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Early physical maturation of female common bottlenose dolphin Tursiops truncatus in the eastern Levantine Basin

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Early physical maturation of female common bottlenose dolphin *Tursiops truncatus* in the eastern Levantine Basin

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Regional resource limitation in the eastern Levantine Basin was predicted to protract the growth of members of the Israeli sub-population of the common bottlenose dolphin (CBD), compared to CBD sub-populations of similar adult size. Growth curves were fitted to length-at-age data available for 24 male and 26 female CBD stranded or incidentally caught along the Israeli coastline between 2000 and 2009. The obtained model growth constants were compared to those of other CBD sub-populations from the southeastern coast of the United States and a correlation to regional seawater primary productivity was sought. As in other sub-populations, local CBD females initially grow faster than males for approximately 3–4 years and remain longer until around eight years old, after which males surpass them in length. Yet the steep early growth of females as well as its high rate of decay was found to be extreme compared to other CBD sub-populations, with 99% of the asymptotic length being reached at the age of six years. A positive correlation between seawater primary productivity and early growth rate as well as growth decay constants could be demonstrated for CBD males from Texas, Florida and Israeli coasts. Females of the same sub-population presented a non-monotonic relationship to primary productivity. Early female attainment of physical maturity in an ultra-oligotrophic region was unpredicted and is not readily explained. It may accompany early reproductive maturation, selected for as partial compensation for lower lifelong reproductive success.

Keywords: common bottlenose dolphin; *Tursiops truncatus;* Gompertz growth model; Israeli coast; primary productivity

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Introduction

For a mammal that has not attained its final adult size, energy balance considerations would dictate:

$$E_G = E_I(=B_{MR}) - E_M - E_S \quad (1)$$

with E_G, the energy allocated for growth, being the left-over of intake energy, E_I, (which equals whole body metabolic rate, B_{MR}) after deducting maintenance energy, E_M, and stored energy, E_S (Sadleir 1969). E_M is invested in fueling resting and active cells and in replacing dead cells. Energy allocated to reproduction is not included, as reproductive maturity is typically reached when the animal has almost attained its final size (Stearns 1992). Two explanations have been proposed to account for the classical sigmoid-shaped asymptotic growth curve: geometric constraints of the fractal-like body transportation systems which cause a diminished capacity to supply the cells as mass increases (West et al. 1997; Banavar et al. 1999) and the tradeoff between the growth potential and the functional capacity of cells and tissues, the latter increasing with age and mass (Ricklefs 2003). When considering growth rate and neglecting stored energy, following West et al. (2001), Equation (1) may be rewritten as:

$$E_{cc}(dN_c/dt) = B_{MR} - N_c E_{mc} \quad (2)$$

where E_{cc} is the energy required to create a cell, N_c is the number of cells and E_{mc} is the metabolic rate of an average cell. Substituting N_c with the ratio of body mass, m, to the mass of an average cell, m_c, we arrive at the familiar basic form of the growth curve:

$$dm/dt = am^{\alpha} - bm^{\beta} \quad (3)$$

with $a = Am_c/E_{cc}$, $b = E_{mc}/E_{cc}$, $\beta = 1$ and $\alpha = {}^3/_4$

The ${}^3/_4$ exponent that underlies the individual's exponential growth curve as well as the taxon-specific constant A are derived from the well-known empirical inter-taxa scaling of metabolism, $B_{MR} = Am^{3/4}$ (Kleiber 1932; Schmidt Nielsen 1984) and predict higher growth rates for taxa with a smaller final adult size, as well as decreasing growth rates as mass increases during ontogeny (Hou et al. 2008).

When comparing the growth characteristics of different sub-populations of a given species, especially with similar adult body size, it is customary to use sigmoid curves fitted to mass or length-by-age data, describing the integral form of Equation (3). The steepness of the growth curves and the times of attaining asymptotic size will be governed, respectively, by constants describing early growth rate and rate of growth decay (Laird 1966), which may have evolved in response to environmental features and constraints. Among the latter, temperature and resource availability are noteworthy. For cetaceans, low water temperature imposes large thermoregulatory energy expenditures on newborns, whence E_S becomes important for building up the isolating blubber layer. An energy balance model which considers

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thermoregulatory as well as other constraints predicts an increase in optimum body size as temperature decreases (Searcy 1980). Cold waters are usually fertile and for resident cetaceans, a relatively large size at birth, enhanced early growth, large final body size and lower lifetime investment in extra-uterine growth as a percentage of total lifetime energy expenditure may be selected for (West et al. 2001). Opposite traits may be expected in species or in sub-populations of a given species exposed to the combination of warm waters and low resources.

