

Growth comparison in striped dolphins, *Stenella coeruleoalba*, from the Atlantic and Mediterranean coasts of France

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Abstract

The growth of striped dolphins stranded on the coast of France has been studied using non linear growth models. Individuals from the Atlantic reach a longer total body length than those from the Mediterranean Sea. Although there is no significant sexual dimorphism for the Mediterranean specimens, males are longer and heavier than females in the Atlantic.

Resume

La croissance du Dauphin bleu et blanc a été étudiée d'après les données récoltées sur des individus trouvés échoués le long des côtes françaises. L'étude statistique de différents modèles de croissance montre que les individus de l'Atlantique atteignent globalement une taille supérieure à ceux de la Méditerranée. D'autre part, tandis qu'aucun dimorphisme sexuel significatif n'apparaît chez les dauphins de Méditerranée, chez les adultes de l'Atlantique, les mâles sont plus grands et plus lourds que les femelles.

Introduction

Perrin (1984) noted that geographical variation in morphology is the norm for most species of dolphins. A qualitative study by Duguy & Robineau (1982) suggested that the total body length of striped dolphins, *Stenella coeruleoalba*, from the Mediterranean Sea differed from those found in the Atlantic Ocean. This study examined possible differences in length and/or weight growth for animals from these two areas.

Material and methods

All of the striped dolphins considered here were found stranded on either the Atlantic (34 males+18

females) or the Mediterranean (22 males+22 females) coasts of France. The total body length of each dolphin was measured to the nearest centimetre and each was weighed to the nearest kilogram. Their age was determined from the number of dental and cemental growth layer groups (GLGs) (Perrin & Myrick, 1980).

Two techniques to highlight GLGs were used: decalcified and stained sections, and unstained thin ground sections, as described by Di-Méglio (1993). Ages were determined using a double cross-reading method (Perrin & Myrick, 1980) under a microscope, using transmitted light for stained sections and polarised light for thin sections.

Since both the Gompertz and Von Bertalanffy models have been used to study mammalian growth (Lebreton & Miller, 1982), fits to test both models were applied. Von Bertalanffy models were rejected because of their poor fit to the weight data for both sexes from the Mediterranean sample, and to length data for Atlantic males and Mediterranean females. By contrast, the Gompertz model provided good fits to both weight and length data (see Table 1). In particular, the Gompertz model (Pavé, Corman & Bobillier-Monot, 1986) was considered acceptable for two reasons: (a) the data provided no evidence of an inflection point but some evidence of almost constant concavity; (b) given that the length (L) is a variable that follows the Gompertz law, any allometric variable such as the weight ($W=a.L^b$) will also follow a Gompertz law. The Gompertz model can be expressed as follows:

$$Y(t) = Y_0 \cdot \exp[\ln(K/Y_0) \cdot (1 - \exp(-at))]$$

where: Y(t)=variable (total body length or weight) at time t; Y₀=initial value of Y at time 0; K=asymptotic value of Y; a=constant growth rate; t=time.

Data are paired:

$$(l_i, t_i) \text{ and } (w_i, t_i) \quad i=1, 2, \dots, M$$

where l_i is the total body length observed at time t_i and w_i is the total body weight observed at time t_i for each area (Atlantic or Mediterranean) and sex (male or female)

Models were fitted to the data by the least squares method, i.e. by minimizing:

$$\sum_i [Y_i - \{Y_0 \cdot \exp(\ln(K/Y_0) \cdot (1 - \exp(-at_i)))\}]^2$$

where $Y_i = l_i$ or w_i , $i=1, 2, \dots, M$.

Parameters K and a were estimated, for each data set, using the NLINE programme for non-linear regression (Romero-Alvarez, 1991b).

Variances of parameters were obtained from the variance-covariance matrix returned by the Marquardt modified algorithm, used to fit the model to the data. While comparison tests using variance in linear models are exact, in non-linear models they give only approximate results based on asymptotic normality (Romero-Alvarez, 1991a).

