Changes in tooth size of *Otaria flavescens*: an indicator of density-dependent effects? (#108774)

First submission

Guidance from your Editor

Please submit by **12 Dec 2024** for the benefit of the authors (and your token reward) .

✓ **Structure and Criteria**
Please read the 'Structure and Criteria' page for guidance.

Author notes
Have you read the author notes on the guidance page?

Raw data check
Review the raw data.

Image check
Check that figures and images have not been inappropriately manipulated.

If this article is published your review will be made public. You can choose whether to sign your review. If uploading a PDF please remove any identifiable information (if you want to remain anonymous).

Files Download and review all files from the materials page.	5 Figure file(s) 1 Table file(s) 2 Raw data file(s) 1 Other file(s)

Structure and Criteria

Structure your review

The review form is divided into 5 sections. Please consider these when composing your review:

1. **BASIC REPORTING**
2. **EXPERIMENTAL DESIGN**
3. **VALIDITY OF THE FINDINGS**
4. General comments
5. Confidential notes to the editor

You can also annotate this PDF and upload it as part of your review

When ready submit online.

Editorial Criteria

Use these criteria points to structure your review. The full detailed editorial criteria is on your guidance page.

BASIC REPORTING

- ✓ Clear, unambiguous, professional English language used throughout.
- ✓ Intro & background to show context. Literature well referenced & relevant.
- ✓ Structure conforms to PeerJ standards, discipline norm, or improved for clarity.
- ✓ Figures are relevant, high quality, well labelled & described.
- ✓ Raw data supplied (see PeerJ policy).

EXPERIMENTAL DESIGN

- ✓ Original primary research within Scope of the journal.
- ✓ Research question well defined, relevant & meaningful. It is stated how the research fills an identified knowledge gap.
- ✓ Rigorous investigation performed to a high technical & ethical standard.
- ✓ Methods described with sufficient detail & information to replicate.

VALIDITY OF THE FINDINGS

- ℹ **Impact and novelty is not assessed.** Meaningful replication encouraged where rationale & benefit to literature is clearly stated.
- ✓ All underlying data have been provided; they are robust, statistically sound, & controlled.
- ✓ Conclusions are well stated, linked to original research question & limited to supporting results.

Standout reviewing tips

The best reviewers use these techniques

Tip	*Example*
Support criticisms with evidence from the text or from other sources	*Smith et al (J of Methodology, 2005, V3, pp 123) have shown that the analysis you use in Lines 241-250 is not the most appropriate for this situation. Please explain why you used this method.*
Give specific suggestions on how to improve the manuscript	*Your introduction needs more detail. I suggest that you improve the description at lines 57- 86 to provide more justification for your study (specifically, you should expand upon the knowledge gap being filled).*
Comment on language and grammar issues	*The English language should be improved to ensure that an international audience can clearly understand your text. Some examples where the language could be improved include lines 23, 77, 121, 128 – the current phrasing makes comprehension difficult. I suggest you have a colleague who is proficient in English and familiar with the subject matter review your manuscript, or contact a professional editing service.*
Organize by importance of the issues, and number your points	*1. Your most important issue* *2. The next most important item* *3. …* *4. The least important points*
Please provide constructive criticism, and avoid personal opinions	*I thank you for providing the raw data, however your supplemental files need more descriptive metadata identifiers to be useful to future readers. Although your results are compelling, the data analysis should be improved in the following ways: AA, BB, CC*
Comment on strengths (as well as weaknesses) of the manuscript	*I commend the authors for their extensive data set, compiled over many years of detailed fieldwork. In addition, the manuscript is clearly written in professional, unambiguous language. If there is a weakness, it is in the statistical analysis (as I have noted above) which should be improved upon before Acceptance.*

Changes in tooth size of *Otaria flavescens*: an indicator of density-dependent effects?

Ailin Sosa Drouville Corresp., [1] , **Federico Heredia** [2] , **Mariano Coscarella** [2, 3] , **Enrique Crespo** [2, 3] , **María Florencia Grandi** [2]

[1] Instituto de Biología de Organismos Marinos (Consejo Nacional de Investigaciones Científicas y Técnicas), Puerto Madryn, Argentina
[2] Centro para el Estudio de Sistemas Marinos (Consejo Nacional de Investigaciones Científicas y Técnicas), Puerto Madryn, Argentina
[3] Universidad Nacional de la Patagonia San Juan Bosco, Puerto Madryn, Argentina

Corresponding Author: Ailin Sosa Drouville
Email address: ailinsosad@gmail.com

Teeth provide valuable information about an individual’s life cycle and serve as a powerful tool for visualizing population-level changes associated with density-dependent processes. In pinnipeds, teeth are used to estimate the age of individuals based on the count of growth layer groups (GLG) in the dentine.In this study, we analyzed changes in tooth size and GLG widths in the canines of*Otaria flavescens*throughout the past 100 years, linking these to fluctuations in population abundance. A total of 76 male individuals from Patagonia were analyzed, classified into two periods: harvest and postharvest.The length and diameter of each tooth were measured prior to sagittal sectioning. Only for the postharvest period body length was recorded. Longitudinal sections of the upper canine were prepared, age was determined and the width of each GLG was measured in the resulting half-tooth. Results indicated that a positive correlation (F = 62.90; $p < 0.001$; n = 50; r^2= 0.59) between body length and tooth length in postharvest individuals, suggesting that tooth growth is a reliable indicator of body growth. Individuals from the harvest period had narrower GLGs (t = 3.75; $p < 0.001$) and smaller tooth size (t = 3.48; $p < 0.001$) compared to those from the postharvest period. These results indicate that somatic growth of individuals may vary with population numbers and resources available. Also, that hard structures like teeth are excellent tools for visualizing density-dependence effects.

Changes in tooth size of *Otaria flavescens*: an indicator of density-dependent effects?

Sosa Drouville A.(1)*, Heredia F.(2), Coscarella M.(2,3), Crespo E. A.(2,3), Grandi M. F.(2)

(1) Instituto de Biología de Organismos Marinos (IBIOMAR-CONICET), Puerto Madryn, Argentina.
(2) Laboratorio de Mamíferos Marinos, CESIMAR-CONICET, Puerto Madryn, Chubut, Argentina.
(3) Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Puerto Madryn, Chubut, Argentina.

* Corresponding Author: ailinsosa@cenpat-conicet.gob.ar

Abstract

Teeth provide valuable information about an individual's life cycle and serve as a powerful tool for visualizing population-level changes associated with density-dependent processes. In pinnipeds, teeth are used to estimate the age of individuals based on the count of growth layer groups (GLG) in the dentine. In this study, we analyzed changes in tooth size and GLG widths in the canines of *Otaria flavescens* throughout the past 100 years, linking these to fluctuations in population abundance. A total of 76 male individuals from Patagonia were analyzed, classified into two periods: harvest and postharvest. The length and diameter of each tooth were measured prior to sagittal sectioning. Only for the postharvest period body length was recorded. Longitudinal sections of the upper canine were prepared, age was determined and the width of each GLG was measured in the resulting half-tooth. Results indicated that a positive correlation ($F = 62.90$; $p < 0.001$; $n=50$; $r^2= 0.59$) between body length and tooth length in postharvest individuals, suggesting that tooth growth is a reliable indicator of body growth. Individuals from the harvest period had narrower GLGs ($t = 3.75$; $p < 0.001$) and smaller tooth size ($t = 3.48$; $p < 0.001$) compared to those from the postharvest period. These results indicate that somatic growth of individuals may vary with population numbers and resources available. Also, that hard structures like teeth are excellent tools for visualizing density-dependence effects.

