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# Spatial variability in responses to environmental conditions in Southern Hemisphere long-finned pilot whales

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ABSTRACT: Investigating past responses to variations in the marine environment can provide insights into how species might respond to future change. Using long-finned pilot whales *Globicephala melas* stranded in New Zealand (2011) and Australia (2012), we investigated relationships between tooth growth chronologies, as a proxy for energy budgets (which underpin population state), and interannual variations in broad-scale climate indices (Southern Oscillation Index [SOI], Indian Ocean Dipole [IOD]) and spatially explicit, seasonally averaged sea surface temperature (SST). Tooth chronologies from pilot whales that stranded in Australia had a positive relationship with the SOI and a negative relationship with the IOD. Those from New Zealand had a positive relationship with the SOI, but at a 1 yr lag. Positive SOI and negative IOD conditions are associated with increased storm activity across the southern Australian/New Zealand region. The resulting changes in regional SST, currents and frontal activity likely influences the distribution of prey resources and associated high-order predators such as pilot whales. Correlation maps between tooth growth chronologies and SSTs suggest differences in habitat utilisation between the 2 regional groups, with pilot whales stranded in Australia associating with the subtropical and subantarctic fronts south of Tasmania, and those stranded in New Zealand associating with a number of regions of seasonally enhanced productivity close to New Zealand. This study greatly enhances our understanding of the environmental conditions influencing populations of an insufficiently studied species in the region.

KEY WORDS: Energy budget · Tooth growth chronology · *Globicephala melas* · Indian Ocean Dipole · Southern Oscillation Index · Sea surface temperature

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## 1. INTRODUCTION

Determining how variability in the marine environment affects higher-level predators is increasingly important for establishing how species might respond over the medium- to long-term under changing environmental conditions (Trathan et al. 2007, Schumann et al. 2013). Fluctuations in broad-scale climate modes can influence oceanographic conditions, such as sea surface temperature (SST), wind and ocean currents at differing spatial and temporal scales (Stenseth et al. 2002, Behrenfeld et al. 2006).

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Variability in environmental conditions driven by broad-scale climate processes have been related to changes in the diet, condition and breeding performance of higher trophic level predators, as a result of changes in productivity and flow-on effects to prey availability and the energy budgets of individuals (Barber & Chavez 1983, Learmonth et al. 2006). Responses to short-term natural variability in oscillating climate signals (e.g. El Niño–Southern Oscillation [ENSO]) and environmental parameters (e.g. SST) can provide insights into how top predators will respond to future changes in their environment (Learmonth et al. 2006, Trathan et al. 2007). Obtaining information on potential responses to environmental variation, however, is inherently difficult for many marine species, as it requires multiple years of data encompassing contrasting conditions. This is particularly so for marine mammals, due to difficulties in collecting long time series from populations that are largely underwater, remote and wide-ranging.

Time series of annual growth increment widths in the teeth of marine mammals (known as growth layer groups [GLGs]) provide proxy records of the annual energy budgets of individuals. This is because the width of each GLG is dependent on an individual's nutritional intake for their rate of formation over each year (Boyd & Roberts 1993, Klevezal 1996). As a result, interannual variation in GLG widths will reflect variability in energy budgets (Klevezal 1996, Hamilton et al. 2013). Similar to tree rings, chronologies developed from time series of GLG widths can then be used to investigate past responses of individuals to their environment.

Previous studies using tooth growth chronologies to investigate the responses of marine mammals to interannual variability in broad-scale environmental drivers have primarily focused on pinnipeds (e.g. Knox et al. 2014, Wittmann et al. 2016). Pinniped species are often easier to monitor than cetaceans due to their life history constraints of land-based breeding and pup provisioning, and associated annual return to rookeries. Only 1 study to date has attempted to investigate environmental drivers of energy budgets in odontocetes (i.e. Hamilton et al. 2013), and was unable to identify relationships with broad-scale climate variables. In addition, varying methodology has limited the repeatability and comparability of those studies conducted. This lack of consistency in methodology led us to investigate dendrochronology (tree-ring science) techniques as a more robust and consistent approach to chronology development in marine mammals (Hamilton & Evans 2018).

Long-finned pilot whales *Globicephala melas* (hereinafter pilot whales) are long-lived (>60 yr for females and 35–45 yr for males; Bloch et al. 1993) and wide-ranging mesopelagic predators in cold temperate waters of the North Atlantic, Mediterranean Sea and Southern Hemisphere (Olson 2009). This longevity potentially enables access to relatively long time series of tooth growth. Individuals occur in stable, matrilineally associated social units of approximately 7–12 individuals that often travel in groups with other matrilineal units (Amos et al. 1993, Augusto et al. 2017). This social structure means animals from the same social unit should have experienced similar environmental conditions throughout the majority of their lifetimes. The species also frequently mass strands, particularly in the southern Australian/New Zealand region, enabling access to samples from multiple animals. Collectively, these factors make pilot whales a potentially suitable species for chronology studies.

