



UNIVERSITY *of*
TASMANIA



IMAS
INSTITUTE FOR MARINE
& ANTARCTIC STUDIES

Using tooth growth chronologies to investigate
responses of marine mammals to variability in the
marine environment

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Submitted in partial fulfilment of the requirements for the degree of
Doctor of Philosophy in Quantitative Marine Science

Institute for Marine and Antarctic Studies, University of Tasmania

July 2018



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“It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living.”

Sir David Attenborough

Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Abstract

In a changing climate, it becomes increasingly important to understand how species respond to variability in their environment, and how their responses might influence overall population dynamics. Such information is important for the assessment of impacts on species, and for modelling variability in ecosystems, however obtaining this information for long-lived, cryptic marine mammal species is difficult.

Growth layers (termed growth layer groups: ‘GLGs’) laid down annually in the teeth of marine mammals can provide a proxy record of the energy budget of individuals; the size of each GLG is a factor of the metabolic energy available for the deposition of the structures associated with each. Chronologies developed from time series of measurement of GLGs, similar to those developed from tree-rings or otoliths, have the potential to be compared with environmental variables, thereby providing insights into environmental drivers of the energy budgets of marine mammals. Although a number of attempts at developing chronologies have been conducted on pinnipeds, they have all varied in their methodology and complexity and have in most cases, been developed for single species, limiting both their repeatability and comparability among studies. Further, the life spans of study species and subsequently their associated chronologies have been relatively short, reducing the ability of these methods in their applicability for investigating the responses of individuals to longer-term environmental variability.

The responses of cetacean species to variability in their environment are poorly understood in the southern Australian/New Zealand region, particularly for wide-ranging pelagic odontocete species such as long-finned pilot whales (*Globicephala melas*) and sperm whales (*Physeter macrocephalus*). This thesis therefore aims to: use dendrochronology (tree-ring science) techniques to establish a standardised methodology for development of tooth growth chronologies, and test the efficacy of these chronologies for investigating responses of long-finned pilot whales and sperm whales to environmental variability. These aims are achieved utilising long-finned pilot whale teeth sourced from New Zealand and Australia and sperm whale teeth sourced from two regions in Australia: Western Australia and Tasmania.

Investigation of the relationship between tooth growth chronologies and environmental variables comprised comparisons at two scales:

- i) Broad-scale annually averaged climate indices of relevance to the region (Southern Oscillation Index: SOI, Southern Annular Mode: SAM, Indian Ocean Dipole: IOD and the Fremantle sea level: FSL)
- ii) Seasonally averaged and spatially gridded environmental measures (sea surface temperature: SST and zonal wind speed).

By modifying the dendrochronology ‘list method’, I established a method to cross-check GLG identification within individuals and refine age estimates. I then established a repeatable approach to the measurement of GLG widths, suitable for both acid etched teeth (sperm whales) and thin sectioned and stained teeth (pilot whales). Dendrochronology detrending techniques were then trialled on time series of GLG measurements to standardise time series and produce chronologies for each individual. Cubic smoothing splines provided the best fit to the GLG width data for both species with both linear models and negative exponential curves found to be unsuitable. Chronologies derived from each of the individual whales from each sample site were then averaged within calendar years to produce master chronologies at the whole group (composite chronology) and each sample group level, thereby enhancing common environmental signals and reducing the influence of individual variability.

Sample site chronologies for pilot whales were 10 and 12 years for the New Zealand and Australian strandings, respectively. A 70 year time series spanning 1935 – 2004 was established for sperm whales by combining tooth samples from the 1960s (whaling archives), 1990s and 2000s (strandings). Regional sample site chronologies for sperm whales were 30 years in length for the southwest Australia samples, 22 years for the Flinders Island stranding, and 38 and 20 years for the 1998 and 2004 Strahan strandings, respectively.

(i) Broad-scale annually averaged climate indices of relevance to the region: Generalised additive models (GAMs) were used to investigate relationships between broad-scale climate indices and tooth growth. GAMs including the sperm whale composite master chronology as the response variable resulted in poor explanatory

power of environmental predictors. Subsequent environmental comparisons were therefore conducted on sample site chronologies and revealed stronger and contrasting relationships among sample groups.

A positive relationship with the SOI at a one year lag was observed for the New Zealand pilot whale chronology. The Australian pilot whale chronology demonstrated a positive relationship with the SOI and a negative relationship with the IOD. Environmental conditions associated with mutual interactions of the SOI and IOD result in changes in wind and increases in storm activity across the southern Australian region, which may drive increased productivity through mixing and upwelling of productive deep waters. These relationships suggest that the more westerly population of pilot whales is influenced by a mixture of both the SOI and IOD, with low or no influence of the IOD on populations to the east that utilise New Zealand waters.