Keywords: density-dependence, *Otaria flavescens*, pinnipeds, South American sea lion, teeth

Introduction

Density-dependent is a mechanism that occurs in K strategist species and is noted or measured when population abundance approaches carrying capacity (McLaren & Smith 1985). The changes caused by density-dependent occur dramatically and can be seen in a relatively short time (Fowler 1981; Lima 1995). Density-dependent regulation can generate physiological or behavioral changes in individuals within a population (Fowler 1990). In particular, hard structures like teeth provide information about individual's life cycle and are powerful tools for visualizing population-level changes associated with density-dependent processes.

Age determination of individuals is one of the most important parameters for studying the population dynamics of mammals (McLaren & Smith 1985; Scheffer & Myrick 1980). In the past, several methods have been used to estimate the approximate age of individuals, such as body length, lens weight, cranial sutures, tooth wear, and corpora albicantia count (McLaren & Smith 1985). However, none of these techniques provided precise information on the age of an individual (Scheffer & Myrick 1980). Since the 1950s, pinniped teeth have been used to estimate ages by counting growth layer groups (GLGs) found in the dentine and/or the cement (Scheffer 1950). This technique is mostly used in marine mammals as it provides more accurate information on the chronological age of the individual (Crespo 1988; Laws 1952, 1953; Loza et al. 2016; Read et al. 2018; Scheffer 1955).

In pinnipeds, it is generally assumed that one GLG corresponds to the amount of tissue accumulated during a year of life. In tooth-thin sections observed with transmitted light, a GLG is composed of a thin, clear band and a broader, opaque band (valley and ridge, respectively, in acid-etched sections of half-tooth) (Crespo 1988; Crespo et al. 1994; Laws 1952, 1953, 1962; Scheffer 1955). The opaque bands correspond to the feeding period, and the light bands correspond to the fasting season usually associated with the reproductive season (Crespo 1988). The deposition of a GLG can be modified by physiological events such as pregnancy, lactation, weaning, fasting, moulting, and sexual maturity (Bengtson 1988; Boyd & Roberts 1993; Mansfield 1991) or by extreme climatic conditions (Heredia et al. 2021; Dellabianca et al. 2012; Wittmann et al. 2016).

The dentine of pinnipeds, like that of other mammals, is composed of 35% organic components mainly collagen fibers and mucopolysaccharides, and 65% inorganic components, including hydroxyapatite and small amounts of zinc, strontium, fluorine, magnesium, manganese, lead, iron and tin (Klevezal et al. 1996). Dentine is formed by the activity of cells called odontoblasts, which are located in the wall of the pulp cavity (Klevezal et al. 1996). Particularly, dentine presents a high sensitivity to diet changes, and the mineralization process of GLGs depends on the contribution of vitamins and minerals ingested with food (Klevezal et al. 1996; Laws 1962). Consequently, the physiological mechanisms of mineralization can be affected by a nutritional deficit, leading to sparse deposition of minerals that structure the GLG (Boyd & Roberts 1993; Hanson et al. 2009; Klevezal et al. 1996; Knox et al. 2014; Wittmann et al. 2016). Since GLGs are deposited from the pulp cavity, it is important to consider the normal progressive decrease in the width of the GLG with the age of the animal before relating this information to food availability or growth (Boyd & Roberts 1993). Therefore, the various events throughout an individual's life cycle are reflected in the dentine deposits on their teeth. This could generate patterns in the tooth growth that could reflect the life history of the individual (Boyd & Roberts 1993; Newsome et al. 2006, 2007).

The South American sea lion (SASL, *Otaria flavescens*) population from Patagonia has experienced a drastic reduction in size over a relatively short period and then began a slow recovery after sealing ended (Crespo & Pedraza 1991; Dans et al. 2004; Grandi et al. 2015; Reyes et al. 1999; Romero et al. 2017). In Argentina, large scale commercial sealing of SASL began in 1917 and ended in 1962 (Romero et al. 2017). Skin and blubber were used for leather, fur and oil production, and the remains of the animals were discarded on the coast, generating ossuaries near the factories (Bastida 1963; Carrara 1952; Crespo & Pedraza 1991). Península Valdés (in northern Patagonia), Tierra del Fuego and Malvinas Islands supported the most heavily exploited stocks of the Atlantic Ocean (Romero et al. 2017, Baylis et al. 2015). The northern and central Patagonian population dropped drastically from an estimated 440,000 individuals in the preharvest period to 20,000 individuals in a few years, a reduction of more than 90% of its original abundance (Romero et al. 2017). After the harvest ceased, the population reached its minimum abundance and then began to recover (Romero et al. 2017). Romero et al. (2017) observed that populations of SASL have a nonlinear relationship with density, assuming an "overcrowding" or compensatory density-dependent process that affects the population growth rate at high densities. These changes in abundance over time provide a favorable scenario for testing possible changes related to density-dependent phenomena. Before the commercial harvest, SALS abundance was probably in equilibrium with the *per capita* food availability in the environment, resulting in individuals of a certain body size. At the end of the harvest, population density was so low that individuals likely had greater *per capita* food availability that ultimately would lead to a larger body size.

The variation in individual size could also be related to the reaction norm of the genotype. Norm of reaction represents the range of phenotypic variation produced by a genotype in response to environmental variation (Woltereck 1909). Studying reaction norms is important for understanding various aspects of phenotypic evolution (Bhumika & Singh 2019). Phenotypic plasticity is defined as the ability of a particular genotype to produce more than one phenotype in response to changing environmental conditions such as temperature, population density, nutrition, etc. (Yang & Pospisilik 2019). Phenotypic plasticity provides species with the ability to facilitate adaptive changes and increase phenotypic diversity, thereby enabling them to better cope with environmental changes (Yang & Pospisilik, 2019). In this context, it is expected that individual growth will be reflected in teeth growth pattern, which could be modified over time due to density-dependent effects and the norm of reaction of the genotype.

Therefore, the objective of this work was to analyze potential changes in the upper canines of male *Otaria flavescens* related to changes in population abundance over the past 100 years.

Materials and methods

Sample and study area

A total of 76 upper canine teeth of male SASL from northern and central Patagonia were analyzed (Fig. 1). The sample belongs to the Osteological Marine Mammal Scientific Collection of CESIMAR - CONICET, Argentina (Table S1).

Individuals were classified into periods according to their time of death: harvest (1917-1962) and postharvest (1963-2017). The individuals from the harvest period ($n = 26$) corresponded to the sealing time when population abundance was high and presumably at carrying capacity. These individuals were obtained from the ossuary at Punta Norte (42°04´S, 63°45´W), Península Valdés, Argentina (Fig. 1). The postharvest period includes individuals (*n* = 50) found dead on the coasts or incidentally caught in commercial trawl fisheries in northern and central Patagonia (Fig. 1). Only sub-adult and adult individuals (*i.e*., older than 4 years are sexually mature, Grandi et al. 2010) were selected to avoid differences related to ontogeny.