The common bottlenose dolphin *Tursiops truncatus* (henceforth CBD) is a cosmopolitan coastal delphinid that avoids surface water temperatures (SWT) <10°C (Wells & Scott 2009). It is a polymorphic species with a maximum adult size range of <2–4.1 m that, other than in the eastern Pacific, tends to show an inverse relationship between size and SWT (*ibid.*). Two genetically and physiologically distinct morphs of CBD, a smaller coastal morph and a more robust offshore morph, have been described in the western North Atlantic (Hersh & Duffield 1990; Mead & Potter 1995). This size dichotomy may be partly tied to differences in mean daily and annual water temperatures to which the two morphs are exposed (Perrin 1984).

Cetacean species pose some methodological problems in studies of growth dynamics. Firstly, all growth models require continuous data which, due to their low accessibility, are very rarely available in wild cetaceans (i.e. Kasuya et al. 1986; Read et al. 1993). As a rule, growth studies of cetaceans acquire point data from carcasses of stranded and/or by-caught animals, from which age can only be estimated on annual scales. With such a source, age biases (relative preponderance of newborns and calves and of senescent animals) as well as sex biases (relative preponderance of males) in the sample are to be expected (Stolen & Barlow 2003 and references therein).

Secondly, an inherent limitation of monotonically changing sigmoid growth-modeling functions is their inadequacy in dealing with secondary growth spurts, which seem to apply to all studied toothed whale species, including CBD (see McFee et al. (2010) for a review). The latter authors, drawing from the largest series of CBD to date – 287 males and 277 females from the southeastern coast of the United States – could best fit their data to a three-staged logistic model: an initial stage of rapid growth with rapidly decaying rate lasting several months post-parturition, succeeded by a slower and slowly decaying growth stage, and then a third stage, more pronounced in males, starting at sexual maturation and ending with cessation of growth. Most authors who reported on smaller samples used a single sigmoid curve for the entire sample (i.e. Stolen et al. 2002; Turner et al. 2006; Neuenhoff et al. 2011), some (Read et al. 1993; Fernandez & Hohn, 1998) avoiding the stage 1 issue by initiating the curves at the age of one year, and others (Neuenhoff et al. 2011) acknowledging the fact that a single-stage model cannot account for the high growth rate observed in young dolphins, particularly when late fetal growth was considered. Mattson et al. (2006) applied two-staged sigmoid curves with the intersection points at the age of about eight years for CBD from Mississippi Sound and got satisfactory results; however, they too had to exclude non-neonate animals younger than one year for part of the calculations.

Within the Mediterranean Sea, the CBD population in the eastern Levantine Basin (ELB) may be a candidate for experiencing size diminution on account of high SWT (Brasseur et al. 1996), limited resources (Yakobi et al. 1995; Krom et al. 2004) and genetic isolation (Natoli et al. 2004, 2005; Viaud-Martinez et al. 2008). A recent study (Sharir et al. 2011) has indeed shown that adult members of the Israeli sub-population of CBD have a smaller mean total body length, as well as condylo-basal length, than conspecifics from western Mediterranean sub-populations. While the Israeli sub-population is known to attain a relatively small adult body size by Mediterranean standards, its final adult length is very similar to that of CBD populations in the western North Atlantic (Sharir et al. 2011), all of which reside in waters that are considerably more fertile (Oregon State University/Ocean Productivity 2010) and with similar or slightly higher mean annual SWT (NOAA/International Comprehensive Ocean-Atmosphere Data Set).

This study is about comparative growth dynamics of the CBD population residing in the ultra-oligotrophic marine environment of the ELB. We hypothesized that limited resources would cause a relative protraction of the growth period in both sexes with a resultant older age upon reaching asymptotic length, as compared to CBD populations of similar adult size in more fertile regions. Accordingly, our specific study objectives were (1) to analyze postnatal growth of local CBD and establish growth curves for males and females and (2) to determine whether growth constants of CBD sub-populations with similar adult size (i.e. southeastern US coast and Israeli coast) would conform to a model where both early growth rate and arrest of growth will be positively correlated to regional primary productivity. As far as we are aware, the latter objective has not previously been addressed.