In the Southern Hemisphere, pilot whales are thought to be nomadic in response to movements of their preferred prey, inhabiting temperate and subantarctic deep oceanic waters and areas of high productivity along the continental slope (Ross 2006). The spatial distribution, movement patterns and responses to environmental variability, particularly in terms of energy budgets, of pilot whales in the southern Australian/New Zealand region are poorly understood. There are no existing photo-identification studies and satellite telemetry tracking has been conducted on only 5 individuals released post-stranding on the northwest coast of Tasmania, Australia in 2008. Within the tagging timeframe of 12–32 d, these individuals travelled a limited range, remaining in the waters of Bass Strait, between Tasmania and the Australian mainland (Gales et al. 2012). Dietary investigations of pilot whales stranded in Tasmania suggest consumption of a broad range of cephalopod species (Beasley et al. 2019). The stomach contents of pilot whales stranded in New Zealand indicate a more limited range of cephalopod species are consumed; however, to date, such studies have focused on small numbers of stranded individuals (Beatson et al. 2007, Beatson & O'Shea 2009). How reflective they might be of the dietary preferences of wider populations in either region remains unknown. Genetic studies suggest population differentiation of pilot whales between New Zealand and Tasmania (Oremus et al. 2009); however, whether or not this reflects separation of foraging ranges is unknown.

Here we apply modified dendrochronology techniques to teeth collected from pilot whales stranded in New Zealand and Australia to establish chronologies of tooth growth (as proxies for energy budgets) in order to:

(1) investigate the responses of pilot whales to short-term, interannual variability in broad-scale climate variables (ENSO, measured by the Southern Oscillation Index [SOI]; the Southern Annular Mode [SAM]; and the Indian Ocean Dipole [IOD]),

(2) investigate spatial variability in relationships between tooth growth and spatially explicit, gridded environmental variables (SST, wind speed) as a guide to identifying potential foraging areas utilised by pilot whales in the Australian/New Zealand region, and

(3) assess any differences in the responses of pilot whales from the 2 geographic regions.

## 2. MATERIALS AND METHODS

### 2.1. Samples

Two teeth per individual (from the middle of the mandibular tooth row) were sampled from deceased pilot whales involved in mass strandings on the coasts of Rakiura (Stewart Island), New Zealand (46.93° S, 167.73° E; n = 12 from a stranding of 107 animals) in 2011, and King Island, Tasmania, Australia (39.67° S, 143.83° E; n = 18 from a stranding of 44 animals) in 2012 (see Table 1). These 2 sites are separated by a distance of ~2000 km (see Fig. 3).

### 2.2. Tooth preparation and GLG identification

Teeth were decalcified, thin-sectioned, stained and mounted on slides before being digitally imaged following methods detailed in Hamilton & Evans (2018).

Annual dentinal GLGs were defined as consisting of a pair of layers of varying staining intensity: one narrow/thin deeply stained layer and a wide/thick lightly stained layer (Perrin & Myrick 1980). GLGs were identified 2 to 3 times for each tooth via blind readings of digital images by V. Hamilton, and a subsample of teeth (n = 12) was cross-verified by another experienced reader, K. Evans. Final GLG identification was based on repeated counts.

A modified visual crossdating process, based on a comparison of distinctive GLGs present in both teeth, was then used to check GLG identification within each individual (Hamilton et al. 2017). Following any adjustments made to the GLG time series as a result (see Table S1 and Text S1 in the Supplement at www.int-res.com/articles/suppl/m629p207_supp.pdf), the tooth with the most central section position and greatest clarity of GLG boundaries was selected for GLG width measurement and chronology development.

### 2.3. Chronology development

Chronology development involving the measurement of GLG widths, further adjustments to GLG identification via statistical crossdating and detrending followed the methods detailed in Hamilton & Evans (2018). Because effective crossdating requires time series long enough to match patterns of wide and narrow GLGs among individuals, we were unable to use statistical crossdating with 4 time series of individuals from New Zealand and 7 time series from Australia, due to their short length (≤8 yr) (Black et al. 2016). As a result, some residual errors in GLG identification and calendar year assignment may have remained for those individuals, and could result in some dampening of the annual signal. Individual GLG width time series from New Zealand whales showed no obvious age-related decline in GLG widths and so were detrended using a cubic smoothing spline with 50% frequency cut-off at *n*-years/2 (i.e. a wavelength of half the series length). Time series from Australian individuals did exhibit an obvious age-related decline in GLG widths, and subsequently were detrended using the 'double detrending' approach of Cook (1985). Negative exponential curves were initially applied to each GLG width time series to account for the age-related trend. The resulting indices were then detrended once more using cubic smoothing splines at a 50% frequency cut-off of 12 yr to accommodate growth variation in the latter parts of the time series. Additional crossdating and detrending details can be found in the Supplement (Text S1).