Data collection and tooth preparation

The length (L) and diameter (D) of each tooth were measured using a digital caliper (Mitutoyo, minimum value 0.01 mm), before sagittal sectioning. For the postharvest period, body length (Standard Length, LS) was recorded using a measuring tape (minimum measurement 1 mm). Subsequently, upper canines were sagittally sectioned through the center of the pulp cavity with a handsaw. The best half-tooth was selected, polished, and etched in 5% nitric acid. Each half-tooth was then rinsed, dried at room temperature, and rubbed with acetone to enhance GLG contrast (Fig. 2) (Crespo et al. 1994).

The inner surface of the half-teeth was photographed using a Cannon Rebel camera. Two observers independently counted the number of GLGs on each half-tooth in different reading sessions, and final age assignments were based on consensus (Table S1). Then GLG width was measured in the dentine using Leica Application Suite V3.4.0 software, which allowed for plotting lines on the edge of each GLG and measuring width considering the scale of the photograph. Measurements were taken on the polished surface of the most concave side of half-tooth (Fig. 2), from the neonatal line (*i.e.,* the line laid at birth) to the pulp cavity in a staggered manner (Fig. 2). As GLG width varies throughout its entire path, the measurements were taken in the most stable width area (*i.e*., the central area of the tooth). Measurements of the first GLG were excluded from the sample, since they presented high variability.

Data analysis

To study the relationship between tooth length (L) and individual size (LS), linear regression was performed to analyze whether tooth size is a good proxy of body size. This was done using postharvest individuals, as body length data from the harvest period individuals were unavailable. *T*-Student analyses were conducted to evaluate differences in tooth length (L) and diameter (D) between the harvest and postharvest periods.

Generalized linear mixed models with a normal error distribution were used to assess whether there were differences in the width of the growth layers (GLGW) between periods. The response variable, GLGW, was modeled using two predictor variables: the period as a categorical variable (harvest and postharvest) and n°GLG as a continuous variable (which is the number of each growing layer). Individual id was used as a random covariable. Two of the most suited autocorrelation structures were used to model the temporal dependence of the response variable within each tooth. The gls function from the "MASS" library (Venables & Ripley 2002) and the lme function of the "nlme" v. 3.1-127 package (Pinheiro & Bates 2000) were implemented with R (R Core Team 2017). The modelling procedures followed Zuur et al. (2009), and models were selected using the Akaike Information Criterion (AIC) (Zuur et al. 2009).

Results

The body length and tooth length in individuals from the postharvest period showed a significant linear regression ($F = 62.90$; $p < 0.001$; $n = 50$; $r^2 = 0.59$), suggesting that tooth growth is a good indicator of body growth (Fig. 3). Additionally, there were differences in tooth length (L) and diameter (D) between harvest and postharvest period, with teeth from the harvest period being significantly shorter ($t = 3.48$; $p < 0.001$; Fig. 4) and thinner ($t = 3.75$; $p < 0.001$; Fig. 4) compared to those from the postharvest period.

The best models are presented in terms of ΔAIC (Table 1), and as a rule of thumb values that are less than two should be given consideration as the selected model (Burnham & Anderson 2004). The Akaike Information Criterion (AIC) favours Model 4, as shown in Table 1. Model 4 includes the predictor variables: period (harvest, post-harvest), n°GLG, individual as a random effect, and an AR1 temporal autocorrelation structure (Table 1). All variables were significant.

The model results indicated that individuals from the harvest period had smaller GLG widths compared to those from the postharvest period (Fig. 5). Additionally, the models slopes are equal, showing that the decrease in the width of the growth layers was the same in both periods.

Discussion

This study demonstrates that the growth of canine teeth is a good indicator of body growth of individuals. The results suggest the existence of a density-dependent response in tooth growth of males SASL of Patagonia, Argentina. GLGs were found to be thinner in individuals from the harvest period, compared to post-harvest individuals, likely due to higher population density in sealing time. Additionally, teeth from the harvest period were thinner and shorter than those from the post-harvest period, indicating changes in somatic growth over time. In turn, the results also suggest that a lesser amount of dentine (i.e. narrower GLG) was deposited in each calendar year in individuals from the harvest period compared to post-harvest individuals.

Changes in population abundance have a significant impact on individual growth. These changes are often related to density-dependent processes that produce physiological or behavioral changes in individuals of a population (Fowler 1990). Therefore, differences in GLG width and tooth size between the two time periods are likely related to changes in *O. flavescens* population abundance. Before commercial harvesting, the population of northern and central Patagonia was estimated at 440,000 individuals (Romero et al. 2017). At its height, intraspecific competition would have been the highest, leading to a lower *per capita* intake, likely investing more energy in searching for food, consuming a smaller amount of prey *per capita* and/or prey of lower nutritional quality. This results in lesser dentine deposits in GLGs and could be ultimately reflected in lower somatic growth (Sosa Drouville et al. 2021). On the contrary, when the population declined, the intraspecific competition was lower, leading to an increase in dentine deposits thickness and larger somatic growth.

Dietary changes caused by density-dependent factors may be reflected in the physical condition of individuals and their somatic growth (Trites & Bigg 1992; Sosa Drouville et al. 2021). The results obtained are consistent with findings in other studies (Boyd & Roberts 1993; Etnier 2004; Hanson et al. 2009; Sosa Drouville et al. 2021; Scheffer 1955). For example, the northern fur seal, *Callorhinus ursinus*, shows a decrease in body size with increased population size (Etnier 2004; Scheffer 1955). In the *Arctocephalus gazella* population from South Georgia Islands, GLG width decreased with increased population density (Boyd & Roberts 1993). A decline in annular tooth growth was observed in male Antarctic fur seal, *A. gazella*, from South Georgia as a consequence of rapid population growth (Hanson et al. 2009).

In pinnipeds, there are marked intra-specific differences in feeding patterns. Diving skills, dive duration, dive depth, distance to shore, and swimming speed increase with age and are acquired progressively throughout their lives (Bekkby & Bjørge 2000; Costa 1991; Chilvers et al. 2005, 2006; Horning & Trillmich 1997). Hence, an increase in population abundance likely increases prey consumption near colonies, leading to higher intraspecific competition (Drago et al. 2010, 2011). Females are particularly affected due to the constrains of raising pups, especially during the early lactation period when foraging trips are restricted in distance and duration by the fasting ability of pups (Drago et al. 2010; Riet-Sapriza et al. 2013). Suboptimal maternal nutrition may result in lower offspring somatic growth and smaller GLG width during lactation. Pups likely spend their early years feeding in areas surrounding the colony with short foraging trips. Drago et al. (2011) found that *O. flavescens* pups grew slower in more abundant colonies than in smaller ones, and this may be due to lower *per capita* food availability for females. Therefore, if food is a limiting factor in the feeding areas near the colony, there may be a nutritional deficit that could be reflected in tooth growth and GLG composition by poor mineral deposition. In this study, we found that males of *O. flavescens* exhibit the same pattern that would be expected for females that feed near the colonies, even though the males feed further away (Koen Alonso et al. 2000; Campagna et al. 2001). This could be the result of an onset effect due to insufficient nutrition during the lactating period, which affects the male's development throughout its life, higher competition in the feeding grounds despite being further away, or a combination of both (Sosa Drouville 2023).

