

Influence of climate oscillations on dentinal deposition in teeth of Commerson's dolphin

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Abstract

Effects of climatic oscillations on populations in marine environments are produced mainly through the lower trophic levels. Marine mammals, as top predators, are affected indirectly by these fluctuations, showing variations in their survival, growth and reproduction. The main objective of this study was to determine whether we could detect the effect of climatic oscillations on Commerson's dolphins (*Cephalorhynchus c. commersonii*) off Tierra del Fuego, Argentina, by examining the presence and proportion of anomalous dentinal growth layer groups (GLGs). The relative deposition of anomalous GLGs was determined using calendar years from 1960 to 2005, and related to the Southern Annular Mode (SAM) and El Niño Southern Oscillation (ENSO) events, and to mean annual sea surface temperatures (SST). Then, growth parameters between animals that did and did not show anomalous dentinal growth layer patterns in one or more of their GLGs were compared. The presence of anomalous GLGs was related to the SAM, increasing in frequency with negative values of the SAM. No relationship was found among anomalous GLGs, ENSO, and SST. There were no significant differences in growth parameters between animals with and without anomalous GLGs. Using recording structures such as teeth provided a unique way of reconstructing time series to evaluate the effects of these climatic patterns on a top predator species in an area where no similar studies have been conducted, primarily due to a lack of suitable long-term data sets.

Keywords: Argentina, dentinal anomalies, ENSO, growth, SAM, SST, Tierra del Fuego

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Introduction

During the last decade, as a result of perceived changes in global climate, there has been increasing interest in determining the impacts of large-scale patterns of climate variability, such as the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO), on natural populations and their ecological responses to these impacts (Stenseth *et al.*, 2002; Walther *et al.*, 2002). Climate variations affect natural populations of plants and animals through numerous pathways and may operate directly by affecting the physiology and phenology of organisms and indirectly through effects on their prey, predators, and/or competitors (Lima *et al.*, 2002a,b; Stenseth *et al.*, 2002; Walther *et al.*, 2002; Forcada *et al.*, 2006).

In marine ecosystems, the major impacts of climate are through their effects on sea surface temperature and wind conditions (Stenseth *et al.*, 2002). Changes in surface temperature and wind condition are likely to have particularly strong effects on organisms at lower trophic levels (Walther *et al.*, 2002), which, in turn, can lead to strong indirect effects on marine mammal populations that occupy higher trophic levels. Thus, the distribution, abundance, growth, reproductive success, and survival of marine mammals may be modified by changes in the availability or quality of their prey that result from changes in climate (Boyd & Roberts, 1993; Gardner & Chavez-Rosales, 2000; Antonelis *et al.*, 2003; LeBoeuf & Crocker, 2005; Crocker *et al.*, 2006). In addition, direct influences of fluctuating environmental conditions on marine mammals have been found. For example, reduction of cover ice and rising sea level can affect seal haul-out sites (Learmonth *et al.*, 2006) and changes in water temperature may modify the geographic ranges of cetaceans (MacLeod, 2009).

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The subantarctic ecosystem is dominated by two patterns of large-scale climate variability: the ENSO and the Southern Annular Mode (SAM) (Thompson & Solomon, 2002; Marshall, 2003; Liu *et al.*, 2004; Murphy *et al.*, 2007). The ENSO variability generates anomalies in sea surface temperature (SST) around the Antarctic Peninsula and South Georgia (Trathan & Murphy, 2003; Trathan *et al.*, 2007; Meredith *et al.*, 2008). The SAM, also referred to as the Antarctic Oscillation or High Latitude Mode, is considered the most important pattern of climatic variability at high latitudes in the Southern Hemisphere (Hall & Visbeck, 2002; Marshall, 2003; Thompson, 2007). It is linked with variations in temperature and distribution of sea ice in Antarctic waters and the SST over the Southern Ocean (Thompson & Solomon, 2002; Marshall, 2007). Climatic variations from these events are known to influence top predator populations. For example, SAM-related variations have generated changes in demographic parameters of several penguin populations at high southern latitudes (Ainley *et al.*, 2005; Forcada & Trathan, 2009). Connections between ENSO and marine mammal populations have also been found in the Southern Ocean and Antarctica (Croxall, 1992; Boyd & Roberts, 1993; Proffitt *et al.*, 2007). Leaper *et al.* (2006) noted a strong negative relationship between breeding success of the southern right whale, *Eubalaena australis*, off Peninsula Valdes and El Niño and SST in South Georgia. Similar results were observed for the Antarctic fur seal, *Arctocephalus* (*cf.* *Arctophoca*) *gazella* (Forcada *et al.*, 2005). However, to date, no studies have been conducted to determine the ecological effects of these climate patterns on top predators in the Tierra del Fuego or Magellanic regions. This is primarily due to a lack of suitable long-term data sets for studying such effects.