Pilot whales are reported to exhibit strong social bonds and co-exist in long-term groups (Amos et al. 1993, Augusto et al. 2017). We therefore assumed that individuals that strand together would comprise individuals with long-term associations and consequently would be exposed to similar environmental conditions for large portions of their lives. Combining chronologies of individuals from each of the strandings into a single GLG width chronology in an effort to represent the common climate signal for a particular region (Cook et al. 1990) could therefore also be

assumed to be appropriate. With this in mind, individual chronologies were averaged with respect to calendar year into a master chronology for each stranding group. To reduce the influence of outliers, Tukey's biweight robust mean was used to calculate the regional master chronologies (Cook et al. 1990). Master chronologies for each of the stranding groups comprised years in which there was a minimum of 6 individuals to ensure individual variability did not obscure common signals (Matta et al. 2010).

Synchrony among chronologies of individuals within each stranding group was assessed using Pearson's correlation coefficient. The strength of this synchrony or the overall common signal for each stranding group was compared quantitatively using $\bar{r}$ (the mean of all pairwise correlations between individual chronologies). Chronology quality was assessed using the expressed population signal (EPS), a measure of how well the chronology represents an 'ideal' chronology from a hypothetical population, where EPS = $n\bar{r}/(1 + (n - 1)\bar{r})$ (Wigley et al. 1984, Cook et al. 1990).

### 2.4. Environmental analyses

Generalised additive models (GAMs; Wood 2006) with a Gaussian error distribution and identity link function were used to investigate relationships between the 2 master chronologies and indices of broad-scale climate-ocean interactions recognised as important determinants of interannual environmental and biological variability in the Australian and New Zealand regions, i.e. the ENSO, the IOD and the SAM (see Table S2 in the Supplement for data sources). The ENSO (measured by the SOI) is a large-scale coupled ocean-atmosphere phenomenon of the Pacific Ocean and overlying atmosphere, operating on interannual timescales (Clarke 2008). The ENSO involves a cyclical fluctuation of air pressure between the western and eastern tropical Pacific from a 'neutral' state to sustained periods of either El Niño events (associated with warming of the central and eastern tropical Pacific Ocean) or La Niña events (cooling of the central and eastern tropical Pacific) (Clarke 2008). The effects of ENSO are strongest in the Pacific; however, teleconnections into adjoining ocean basins result in the influence of the ENSO extending across the globe, with effects on climate and bological processes varying regionally (Clarke 2008). The IOD (measured by the dipole mode index) is a coupled ocean-atmosphere interaction of the Indian Ocean basin, associated with an oscillation of SST anomalies between the eastern and western tropical Indian Ocean, and affects climate across the Indian Ocean and southern Australian region (Saji et al. 1999). When the IOD is in a positive (negative) phase, SSTs are warmer (cooler) in the western Indian Ocean relative to the east, and there is an east-west shift in zonal wind anomalies over the equatorial Indian Ocean (Saji et al. 1999). The SAM describes the atmospheric phenomenon of the north-south oscillation of the westerly wind belt surrounding Antarctica (Thompson & Wallace 2000). Positive phases of the SAM are associated with southward contraction and strengthening of the westerly winds south of 45° S, and weaker westerlies in the mid-latitudes (Thompson & Wallace 2000, Hall & Visbeck 2002).

Model covariates and chronologies were tested for autocorrelation and collinearity (covariates retained if $r < 0.7$) and residual diagnostics checked to confirm normality and homogeneous variance. Pilot whales are higher trophic level predators and as a result, their responses to variations in broad-scale climate phases could potentially occur at a temporal lag, as environmentally driven changes in productivity may take time to propagate through trophic levels (Mann & Lazier 2006, Poloczanska et al. 2007). Pilot whales feed primarily on cephalopods, which typically have a relatively short life cycle of 1–2 yr, and respond rapidly to fluctuations in their environment (Clarke 1996, Boyle & Rodhouse 2005). With this knowledge of prey dynamics in mind, pilot whales might be expected to show a relatively short lagged response to changes in conditions that influence productivity and prey resources. Therefore, climate indices were included in the models both concurrently with the chronologies and at a lag of 1 yr. Covariates were means-centred prior to smoothing to account for differing measurement scales. The degree of smoothing for model terms was estimated using the restricted maximum likelihood (REML) approach, which provides greater resistance to overfitting and less variability in smoothing parameter estimates (Wood 2011). Models were trialled by sequential addition of each predictor covariate. Final model selection was based on minimisation of the second-order Akaike's information criterion ($AIC_c$) scores, accounting for small sample sizes (Burnham & Anderson 2002) and model fit assessed by the amount of deviance explained by the model.