Differences found in tooth size between the two periods may also be related to the Norm of reaction of the genotype, producing different phenotypes under a gradient of environmental conditions such as population abundance, diet, and behavioral changes (Forsman 2015). Genes that code for tooth growth can have different phenotypic outputs that can be influenced by environmental conditions. Optimal environmental conditions yield maximum growth values, while suboptimal conditions result in minimum value (Woltereck 1909). Therefore, we propose that the difference in tooth size observed in the present work could likely due to the intense intraspecific competition generated by the high population density during the harvest period, preventing teeth from reaching their maximum growth potential determined by the genotype of the species.

Tooth structure can also provide powerful and relevant information about individual and population life history. The upper canines of SASL males are large and robust, with clearly visible GLGs in the dentine. Pinniped growth patterns reflect species characteristics and environmental features (McLaren & Smith 1985). Climate patterns can have a great impact on the somatic growth of individuals and may affect the availability of resources in the environment (Heredia et al. 2021; Sielfeld et al. 2018; Sprogis et al. 2018). For example, SASL population in Chile alters their diet during El Niño-Southern Oscillation (ENSO) events, leading to nutritional stress and affecting somatic growth, survival rates, birth rates, and increased susceptibility to disease (Sielfeld et al. 2018). Another example in Patagonia, SASL female GLG width was influenced by the Southern Annular Mode (SAM) climate pattern (Heredia et al. 2021). Regarding SASL males from Patagonia, there was no alteration in GLGs growth associated with SAM or ENSO (Heredia et al. 2021).

On the other hand, changes in the diet of a species or changes in prey availability are often associated with industrial fishing and could generate an impact in the somatic growth (Crespo et al. 1997; Dans et al. 2003). In the Argentine Sea, fishing activity targeting hake (*Merluccius hubbsi*), shrimp (*Pleoticus muelleri*) and squid (*Illex argentinus*) increased considerably since the 1970s (Bertolotti et al. 2001; Bezzi & Dato 1995; Brunetti 1990), leading to the decline of several stocks due to over-exploitation by the 2000s (Cordo 2004). These species are the main prey in the diet of SASL (Koen Alonso et al. 2000; Sosa Drouville 2023), making the fishing industry a crucial factor affecting food availability from the post-harvest period.

This study covers over 100 years of the life history of the northern and central Patagonian sea lion population, confirming that hard structures like teeth are excellent tools for visualizing the effects of density-dependence. Teeth degrade slowly, making them ideal for studying long-term changes in individual and population life histories.

Acknowledgments

We wish to express our gratitude to the staff of the Administración de Parques Nacionales, Dirección de Fauna y Flora Silvestre of Chubut and Secretaría de Ambiente y Cambio Climático of Río Negro, for permits to conduct research in protected areas. This research was funded by the Agencia Nacional de Promoción Científica y Tecnológica (PICTs 2110, 33934, 11679, 2063), Amnéville zoo France (2004-2020), the Mohamed Bin Zayed species conservation fund (2011-2014), Yaqupacha, Heidelberg zoo (2012), BBVA (BIOCON_08, 2009-2012) and CONICET (PIP 0111/2016), granted to EAC. Additionally, by The Explorers Club (granted to ASD).

References

Bastida, R., 1963. Algo sobre los carnívoros marinos. *Revista Diana*. Buenos Aires, 45.

Baylis, A. M., Orben, R. A., Arnould, J. P., Christiansen, F., Hays, G. C., & Staniland, I. J. 2015. Disentangling the cause of a catastrophic population decline in a large marine mammal. *Ecology*, *96*(10), 2834-2847.

Bekkby, T. & Bjørge, A., 2000. Diving behaviour of harbour seal *Phoca vitulina* pups from nursing to independent feeding. *Journal of Sea Research* 44(3-4):267-275.

Bengtson, J., 1988. Long-term trends in the foraging patterns of female Antarctic fur seals at South Georgia. *Antarctic Ocean and Resources Variability*. Springer, 286-291.

Bertolotti, M. I., Verazay, G. A., Errazti, E., Pagani, A. N., Buono, J. J. & Akselman, R., 2001. Flota pesquera argentina. Evolución durante el período 1960-1998, con actualización al 2000. *El Mar Argentino y sus Recursos Pesqueros* 3:9-53.

Bezzi, S. I. & Dato, C. V., 1995. Conocimiento biológico pesquero del recurso merluza (*Merluccius hubbsi*) y su pesquería en la República Argentina. *Revista de Investigación y Desarrollo Pesquero (INIDEP) N°4: 1-52*.

Bhumika, & Singh, A. K., 2019. Patterns of morphological divergence in fruit fly: Response to nutritional variations through changes in allometric relationships and trait sizes. *Journal of Zoology*, 309(1), 22–34.

Boyd, I. & Roberts, J., 1993. Tooth growth in male Antarctic fur seals (*Arctocephalus gazella*) from South Georgia: an indicator of long-term growth history. *Journal of Zoology* 229(2):177-190.

Brunetti, N. E., 1990. Evolución de la pesquería de *Illex argentinus* (Castellanos, 1960). Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), 1-19.

Burnham, K. P. & Anderson, D. R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33(2):261-304.

Cabrera, A., 1940. Notas sobre carnívoros sudamericanos [Notes on South American carnivores]. *Notas del Museo de La Plata* (Zoología), 5(29), 1–22.

Carrara, I. S., 1952. Lobos marinos, pingüinos y guaneras, de las costas del litoral marítimo e islas adyacentes de la República Argentina. *Facultad de ciencia veterinarias, Universidad Nacional de La Plata, 1-16.*

Cordo, H., 2004. Evaluación del estado del efectivo sur de 41°S de la merluza (*Merluccius hubbsi*) y estimación de la captura biológicamente aceptable correspondiente al año 2004. *Revista de Investigación y Desarrollo Pesquero (INIDEP)* N°17/04.

Costa, D. P., 1991. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. *The behaviour of pinnipeds*. American Zoologist, (31):111-130.

Chilvers, B. L., Wilkinson, I. S., Duignan, P. J. & Gemmell, N. J., 2005. Summer foraging areas for lactating New Zealand sea lions *Phocarctos hookeri*. *Marine Ecology Progress Series* 304:235-247.

Chilvers, B., Wilkinson, I., Duignan, P. & Gemmell, N., 2006. Diving to extremes: are New Zealand sea lions (*Phocarctos hookeri*) pushing their limits in a marginal habitat? *Journal of Zoology* 269(2):233-240.

Crespo, E. A., 1988. Dinámica poblacional del lobo marino de un pelo *Otaria flavescens* (Shaw, 1800), en el norte del Litoral Patagónico. Tesis Doctoral, Universidad de Buenos Aires, Argentina.

Crespo, E. A. & Pedraza, S. N., 1991. Estado actual y tendencia de la población de lobos marinos de un pelo (*Otaria flavesces*) en el litoral norpatagónico. *Ecología Austral* 1(02):087-095.

Crespo, E., Schiavini, A., Pérez Macri, G., Reyes, L. & Dans, S., 1994. Estudios sobre determinación de edad en mamíferos marinos del Atlántico Sudoccidental. *IV Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur*: 31-55.

