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Establishing growth chronologies from marine mammal teeth: A method applicable across species

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ABSTRACT

Multidecadal datasets are important for investigating the effects of a changing climate on top predators, particularly if short-term variations are to be differentiated from long-term trends. Annual increments (growth layer groups: GLGs) formed in the teeth of marine mammals have the potential to provide multidecadal proxy records or chronologies of energy budgets associated with growth, allowing for the investigation of potential environmental drivers of interannual variability and longer-term changes in growth. To date, methodology universally applicable across marine mammal species for developing such chronologies has not been established. Methodologies developed are often “bespoke” being developed specifically for individual species and datasets. This thereby limits the applicability of such methodologies to other species and regions and introduces difficulties in the replication of methods.

By modifying dendrochronology (tree-ring dating) techniques, we provide a method for developing chronologies from GLG widths using sperm whales (*Physeter macrocephalus*) and long-finned pilot whales (*Globicephala melas*) as examples. The method firstly utilizes statistical crossdating to identify and correct potential errors in GLG identification ensuring assignment of GLGs to the correct calendar year. Common dendrochronology “detrending” methods were then tested for applicability and the most appropriate applied to remove age-related trends and variability specific to each individual in the example dataset. Finally, individual chronologies comprised of a standardized growth index were calculated and then averaged into a master chronology for each dataset, maximizing common patterns in growth across individuals and reducing noise in the data due to individual variability.

The described approach to chronology development provides a number of advantages over others previously used on marine mammals; first, it has been formed on the basis of well-established and tested techniques and second provides a step-by-step process that is readily repeatable, thereby allowing direct comparisons between similarly developed chronologies from different species or regions. Once developed, chronologies can be used in modeling studies and compared with annually resolved climate indices to explore sensitivities in tooth growth and associated energetic budgets to environmental conditions.

1. Introduction

The population dynamics of many marine species are likely to be influenced by climate-mediated changes in environmental conditions that affect prey availability and distribution (Simmonds and Isaac, 2007). To understand how these changes in the environment influence long-lived marine species, there is a need for multidecadal datasets that cover cycles incorporating both natural and anthropogenic induced changes, and an effective method for separating such signals from noise at appropriate temporal and spatial scales (Black et al., 2008; Edwards et al., 2010; Hare and Mantua, 2000; Moore, 2005). Long-term datasets in the marine environment can be lacking due to the expense and commitment required for their acquisition. Retrospective studies using naturally occurring multidecadal records of indices that are influenced by environmental conditions are therefore important resources for increasing general understanding of the potential responses of species to variability in their environment and their resilience under future scenarios of climate change (Brown et al., 2011; Chambers et al., 2015; Morrongiello et al., 2014).

Annual growth increments deposited in marine mammal teeth over an animal's lifetime (known as growth layer groups, or GLGS) are commonly used to estimate age. Growth layer groups are metabolically

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Table 1
Details of individual sperm whales and long-finned pilot whales (number of teeth available per individual sperm whale in parentheses after ID #), tooth state and GLG width time series (T-S length) included in chronology development.

Stranding date	Stranding location	Species	Whale ID #	Sex	Age estimate (T-S length)	Pulp cavity state	Tooth wear
28/11/2003	Flinders Island	*P. macrocephalus*	1928 (2)	M	30 (29)	Open	Low – moderate
28/11/2003	Flinders Island	*P. macrocephalus*	1929 (2)	M	23 (21)	Open	Low – moderate
28/11/2003	Flinders Island	*P. macrocephalus*	1930 (2)	M	26 (24)	Open	Low – moderate
28/11/2003	Flinders Island	*P. macrocephalus*	1931 (2)	M	23 (22)	Open	Low – moderate
28/11/2003	Flinders Island	*P. macrocephalus*	1932 (2)	M	19 (18)	Open	Low – moderate
28/11/2003	Flinders Island	*P. macrocephalus*	1933 (2)	M	31 (29)	Open	Low
28/11/2003	Flinders Island	*P. macrocephalus*	1934 (2)	M	25 (22)	Open	Low – moderate
28/11/2003	Flinders Island	*P. macrocephalus*	1935 (2)	M	26 (25)	Open	Low – moderate
29/12/2004	Strahan	*P. macrocephalus*	2156 (2)	F	33 (33)	Full	Low – moderate
29/12/2004	Strahan	*P. macrocephalus*	2157 (2)	F	29 (28)	Closing	Low – moderate
29/12/2004	Strahan	*P. macrocephalus*	2158 (4)	F	20 (17)	Open	Moderate
29/12/2004	Strahan	*P. macrocephalus*	2161 (4)	F	29 (27)	Open	Low – moderate
29/12/2004	Strahan	*P. macrocephalus*	2163 (3)	F	26 (17)	Open	Low – moderate
29/12/2004	Strahan	*P. macrocephalus*	2166 (4)	F	21 (18)	Open	Moderate
29/12/2004	Strahan	*P. macrocephalus*	2168 (4)	F	27 (25)	Open	Low – moderate
29/12/2004	Strahan	*P. macrocephalus*	2169 (2)	F	19 (18)	Open	Moderate
29/12/2004	Strahan	*P. macrocephalus*	2172 (4)	F	25 (20)	Open	Moderate
29/12/2004	Strahan	*P. macrocephalus*	2174 (3)	F	29 (22)	Open	Moderate
03/11/2012	King Island	*G. melas*	KI-GM1	M	8	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM2	F	9	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM3	F	13	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM4	M	12	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM5	F	9	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM6	F	11	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM7	M	11	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM9	M	15	Closing	Nil
03/11/2012	King Island	*G. melas*	KI-GM10	M	7	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM11	F	7	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM12	M	13	Closing	Nil
03/11/2012	King Island	*G. melas*	KI-GM13	F	13	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM14	F	12	Closing	Nil
03/11/2012	King Island	*G. melas*	KI-GM15	M	8	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM16	F	8	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM21	M	8	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM28	F	8	Open	Nil
03/11/2012	King Island	*G. melas*	KI-GM29	F	13	Open	Nil