Materials and methods

Database

A total of 59 CBD specimens, collected along the Mediterranean coast of Israel (190 km of coastline) between 1994 and 2009, were studied. Of these, 51 were stranded carcasses, six were bottom-trawl by-catches and two were gill-net by-catches. The stranded and by-caught animals were sampled in the course of stranding network activity of the Israeli Marine Mammal Research & Assistance Center (IMMRAC). Over that period, the mean annual number of dead CBD recorded by IMMRAC was 8.6. However, this rate includes reported by-catches with the carcass thrown overboard, dead specimens known only from skeletal elements retrieved from the sea bottom (e.g. skulls found in bottom-trawl hauls) and mummified or disintegrated carcasses incompatible with length measurements. Advanced decay and/or shark scavenging of the genital area were the main reasons for the inability to determine gender in nine animals in the database. The

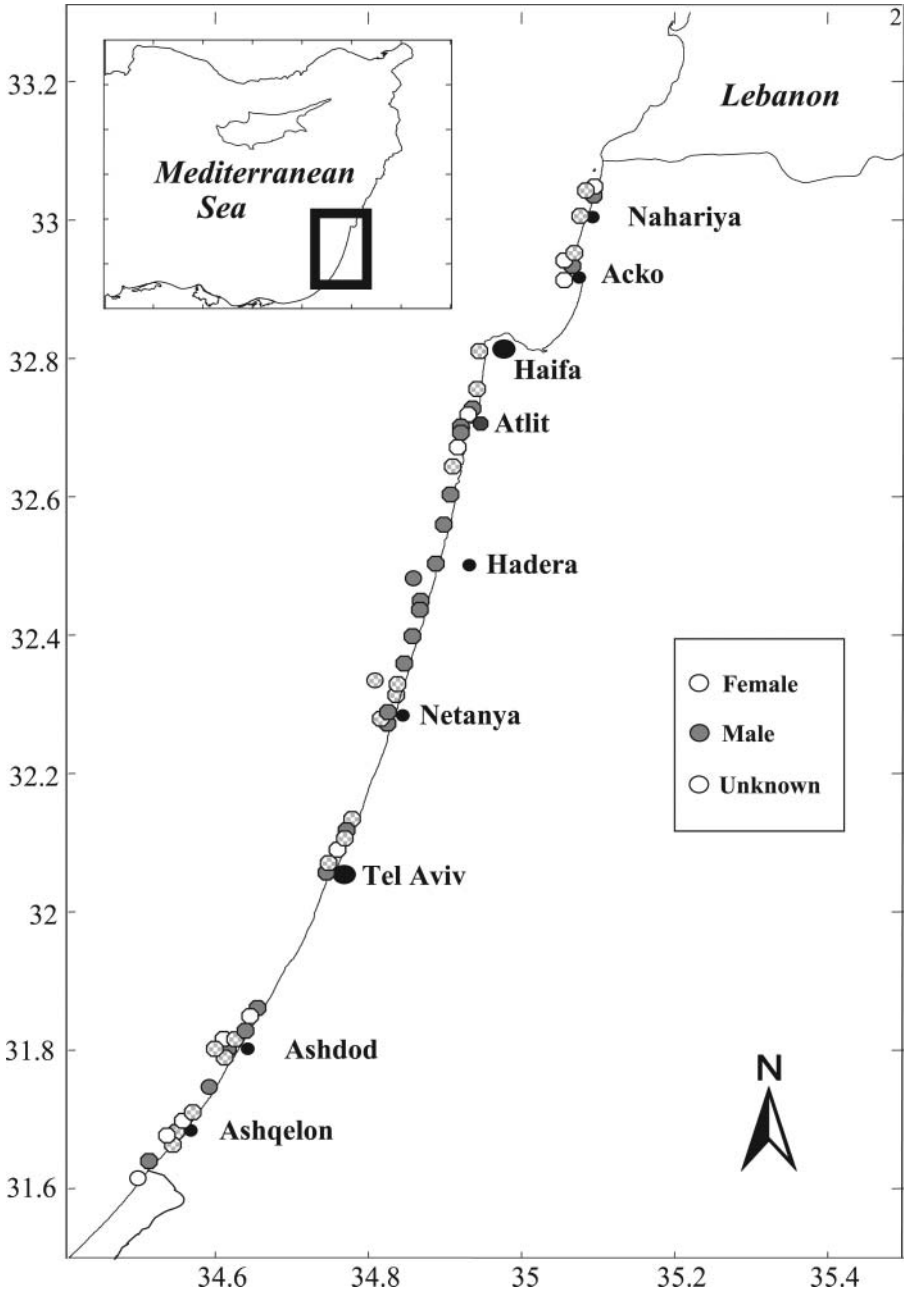

Figure 1. Stranding and by-catch locations along the Israeli Mediterranean coastline. The sites of the two gill-net entanglements are shown detached from shoreline. Trawl by-catch locations are unknown and not marked.

remainder was composed of 26 males and 24 females. Strandings and by-caught animals were distributed along the entire length of the Israeli coast (Figure 1).