In this context, the study of teeth offers a valuable opportunity to look at the effects of climate change on a particular species since teeth are permanent recording structures for an individual (Klevezal, 1996). Dentine and cement in teeth 'respond to changes of physiological condition of an organism by changing their morphological characteristics as they grow' (Mina & Klevezal, 1970; Klevezal, 1996). These two structures normally are not subjected to resorption, and thus, once formed, their records remain for life (Klevezal, 1996). In marine mammals, these recording structures have been used primarily for age estimation (Hohn, 1980, 2009; Perrin & Myrick, 1980; Stewart *et al.*, 1996; Lockyer *et al.*, 2001; Dellabianca *et al.*, 2012). However, it is possible to obtain additional information, such as an individual's life history or the effects of particular environmental events, from accessory layers and mineralization anomalies present within the layering pattern of the teeth (Klevezal & Myrick, 1984; Manzanilla, 1989; Lockyer, 1993, 1995;

Klevezal, 1996). Since growth patterns in individuals are determined by hormonal variations, any factor strong enough to interfere with a seasonal hormonally linked response could potentially affect the formation pattern in teeth, generating anomalies in zonation and mineralization (Lockyer, 1995). It has been suggested that the occurrence of dentinal anomalies are due to systemic causes linked to life-history events such as birth, pregnancy, parturition, lactation, and achievement of sexual maturity (Klevezal & Myrick, 1984; Bengtson, 1988; Lockyer, 1993, 1995; Klevezal, 1996; Luque *et al.*, 2009). They may also be caused by other factors such as nutritional deficiencies, captivity, disease (Lockyer, 1993) or climatic events (Manzanilla, 1989).

In addition, teeth may also be used as indicators of the growth of individuals, reflecting the changes that occur in their growth rates (Klevezal, 1980, 1996). In terrestrial mammals, Mina & Klevezal (1970) found that changes in growth of individuals were recorded in growth of the teeth, even if those changes had been induced artificially. These associations between the growth of the recording structure and the growth of the animal were also observed in marine mammals (Sergeant, 1973; Hohn, 1980; Baker & Fowler, 1990; Boyd & Roberts, 1993). The latter authors found a significant correlation between variations in tooth growth and the Southern Oscillation Index (SOI) in Antarctic fur seals.

The goal of this study was to determine whether we could detect the effect of climate oscillations, SAM and ENSO, on Commerson's dolphins (*Cephalorhynchus c. commersonii*) off Tierra del Fuego, Argentina, by examining the presence of anomalous dentinal growth layer groups (GLGs, Perrin & Myrick, 1980; Dellabianca *et al.*, 2012). We also compared growth curves between specimens with and without dentinal mineralization anomalies. Since Commerson's dolphins have a distribution restricted to cool coastal and shelf waters (Riccialdelli *et al.*, 2010), investigating the effects of ENSO and SAM on this species in subantarctic waters will contribute to a better understanding of general changes in ecosystems at these latitudes.

Materials and methods

Species and study site

The Commerson's dolphin, one of the world's smallest cetaceans, occurs in the southwestern South Atlantic from about 41°30'S to 56°S (Goodall, 1978; Goodall *et al.*, 1988). Along the northeastern coasts of Tierra del Fuego, Argentina, and the eastern Strait of Magellan, Chile (Fig. 1), it is the cetacean species most often seen near the shore and the species most affected by bycatch in artisanal shore-based fisheries (Goodall, 1978, 1994; Goodall *et al.*, 1994). In addition, MacLeod (2009)



Fig. 1 Location of Tierra del Fuego.

predicted that this genus is one of the taxa at highest risk due to range changes and contractions caused by climate change.

Teeth sample

We examined teeth from 172 incidentally caught Commerson's dolphins from the Goodall (RNP) collection at the Museo Acatashún de Aves y Mamíferos Marinos Australes (AMMA) at Estancia Harberton, Tierra del Fuego, Argentina. Specimens were collected during the RNP program of beach surveys along the coast of northeastern Tierra del Fuego, Argentina, from 1974 to present (Goodall, 1978; Goodall *et al.*, 1994, 2008). Data on collection date, stranding location, total length and sex were available for all specimens.

The teeth were collected from the center of the lower jaw and were processed following the method described by Myrick *et al.* (1983) and Hohn *et al.* (1989). The teeth were decalcified in RDO[®] (Apex Engineering Products Corporation, Plainfield, IL, USA) (a commercial decalcifying agent) and sectioned longitudinally on a sliding microtome with a freezing stage to 25 μ m thickness. The sections were stained in Mayer's hematoxylin and 'blued' in a weak ammonia solution. The best sections were selected and mounted on microscope slides in 100% glycerin.

