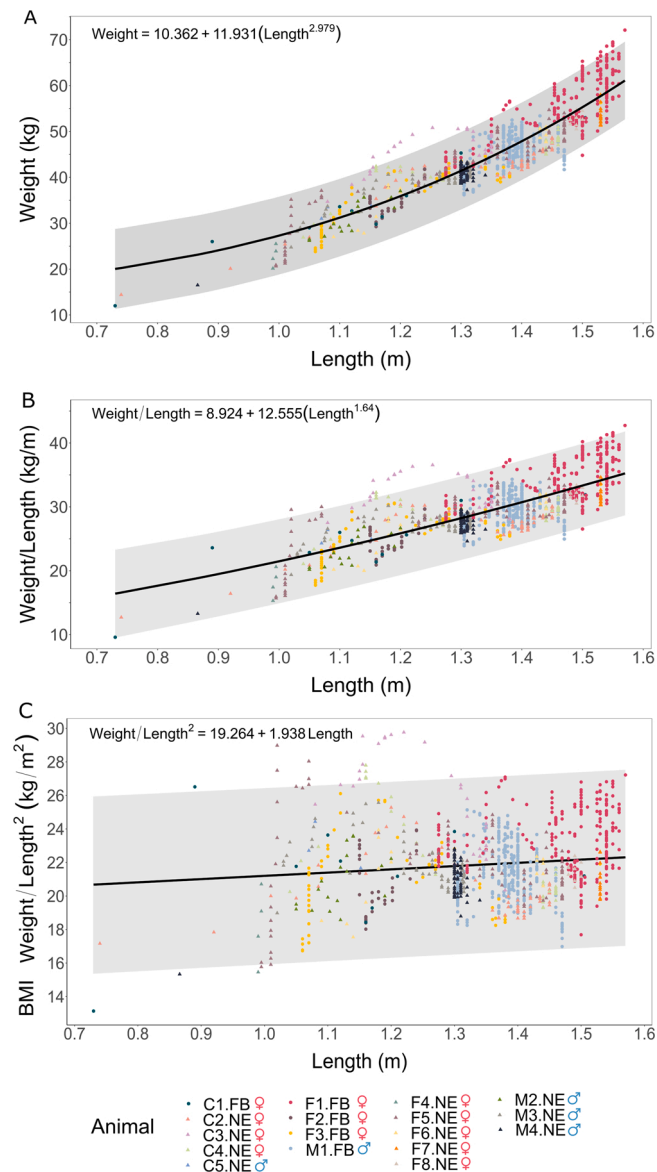


Fig. 5. Relationships and least-squares regressions of length and three indicators of body mass index: **A)** $Weight = 10.361 + 11.931(Length^{2.980})$, **B)** $Weight/Length = 8.923 + 12.555(Length^{1.64})$, and **C)** $Weight/Length^2 = 19.264 + 1.938 Length$. Four individuals were at FB (circles) the twelve animals at DH, SD, and EC in the Netherlands (triangles). Grey area is the 95% confidence interval. For gender variations in BMI see Appendix.

and R_c^2 varying from 43% to 67.6% (Table 3). Only the blubber thickness L2 and V3 had a R_m^2 below 50%; therefore, these measurements cannot be validated as predictors. Overall, the girths G2, G3 and G6 appeared to be the best predictors of individual blubber thickness, and length had a strong significant effect for all models ($p < 0.001$). (Table 4).

By comparing body mass with length, we estimated the parameters of the [Hayes and Shonkwiler \(2001\)](#) equation: $Body\ Mass \sim \delta + \alpha (Length^\beta)$ by least-squares regression, with $\delta = 10.36$ and $\beta = 2.98$. As illustrated in Fig. 5A, $\beta \dagger 1$ and δ is not close to 0, suggesting that *Body Mass* is highly dependent on length, and hence not in itself a good predictor of body condition. Likewise, the *Body Mass/Length* ratio correlates positively with $\delta = 8.92$ and $\beta = 1.64$, again suggesting that length is a poor predictor of body condition (Fig. 5B). In contrast, body mass index, $BMI = Body\ Mass/Length^2 = 19.26 + 1.94(Length)$, provided a reliable index of individual harbour porpoise body condition because it was not significantly dependent of body length (Fig. 5C). The parameters from [Hayes and Shonkwiler \(2001\)](#) can only be applied for non-linear models and so the parameters from the body mass index are based on a linear regression.