Measurements

Total body lengths, to the nearest 0.5 cm, from the tip of the rostrum to the fluke notch (Norris 1961) were measured either on site or during necropsy. For age determination, teeth from mid-length lower jaws were extracted; when not available (six cases), teeth from mid-length upper jaw were used. Aging was conducted by the authors (n = 40) and by Christina Lockyer (Age Dynamics, Denmark) (n = 19) using the following methods: two to three teeth were examined in adult animals; one tooth was generally examined in young animals, and the second tooth was examined in case of complicated tooth layering structure (such as multiple accessory layers). The teeth were decalcified in 5% solution of nitric acid. Thin longitudinal sections were made using a sliding microtome with a freezing stage, then stained by Mayer's haematoxylin and mounted on slides in glycerin. Age was estimated as the number of complete growth layer groups (GLG) (Hohn 1980; Hohn et al. 1989).

The following exceptions were made for some animals at the age of four years or younger:

(1) Five animals were judged to be neonates from external appearance: folded dorsal fin and/or vestiges of umbilical cord. Another animal was so judged for lack of dentine past the neonatal line in its tooth section.

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(2) Animals were judged to be <0.5 years old if they were non-neonates and had neonatal line present in teeth and a thinner layer of postnatal dentine (compared with prenatal dentine).
(3) Animals were judged to be of 0.5, 1.5, 2.5 or 3.5 years old if their latest GLG was forming but not completed.

GLGs were counted twice: the first "blind" count was made before the reader had access to the information about sex and body length, and the second count was made taking into account this information, a considerable time after the first count. If the estimates did not agree, a third resulting count was made; if the third count did not lead to agreement (e.g. in old animals), the age was estimated as the mean value of two first counts.

Growth curve fitting

Zullinger et al. (1984) report that among sigmoidal growth models, the Gompertz model provides good estimates for the largest number of mammalian species, and, indeed, it has been used to describe the growth of many toothed whales (Perrin et al. 1976, 1977; Bloch et al. 1993; Ferrero & Walker 1995, 1996, 1999; Marsili et al. 1997; Siciliano et al. 2007) as well as several populations of CBD on the eastern coasts of the United States (Read et al. 1993; Fernandez & Hohn 1998; Stolen et al. 2002; Neuenhoff et al. 2011). In this study, von Bertalanffy as well as Gompertz growth models were fitted to length-at-age data.

The von Bertalanffy equation was used in the following form:

$$L_t = L_\infty(1 - be^{-kt})$$

The Gompertz equation was used in the following form:

$$L_t = L_\infty \cdot e^{-be^{-kt}}$$

Where:

L_t – length at time t
L_∞ – asymptotic length
b – integration constant
k – growth constant
t – time (age in years, with birth being time 0)

The biological meaning of the constants, as explicitly reported by some researchers, is that b = G/g, G being the rate of absolute growth, and g = k, being the rate of growth decay (Laird 1966).

The first half-year of life of CBD has been suggested to be a separate growth stage with its own parameters (Kasuya et al. 1986; McFee et al. 2010) or with parameters common to late uterine growth (Neuenhoff et al. 2011). This perinatal period is characterized by a high growth rate resulting in a 1.7–1.75-fold increase in body length (as predicted by both Gompertz and von Bertalanffy growth models). The growth rate appears to decline during this six-month period, since the body length difference between neonates and 0.25-year-old calves is greater than that between 0.25-year-old and 0.5-year-old calves. However, accurate calculation of growth parameters during this period is impossible because the exact age of very young stranded calves is unknown. For this reason, we used models describing the growth from the age of 0.5 years on. Two adult animals, a 16-year-old female with a body length of 303 cm and a 20-year-old male with a body length of 308 cm, with coloration, stomach content and/or morphometric evidence of not belonging to the local population, were also excluded from the growth curve calculations, leaving 21 males and 21 females on whose measurements the curves were fitted.

Single-stage growth curves were produced separately for each sex. A two-stage growth curve based on two Gompertz equations, each describing the growth for the given age range, was additionally applied for males (details in Results). Goodness of fit of all curves, acquired by least squares iterations, was judged by R^2 values, residual sum of squares and Akaike's Information Criterion (AIC) values.