Aging and identification of anomalies

The tooth sections were examined under a stereo microscope with transmitted light at 40 \times and 100 \times magnification. Age was estimated by counting the number of GLGs in the dentine. Following Lockyer *et al.* (1981, 1988) and by analogy to related species (Hohn, 2009), we assumed that in this species one GLG, consisting of a thin unstainable layer and a wide stainable layer (Dellabianca *et al.*, 2012), represents 1 year's

growth. In addition, because Commerson's dolphins exhibit relatively synchronous calving and thus, predictable dentinal deposition patterns, we were able to confirm the deposition of the first annual layer, which supported the assumption that we were identifying an annual deposition pattern. Three readings for each specimen were conducted (without access to biologic data) by NAD. A subsample of teeth ($n = 60$) was read independently by AAH and the readings were compared. Readings were within ± 1 year for 48 animals (80%), within ± 2 years for another eight (13.3%), and the remaining four differed by 4 years. Absent initial agreement, a consensus between readers was achieved.

For each specimen estimated to be older than 6 months ($n = 168$), the tooth section was checked for anomalous GLGs. As noted in Dellabianca *et al.* (2012), the relative width of GLGs was consistent in all specimens. Thus, to estimate 6 months, we considered (qualitatively) the proportional width of the first GLG at the time of death. GLGs were considered anomalous when they had one or more conspicuous, wavy, dark accessory layers (as defined by Lockyer, 1993, 1995) or a relatively 'hypocalcified' (hypochromatic, Klevezal, 1996) appearance (Dellabianca *et al.*, 2012) (Fig. 2). When one or more of these anomalies occurred within a GLG, we refer to that GLG as being anomalous. For example, if a specimen had one GLG with wavy, dark accessory layers, another GLG hypocalcified, and a third with both characteristics, we refer to this specimen as having three anomalous GLGs.

Anomalous GLGs and climate

We used two large-scale climatic indices and a local weather variable to represent environmental conditions. We used the Southern Oscillation Index (SOI) to measure the strength and

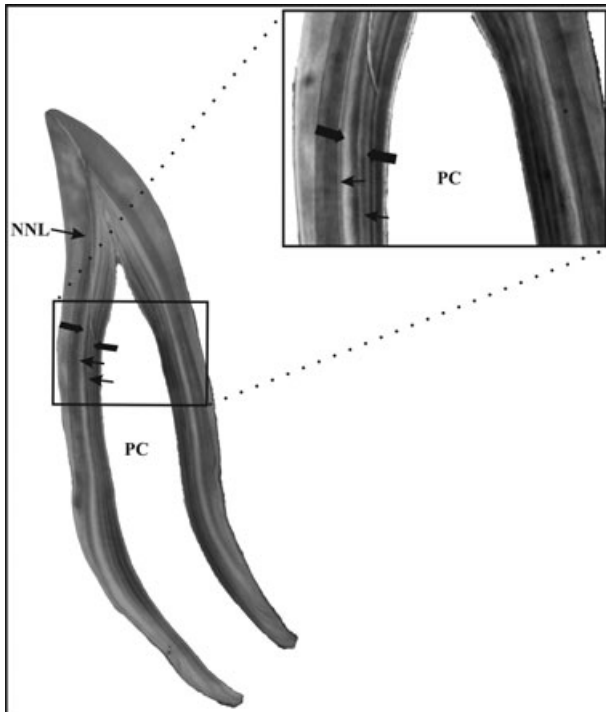


Fig. 2 Accessory layers (thin arrows) and 'hypocalcified' appearance (wide arrows) in a section from a 3 years old male *C. commersonii* (RNP 1837) at 25 \times and 50 \times magnification (top right corner). PC = pulp cavity, NNL = neonatal line.

the phase of the ENSO events (positive SOI values are associated with La Niña conditions and negative values with El Niño conditions). Annual SOI data were obtained from 1951 to 2005, from the US National Center for Atmospheric Research (NCAR, web page: <http://www.cgd.ucar.edu/cas/catalog/climind/>). Annual values for the SAM were obtained from 1957 to 2005, from the British Antarctic Survey web page (<http://www.nerc-bas.ac.uk/icd/gjma/sam.html>).

We used mean annual SST from the study site as a local environmental variable. It was calculated from the average monthly SST values, at 51.5°S–55.5°S and 65.5°W–68.5°W. These data were obtained from Met Office HadiSST data set (see Rayner *et al.*, 2003 for details) by CDM. Temperatures were extracted for the period 1950–2005. Time series of these environmental data are shown in Fig. 3.