Within this context, in order to compare the samples from both areas (Atlantic and Mediterranean coasts) and to investigate the effects on the individual growth of both factors (area and sex), the following statistical tests have been applied:

(1) To test the equality of parameters $H_0: \Theta_i = \Theta_j$

$$Z = \frac{\hat{\Theta}_i - \hat{\Theta}_j}{\sqrt{S^2_{\hat{\Theta}_i} + S^2_{\hat{\Theta}_j}}}$$

where $\hat{\Theta} = \hat{a}$ or \hat{K}

$$i \neq j \quad i, j = f, f', m, m'$$

with f =Mediterranean females; f' =Atlantic females; m =Mediterranean males; m' =Atlantic males; $S^2_{\hat{\Theta}_i}$, $S^2_{\hat{\Theta}_j}$ =estimated variance of $\hat{\Theta}_i$, $\hat{\Theta}_j$.

(2) To test the main effects (sex or area) sex: $H_0: \Theta_f = \Theta_m$ and $\Theta_{f'} = \Theta_{m'}$; area: $H_0: \Theta_f = \Theta_{f'}$ and $\Theta_m = \Theta_{m'}$.

$$\frac{Z_1 + Z_2}{\sqrt{2}} \sim N(0, 1)$$

where Z_1 and Z_2 are calculated as in (1).

(3) To test the interaction between two factors (sex . area):

$$\frac{(Z_1 + Z_2)^2}{\sqrt{2}} \sim N(0, 1)$$

An accurate value for Y_0 is important for a good fit to be obtained. As the present samples do not include any newborn animals, and only a few very young dolphins, the estimate of Y_0 obtained by the

model cannot be considered reliable (106.5 ± 6.3 cm for the Mediterranean sample and 160.1 ± 5.4 cm for the Atlantic sample). A logical way to solve this problem is to fix Y_0 and again fit the models. As an initial value for both length and weight is needed, they were calculated for each sample. The body length at birth for the Mediterranean sample is calculated from 3 records found in the literature for this area (Duguay, 1979 and Aguilar, 1991: 87, 92 and 105 cm), providing an average of 94.7 cm.

Aguilar (1991) calculated a newborn weight of 11.3 ± 5.6 kg for a 92.5 cm long Mediterranean striped dolphin. Following the allometric law: $W = aL^b$ (under its logarithmic form: $\ln W = \ln a + b \ln L$) an initial weight of 10.8 kg was obtained for an initial length of 94.7 cm, according to:

$$W = 5.628 \cdot 10^{-5} L^{2.6734}$$

As no data are available in the literature for the Atlantic specimens, we chose the newborn size of 100 cm provided by Kasuya (1972) for striped dolphins from the Japanese coast, given that their maximum adult sizes (238 cm for males, 225 cm for females) are close to those from our sample (241 cm for males, 215 cm for females). Assuming the length/weight relationship above results in an initial weight of 11.5 kg:

$$W = 3.328 \cdot 10^{-5} L^{2.7701}$$

Results

The quality of the fit of the models to the data can be looked at using the residual sum of squares (RSS) and the correlation coefficients between observed and calculated Y (corr. Y vs \hat{Y}). The latter values, apart from one exception, are always greater than 0.77 (Table 1). The acceptable behaviour of the method is shown by the moderate correlation (always below 0.70) between \hat{K} and \hat{a} . All tests have been applied using a rejection level of $\alpha=0.05$.

Growth in total body length

Mediterranean sample Although the curves obtained (Fig. 1) suggest that males grow faster than females up to 8 years old, statistical tests show no sexual difference in growth rate ($P=0.093$) nor in asymptotic length ($P=0.378$). We assumed therefore that growth in total body length for striped dolphins from the Mediterranean Sea can be expressed as:

$$Y(t) = 94.7 \exp[0.716 (1 - \exp(-0.498 t))]$$

Separate models by sex were:

for males:

$$Y(t) = 94.7 \exp[0.703 (1 - \exp(-0.653 t))]$$

Table 1. Fits results for each sample of striped dolphins (total body length, total body weight, Mediterranean and Atlantic samples)