Crespo, E. A., Pedraza, S. N., Dans, S. L., Koen Alonso, M., Reyes, L. M., García, N. A., Coscarella, M. & Schiavini, A. C., 1997. Direct and indirect effects of the high seas fisheries on the marine mammal populations in the northern and central Patagonian coast. *Journal of Northwest Atlantic Fishery Science* 22:189-207.

Dans, S. L., Koen Alonso, M., Crespo, E. A., Pedraza, S. N. & García, N., 2003. Interactions between marine mammals and high seas fisheries in Patagonia: an integrated approach. *Marine mammals: fisheries, tourism and management issues.* (Gales, Hindell, Kirkwood eds), CSIRO Publishing, Collingwood, 100-115.

Dans, S.L., Crespo, E.A., Pedraza, S.N. & Koen Alonso, M., 2004. Recovery of the south american sea lion population in northern Patagonia. Canadian J. Fisheries and Aquatic Science. 61:1681-1690.

Dellabianca, N. A., Hohn, A. A., Goodall, R. N. P., Pousa, J. L., MacLeod, C. D. & Lima, M., 2012. Influence of climate oscillations on dentinal deposition in teeth of Commerson's dolphin. *Global Change Biology* 18(8):2477-2486.

Drago, M., Cardona, L., Crespo, E. A., García, N., Ameghino, S. & Aguilar, A., 2010. Change in the foraging strategy of female South American sea lions (Carnivora: Pinnipedia) after parturition. *Scientia Marina* 74(3):589-598.

Drago, M., Cardona, L., García, N., Ameghino, S. & Aguilar, A., 2011. Influence of colony size on pup fitness and survival in South American sea lions. *Marine Mammal Science* 27(1):167-181.

Etnier, M. A., 2004. Reevaluating evidence of density-dependent growth in northern fur seals (*Callorhinus ursinus*) based on measurements of archived skeletal specimens. *Canadian Journal of Fisheries and Aquatic Sciences* 61(9):1616-1626.

Fowler, C. W., 1981. Density dependence as related to life history strategy. *Ecology 62(3):602-610.*

Fowler, C. W., 1990. Density dependence in northern fur seals (*Callorhinus ursinus*). *Marine Mammal Science* 6(3):171-195.

Forsman, A., 2015. Rethinking phenotypic plasticity and its consequences for individuals, populations and species. *Heredity 115*(4), 276-284.

Grandi, M. F., Dans, S. L., García, N. A., & Crespo, E. A., 2010. Growth and age at sexual maturity of South American sea lions. *Mammalian Biology*, 75(5), 427-436.

Grandi, M. F., Dans, S. L., & Crespo, E. A., 2015. The recovery process of a population is not always the same: The case of *Otaria flavescens*. *Marine Biology Research*, 11(3), 225-235.

Hanson, N. N., Wurster, C. M., Bird, M. I., Reid, K. & Boyd, I. L., 2009. Intrinsic and extrinsic forcing in life histories: patterns of growth and stable isotopes in male Antarctic fur seal teeth. *Marine Ecology Progress Series* 388:263-272.

Heredia, F. M., Sosa Drouville, A., Srur, A. M., Crespo, E. A. & Grandi, M. F., 2021. Climate anomalies influence tooth growth patterns of South American sea lion. *Marine Mammal Science, (1):1-15*.

Horning, M. & Trillmich, F., 1997. Ontogeny of diving behaviour in the Galapagos fur seal. *Behaviour* 134(15-16):1211-1257.

Klevezal, G. A., Mina, M. V. & Oreshkin, A., 1996. *Recording structures of mammals: determination of age and reconstruction of life history*. A. Balkema Publishers. London.

Koen Alonso, M., Crespo, E. A., Pedraza, S. N., Garcia, N. A. & Coscarella, M. A., 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin*, 98:250–263.

Knox, T. C., Stuart-Williams, H., Warneke, R. M., Hoskins, A. J. & Arnould, J. P., 2014. Analysis of growth and stable isotopes in teeth of male Australian fur seals reveals interannual variability in prey resources. *Marine Mammal Science* 30(2):763-781.

Laws, R., 1952. A new method of age determination for mammals. *Nature* 169(4310):972-973.

Laws, R., 1953. The seals of the Falkland Islands and Dependencies. *Oryx* 2(2):87-97.

Laws, R. M., 1962. Age determination of Pinnipedia with special reference to growth layers in the teeth. *Z Saugetierkunde* 27:129-146.

Lima, M., 1995. Regulación poblacional, denso-dependencia y métodos para su detección en series de tiempo. *Revista Chilena de Historia Natural* 68:251-269.

Loza, C. M., Soibelzon, L. H., Tarnawski, B. A., del Corrro, M. E., Negrete, J., & Ciancio, M., 2016. Determinación de edades en Otariidae y Phocidae (Carnivora) sobre piezas dentarias, técnicas alternativas. *Revista del Museo de la Plata*, *1*(1), 39-56.

Lucero, S., Rodríguez, S. M., Teta, P., Cassini, G., & D'elia, G., 2019. Solving a long-standing nomenclatorial controversy: Designation of a neotype for the southern sea lion *Otaria flavescens* (Shaw, 1800). *Zootaxa*, *4555*(2), 296-300.

Mansfield, A., 1991. Accuracy of age determination in the grey seal *Halichoerus grypus* of eastern Canada. *Marine Mammal Science* 7(1):44-49.

McLaren, I. A. & Smith, T. G., 1985. Population ecology of seals: retrospective and prospective views. *Marine Mammal Science* 1(1):54-83.

Newsome, S. D., Koch, P. L., Etnier, M. A. & Aurioles-Gamboa, D., 2006. Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Marine Mammal Science* 22(3):556-572.

Newsome, S., Etnier, M., Kurle, C., Waldbauer, J., Chamberlain, C. & Koch, P., 2007. Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: isotopic analysis of northern fur seal teeth. *Marine Ecology Progress Series* 332:211-224.

Pinheiro, J. C., & Bates, D. M., 2000. Linear mixed-effects models: basic concepts and examples. *Mixed-effects models in S and S-Plus*, 3-56.

R Core Team., 2017. R: A language and environment for statistical computing [Computer software]. R Foundation for Statistical Comput

Read, F. L., Hohn, A. A., & Lockyer, C. H., 2018. A review of age estimation methods in marine mammals with special reference to monodontids.

Reyes, L. M., Crespo, E. A. & Szapkievich, V., 1999. Distribution and population size of the southern sea lion (*Otaria flavescens*) in central and southern Chubut, Patagonia, Argentina. *Marine Mammal Science* 15(2):478-493.

Rice, D. W., 1998. Marine mammals of the world. Special Publication No. 4. *Society for Marine Mammalogy.*

Riet-Sapriza, F. G., Costa, D. P., Franco-Trecu, V., Marín, Y., Chocca, J., González, B., Beathyate, G., Chilvers, B. L. & Hückstadt, L. A., 2013. Foraging behavior of lactating South American sea lions (*Otaria flavescens*) and spatial–temporal resource overlap with the Uruguayan fisheries. *Deep Sea Research Part II: Topical Studies in Oceanography* 88:106-119.

Rodríguez, D. H., & Bastida, R. O., 1993. The southern sea lion, *Otaria byronia* or *Otaria flavescens*? *Marine Mammal Science*, 9(4), 372–381.