Data analysis

Presence of anomalous GLGs. To assess the influence of environmental variables on dentine deposition, we used generalized linear mixed-effects models. Mixed models account for the non-independence of data among repeated measures (in this case, GLGs from the same specimen; Pinheiro & Bates, 2000). The presence of anomalous GLGs was modelled as the response variable; calendar year, SAM, SOI, and SST were modelled as fixed effects. The specimen's identity, age, and sex were included in all the models as random effects. We used models with a binomial error distribution and a logit link

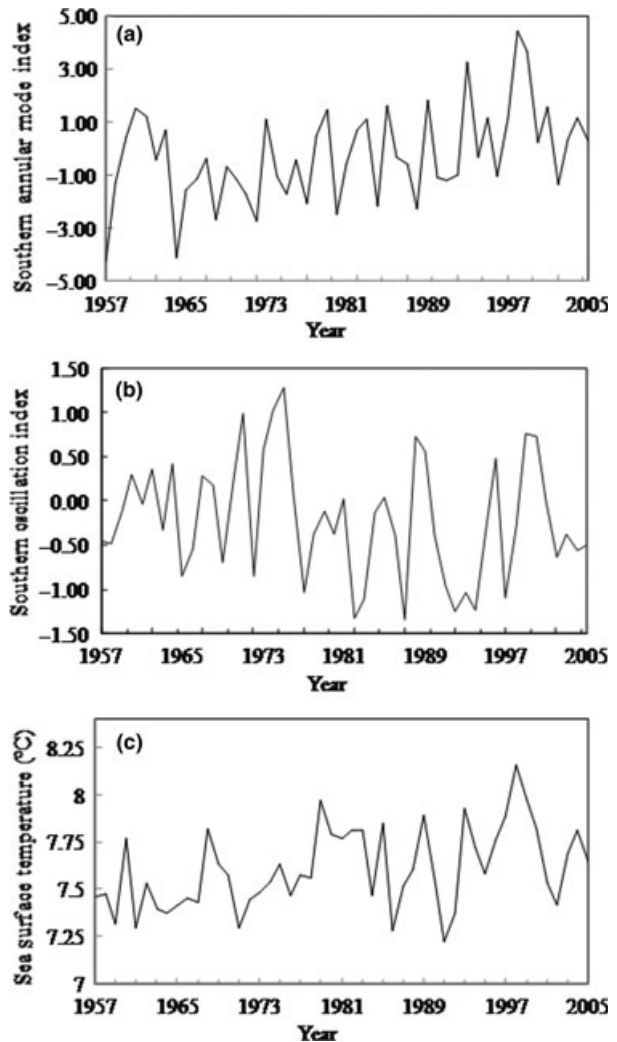


Fig. 3 Time series (1957–2005) of environmental variables used in the study. Annual SAM index (a), Annual SOI index (b) and SST in Tierra del Fuego area (51.5°S–55.5°S, 65.5°W–68.5°W) (c).

function. We used a maximum likelihood method of parameter estimation, with the specific packages nlme4 and lme4 in the statistical package R (R Version 2.9.2, R Development Core Team, 2009). The significance of the random effect was assessed using a maximum likelihood method (Pinheiro & Bates, 2000; Crawley, 2007).

Data for GLG (anomalous and non-anomalous) deposition were available for all years, from 1960 to 2005, by back-calculating to calendar year from the date and age at death. We used values from the current year (t) and those from the three previous years ($t-1$ – $t-3$) for SAM and SOI, and from t and the previous year ($t-1$) for SST, to assess possible delayed effects of climatic variables on the deposition of dentine. Since initial data exploration indicated that SST from the study area is correlated with the SAM and the ENSO, and interaction between the two climate modes has been suggested (Liu *et al.*, 2004; Fogt & Bromwich, 2006; L'Heureux & Thompson, 2006), we fitted separate models for each of the explanatory variables.

Models were selected using Akaike Information Criterion (AIC). The model with the lowest AIC value was taken to be the best approximating model, and subsequent models with an Akaike difference (ΔAIC) < 2 were considered to also have substantial support from data (Burnham & Anderson, 2002). ΔAIC , Akaike weights (w_i) and evidence ratio (w_1/w_i) were calculated for each model (Burnham & Anderson, 2002).