Samples	N	Y_0	\hat{K}	$\sigma\hat{K}$	\hat{a}	$\sigma\hat{a}$	corr. \hat{K}, \hat{a}	RSS	corr. Y vs \hat{Y}
Atlantic									
Length:									
males	34	100.0	216.07	2.65	0.507	0.043	-0.54	4111.52	0.870
females	18	100.0	200.10	4.51	0.637	0.117	-0.63	2877.75	0.580
both sexes	52	100.0	211.29	2.55	0.519	0.043	-0.58	8436.85	0.787
Weight									
males	20	11.5	104.24	4.92	0.407	0.056	-0.51	3679.62	0.880
females	12	11.5	90.49	4.48	0.422	0.054	-0.67	818.14	0.860
both sexes	32	11.5	100.31	3.83	0.390	0.039	-0.59	5212.33	0.860
Mediterranean									
Length:									
males	22	94.7	191.20	2.95	0.653	0.142	-0.37	2841.75	0.890
females	22	94.7	194.75	2.70	0.383	0.073	-0.45	2198.45	0.910
both sexes	44	94.7	193.72	2.04	0.498	0.070	-0.41	4787.29	0.870
Weight:									
males	11	10.8	78.05	7.28	0.252	0.082	-0.70	1824.00	0.790
females	11	10.8	78.95	3.10	0.267	0.047	-0.64	466.36	0.770
both sexes	22	10.8	78.99	3.66	0.257	0.047	-0.65	2298.90	0.790

N=number of individuals per sample, Y_0 =initial value (see text), \hat{K} =asymptotic length or weight (see text), \hat{a} =constant growth rate (see text), RSS=residual sum of squares (dependent of the model)= $\sum[y_i - \hat{y}_i]^2$, corr. Y. vs \hat{Y} =correlation of Y versus \hat{Y} (independent of the model)= $\rho_{y,\hat{y}} = \text{cov } Y\hat{Y} / \sigma_Y \sigma_{\hat{Y}}$.

for females:

$$Y(t) = 94.7 \exp[0.721 (1 - \exp(-0.383 t))]$$

Atlantic sample Atlantic striped dolphins from both sexes (Fig. 2) appear to grow in the same way up to the age of 3 to 4 years ($P=0.298$). Then, because males grow larger than females (maximal lengths respectively: 216.07 and 200.10 cm, $P=0.002$) and reach their asymptotic length later than females (respectively: 8-9 and 5-6 years of age), the patterns of growth differ and two models were needed:

for males:

$$Y(t) = 100 \exp[0.770 (1 - \exp(-0.507 t))]$$

for females:

$$Y(t) = 100 \exp[0.694 (1 - \exp(-0.637 t))]$$

Comparison of Mediterranean and Atlantic samples

The comparison of growth by sex shows that Atlantic and Mediterranean females reach similar asymptotic lengths ($P=0.312$) with similar growth rates ($P=0.067$), although the former seem to grow faster at young ages (Fig. 3). For males, both samples, have a similar growth rate ($P=0.327$), but their maximal lengths significantly differ ($P=0.000$).

In conclusion, the main difference in the growth of striped dolphins is due to the Atlantic males, since Atlantic females and both sexes in the

Mediterranean sample show similar growth rates and asymptotic lengths.

Growth in total body weight:

Mediterranean sample Growth in weight for Mediterranean individuals of both sexes (Fig. 4) is not statistically different in either rate ($P=0.872$) or asymptotic value ($P=0.912$). A single model may then be applied for the whole sample:

$$Y(t) = 10.8 \exp[1.990 (1 - \exp(-0.257 t))]$$

Atlantic sample As shown on Figure 5, the male asymptotic weight (104.24 kg) is significantly higher ($P=0.039$) than for the females (90.49 kg), although growth rates are similar ($P=0.849$). Separate models are needed for each sex:

for males:

$$Y(t) = 11.5 \exp[2.204 (1 - \exp(0.407 t))]$$

for females:

$$Y(t) = 11.5 \exp[2.063 (1 - \exp(-0.422 t))]$$

Comparison of Mediterranean and Atlantic sample

Fig 6 plots the estimated growth curves by weight for the Mediterranean and Atlantic. Differences in asymptotic weights are significant for both sexes ($P=0.003$ for males, $P=0.035$ for females). The growth rate for Atlantic females is higher than for