There was a seasonal variation in the BMI of around 2 for both males and females, with females ranging from 24 to 22 from December/January to June/August, and males from 23 to 21 from December-July to August-November respectively (Fig. 6).

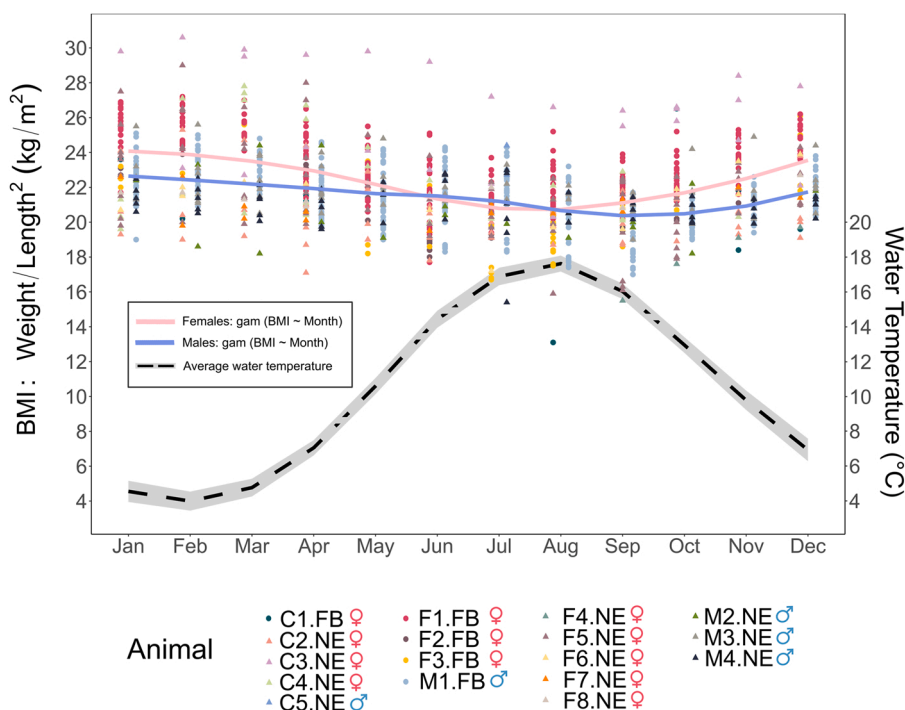


Fig. 6. Seasonal variations in Body Mass Index (BMI) of individual harbour porpoises. Points of individual variations in BMI for March 1997 to August 2020 for one male (M1) and three female (F1–F3) harbour porpoises at Fjord&Bælt, and for six females (C2–4, and F5–7) and three males (M2–4) at Dolfinarium Harderwijk and Ecomare from August 2007 to April 2019. The black line illustrates the seasonal variations in ambient average monthly water temperature ($^{\circ}\text{C}$) through the same period. The fit for females (pink line), males (blue line) based on *gam* ($\text{BMI} = \text{Month}$).

4. Discussion

Harbour porpoises face formidable challenges. They must grow 66% within their first year of life, be equipped with a sufficient layer of blubber to uphold a high energetic demand and adapt to seasonal and environmental changes. Our results supply detailed insights into the long-term growth of individual harbour porpoises under human care, from birth until sexual maturity and in some cases all the way until senescence. We describe seasonal and age-dependant variations in body mass, body condition, girth, and blubber thickness with a degree of detail that has not been reported previously. We provide the first model for age determination in young calves, with a resolution of a month, as well as models using length and girth as predictors of individual body mass, body mass index and blubber thickness in porpoises.

4.1. The growth of individual harbour porpoises

Our longitudinal data substantially add to knowledge gained by earlier studies of Lockyer et al. (2003a) and Kastelein et al. (1997a, 1997b, 2018), by being collected during longer time spans through the lives of porpoises, and by including more individuals at various life stages, from new born calves less than a month old, to adults up to 25 years of age. The data demonstrate a rapid growth of 66% in length and 288% in body mass of harbour porpoises within the first year of life, levelling off after 3–4 years. For example, F1 and F2 reached a length of ~ 150 – 155 cm at age 4 years and kept this length until age 25 and 13 years, respectively. Growth is thus stalled around the time when harbour porpoises reach sexual maturity, between 2 and 5 years (Möhl, 1954; Lockyer, 1995b, 2003; Read, 1999; Kesselring et al., 2017, 1995c). The growth during these first couple of years is consistent with the growth of the wild porpoises sampled and aged by other studies (Lockyer and Kinze, 2003; Fisher and Harrison, 1970; van Bree, 1973; Gaskin and Blair, 1977; Bjørge et al., 1991; Richardson et al., 2003).