A negative relationship with the IOD was identified for sperm whales from southwest Australia, while modelled relationships suggested a combination of a positive relationship with the SAM and negative relationship with the IOD were important drivers of tooth growth and energy budgets for the Flinders Island group. In contrast, a positive relationship with the SAM as a single predictor variable was observed for the 1998 Strahan group. Both negative IOD and positive SAM conditions lead to increased westerly winds and storm activity in the southern Australian region, resulting in higher productivity via increased upwelling and mesoscale activity in frontal zones. A positive relationship with the SOI and varying relationship with the IOD (decreasing with negative IOD values and increasing with positive IOD values) were observed for the 2004 Strahan group. Positive SOI conditions are associated with increased storm activity and variations in strength and SST of major currents in the Australian region, leading to regional increases in biological productivity. The effects of the SOI in combination with the IOD are likely to vary depending on the connectivity of SOI and IOD events. Differences in environmental drivers among sample sites suggest spatial variability in foraging patterns among sperm whale social groups, leading to differential responses in energy budgets, most likely associated with spatial variability in prey availability.

(ii) Seasonally averaged and spatially gridded environmental measures:

Correlations between the regional chronologies and seasonal averages of gridded sea surface temperature and zonal wind speed were carried out across a domain bounded by 30°S – 60°S, 94°E – 190°E. Spatial maps of correlations were then produced to identify potential areas associated with higher and lower tooth growth (energy budgets). Areas associated with higher tooth growth for pilot whales from Australia consistently occurred in frontal regions south of Tasmania across all seasons, whereas areas associated with higher tooth growth for New Zealand pilot whales varied among seasons. These differences in spatial correlations suggest consistent utilisation of highly productive frontal regions by the more westerly population of pilot whales, whereas the population in the east may alter foraging movements in response to seasonal variability in regions of high prey biomass. Areas associated with higher tooth growth for sperm whales were consistent with regions of known sperm whale habitat (e.g. southwest of Western Australia and frontal regions south of Australia). Both regions are influenced by variability in the SOI, the IOD and the SAM, with effects on SST, wind direction and storm activity resulting in changes to food webs. Spatial correlations for the southwest, Flinders Island and 2004 Strahan groups consistently occurred in the region southwest of Western Australia in austral winter, but regions associated with higher tooth growth differed across other seasons. In contrast, the 1998 Strahan group showed a consistent pattern of higher tooth growth associated with frontal regions south of Australia across all seasons. Differences in spatial correlations among sample sites suggest previously unknown differences in habitat preferences between sperm whale groups in the southern Australian region.

Conclusions: Through the adaptation of dendrochronology techniques to time series of GLG widths a standardised, transparent and repeatable methodology broadly applicable to long-lived mammal species has been developed. For the first time, relationships between variability in annual GLG widths and broad-scale climate indices have been identified in Southern Hemisphere odontocetes. In doing so, this study has provided a step change in our ability to quantify how a changing environment might influence populations of these and other marine mammals in the future.

Statement of Publication and Co-authorship

Chapters 2 and 3 comprise manuscripts published in peer-reviewed journals. Chapter 4 has been submitted and chapter 5 is in preparation for submission to peer-reviewed journals.

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

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Emma Betty, Auckland University of Technology = Author 4

The candidate was the lead author for each of the manuscripts and responsible for the experimental design, some sample collection, laboratory work/sample preparation, data analyses and interpretation, and preparation of manuscripts. The co-authors contributed to either the collection of data from sample sites, some data analyses, interpretation of results and played a role in supervision of the PhD and revisions of manuscripts for publication. Contributions of co-authors are outlined below:

Paper 1

Hamilton, V., Evans, K. and Hindell, M.A. 2017. From the forests to teeth: Visual crossdating to refine age estimates in marine mammals. *Marine Mammal Science*, 33: 880-888.

Chapter 2 of this thesis

Hamilton, V. (60%), Evans, K. (25%), Hindell, M.A. (15%).

Co-author contributions: Karen Evans helped with study design, cross-verified age estimates, assisted with interpretation of results and contributed to manuscript preparation. Mark Hindell assisted with interpretation of results and contributed to manuscript preparation.

Paper 2

Hamilton, V. and Evans, K. 2018. Establishing growth chronologies from marine mammal teeth: a method applicable across species. *Journal of Experimental Marine Biology and Ecology*, 505, 24-34. doi.org/10.1016/j.jembe.2018.04.006.

Chapter 3 of this thesis

Hamilton, V. (70%), Evans, K. (30%).

Co-author contributions: Karen Evans helped with study design, cross-verified age estimates, assisted with interpretation of results and contributed to manuscript preparation.