Mediterranean

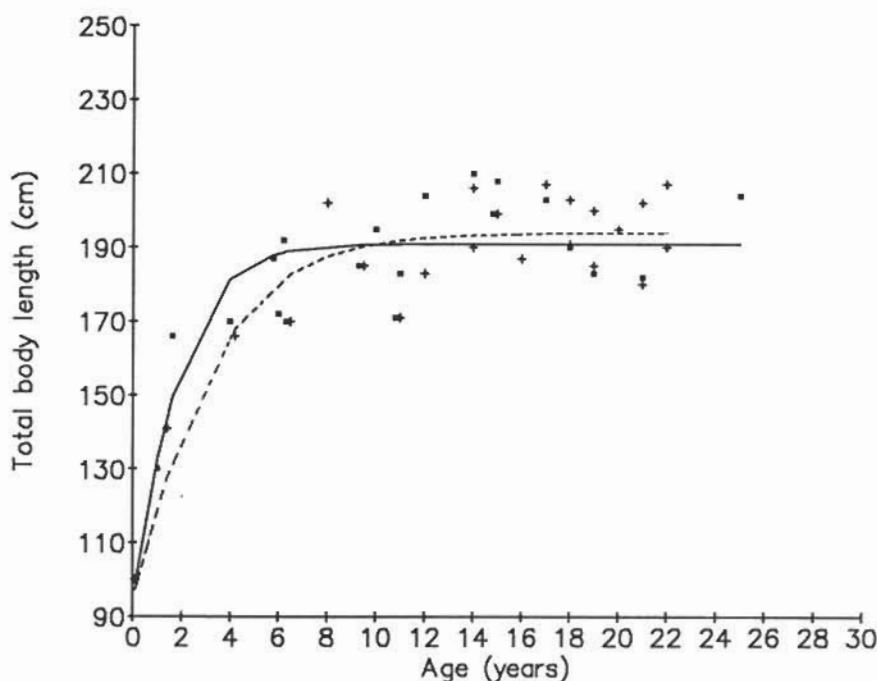


Figure 1. Fitted growth curves of total body length, for male (plain line and ■) and female (dotted lined and +) Mediterranean striped dolphins.

those from the Mediterranean ($P=0.032$) but despite the different asymptotic weight in males from the Atlantic, male growth rates from both areas are not significantly different ($P=0.123$).

In conclusion, contrary to the results obtained for the total body length, the growth differences in weight observed between the two areas is due to the whole Atlantic sample whose asymptotic weight is always higher.

Interactions and main factors

The results obtained for length and weight growth show clearly the influence of the area (Mediterranean or Atlantic) and the sex. The tests described in the methods section, have been applied to determine the interaction of these factors, the effect of a main factor, or the combination of both.

The interaction effect A sex-area interaction affects the asymptotic length ($P=0.000$) and the growth rate ($P=0.046$), but is not significant for weight growth rate and asymptotic weight.

The main effect Influence of the area as main factor is noted on the growth rate in weight and the asymptotic weight ($P=0.004$ and 0.000 respec-

tively). No effect of sex is found for either parameter ($P=0.401$, $P=0.084$). In other words, the effect of the area or the sex differs for each sample, because of the interaction between them. While the asymptotic length and weight differ for males and females from the Atlantic sample, no significant sexual variation appears in the Mediterranean sample. With regard to their length growth, females from both areas are similar, while Atlantic males are larger (and heavier) than Mediterranean males (asymptotic length and weight significantly different).