For older animals, our growth curves based on longitudinal data differ from those by Lockyer and Kinze (2003), which were based on cross-sectional data. Whereas Lockyer & Kinze's growth curves imply that porpoises continue growing all their lives, our growth curves indicate that growth stops or is drastically reduced at around 4 years of age, which is consistent with the findings in wild porpoises from Richardson et al. (2003). Gompertz and von Bertalanffy growth curves explicitly include maximum animals' length (L_{∞}) and are therefore expected to fit better to observed data for animals that eventually stop growing, as is the case for harbour porpoises. This is an important finding, because harbour porpoise researchers have previously used the growth curve from Lockyer and Kinze (2003) to determine the age of wild-born porpoises when dental or bone ossification data have not been available.

The difference between our findings and those of Kastelein et al. (1997a) could also partly be due to differences between wild and captive animals. Most of the animals used in our study were brought to the facilities either for rehabilitation or for public display and

research purposes at an early age. Transferring wild animals to a captive facility could influence the growth rate during the first years if conditions at weaning are affected (Hall et al., 2001). Another possibility is that the growth curves of porpoises have changed during the two decades spanning the bulk of our data and the one used by Lockyer and Kinze (2003) by e.g., changes in the animals' environment, which highlights the importance of using recent established growth curves when assessing the age and condition of porpoises.

Relying on animals kept in captivity to determine growth may also introduce other biases. The animals in our study were all regularly monitored and treated for diseases and parasites, and they were always fed the amount of food needed to keep them in good physiological, anatomical, and behavioural shape. They do represent the growth and seasonal variation when assuming *optimal* nutritional state. Thus, the conditions in captivity may not be representative for the conditions in which wild animals are living. On the other hand, harbour porpoises kept in human care under semi-natural conditions may be the best sample to set the baseline for free-living animals, as previously shown for e.g., blood analyses (Siebert et al., 2020a).

4.2. Porpoises show large seasonal variations in body measurements

The animals kept in the semi-enclosed natural environment at Fjord&Bælt exhibited marked intra-seasonal variations in body mass and girths (Fig. 3). The averaged body mass of the three females varied by 27–28%, whereas the male's body mass only varied by 12%. Body mass, girths and blubber thickness of females were lowest between May and August, the same period in which they would give birth in nature (Møhl, 1954). In contrast, the male showed a small increase in G4 and G5, as well as in BMI from May to August, perhaps due to the 4% increase in body mass that is attributed to testicular growth during the mating season (Neimanis et al., 2000). Seasonal variations in body mass were previously observed by Lockyer et al. (2003a) from some of the individuals used in our data set. Even though Lockyer and Kinze (2003) fitted trend lines to their data that smoothed putative seasonal variations, a later analysis by Lockyer (2007) of the same data reported marked seasonal variations in body mass for free adult living porpoises from Danish waters, similar to our findings.

Seasonal variations in both body mass, blubber thickness, girth, food intake and respiration rate were also described for a 2–10 year old male harbour porpoise in the Kastelein et al. (2018) study. This animal was kept in a pool with seawater being pumped directly from a lagoon of the North Sea and showed 12.5–25% variation in body mass from the age of 4–5 years. When exposing another animal to near-fasting conditions, Kastelein et al. (2019a) found that the greatest loss of mass occurred in autumn and was smallest during the summer. These patterns are similar to the ones we observed in non-fasting males with little to no change in BMI from May–July, and a reduction of 2 from August–September/October (Appendix Figure A2).

In contrast, the porpoises from the Netherlands used in this study showed very little seasonal variation in body weight (Fig. 3). The smaller blubber thickness variations in the animals at the Dutch facilities may in part be explained by the higher winter temperatures in the facilities in the Netherlands compared to the one in Denmark. In addition, the animals kept in an open pen enclosure in Denmark were more exposed to seasonal differences in biota and visibility, which may affect hormonal functions in the animals that affects the formation of blubber. Harbour porpoises adjust their metabolism and energy reserves according to e.g., ambient water temperatures (Lockyer et al., 2003a; Rojano-Doñate et al., 2018). This factor is important to take into consideration when evaluating the status of free-ranging populations, as there are large differences between body mass and girths within age, sex, and time of year.