Physical oceanographic variables, such as SST and zonal winds, have been linked to the spatial distribution of primary productivity and the prey of higher predators (Hindell et al. 1991, Wilson &

Adamec 2002). Although higher predators are separated from physical variables and primary productivity by several intermediate trophic levels, direct measurements of prey abundance are difficult to obtain in pelagic environments, and physical oceanographic features may reflect the foraging habitats of marine predators (e.g. Arthur et al. 2017). Gridded measurements of SST and zonal near-surface wind speed (Table S2) were aggregated into seasonal averages within each year for the austral summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). The regional chronologies were then spatially correlated (Spearman's rank) with the SST/wind speed seasonal averages within 2.0°/2.5° grid cells across a spatial domain based on pilot whale sighting and stranding records (Ross 2006), bounded by 30°–60° S, 110°–190° E to identify regions associated with increased tooth growth. Spatial maps were used as indicative guides to possible foraging regions utilised by pilot whales.

Annual GLG widths were measured using a plug-in ('IncMeas'; Rountrey 2009) written for ImageJ, an open-source image processing program (version 1.47; NIH 2016). All statistical analyses were conducted within the R statistical programming environment (version 3.0.2; R Core Team 2013). The Dendrochronology Program Library in R package 'dplR' (Bunn 2008) was used for crossdating, detrending and chronology building and GAMs were implemented using the R package 'mcgv' (Wood 2011).

Table 1. Age estimate/growth layer group (GLG) width time series length (T-S length) and tooth state of individual long-finned pilot whales *Globicephala melas* stranded at Rakiura, New Zealand (20 Feb 2011; ID: R-) and King Island, Tasmania, Australia (3 Nov 2012; ID: KI-) included in tooth growth chronologies

| Whale ID # | Sex | Age estimate/ T-S length (yr) | Pulp cavity state | Tooth wear |
|---|---|---|---|---|
| R-GM1 | M | 13 | Closing | Low |
| R-GM2 | M | 13 | Open | Low |
| R-GM3 | F | 12 | Closing | Nil |
| R-GM4 | M | 9 | Open | Low–moderate |
| R-GM5 | M | 8 | Open | Nil |
| R-GM6 | M | 10 | Open | Low |
| R-GM7 | M | 11 | Open | Nil |
| R-GM8 | M | 7 | Open | Nil |
| R-GM9 | M | 7 | Open | Low–moderate |
| R-GM10 | M | 10 | Open | Nil |
| R-GM11 | M | 6 | Open | Nil |
| R-GM12 | M | 11 | Open | Low |
| KI-GM1 | M | 8 | Open | Nil |
| KI-GM2 | F | 9 | Open | Nil |
| KI-GM3 | F | 13 | Open | Nil |
| KI-GM4 | M | 12 | Open | Nil |
| KI-GM5 | F | 9 | Open | Nil |
| KI-GM6 | F | 11 | Open | Nil |
| KI-GM7 | M | 11 | Open | Nil |
| KI-GM9 | M | 15 | Closing | Nil |
| KI-GM10 | M | 7 | Open | Nil |
| KI-GM11 | F | 7 | Open | Nil |
| KI-GM12 | M | 13 | Closing | Nil |
| KI-GM13 | F | 13 | Open | Nil |
| KI-GM14 | F | 12 | Closing | Nil |
| KI-GM15 | M | 8 | Open | Nil |
| KI-GM16 | F | 8 | Open | Nil |
| KI-GM21 | M | 8 | Open | Nil |
| KI-GM28 | F | 8 | Open | Nil |
| KI-GM29 | F | 13 | Open | Nil |

## 3. RESULTS

### 3.1. Chronologies

The number of GLGs measured for each individual ranged 6–13 yr, spanning 1998–2010 for pilot whales from New Zealand, and 7–15 yr, spanning 1997–2011 for pilot whales from Australia (Table 1). Master chronology lengths were 10 and 12 yr for the New Zealand and Australian strandings, respectively (Fig. 1). Chronologies of individuals from each of the strandings varied from low to high similarity, with Pearson's correlation coefficients ranging from –0.86 to 0.88 and from –0.85 to 0.91 for the New Zealand and Australian chronologies respectively (see Fig. S1 in the Supplement). The strength of the common signal ($\bar{r}$) and the EPS were 0.069 and 0.475 for the New Zealand chronology and 0.038 and 0.415 for the Australian chronology, respectively, reflecting variability among chronologies of individuals (see Text S1 and Fig. S2 in the Supplement). Little correlation was evident between the New Zealand and Australian master chronologies (Pearson's r = –0.09).