inert after deposition, and reflect seasonal changes in tooth growth rate and the physiological condition of the animal at time of deposition (Klevezal', 1996). Deposition of each GLG therefore represents the balance between energetic intake and the costs of movement and foraging, maintenance of body functions and condition and reproductive output (Boyd and Roberts, 1993; Hamilton et al., 2013; Hanson et al., 2009). A deficit (i.e., a "poor" year) will lead to relatively narrow/below average GLG deposition, while a surplus (i.e., a "good" year) will lead to relatively wide/above average GLG deposition (Hamilton et al., 2013; Klevezal', 1996; Lockyer, 1993; Medill et al., 2010). As such, time series of measurements of GLG widths provide annually resolved proxies of variability in annual energetic budgets for marine mammals that are otherwise difficult to obtain.

To date, chronologies of growth increment widths in the teeth of marine mammals have predominantly been developed for pinnipeds (Boyd and Roberts, 1993; Hanson et al., 2009; Knox et al., 2014; Wittmann et al., 2016). Growth chronologies of individuals developed so far however have used varying GLG measurement, standardization and modeling techniques across studies that have often been "bespoke" to each study and each dataset. They are also restricted by the species' lifespans, which are normally < 25 years (Arnould, 2009; McKenzie et al., 2007). The resultant chronologies are generally insufficient in length to identify long-term environmental cycles, and differing methodology precludes comparisons across species and studies. Growth increment width chronology development for odontocetes has received little attention (e.g., Hamilton et al., 2013), yet has the potential to provide multidecadal time series for analysis, due to the extended life span of many medium to large odontocete species.

The field of dendrochronology (tree-ring science) has long-standing robust methods for producing multidecadal time series in terrestrial environments, with the isolation of a common climatic signal among individuals a foremost aim. Crossdating is a fundamental principle of dendrochronology, and facilitates assignment of growth increments to the correct calendar year, to generate chronologies with accurate annual resolution (Stokes and Smiley, 1996). Effective crossdating relies on the assumption that environmental conditions will have a synchronizing effect on the growth of individuals, resulting in similar patterns of wide and narrow growth increments among individuals of the same species within a region (Fritts, 1976; Speer, 2010; Stokes and Smiley, 1996).The application of crossdating and chronology building techniques pioneered by dendrochronologists remain relatively unexplored for marine mammal teeth. Such methods have proven effective for establishing relationships between environmental drivers and continuous, long-term chronologies for a number of marine species with hard structures that exhibit incremental growth (the discipline termed "sclerochronology"), particularly bivalves and teleost otoliths (e.g. Black, 2009; Black et al., 2008; Helama et al., 2006; Matta et al., 2010; van der Sleen et al., 2016). Development and refinement of dendrochronology techniques that can be consistently applied across different marine mammal species has the potential to provide considerable information on the responses of species to climate variability (Helama et al., 2006; Rypel et al., 2008) and allow for multi-species comparisons.

Sperm whales (*Physeter macrocephalus*) and long-finned pilot whales (*Globicephala melas*) are good case study species for developing methods associated with establishing growth increment chronologies. They possess homodont tooth structure and accordingly, each tooth from the same individual should manifest similar patterns of GLG deposition.