Correlation with regional primary productivity

To this end, we could only find four other studies that fitted single Gompertz curves to a point database from dead CBD and reported G and g constants for both genders: three from the coast of Texas (Fernandez & Hohn 1998; Turner et al. 2006; Neuenhoff et al. 2011) and one from the Indian River Lagoon, Florida (Stolen et al. 2002). The values of the first three studies were averaged and the three regional sets of male and female G and g values were log transformed and correlated (Pearson's product correlation coefficient) to corresponding log transformed regional mean annual primary productivity rates obtained from the literature.

Results

Age by gender distribution

The age distribution of the sample is markedly uneven, with a preponderance of young animals of both genders (Figure 2). Except for a 32-year-old individual, all animals with undetermined gender were less than four years old.

Growth in body length

Descriptive statistics for lengths of neonates and adults show mean neonatal length, calculated for both genders combined, to be 104.4 cm and indicate that males attain a larger mean adult length than females (Table 1). By the age of one year, males had grown to a maximum length of 194 cm and females to 225 cm. The median length of adult males (15 years and older in the examined sample, n = 9), 268 cm, is significantly longer than that of

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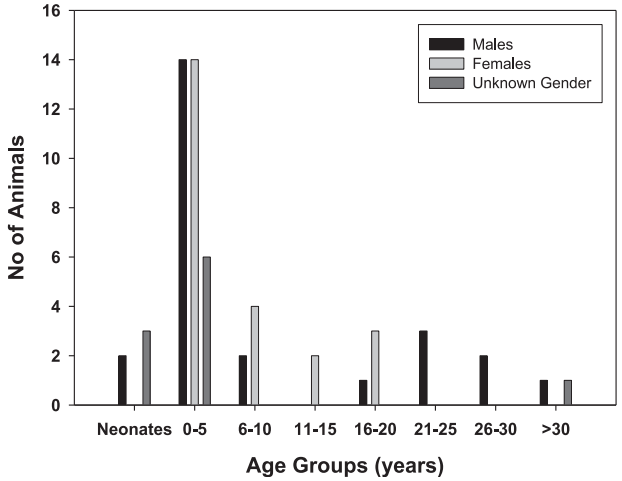

Figure 2. Composition of the Israeli CBD data-set by age and gender. The dominant 0–5 age group is composed of calves and weaned juveniles, all of the latter being by-catch victims.

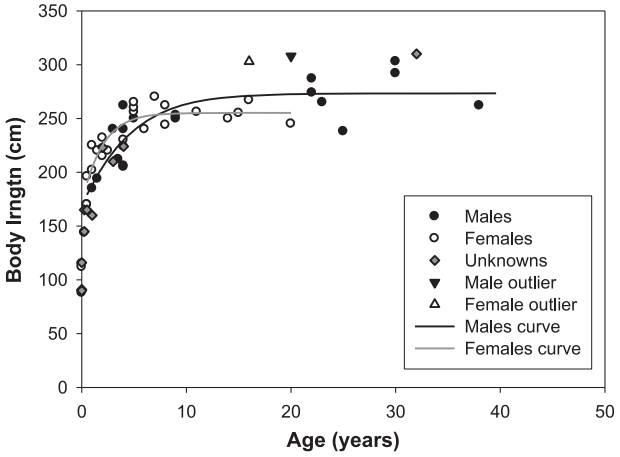

Figure 3. Single growth curves for length vs. age data for both genders of CBD in Israel. The scatter-plot also includes data points of animals with undetermined sex and two outliers, all of which did not partake in the model-fitting. The curves produced by the Gompertz and von Bertalanfy models virtually overlapped.

254.5 cm for six adult females (≥10 years) (Mann–Whitney U test: p = 0.034; Kolmogorov–Smirnov test: p = 0.047). The gender of the 32-year-old and 310 cm-long animal (the maximum length recorded in the examined sample) was not identified. For both sexes, single Gompertz and von Bertalanffy equations produced curves with virtually identical predicted values at given ages (Figure 3). All model-fit criteria were very similar for the two growth models, with both models predicting divergent patterns for the two sexes (Table 2).

Curves based on a single equation appear to satisfactorily describe the growth of females older than 0.5 years, but produce less certain results for males (expressed by the relatively low R^2 value and large residual sum of squares). For this reason, we tried to fit a growth model with two successive Gompertz curves for males: the first describing the growth for the period of 0.5–3.5 years and the second for four years and over. The two-stage model does not fit the data significantly better than the single-stage Gompertz model, and considering the higher number of parameters involved, it is even slightly worse (values of Akaike's Information Criterion are 126.4 for the one-staged model and 129.6 for the two-staged model). However, residual analysis showed the two-staged model to better predict the growth trajectory at ages of less than five years.