Proportion of anomalous GLGs and climate. To assess the relationship between the number of anomalous GLGs per calendar year (response variable) and climatic variables (explanatory variables), we performed generalized linear models with binomial error structure and a logit link function. The number of anomalies per year was expressed as a proportion (between 0 and 1), and was calculated as the absolute frequency of anomalies in relation to the number of animals present that year. We used data from specimens from the period between 1976 and 2001 to ensure a minimum n of 18 individuals per year. To rule out the existence of auto regressive effects on the number of anomalous GLGs (i.e., anomalous GLGs in time t are a function of anomalous GLGs in t_{-1}), the proportion of GLG anomalies in t_{-1} was used as another independent variable. As in the previous section, there were different models to evaluate the possible relationship between the proportion of anomalous GLGs and calendar year, SAM, SOI, and SST. We used environmental variable values from the current and previous years as detailed in the previous section.

We selected the best model using AIC corrected for small-sample bias (AICc, Burnham & Anderson, 2002), ΔAICc , w_i and w_1/w_i . Analyses were performed using the statistical package R version 2.9.2 (R Development Core Team, 2009).

Growth

To evaluate the correlation of anomalous dentinal deposition on somatic growth rate, we estimated growth parameters in specimens with the typical growth layer pattern (Dellabianca *et al.*, 2012) in all their GLGs and in those with anomalous dentine in one or more GLGs. Growth was determined fitting the nonlinear Gompertz model (Laird, 1966) to length at age data:

$$L(t) = Ae^{-be^{-ct}}$$

where L corresponds to the length (cm) at age t (yr); A is asymptotic length; b is the constant of integration, and c is rate of growth constant. Neonatal specimens ($n = 4$) were included in the data set of both subsamples (with and without anomalous GLGs) to improve the growth parameter estimation.

Results

Anomalous GLGs and climate

The presence of one or more anomalous GLGs was recorded in 88 of the 168 specimens analyzed. There was no significant difference in the presence of anomalous GLGs between males ($n = 105$) and females ($n = 63$) (test of difference of proportions: $z = 0.025$,

$P = 0.75$). The relative frequency of anomalous GLGs (expressed as number of specimens with anomalous GLGs relative to the total number of specimens at each age) was higher in the first three GLGs (chi-square test, $P < 0.001$; Fig. 4).

The best-supported model to explain the presence of anomalous GLGs included SAM at time t as the only explanatory variable. This model had a w_i of 0.65. The second best model included SAM in t and t_{-1} , which showed a w_i of 0.23 and a ΔAIC 2.07, whereas other alternative models had essentially no support from data (Table S1). Parameter estimates for the best model indicated a negative relationship (-0.26 , $\text{SE} = \pm 0.12$) between the presence of anomalous GLGs and SAM. The variability explained by the random effects was significant in all models (PCV, $P \leq 0.001$).

The proportion of anomalous GLGs showed a negative trend from the early 1980s until 1995, when no specimen had anomalous GLGs. Afterwards, it appears that a positive trend may have begun and continued until 2001 (Fig. 5). The null model (intercept term only) had the lowest AICc score, indicating a better overall fit than the other models, to explain the proportion of anomalous GLGs in different calendar years. In addition, ΔAICc between the best model and the next best models was ≥ 2.3 units (Table S2). These results suggest that none of the variables selected (year, SAM, SOI and SST) was related to the proportion of anomalous GLGs deposited each calendar year.

Growth

The results of the Gompertz growth model for specimens with the non-anomalous growth layer pattern in all their GLGs and in those which presented anomalous dentine in one or more GLGs are presented in Table 1 and Fig. 6. Although the estimated parameters were higher in animals with non-anomalous deposition pat-

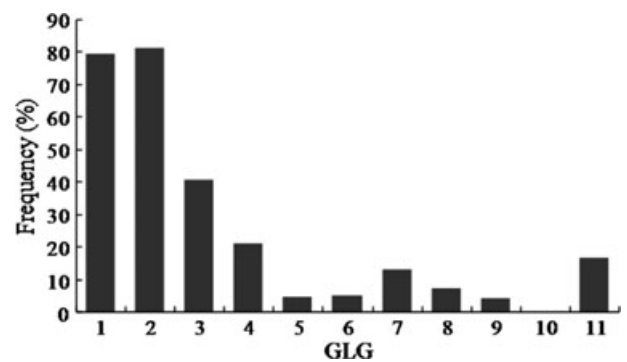


Fig. 4 Frequency of anomalous dentine in each growth layer group (GLG) relative to the total number of specimens at each age.