### 3.2. Relationships with broad-scale climate indices

The highest-scoring model ($AIC_c$) for the New Zealand chronology included the SOI with a 1 yr lag and explained 50.8% of the deviance in the data (Table 2). Below-average tooth growth was associated with SOI values less than approximately –2 and above-average tooth growth was associated with SOI

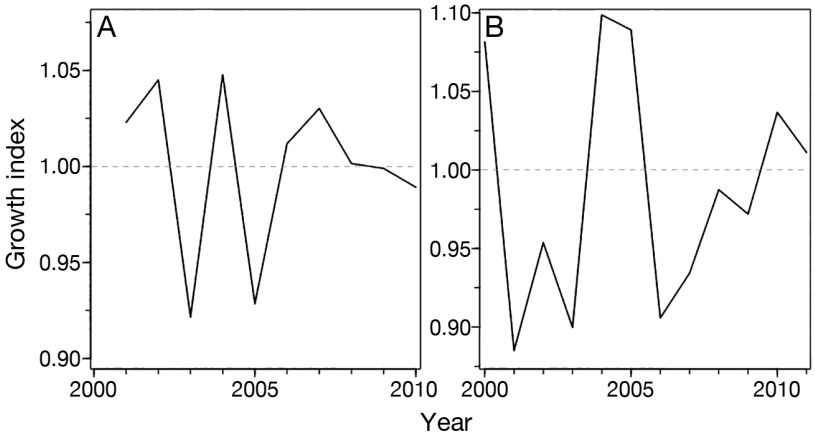


Fig. 1. Tooth growth master chronologies for long-finned pilot whales *Globicephala melas* from (A) New Zealand (n = 12) and (B) Australia (n = 18). Dashed horizontal line: the mean

values greater than –2 (Fig. 2A). The highest-scoring model ($AIC_c$) for the Australian chronology included the SOI and the IOD and explained 40.1% of the deviance in the data (Table 2). The relationship with the SOI was positive; above-average tooth growth was associated with SOI values greater than approximately 2. The relationship with the IOD was negative and linear, with above-average growth associated with IOD values of 0–0.25, above which tooth growth was below-average (Fig. 2B).

### 3.3. Relationships with gridded spatially explicit environmental variables

The spatial distribution of correlations between the New Zealand chronology and seasonally averaged SST varied seasonally (Fig. 3A). Lower SSTs correlated with high tooth growth in areas to the east and north of New Zealand (30–40° S, 175–190° E). Similar correlations were observed in the eastern area of the Great Australian Bight during the austral winter and to the southeast of New Zealand in the region of the Campbell Plateau (45°–55° S, 160°–190° E) in the austral spring. Higher SSTs correlated with high tooth growth in areas to the east of New Zealand (35°–45° S, 175°–190° E) during the austral summer, shifting progressively west and south across the austral autumn and winter, until in the austral spring, correlations between higher SSTs and high tooth growth occurred in a region to the southwest of Australia (Fig. 3A).

In contrast, the spatial distribution of correlations between the Australian chronology and SST was more seasonally consistent. Lower SSTs correlated with high tooth growth across a region south of Tasmania (45°–55° S, 130°–160° E) in all seasons, with correlations strongest in the austral autumn and winter (Fig. 3B). Higher SSTs correlated with high tooth growth consistently in the western Tasman Sea (30°–40° S, 152°–165° E) across all seasons, with correlations strongest in the austral autumn and spring. Similar correlations dominated most of the spatial domain during spring.

The spatial distribution of correlations between seasonally averaged zonal wind speed and the chronologies did not reveal any biologically meaningful patterns, and so were not considered further (Fig. S3 in the Supplement).

Table 2. Outputs from the top-ranked generalised additive models fitted to New Zealand and Australian long-finned pilot whale (*Globicephala melas*) tooth growth chronologies. $AIC_c$: Akaike's (2nd-order) information criterion; GI: chronology; SOI: Southern Oscillation Index; lag1 (subscript): lagged covariate; SAM: Southern Annular Mode; IOD: Indian Ocean Dipole. **Bold**: the model that was accepted

| Candidate models | $AIC_c$ | % Deviance explained |
|---|---|---|
| *New Zealand* | | |
| 1. **GI ~ $SOI_{lag1}$** | –23.944 | 50.8 |
| 2. GI ~ SAM | –19.364 | 43.6 |
| *Australia* | | |
| 1. **GI ~ SOI + IOD** | –20.470 | 40.1 |
| 2. GI ~ SOI + $SAM_{lag1}$ | –16.047 | 24.1 |

## 4. DISCUSSION

Here, we applied modified dendrochronology techniques to establish chronologies of tooth growth, and by proxy, energy budgets, in odontocetes. We then used the chronologies to investigate relationships between energy budgets in Southern Hemisphere pilot whales with environmental factors for the first time.