Models based on a single equation predict the following growth characteristics for the local CBD population:

(a) Patterns of sexual dimorphism in average body length change during life: females become larger than males between 0.5 and one year old, grow faster than males for approximately 3–4 years, and remain longer than males until around eight years old, after which males surpass them in length.
(b) Growth of males lasts longer: females attain 95% of the asymptotic length at the age of four years and 99% at the age of six years while the values for males are nine years and 16 years, respectively.
(c) The steep early growth in females, as well as the early cessation of growth resultant from a high rate of growth decay (large k), are extreme compared to western North Atlantic populations of the species, as detailed and discussed below.

Table 1. Body lengths (cm) in age and sex groups of CBD, stranded and by-caught in Mediterranean waters of Israel.

Group	*n*	Range	Median	Mean	SD
Neonates	6	88–115	90.5	104.4	13.7
Adult females	6	250–267	254.5	255.0	6.6
Adult males	9	238–303	268.0	272.8	19.2

Table 2. Parameters of the growth models for CBD stranded and by-caught in Mediterranean waters of Israel.

Equation	Gender	*n*	Age range	$L_\infty \pm$ SE	$b \pm$ SE	$k \pm$ SE	*RSS*	R^2
Gompertz	females	21	0.5 and over	255.2 ± 4.0	0.39 ± 0.06	0.57 ± 0.16	2252.5	0.82
von Bertalanffy	females	21	0.5 and over	255.3 ± 4.1	0.33 ± 0.05	0.53 ± 0.15	2242.2	0.82
Gompertz	males	21	0.5 and over	273.1 ± 7.1	0.50 ± 0.09	0.27 ± 0.08	6514.6	0.75
von Bertalanffy	males	21	0.5 and over	273.4 ± 7.2	0.40 ± 0.06	0.24 ± 0.07	6437.3	0.75
Gompertz (two stages)	males	21	0.5 –3.5	232.0	0.52 ± 0.21	0.91 ± 0.80	655.0	0.77
			4 and over	276.6	0.31±0.21	0.145 ± 0.17	5387.9	

L_∞ – asymptotic length; *RSS* – residual sum of squares

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Discussion

Reasons for paucity of data

The stranding rate normalized to shoreline length is remarkably lower in Israel (3.1 carcasses per 100 km of shoreline per year (IMMRAC, unpublished observations)) than in southeastern US coasts for which information is available: Indian River Lagoon – 10.9/100 km/y (Stolen & Barlow 2003), South Carolina – 12.8/100 km/y (McFee et al. 2010) and Texas – 15/100 km/y (Fernandez & Hohn 1998). This low rate, most probably indicative of the low carrying capacity for top predators in the ultra-oligotrophic easternmost Mediterranean (Malanotte-Rizzoli et al. 1999; Herut et al. 2000), is mainly responsible for the small sample size relative to comparable studies of CBD growth dynamics. While acknowledging this limitation, we believe that our main findings are sufficiently robust.

Potential biasing by inclusion of non-local specimens

In the western Mediterranean (Cañadas et al. 2002) as well as in the ELB (Kent et al. 2006), CBD are sighted in deep water, but differences (if any) in their size relative to inshore animals have not been reported. In the case that they are larger and unidentified in the data-set, they are expected at best to contribute to the scatter or, worse, to cause an upward shift of the growth curve. Another source of bias in our sample would be immigrants from larger-sized inshore CBD populations residing in the western Mediterranean (Sharir et al. 2011). The two excluded outliers in the data-set were probably migrants: these were an exceptionally long female with unusual coloration and gill-net fragments of nine different types in her stomach, none of which are in use by Israeli fishermen, and a 308 cm-long male, the craniometric features of which did not conform to the characteristics of the local population and more resembled those of Tyrrhenian and Ligurian populations (Sharir 2008).

Size sexual dimorphism

Size sexual dimorphism of western North Atlantic coastal CBD, with males being slightly larger, was described by almost all investigators employing large enough series (Sergeant 1973; Read et al. 1993; Tolley et al. 1995; Fernandez & Hohn 1998; Stolen et al. 2002; Mattson et al. 2006; Turner et al. 2006; McFee et al. 2010; Neuenhoff et al. 2011). Asymptotic lengths of males in the southern US Atlantic coast and Gulf of Mexico range between 10 and 20cm (4–8%) higher than those of females, and this relationship seems to hold for the population hereby reported.