Paper 3

Hamilton, V., Evans, K., Raymond, B., Betty, E. and Hindell, M.A. (In review.).
Spatial variability in responses to environmental conditions in Southern Hemisphere long-finned pilot whales.

Chapter 4 of this thesis

Hamilton, V. (55%), Evans, K. (25%), Raymond, B. (5%), Betty, E. (5%), Hindell, M.A. (10%).

Co-author contributions: Karen Evans cross-verified age estimates, assisted with interpretation of results and contributed to manuscript preparation. Ben Raymond provided assistance with the environmental analyses. Emma Betty undertook fieldwork and collection of samples from long-finned pilot whales at Rakiura (Stewart Island), New Zealand. Mark Hindell helped with study design and contributed to interpretation of results. All authors contributed to manuscript preparation.

Paper 4

Hamilton, V., Evans, K., Raymond, B. and Hindell, M.A. (In prep.). Long in the tooth? Insights into environmental influences on energy budgets in marine mammals.

Chapter 5 of this thesis

Hamilton, V. (55%), Evans, K. (25%), Raymond, B. (10%), Hindell, M.A. (10%).

Co-author contributions: Karen Evans helped with study design, cross-verified candidate's age estimates, was responsible for sample preparation and age estimates of teeth from the 1998 stranding, assisted with interpretation of results and contributed to manuscript preparation. Ben Raymond provided analytical advice and assistance with the environmental analyses and contributed to manuscript preparation. Mark Hindell helped with study design and contributed to interpretation of results and manuscript preparation.

We the undersigned agree with the above stated 'proportion of work undertaken' for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

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Acknowledgements

There have been so many people that have helped me over this long journey, first and foremost my supervisors: Karen Evans and Mark Hindell. I cannot thank you both enough for your unwavering support and guidance and extreme patience when family had to take precedence over PhD. Karen – you have been my strongest ally and the best mentor I could have hoped for, I could not have made it to the finish line without you. Mark – thank you for giving me the impetus and confidence to get over the line.

My friends in ‘The Lab’ – most of you moved on but still stuck with me in spirit until the end: Andrea, Ben, Jaimie, Deb, Malcolm, Owen and especially Nat (my PhD co-dependent). Extra special thanks go to Nat, Andrea and Ben for their encouragement and Ben for all the laughs over the years and reading drafts at the end. Ben Arthur, Owen Daniel and Delphi Ward accompanied me on my only trips into the field, fondly remembered for all time by Ben as ‘The most interesting – and least looked forward to second day of – field work ever!’ King Island was quite the adventure, and I am very grateful for your willing support (even though you didn’t know what you were getting yourselves into when you volunteered!).

Ben Raymond was always happy to give statistical advice, make magic happen in the shape of pretty coloured maps and lighten the mood with witty repartee! My eternal gratitude is yours. Dale Maschette who I met at IMAS one night when we were both working late became a good friend and also taught me how to use IncMeas.

DPIPWE Tasmania, specifically Kris Carlyon was a big supporter of my project from the outset, and without his willingness to allow access to sperm whale teeth samples and trusting me with the King Island pilot whale stranding I would have had very few samples! I very much appreciated his encouragement and friendship over the course of my PhD. I was also fortunate to have sample loans from the South Australian Museum, the National Archives of Australia, the Port Elizabeth Museum and Auckland University of Technology. I am grateful to Cath Kemper and David Stemmer (SAM), Greg Hofmeyer and Gill Watson (PEM), Emma Betty (AUT),

Larissa Townsend (NAA), as well as John Bannister for their faith in my project and trusting me with their samples.

I was dependent on a number of people and institutions for lab access and equipment and I am extremely grateful to all for their assistance and support: Cath Kemper at The South Australian Museum allowed me much needed access to the Marine Mammal Aging Lab, taught me so much and gave me her friendship, which I treasure. Along with Cath, David Stemmer, Ikuko Tomo and Peter Shaughnessy treated me like part of the SAM family every time I visited the lab. Cath and David willingly opened the SAM Cetacean collection to me (and let me help dissect the projectile baby sperm whale!). Dirk Welsford, Bryn Farmer, Gabrielle Nowara (Australian Antarctic Division) gave me access to the diamond saw in the Smelly Lab (possibly more aptly named the freezing cold lab!) to wafer pilot whale teeth. Kerrie Swadling (IMAS) allowed me to use her microscope and camera attachment to image pilot whale teeth slides.