If geographical or temporal differences in body size are compared, the seasonal variations should always be considered, as well as the differences between sexes and age-classes. For instance, Heide-Jørgensen et al. (2011) suggested that porpoises from West Greenland waters increased in mass and body condition due to increased prey availability caused by global warming. However, these animals were collected in slightly different seasons — August–September in 1995 (Lockyer et al., 2003b) versus September–October in 2009 (Heide-Jørgensen et al., 2011). In Denmark, our data suggest an approximate 15% increase in body mass of individual female porpoises from early September until early October. A similar body mass increase might also take place in the female porpoises from Greenland waters. Autumn could potentially be the most critical period for a porpoise to allocate energy and isolation reserves, to be able to cope with decreasing water temperatures, as found in the study by Kastelein et al. (2019a). Thus, part of the patterns observed by Heide-Jørgensen et al. (2011) may owe to seasonal variations in body condition. However, this must be confirmed by analysis of seasonal body mass variation in porpoises from Greenland waters, which may be different to that of porpoises from Danish waters due to environmental differences between the Arctic and inner Danish waters.

4.3. Girth and length as predictors of harbour porpoise nutritional status

Besides using our data to estimate porpoise age from length measurements, it can be used to assess the nutritional state of porpoises in the field. Free-living harbour porpoises in the North and Baltic Seas often suffer from many types of diseases and parasites (Beineke et al., 2005; Das et al., 2006; Jauniaux et al., 2002; Jepson et al., 2000, 2016, Siebert et al., 2001, 2020b; Siebert et al., 2009, 2020b), and there is great concern that porpoises are vulnerable to any additional health issues imposed on the animals due to additional anthropogenic activities (Carlén et al., 2021). Applying the findings in this study enables assessments of stressors impact on growth rates and nutritional states, and how it may vary between seasons and years.

To predict any changes in the nutritional status of wild animals, it would be valuable to estimate changes in BMI over time. Our prediction models for determining body mass and blubber thicknesses of individual harbour porpoise identified the measures length and girth as good predictors. In our study, this was measured on healthy and well-fed individuals. Our prediction models can therefore be considered as a baseline to judge the nutritional state of free-living harbour porpoises. We found that measuring G3 and body length enables predictions of the body mass, and thereby of BMI, with a precision similar to other findings for harbour porpoises (Lockyer

et al., 2003a; Kastelein and van Battum, 1990), pilot whales (Lockyer, 1993) and baleen whales (Lockyer, 1986; Lockyer and Waters, 1986). If G3 can be assessed from wild animals through e.g., aerial photometry, the high level of precision in estimates of BMI indicates that the harbour porpoise body condition can be monitored on a regular basis with e.g., aerial drone measurements of length and G3. This does require establishment of the relationship between the diameter at G3, and the girth itself for different age groups, sexes and seasons.

For the animals used in our study, kept under optimal conditions concerning health and food intake, BMI ranged from 15 to 27, which is comparable with the free-living porpoise populations in the study of Kershaw et al. (2017), ranging from 18 to 22 for porpoises that died from acute cases (bycatch, entanglement, storm damage, and bottlenose dolphin attacks). This may indicate that the nutritional status is not critical, at least for this porpoise population. The slightly higher BMI of captive animals is not surprising given their optimised food intake and cures for diseases. The seasonal variation in BMI was about 2 points for both males and females from highest (December/January for females and December-July for males) to lowest (June/August for females and August-November for males). Comparisons of this kind of data to wild populations are needed to assess how well different porpoise populations can adapt to various types of environments and environmental changes.

5. Conclusion

In conclusion, the longitudinal data presented here suggests that it is possible to determine the age, body mass, body mass index, and blubber thickness using solely length and girth measurements. We found that the growth and body condition of porpoises under human care were comparable with wild porpoises. This study enables monitoring population composition and individual nutritional condition for free-ranging harbour porpoises (e.g., through photogrammetry), and support the understanding of the seasonal and geographical variation in harbour porpoise populations, that are exposed to anthropogenic activities, such as, bycatch, chemical pollution, food depletion and noise.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02384](https://doi.org/10.1016/j.gecco.2023.e02384).

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