Romero, M. A., Grandi, M. F., Koen Alonso, M., Svendsen, G., Ocampo Reinaldo, M., García, N. A., Dans, S. L., González, R. & Crespo, E. A., 2017. Analysing the natural population growth of a large marine mammal after a depletive harvest. *Scientific Reports* 7(1):1-16.

Scheffer, V. B., 1950. Growth layers on the teeth of Pinnipedia as an indication of age. *Science* 112(2907):309-311.

Scheffer, V. B., 1955. Body size with relation to population density in mammals. *Journal of Mammalogy* 36(4):493-515.

Scheffer, V. B. & Myrick, A., 1980. A review of studies to 1970 of growth layers in the teeth of marine mammals. *Report Intternational Whaling Commnission* Special Issue3:51-63.

Sielfeld, W., Barraza, J. & Amado, N., 2018. Patrones locales de alimentación del león marino sudamericano *Otaria byronia*: el caso de Punta Patache, Norte de Chile. *Revista de Biología Marina y Oceanografía* 53(3):307-319.

Sosa Drouville, A., Paschetta, C., Crespo, E. A., & Grandi, M. F., 2021. Do changes in skull size of South American sea lions reflect changes in population density?. *Marine Mammal Science*, *37*(3), 934-948.

Sosa Drouville A., 2023. Evaluación de la respuesta denso-dependiente en lobos marinos comunes como consecuencia de cambios ocurridos en el ecosistema marino patagónico. Tesis Doctoral, Universidad Nacional del Comahue, Bariloche, Argentina.

Sprogis, K. R., Christiansen, F., Wandres, M. & Bejder, L., 2018. El Niño Southern Oscillation influences the abundance and movements of a marine top predator in coastal waters. *Global Change Biology* 24(3):1085-1096.

Trites, A. W. & Bigg, M. A., 1992. Changes in body growth of northern fur seals from 1958 to 1974: density effects or changes in the ecosystem?. *Fisheries Oceanography* 1(2):127-136.

Vaz Ferreira, R., 1982. '*Otaria flavescens* (Shaw), South Aoerican sea lion'. *Mammals in the Seas.* Fisheries Series 6:477-495.

Venables, W. N. & Ripley, B. D., 2002. Random and mixed effects Modern applied statistics with S. Springer, New York, 271-300.

Wittmann, T. A., Izzo, C., Doubleday, Z. A., McKenzie, J., Delean, S. & Gillanders, B. M., 2016. Reconstructing climate–growth relations from the teeth of a marine mammal. *Marine Biology* 163(4):1-11.

Woltereck, R., 1909. Weitere experimentelle Untersuchungen uber Artveranderung, speziell uberdas Wesen quantitativer Artunterschyiede bei Daphniden. *Verh. D. Tsch. Zool. Ges*, *1909*, 110-172.

Yang, C. H., & Pospisilik, J. A., 2019. Polyphenism – a window into gene-environment interactions and phenotypic plasticity. *Frontiers in Genetics*, 10, 132.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M., 2009. *Mixed effects models and extensions in ecology with R*, V. 574. Springer.

Figure 1

Figure 1: Study area indicating sampling locations of South American sea lions in northern and central Patagonia, Argentina (●) and Punta Norte ossuary (▲).

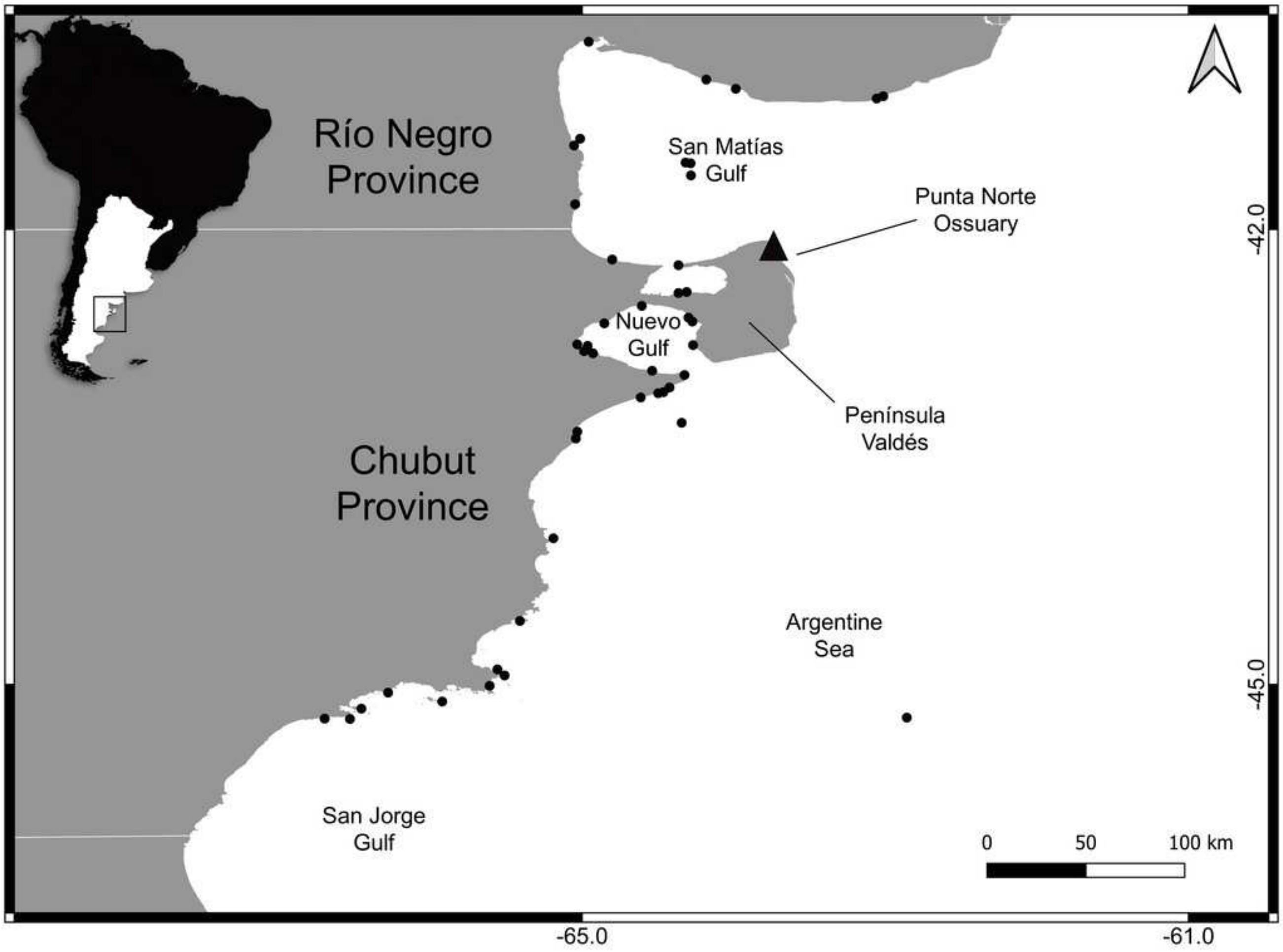

Figure 2

Figure 2: Sagittal section of the upper canine of a South American sea lion male. It is noted the pulp cavity, dentine, cement and enamel. In the dentine the GLGs are marked with graphite.