Discussion

Three main results can be pointed out from this study: (1) in the Mediterranean sample, neither length nor weight growth differ significantly between males and females; (2) in the Atlantic sample, both asymptotic length and weight differ significantly with sex; (3) individuals from the Atlantic sample are generally larger and heavier than those from the Mediterranean sea.

Hence, the effect of the sample area is superior to the effect of the sex. This is supported by several references in the literature that provide different

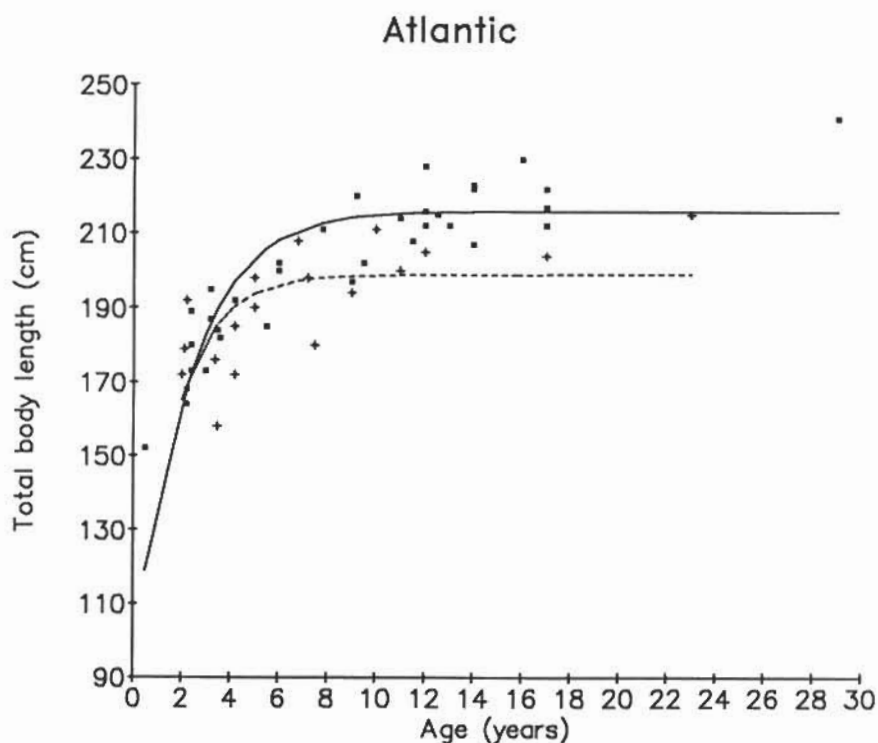


Figure 2. Fitted growth curves of total body length, for male (plain line and ■) and female (dotted line and +) Atlantic striped dolphins.

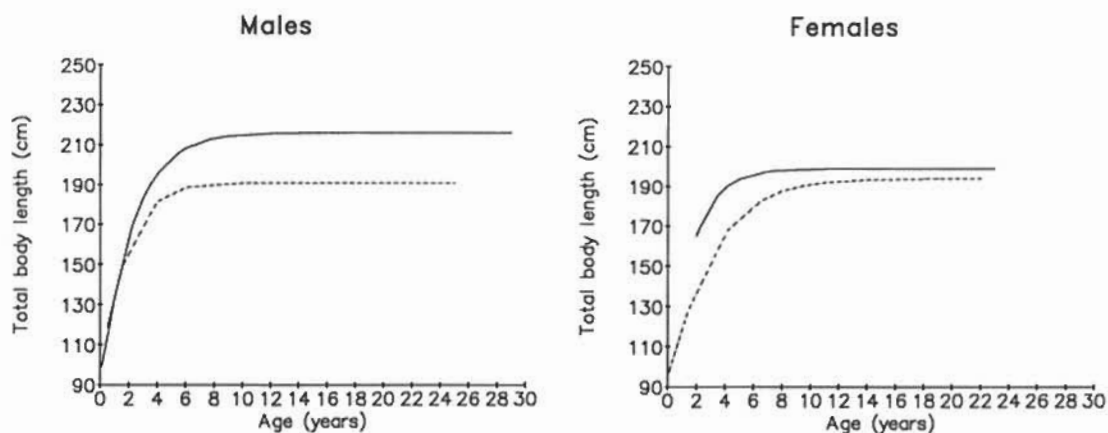


Figure 3. Fitted total body length growth curves for male and female striped dolphins, from the Mediterranean (dotted line) and Atlantic (plain line) samples.

asymptotic total body lengths for various striped dolphin populations (Table 2).