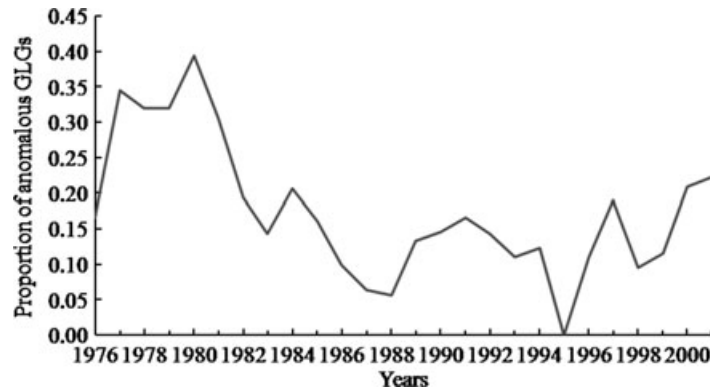


Fig. 5 Proportion of anomalous growth layer groups (GLGs) per year (relative to the number of animals present that year) during the period 1976–2001.

Table 1 Parameters values from the Gompertz growth model fit to age-at-length data for Commerson's dolphin from Tierra del Fuego with the typical deposition pattern (T) and those with anomalous dentine in one or more growth layer groups (A)

	<i>n</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>r</i> ²
T	84	132.01 (0.9)	0.51 (0.05)	1.56 (0.18)	0.73
A	92	131.17 (1.0)	0.48 (0.04)	1.11 (0.13)	0.75

a = asymptotic length (cm), *b* = constant of integration, *c* = growth rate and *r*² = the variance in the data explained by the model. Values in parentheses are standard errors of the estimated parameters.

tern, the differences were not statistically significant (confidence intervals at 95% significance).

Discussion

Anomalous GLGs and climate

The presence of anomalous GLGs was inversely related to the SAM index values at time *t* in Commerson's dolphins. A similar relationship between climatic oscillations and anomalous deposition of dentine was reported by Manzanilla (1989) for dusky dolphins (*Lagenorhynchus obscurus*) in Peruvian waters. In particular, the El Niño event of 1982–1983 was recorded in the teeth of dusky dolphins, primarily in mature females, as a pair of hypocalcified layers in the GLG corresponding to that El Niño event. Concurrent with the El Niño was the collapse of the Peruvian anchovy (*Engraulis ringens*) stocks, the primary prey species of those dusky dolphins (Manzanilla, 1989). Manzanilla's study was the first to show evidence of an environmental effect on dentine deposition during periods of singular climatic conditions, and the only one reported for marine mammals previous to our study. The presence

of dentinal anomalies in particular years was also recorded in long-finned pilot whale (*Globicephala melas*); however, no obvious relationship with environmental variables was found (Lockyer, 1993).

The SAM generates anomalies in SST, as well as variations in oceanic circulation and in the extension of sea ice (Hall & Visbeck, 2002; Thompson, 2007). However, no association was found between the presence of anomalous GLGs and SST, regardless of the correlations between SST and the SAM. This suggests that other local environmental variables regulated by the SAM are responsible for the link between SAM and anomalous GLG deposition. Positive values of the SAM are associated with greater intensity of the circumpolar current, anomalous upwelling in the Antarctic region, and anomalous downwelling near 45°S (Hall & Visbeck, 2002). It is important to note that SAM and ENSO indices appear to have a strong spatial coupling with SST. Whereas SAM seems to be strongly correlated with SST at the Antarctic Peninsula area, ENSO effects on SST are more pronounced off the Ross Sea (negative correlation) and in the sector off the George V and Oakes coasts (Kwok & Comiso, 2002). One effect is that a positive SAM results in cold anomalies over most of Antarctica except for the Antarctic Peninsula (Kwok & Comiso, 2002), resulting in a dipolar response in sea ice coverage, with an increase in sea ice cover except in the Antarctic Peninsula and Weddell Sea where sea ice decreases (Lefebvre *et al.*, 2004; Stammerjohn *et al.*, 2008). Additional knowledge of the influence of the SAM on other local oceanographic variables and access to productivity time series data for 1960–2005 will allow for a better understanding of the connection between this pattern of climate variability and dentine deposition in Commerson's dolphin teeth.

Several authors have reported evidence of ENSO effects on different populations of seabirds and marine mammals in the South Atlantic and Antarctica (Forcada