Although variations in synchrony could be considered relatively high when compared to sessile species, such as trees and bivalves (e.g. $\bar{r}$ = 0.3–0.6; Frank & Esper 2005, Brocas et al. 2013), when compared with those observed in other mobile marine species, they are similar (e.g. Rountrey et al. 2014, Ong et al. 2015). Individual responses will vary, particularly in higher trophic level species, as the effect

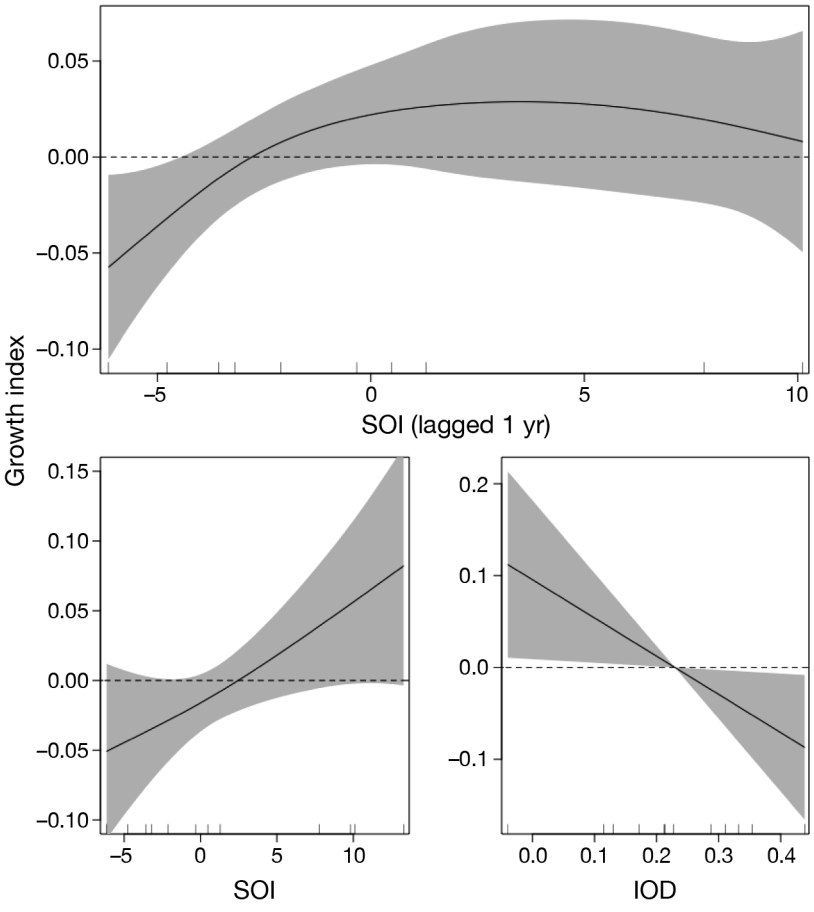


Fig. 2. Results of generalised additive models for predicted tooth growth in relation to the broad-scale climate indices the Southern Oscillation Index (SOI) and the Indian Ocean Dipole (IOD) in long-finned pilot whales *Globicephala melas* from (A) New Zealand and (B) Australia. Shading: 95% confidence limits; dashed horizontal line: the mean

of the environment on energy budgets and growth will be indirect, and driven by factors such as changes in prey density (and energetic intake). However, the overall regional population signal should reflect relationships across longer time frames between tooth growth and environmental influences (Speer 2010, Black et al. 2016). Further, when environmental factors do not strongly limit or enhance prey availability and subsequent energetic intake and growth throughout the year (e.g. such as a lack of strong ENSO events), individual-level responses may be more variable (Black et al. 2005, Speer 2010). Differences in physiological demands among individuals can also introduce asynchrony in energy budgets. For example, energetic requirements associated with reproductive state (e.g. pregnancy, lactation) will place additional energetic demands on individuals and reduce the available energy for tooth growth (Lockyer 2007, Costa 2009). Additionally, in the case of large stranding groups, these might comprise a number of pilot whale matrilines or social units that have come together in the same area just prior to stranding. In this case, samples might be derived from multiple units and therefore individuals that may not necessarily have had similar histories until relatively recently.

The ENSO was an important predictor of tooth growth for both sample groups, with above-average tooth growth associated with positive SOI values. While the relationship was concurrent for the Australian chronology, the relationship with the New Zealand chronology occurred at a 1 yr lag. The underlying reasons behind the differing responses to ENSO are unclear but may be related to food web differences driven by regional specific interactions between climate indices, oceanic processes and resulting food webs. Further, in this study, we have investigated the effects of 3 climate indices, i.e. the ENSO, IOD and SAM, and there are other longer-term phenomena that operate across the region (e.g. the Interdecadal Pacific Oscillation: a large-scale pattern of climate variability of the Pacific basin influencing SSTs at multidecadal timescales) that are likely to interact with these shorter-term phenomena. Understanding of these phenomena and their interactions with each other is not fully understood.