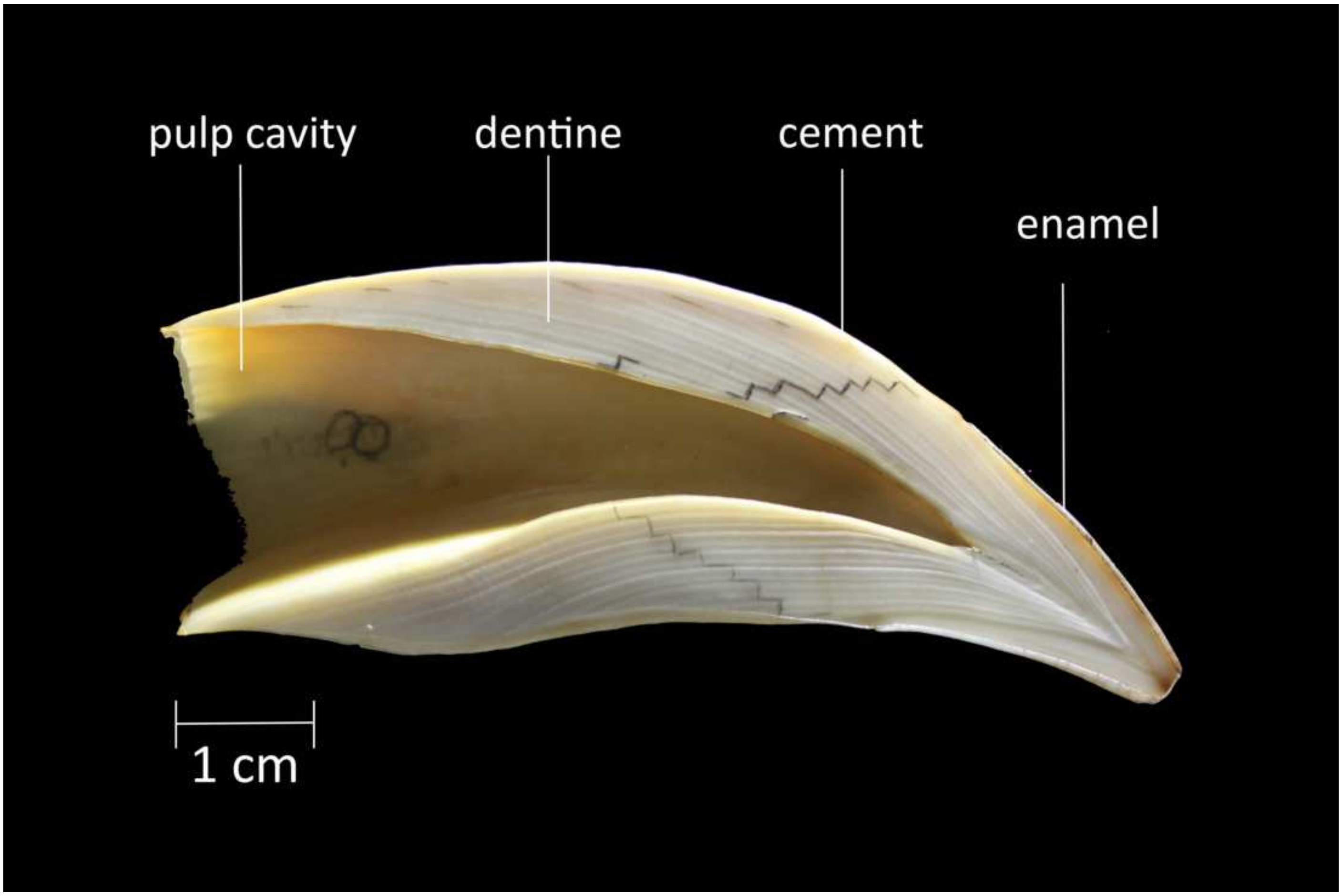

Figure 3

Figure 3: Scatter plot and linear regression between body length and tooth length of SASL males during the post-harvest period.

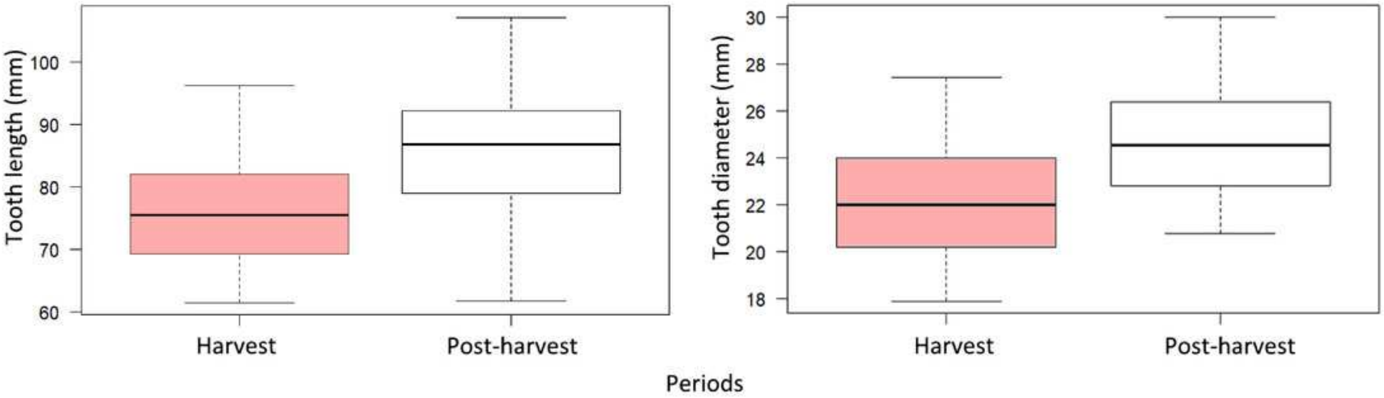

Figure 4

Figura 4: Arriba: Diagrama de caja de la longitud de los dientes de los machos SASL de ambos períodos. Abajo: Diagrama de caja del diámetro de los dientes de los machos SASL de ambos períodos. (●) Período de cosecha y (●) Período de poscosecha.