Sex differences in growth

Results on this aspect vary, with some studies (Fernanadez & Hohn 1998; Stolen et al. 2002) showing similar growth trajectories of the two sexes during the first years of life, after which they diverge, with males growing longer. Read et al. (1993) and McFee et al. (2010) reported the same general pattern of inter-sexual difference in growth that we observed: females were larger than males during the first six years of life, and then males gradually became larger. These differences may arise from sex-divergent reproductive strategies. Females initially invest much energy into growth, such that both physical and reproductive maturity is attained at an early age (Reynolds et al. 2000). Males follow a less steep and more protracted growth rate, allocating more energy than females into social activity throughout the attainment of puberty at a later age (Cockroft & Ross 1990; Read et al. 1993) or possibly throughout life.

Geographical variation in neonatal length, growth rate and adult body length

Published information on actual length at birth in CBD is sparse (Table 3). The only data allowing statistical comparison with our very limited sample is that reported by Mead and Potter (1990), showing CBD newborns in the ELB to be significantly smaller (Mann–Whitney U test: $p=0.024$). With similar asymptotic lengths in the two populations, this difference translates to a ~10% higher ratio of asymptotic to neonatal length and mass and to a higher lifetime investment in extra-uterine growth. High mean annual water temperatures and scarcity of natural predators may be factors allowing a smaller size at birth in ELB dolphins.

Table 4 summarizes growth constants and predicted final lengths for both genders of CBD populations along the southeastern coasts of the US, together with the results from this study. Here, our working hypothesis of relatively drawn-out growth in Levant Basin CBD is seen to be borne out for males. However it is totally contradicted for females, which stand out for their high G and g values, causing a very fast initial growth and an early arrest of growth. In figure 4, male and female CBD growth constants are plotted against local mean annual seawater productivity rates for the Israeli coast, Texas coast (means of the three studies listed in Table 4) and Indian River Lagoon, Florida. Judging by this very small series, both G and g constants in males seem to be positively related to productivity in a monotonic, curvilinear manner, conforming to the premise of accelerated growth in fertile waters (Pearson product correlation coefficients for

Table 3. Mean actual newborn lengths (cm) of selected CBD populations.

Region	N	Mean length	Range	L_∞/L_0	Source
North Carolina	13	117	106–132	2.14	Mead & Potter, 1990
Texas	21	109.5	91–128	2.25	Fernandez & Hohn, 1998
Mississippi	56	94.2	69–113	2.68	Mattson et al, 2006
Israel	6	104.4	88–115	2.34	This study

Table 4. Growth curve constants and predicted asymptotic body lengths (cm) of CBD in southeastern United States and Israeli coasts.

Region	N_M	N_F	$L_{\infty M}$	$L_{\infty F}$	G_M	G_F	G_F/G_M	g_M	g_F	g_F/g_M
Indian River Lagoon, Florida[1]	118	72	258	247	0.26	0.35	1.35	0.36	0.45	1.25
Sarasota Bay, Florida [a ; 2]	49	47	265	250	0.07	0.12	1.7	0.18	0.29	1.61
Texas coast [a ; 3]	78	81	268	247	0.14	0.14	1.0	0.23	0.29	1.26
Texas coast[4]	18	18	258	244	0.25	0.25	1.0	0.33	0.34	1.03
Texas coast[5]	112	70	238	241	0.26	0.31	1.19	0.38	0.42	1.11
Coast of Israel[6]	21	21	277	245	0.12	0.45	3.75	0.26	0.57	2.19

N-number; M-males; F-females; L_∞-asymptotic length; [a]-Animals <1.0 y excluded; [1]Stolen et al. 2002; [2]Read et al. 1993; [3]Fernandez & Hohn 1998; [4]Turner et al. 2006; [5]Neuenhoff et al. 2011; [6]Present study. Bold numbers mark outstanding F and F/M values.

Table 5. Landmark lengths of females in selected CBD populations.