The Australian pilot whale chronology also demonstrated a negative relationship with the IOD, with above-average tooth growth associated with IOD values lower than approximately 0.25. This suggests that the Australian pilot whales were likely to have spent more time in regions influenced to a higher degree by the IOD than the New Zealand pilot whales, and in association, may not have totally overlapping foraging ranges. The influence of the IOD on climate is strongest across the Indian Ocean basin and southern Australian region (Saji et al. 1999). This is consistent with spatial correlations between the Australian chronology and SST, which demonstrated seasonal consistencies with regions south of Australia.

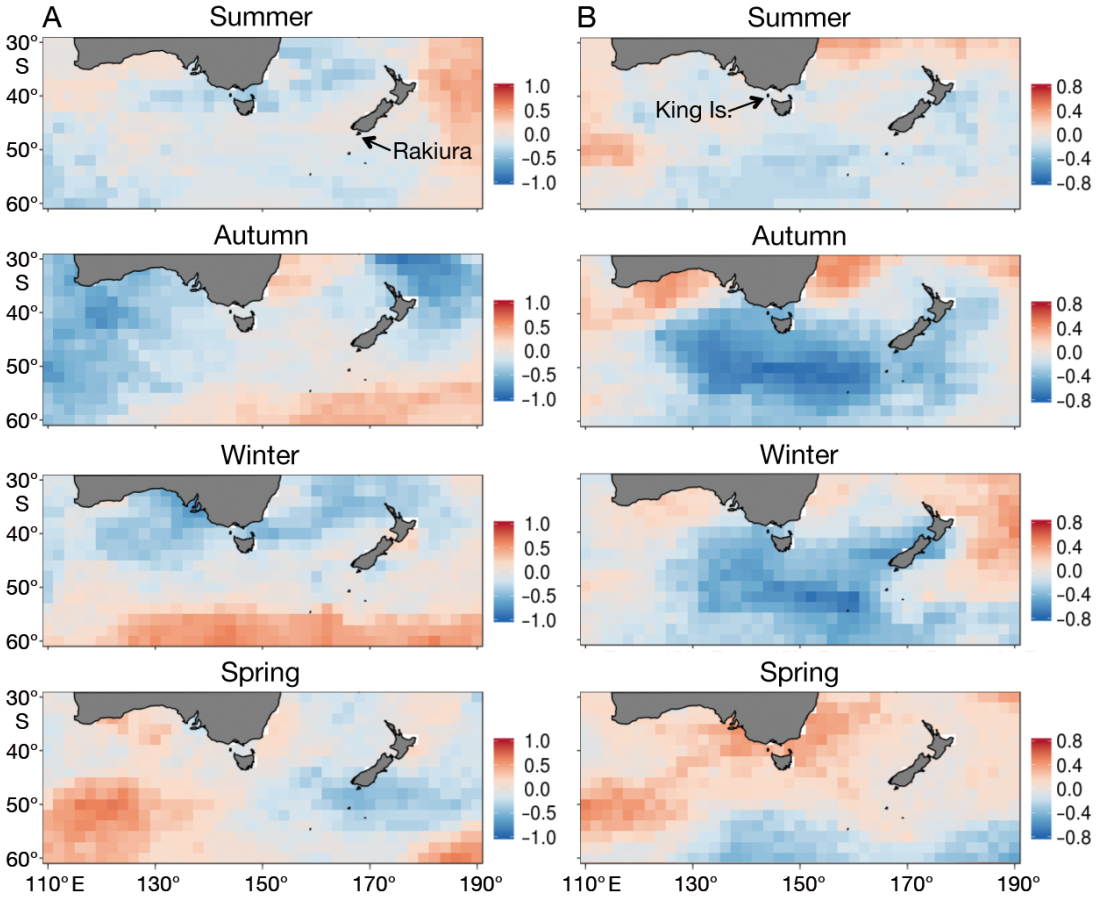


Fig. 3. Spatial maps of correlations between gridded seasonal averages (austral summer: Dec, Jan, Feb; autumn: Mar, Apr, May; winter: Jun, Jul, Aug; spring: Sep, Oct, Nov) of sea surface temperature and long-finned pilot whale (*Globicephala melas*) tooth growth chronologies from (A) New Zealand (2001–2010) and (B) Australia (2000–2011). Red shades: positive correlations; blue shades: negative correlations. Stranding sites (Rakiura and King Island) marked on summer maps

Environmental conditions associated with ENSO and the IOD vary across the marine regions of southern Australia and New Zealand, but generally manifest as changes in wind strength and direction, storm track activity and SSTs (Gordon 1986, Ashok et al. 2007). When ENSO is in a positive phase (i.e. a La Niña phase), storm track activity and SSTs tend to increase (Ashok et al. 2007, Holbrook et al. 2009). The ENSO cycle also has a strong influence on seasonal wind regimes in the New Zealand region (Gordon 1986, Mullan 1995). Positive (negative) IOD events are associated with a weakening (strengthening) of westerly winds and storm activity during winter off Australia (Ashok et al. 2007).