One should of course keep in mind that this first scientific study on the comparison of growth parameters is based on a limited sample, in terms of quantity (96 specimens) and quality: striped

dolphins found stranded on the coast of France are not to be considered as strictly representative of the Mediterranean and Atlantic populations. The animals have been found on large portions of coast (several hundreds kilometres in both areas), over a long period of time (almost 15 years covering every

Mediterranean

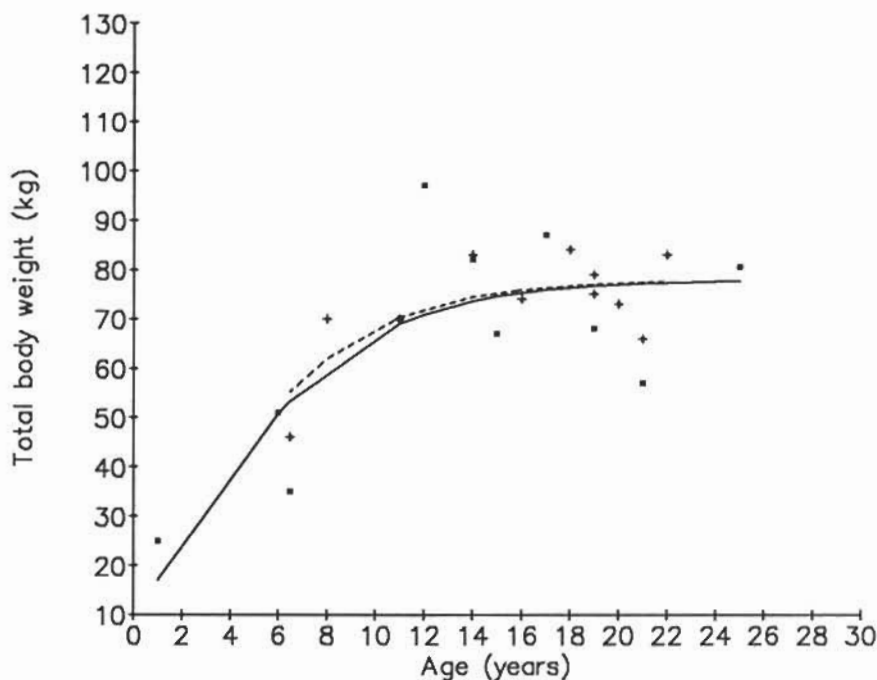


Figure 4. Fitted growth curves of total body weight, for male (plain line and ■) and female (dotted line and +) Mediterranean striped dolphins.

month). In addition, although nothing is known about possible seasonal movements of striped dolphins in the areas considered here, it might be suspected that, because stranded animals have probably died close to the shore and been carried to the beach by the tide and local currents, the dolphins collected for this study come from only a portion of the Mediterranean and Atlantic 'stocks'.

Despite the fact that this study needs to be confirmed with larger and more homogeneous samples, it is of value to consider factors that might explain the differences observed. These might include: predation pressure; population density; the thermal environment; and food resources (Lamotte & Bourlière, 1975; Margalef, 1982).

Very little is known on the first three factors: striped dolphins are affected by incidental catches in both areas (Collet, 1983), but these have not been quantified for the Mediterranean Sea (Notarbartolo di Sciara, 1990) and the study by Collet, Antoine & Danel (1992) concerns only a portion of the northeastern Atlantic.