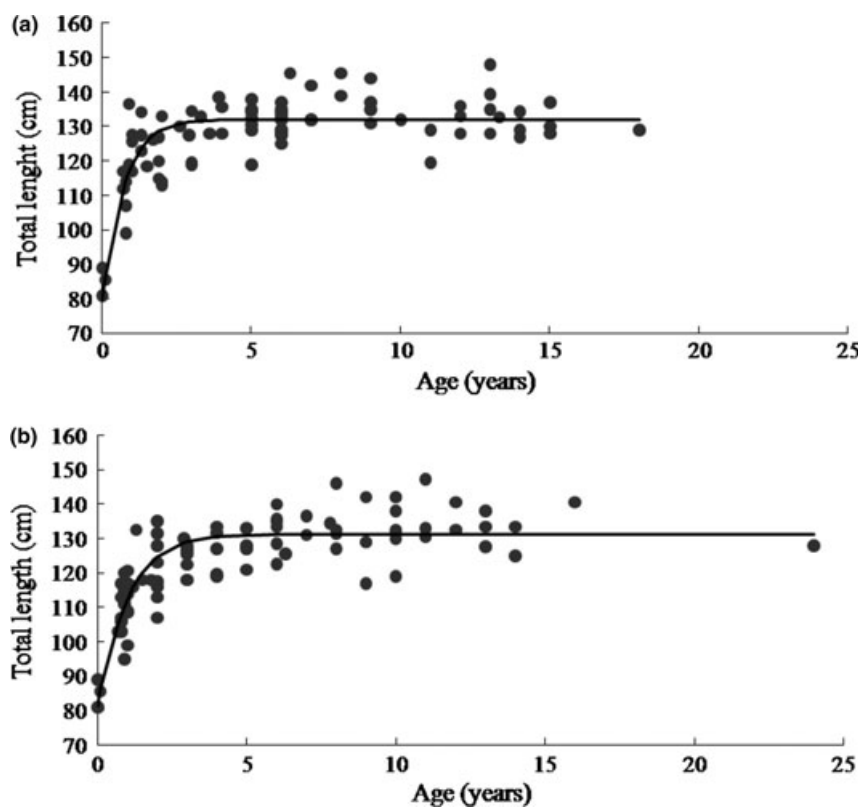


Fig. 6 Length at age, with fitted Gompertz curve, of Commerson's dolphins off Tierra del Fuego with the typical deposition pattern (a) and with anomalous dentine in one or more growth layer groups (b).

et al., 2005; Jenouvrier *et al.*, 2005; Proffitt *et al.*, 2007; Trathan *et al.*, 2007). These ENSO effects on top predators could be related to effects on their prey base. In particular, these species feed primarily on krill, and krill recruitment and availability are known to be affected by sea ice and ENSO in the Southern Ocean (Quetin & Ross, 2003; Ducklow *et al.*, 2007; Murphy *et al.*, 2007).

Although not directly comparable to these previous studies, we found no association between ENSO and the presence of dentinal anomalies in Commerson's dolphins, suggesting that ENSO may not have similar effects on this species. Commerson's dolphin is an opportunistic predator, feeding on coastal and shelf fish, cephalopods, and crustaceans (Bastida *et al.*, 1988; Clarke & Goodall, 1994; Crespo *et al.*, 1997; Berón-Vera *et al.*, 2001; Pedraza, 2008; Riccialdelli *et al.*, 2010). It may be that this wide prey base buffers them from major impacts associated with ENSO effects on individual prey species, as was found for cetaceans off the coast of Peru; while a mark was apparent in teeth of dusky dolphins, the specialist feeder on anchovies, following the collapse of the anchovy stock, it was not apparent in two other species, Burmeister's porpoise (*Phocoena spinipinnis*) and bottlenose dolphin (*Tursiops truncatus*), that were generalist feeders (Manzanilla, 1989).

The results from the models do not show a direct relationship between the proportion of anomalous GLGs and environmental variables. However, there was a high frequency of this dentinal anomaly between the mid-1970s and the beginning of the 1980s, followed by a sharp decrease in its presence (Fig. 5), coinciding with the period of greatest changes in the values of the SAM index (Marshall, 2003). During this time there was also a positive trend in SST in the Tierra del Fuego area. It is interesting to note that changes in demographic parameters were observed during the same period for different top predators of the Antarctic region. The number of breeding pairs of southern fulmar, *Fulmarus glacialisoides*, in Terre Adélie, Antarctica, was very low during the 1975–1980 period, followed by high variability after 1980. The same pattern was observed in the number of birds which attempted to breed. In both cases, there was an association with sea ice cover. Juvenile survival rate was also low between 1975 and 1980, but not associated with climatic variables (Jenouvrier *et al.*, 2003). Barbraud & Welmerskirch (2001) also documented effects on adult emperor penguins (*Aptenodytes forsteri*) in the same Antarctic area. The breeding population of these penguins remained stable until the mid-1970s then declined sharply to 50% toward the end of that decade due to a high

mortality of adults. The decline in adult survival coincided with an extended period of abnormal warm temperatures and a reduced extension of sea ice.