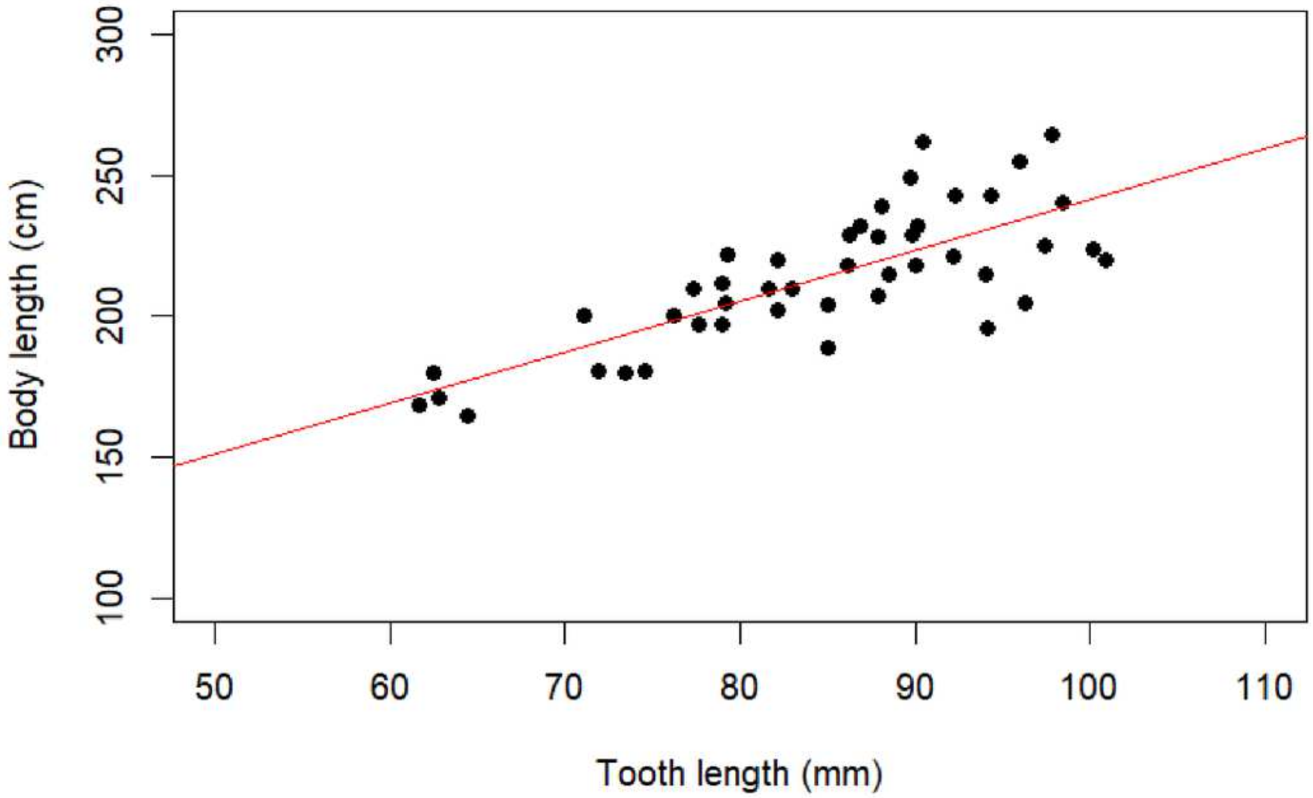

Figure 5

Figure 5: Relationship between GLGW and the N° GLG in both time periods (with confidence interval of 95%). (●) Harvest and (●) Post-harvest.

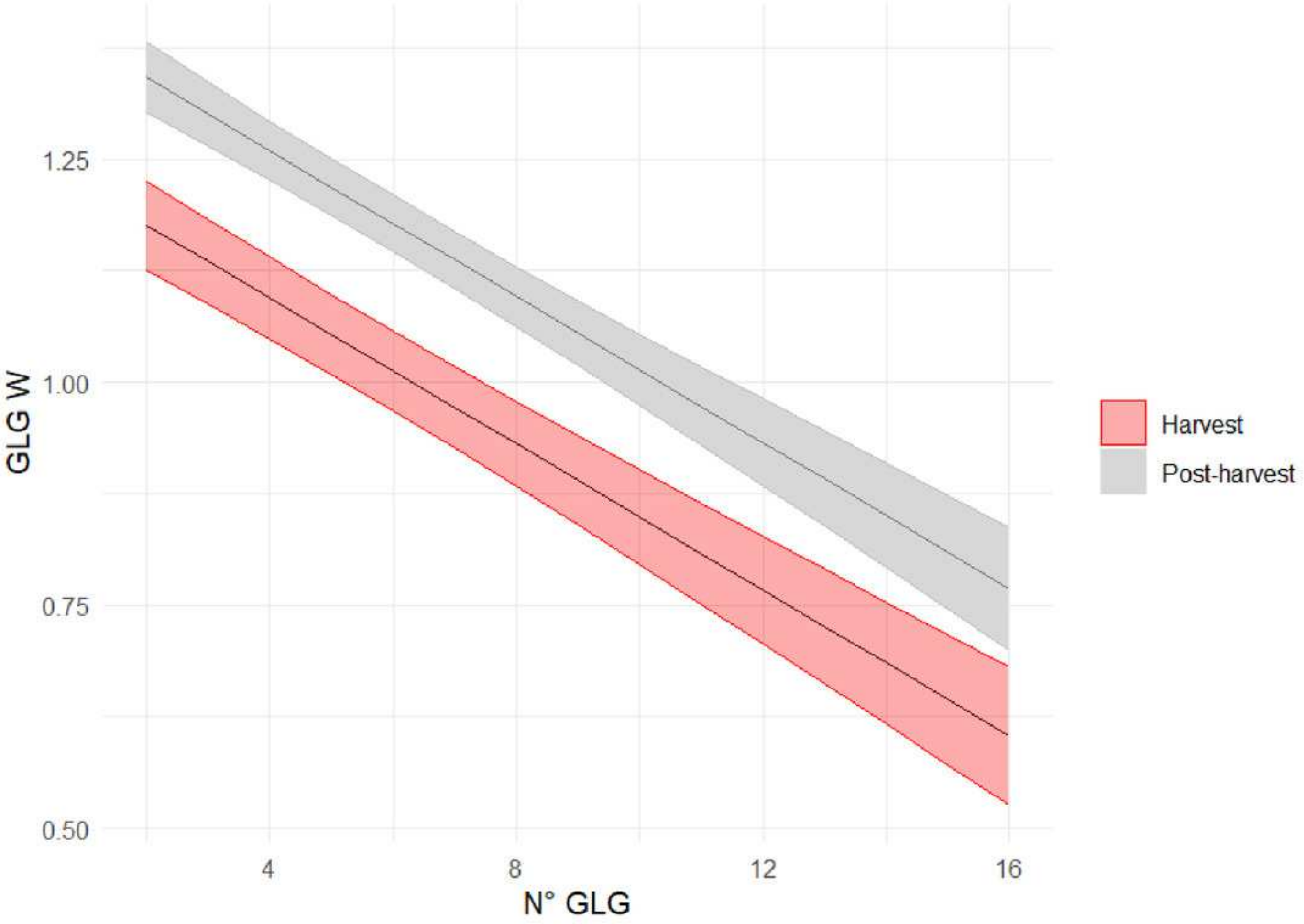

Table 1(on next page)

Table 1: Summary of the generalized linear mixed models used. The structure for each model, ΔAIC and df values are shown.

Table 1: Summary of the generalized linear mixed models used. The structure for each model, ΔAIC and df values are shown.

models	Models	ΔAIC	df
M4	Lme (GLGW ~ n°GLG * period, random = ~1|id, na.action=na.omit, correlation=corCompSymm (form =~ 1|id/glb))	7,5	7
M2	Lme (GLGW ~ n°GLG * period, random = ~1|id, correlation=corAR1(form =~ 1| id/glb))	5,1	7
M3	Lme (GLGW ~ n°GLG * period, random = ~1|id, na.action=na.omit, correlation=corCompSymm (form =~ 1|id/glb))	7,5	7
M1	Lme (GLGW ~ n°GLG * period, random = ~ 1 | id)	108,4	6