Although population density has been estimated in various areas of the Western Mediterranean (Forcada, Aguilar, Hammond, Pastor & Aguilar, 1991; Gannier & Gannier, 1993; Notarbartolo di

Sciara, Forcada, Acquarone & Fabbri, 1993) and in one northeastern Atlantic fishery area (Goujon, Antoine, Collet & Fifas, 1993), the areas and survey periods are too restrictive to be compared, to estimate the impact of striped dolphins on food resources, or to evaluate the possibility that over-population is influencing the individual growth.

The population density in the Mediterranean Sea has probably been affected by the important die off which affected the striped dolphins in 1990 (Bompar, Dhermain, Poitevin & Cheylan, 1991), but the comparison of growth in samples collected before, during or after the die off has not shown any significant difference. Raga & Aguilar (1991) noted that the high PCB concentrations found in the tissues of striped dolphins stranded during the 1990 die off, might be responsible for alterations in the immune system, and then could have facilitated the action of bioaggressive elements, such as the morbillivirus involved. However, because Borrell & Aguilar (1990) showed that samples collected from badly preserved tissues (which is the case for most stranded dolphins) do not produce reliable PCB ratios, we have not attempted to examine possible differences in pollutant contamination between

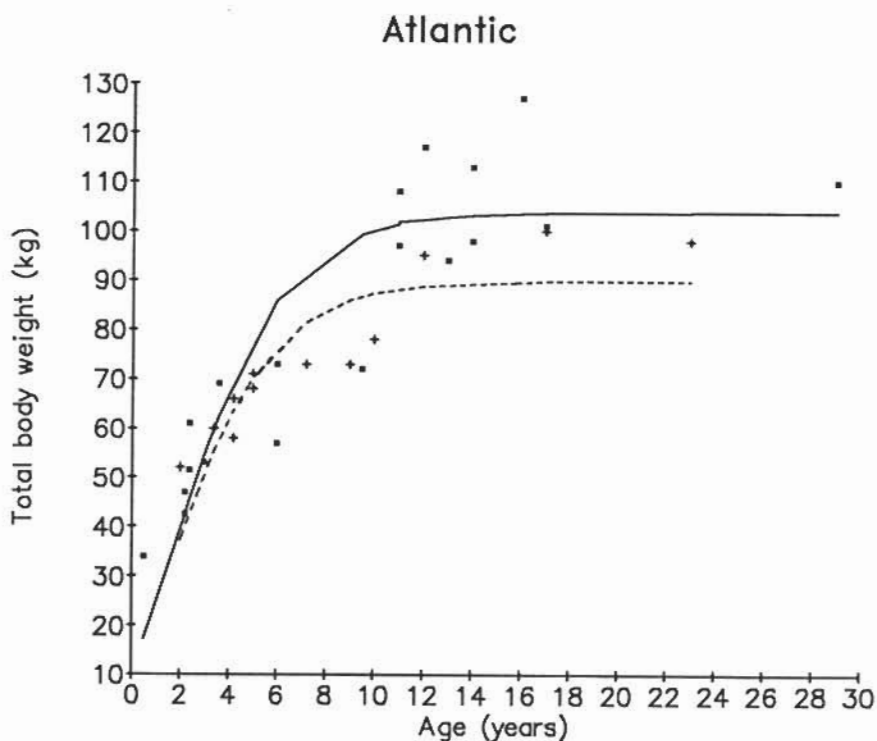


Figure 5. Fitted growth curves of total body weight, for male (plain line and ■) and female (dotted line and +) Atlantic striped dolphins.