Region	Age at L_0 $+1/2(L_\infty - L_0)$	Age at $3/4L_\infty$	Age at $2L_0$	Age at first attaining L_∞
Gulf of Mexico[1]	1.3	1.7	4.9	14.5
IRL, Florida[2]	2.0	2.1	6.3	11
South Carolina[3]	1.4	2.4	8.5	13.5
Israel[4]	<0.5	0.9	1.2	7

[1]Fernandez & Hohn 1998; [2]Stolen et al. 2002; [3]McFee et al. 2010; [4]present study.

log-log transformed values are 0.962; p = 0.177 and 1.0; p = 0.003 for G and g, respectively). Obviously, this relation has to be shown to hold with more studies. In marked contrast, female constants show a non-monotonic behavior with high growth rates at both ends of the productivity range.

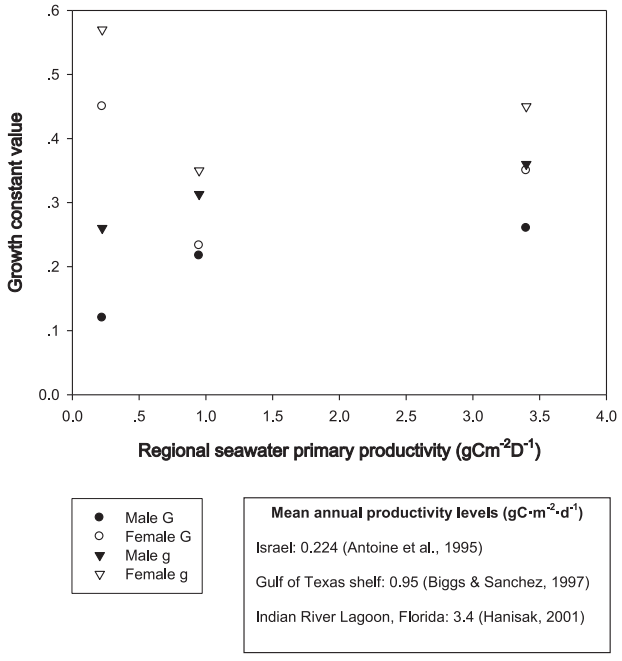

Figure 4. Plots of growth constants as a function of regional seawater productivity. Gompertz growth constants (G – rate of early growth and g – rate of growth decay) for coastal male and female CBD sub-populations in Israel, Texas and Indian River Lagoon, Florida are plotted against local seawater productivity levels, the latter listed in the lower right panel.

The distinction of Israeli CBD female growth dynamics is further stressed by comparing ages of females of the sub-populations at various landmark lengths, as predicted by the growth curves (Table 5). All listed landmark lengths are reached at a much earlier age in the Israeli sub-population, with final length attainment being 5–8 years earlier than their western North Atlantic counterparts. It thus seems that while carrying capacity for CBD and other top predators may be lower in the ELB, growth dynamics of residing individuals are not necessarily resource-limited. It should however be kept in mind that environmental effects on size and growth cannot be inferred or discussed in isolation, as organisms in general and mammals in particular exhibit species-specific and gender-specific trade-offs regarding growth, reproductive and survivability traits (Bronson 1989, Stearns 1992). Since we do not have enough data on the age of attainment of female sexual maturity, calf survivability, inter-birth interval etc. in the local CBD population, explicit interpretation of female growth dynamics is not possible.

The occurrence of relatively accelerated growth in an ultra-oligotrophic region is not intuitive. When energy expenditure is at, or near, the maximal rate dictated by environmental resources, mammalian females might be expected to distribute their energy expenditure between maintenance and reproduction with parsimony (McNab 1980). If lifelong female reproductive success is lower on account of lower food resources and associated higher foraging energetic and time-budget demands as well as protracted lactation, earlier sexual maturity may be selected for as partial compensation. Reproduction and growth of cetacean females in general (Whitehead & Mann 2000) and in CBD in particular (Sergeant et al. 1973) are tied together, as they start reproducing at ~90% of final adult length, the latter being a better predictor of sexual maturity than age. Therefore, early sexual maturity would entail accelerated early growth which may be facilitated due to the lower thermoregulatory demands of residing in the warm ELB. Most of the early female growth is realized before weaning. Whether local female calves are born more efficient at food assimilation or whether they receive preferential maternal investment are intriguing questions worthy of continued research.

Summary

The following growth attributes appear to characterize the common bottlenose dolphin population residing in the

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ELB, which may directly or indirectly result from the region's low productivity:

(1) High M_∞/M_0 and lifelong investment in extra-uterine growth.
(2) Exceptional postnatal growth rate of females such that doubling of length at birth is attained after little more than a year.
(3) A marked decay of growth in females such that asymptotic length is attained by the age of seven.
(4) Male growth dynamics demonstrating protraction and relatively late attainment of asymptotic length, consistent with the study's prediction.

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