Increases in regional wind conditions and strengthened storm activity associated with neutral or lower IOD and/or positive ENSO phases are likely to increase mixing and upwelling in frontal regions and upwelling zones, leading to increases in prey abundance via biological (i.e. production) or physical (e.g. advection with currents) processes (Genin et al. 1988, Bost et al. 2009). Warmer SSTs and increases in SST gradients can influence the timing of spawning, growth and survival or distribution of prey species (Pecl & Jackson 2008, Chambers et al. 2011). These processes are likely to have flow-on positive effects on the energy budgets of marine predators, such as pilot whales, utilising such regions for foraging.

The spatial distributions of long-finned pilot whales in the Northern Hemisphere have been linked to regions of both cooler (Hamazaki 2002) and warmer SSTs (Hooker et al. 1999), likely reflecting seasonal or temperature-regulated movements of prey species (Fullard et al. 2000). Similar associations with both high and low SSTs most likely reflects some flexibility in prey preferences by pilot whales. Current limited understanding of the diet of pilot whales across the Australian and New Zealand regions suggests that those stranded on the southern Australian coastline consume a variety of cephalopod

species (Beasley et al. 2019), while those stranded on the New Zealand coastline consume a limited diversity of cephalopod species (Beatson et al. 2007, Beatson & O'Shea 2009, E. Betty pers. obs.). Noting the limitations of hard-part dietary studies and biases associated with stranded animals (Evans & Hindell 2004), these potential differences in dietary preferences might be driving the varied associations with seasonal SST and spatial foraging habitat of pilot whales across the Australian and New Zealand regions.

The higher variability in the spatial distributions of correlations between the New Zealand chronology and SSTs, when compared to the Australian dataset, suggests that the New Zealand pilot whales are likely associating with more highly dispersed foraging habitats than the Australian whales. Variability or stability in oceanographic conditions and subsequently the location and availability of prey resources can drive differing foraging strategies in higher predators. Individuals or groups may consistently rely on regions of predictable prey resources (Weimerskirch 2007, Bost et al. 2009), or alternatively, in less temporally stable environments, predators may vary their foraging movements to take advantage of regions of seasonally high productivity (e.g. Baylis et al. 2008). Some of the patterns observed in correlations between the New Zealand chronology and SSTs are consistent with the distribution of other predators that consume cephalopods. The Campbell Plateau region south-southeast of New Zealand encompasses important foraging zones for marine mammals and seabirds and commercially important fisheries including squid (Jackson et al. 2000, Bradford-Grieve et al. 2003). The Tasman Sea and regions northeast of New Zealand support high seasonal productivity, driven by the complex oceanography and bathymetry of the region (Tilburg et al. 2001, Ridgway & Dunn 2003). Catches of sperm whales *Physeter macrocephalus* (which are also cephalopod predators) by whaling vessels across the Tasman Sea and New Zealand region occurred in the Campbell Plateau region in austral spring, with a northwards movement of catches in autumn. These shifts in the distribution of catches have been associated with seasonal movements of sperm whales in association with seasonal movements of their prey in response to environmental conditions (Gaskin 1973).

In contrast, correlations between the Australian chronology and SSTs demonstrated seasonal consistencies with regions south of Australia and in the vicinity of the subtropical and subantarctic fronts. These frontal regions are highly productive due to the convergence of subtropical and subantarctic waters, wind-driven upwelling of cooler waters and eddy formation (Tomczak et al. 2004, Westwood et al. 2011). Spatial SST correlations with the Australian tooth growth chronology potentially reflect utilisation of relatively stable areas of high biological productivity, and potentially differing foraging ecology to pilot whales utilising New Zealand waters. Future studies investigating the trophic histories of individuals, e.g. by combining stable isotope analysis of dentinal GLGs with GLG width chronologies, may assist in determining if differences in responses to climate indices reflect spatial variation in the diet of regional populations.

This study is the first to identify relationships between variability in tooth growth and by proxy, energy budgets, and broad-scale environmental drivers for Southern Hemisphere pilot whales. This represents new insights into the responses of pilot whales to environmental variability and associated regional differences in the foraging ecology of pilot whales from New Zealand and Australia. Further, a clear process for progressing our understanding of the energetic responses for these and other toothed marine mammals has been established, comparable among regions and species. Although sample availability in this study resulted in individual time series ≤15 yr, responses to broad-scale indices could be identified. This indicates applicability of the method not only for long-lived marine mammals, but also for species with shorter life spans, such as smaller delphinids and pinnipeds. Future studies would benefit from inclusion of samples from different temporal periods. This would allow for the encompassing of a range of variability in climate oscillations and extreme events, thereby enabling responses to future environmental variability under changing conditions and climate interactions to be established.

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