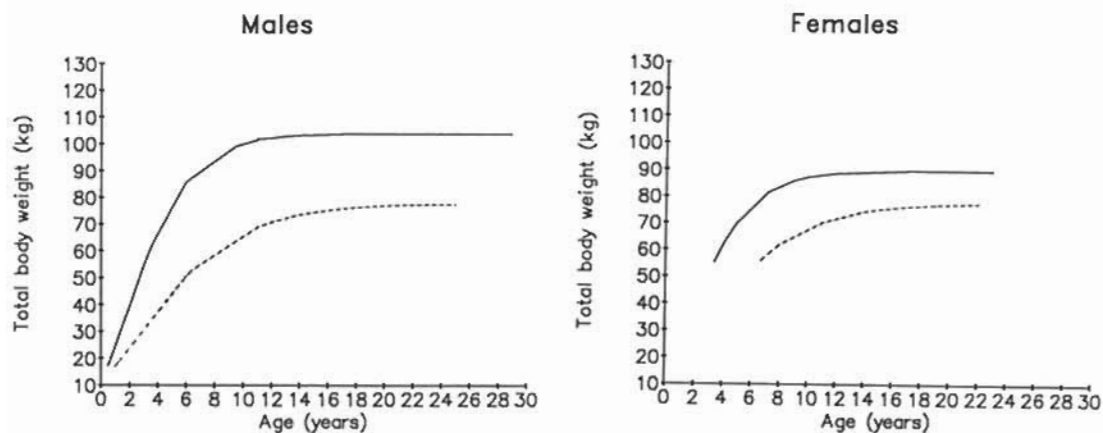


Figure 6. Fitted total body weight growth curves for male and female striped dolphins, from the Mediterranean (dotted line) and Atlantic (plain line) samples.

both areas from our sample. In fact, present scientific knowledge is still far from being able to demonstrate if and how pollution might affect the growth of dolphins.

Bergmann's (1847) law is one of the most established thermal ecological laws. In the same thermal

environment, homeotherms lose the same quantity of heat per unit of surface area. As body volume and mass increase as the cube of linear length while surface area only increases as the square of length, within a given taxonomic group, the largest sizes will be reached in the coldest part of distribution

Table 2. Asymptotic total body length for striped dolphins from various areas

Areas	Males	Females	References
SW Indian	244	217	Ross, 1984
NW Pacific	238	255	Miyasaki, 1977
NE Atlantic	216	200	Present study
E tropical Pacific	205	195	Gurevich & Stewart, 1979
Mediterranean	191	194	Present study

(Sacchi & Testard, 1971; Margalef, 1982). As the Atlantic minimum sea temperatures are lower than the Mediterranean (respectively: 5–7°C and 13°C, Vanney, 1991), the larger size and mass of Atlantic striped dolphins could be explained by Bergmann's rule. While in females, only the asymptotic mass of Atlantic specimens is significantly higher than the one of Mediterranean dolphins, which reflects a proportionally higher volume to save energy.

Sea temperature may also have an indirect effect on dolphin growth in that it also influences the environment's productivity. Our present knowledge of the striped dolphin diet is too scarce to allow any comparative study between the two areas (Desportes, 1985; Wurtz & Marralle, 1991), but an examination of the general oceanographic conditions reveals some fundamental differences between the Mediterranean Sea and the Atlantic Ocean. The semi-closed Mediterranean is considered as rather unproductive whereas the North Atlantic is considered as a particularly productive area (Vanney, 1991). Consequently, the higher total body length and/or weight of Atlantic striped dolphins might be a result of thermal energetics and more abundant food resources.

As noted previously, because of the limited quantity and quality of samples available for the present analysis, these results have to be confirmed on a larger scale. Similar studies carried out on representative samples from other populations, within various dolphins' species, should also improve our understanding of the quality of the oceanic environment.

Acknowledgements

The material used in the present study has been collected by the correspondents of the Centre National d'Étude des Mammifères Marins of La Rochelle, thanks to all of them, in particular to those of the Groupe d'Étude des Cétacés de Méditerranée and to C. Mercier who is in charge of the collections in the Musée Océanographique de La Rochelle. We are most grateful to Dr. J. D. Lebreton for his help with the statistical analysis and to P. Beaubrun for his comments on the

manuscript. Dr. S. Chivers and G. Donovan gave us the honour of reviewing the article, we warmly thank both of them. R.R-A has been supported by the National Council of Sciences and Technology (CONACYT, grant number 44186) and the Zacatecas Autonomous University, both organizations from Mexico.

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