A similar trend to that found in emperor penguins was observed for Weddell seals (*Leptonychotes weddelli*), which showed a decline in the number of individuals between 1973 and 1978. Habitat requirements and feeding behavior are similar in the two species (Ainley *et al.*, 2005). In the same study, an increase in the population of Adelia penguins (*Pygoscelis adeliae*) from 1980 was related to the SAM index. These examples indicate environmental changes in the marine ecosystem, with intensity strong enough to produce responses in different species of top predators in the area.

Given that dentinal anomalies are produced as a response to different stress factors (Lockyer, 1993, 1995), it is not possible, at present, to determine which mechanisms in the environment influence the deposition of anomalous dentine in Commerson's dolphin teeth from Tierra del Fuego. Part of this uncertainty could be answered by determining the presence (or absence) of dentinal anomalies during the same period for other species of subantarctic toothed whales and pinnipeds, with the same (or different) ecological role.

Growth

Differences in the growth model parameters obtained in the present study were not significant between specimens with and without dentinal anomalies, but the values were higher in individuals with non-anomalous patterns in all their GLGs. Given that the frequency of anomalous GLGs corresponded to the period with highest growth in marine mammals (Laws, 1959), the lower growth rate in animals with one or more anomalous GLGs could indicate an effect on growth detectable with a larger sample size.

Correlations between tooth growth and animal growth were found in Antarctic fur seals from South Georgia and individuals with lower growth rates had lower survival rates (Boyd & Roberts, 1993). Also, these authors observed significant variation in the width of the GLGs depending on the deposition year, which suggests that the growth had been higher in some years than others. Variations in growth were positively related to SOI. Years in which male tooth growth was lower were also years in which reproduction rate, survival rate of newborns, and growth rate of newborns during lactation had also been low in the colony (Boyd & Roberts, 1993).

In the present study it was not possible to directly evaluate the effects of climate on individual growth of Commerson's dolphins. However, we can make indirect inferences if we consider the effects on dentinal anomalies.

The presence of these anomalies was associated with the SAM, being less frequent with positive values of the index. Considering that specimens that had anomalous dentine in one or more of their GLGs tended toward lower growth rates, we would expect that Commerson's dolphin of Tierra del Fuego may show slower growth during years with more negative values of SAM. However, these inferences should be taken with caution since other factors which might affect growth have not been investigated in this study.

Biological recording structures as indicators of climate change effects

Effects of climate change on marine mammals have primarily focused on changes in distribution (e.g., MacLeod *et al.*, 2005; Salvadeo *et al.*, 2010), abundance (Siniff *et al.*, 2008), prey availability, body condition (Stirling *et al.*, 2008), recruitment (Ferguson *et al.*, 2005), and fecundity or juvenile survival (Greene & Pershing, 2004; Forcada *et al.*, 2005). Detecting changes in these parameters requires having baseline or sufficient historical data for the change to be detectable. For poorly known species, for which it is also a challenge to collect the necessary data, determining whether or not climate change is having an adverse effect may require other than traditional indicators (e.g., Newsome *et al.*, 2009).

Permanent recording structures, such as teeth, may provide a cost-effective mechanism for detecting the effects of climate on long lived, difficult to study marine species because they contain an archival record of past conditions. In addition, the ability to obtain ages for individuals from those teeth provides the opportunity to back calculate to year of birth and, in this case, to the year and age of deposition of anomalous or non-anomalous dentine. For this study, we examined specific anomalous characteristics in Commerson's dolphin teeth. Additional anomalies have been identified in other species, such as the hypocalcified mark in dusky dolphins (Manzanilla, 1989), dentinal resorption in harbor porpoises (*Phocoena phocoena*; Luque *et al.*, 2009), and other mineralization interference (e.g., pilot whales, *Globicephala* sp. (Lockyer, 1993) that may correlate with climate events or local environmental factors.

This study represents the first evidence of effects of SAM on marine mammals and the first assessment of the effect of climatic oscillations on a top predator species in the Tierra del Fuego and Magellan regions. Although not conclusive, our results suggest that climate influences somatic growth rates, albeit the specific nature of the effects on the Commerson's dolphin population off Tierra del Fuego remains unclear and deserves additional research. Examining the effects of climate change on Commerson's dolphin could also

help our understanding of general changes in subantarctic ecosystems since top predators might amplify those effects via trophic dynamics.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary of the 10 best models for evaluating the influence of calendar year and environmental variables on the presence of dentinal anomalies in teeth from Commerson's dolphins, *Cephalorhynchus c. commersonii*.

Table S2. Summary of the 10 best models for evaluating the influence of calendar year and environmental variables on the proportion of dentinal anomalies in teeth from Commerson's dolphins, *Cephalorhynchus c. commersonii*.

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