During my PhD I was supported through an Australian Government Research Training Program Scholarship and QMS Top-up scholarship and by funding from the Winifred Violet Scott Charitable Trust, the Ethel Mary Read Research Grant and the Australian Geographic Society. I am extremely grateful to these organisations for offering financial support to my project, when so many other funding bodies were not interested in ‘dead stuff’! I am also grateful for the generous funding provided by IMAS and the QMS Program and the Graduate Research Office (UTAS) and the Society for Marine Mammalogy Student Travel Grants Committee for funding to present my work at the Society for Marine Mammalogy 21st Biennial Conference. During my PhD my horizons have been well and truly expanded.

Cory Matthews, who I met at the Dunedin Marine Mammal conference, was always generous with advice, introduced me to Bryan Black and suggested I would find the NADEF dendrochronology workshop helpful, which changed the course of my PhD for the better and introduced me to a new discipline and new friends. Chris Underwood, who I met at NADEF in 2014, became a colleague, co-author and good friend. I am grateful for his encouragement and advice.

A number of dear friends had faith in me, not wanting to disappoint them kept me going, and for that I am extremely grateful: as well as my friends within the PhD bubble, I also need to thank Amanda Winter, Rob Hicklin and Mark Carwardine for their encouragement. Finally, my family: my husband Rob – I know you are glad this is over! Thanks for hanging in there hon. Mads – thanks for the company and keeping my lap warm, even though you made typing difficult! Steph, Alex, Katie and James – I did this for you (and despite you! I'm sure you feel like I did this *to* you!) as well as for myself. It is never too late to follow your heart and finish that unfinished business.

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Chapter 1 General Introduction

Influence of the environment on population dynamics of marine predators

Environmental variability influences physical and biological processes in the marine environment across a range of temporal and spatial scales (Murphy et al., 2007; Stenseth et al., 2002). Broad-scale climatic phenomena are physical drivers of regional oceanographic and weather conditions such as sea surface temperature (SST), wind speed and development of frontal zones and other oceanographic features on varying temporal and spatial scales. Changes to these physical processes have the potential to significantly impact the structure and function of marine ecosystems, through alterations in ocean circulation, nutrient supply and productivity (Doney et al., 2012). Marine ecosystems are underpinned by primary productivity, which is driven by interacting processes of ocean circulation, mixed-layer dynamics, upwelling and nutrient supply (Behrenfeld et al., 2006; Chavez et al., 2011). Variability in the timing, distribution and abundance of phytoplankton blooms will affect secondary productivity (zooplankton), with flow-on effects for prey availability to higher trophic levels (Francis et al., 1998). Biological productivity and prey availability and distribution can vary from year to year, due to short-term environmental fluctuations, or over longer term climatic cycles (Berta et al., 2006). Climate-driven variability in the abundance, distribution and quality of prey resources can affect the foraging success of higher trophic level predators (Learmonth et al., 2006; Österblom et al., 2008).

Prey availability and foraging success determine energetic intake, and acquisition of adequate food and nutrients is essential for an organism to survive and reproduce successfully (Boggs, 1992). Energy obtained from food is allocated to metabolism, growth and reproduction, and organisms must balance their energy intake with energy expenditure across these activities, with the aim of maintaining a positive energy balance (energy intake greater than expenditure); i.e., their *energy budget* (Boyd, 2002; Costa, 2009; Lockyer, 2007). In circumstances where an individual's prey intake is insufficient, growth or body condition will be compromised, and

reproductive activities or survival may be affected (Costa, 2009; Jeanniard-du-Dot et al., 2017; Lockyer, 2007; Trites et al., 2007). Variability in environmental conditions that affect prey resources can subsequently have flow-on effects to population dynamics of marine predators (Bowen et al., 2002; Learmonth et al., 2006; Schumann et al., 2013).

The effects of climate variability on the population dynamics of marine predators are recognised across many taxa (Stenseth et al., 2002). Such relationships can be complex at higher trophic levels as changes in population state may occur at a lag to environmental changes, and can vary in magnitude and effect depending on region, food web transfer and life history of species (Bakun and Broad, 2003; Trathan et al., 2007). Changes in the availability or quality of prey resources related to regional effects of climate oscillations has been observed to impact reproductive success of marine mammal populations, through reduced maternal transfer to offspring or deferred reproduction (Forcada et al., 2005; Greene and Pershing, 2004; Seyboth et al., 2016). For example, foraging success and first year survival of southern elephant seals (*Mirounga leonina*) has been related to the effects of El Niño-Southern Oscillation (ENSO) events on prey availability and maternal foraging success and provisioning to pups prior to weaning (McMahon and Burton, 2005). Reproductive failure and high mortality of seabird and pinniped species near the Galápagos and on the coast of Peru was linked to the effects of the strong 1982 El Niño on prey availability and distribution (Barber and Chavez, 1983; Trillmich and Limberger, 1985). Conversely, annual body fat accumulation for energy storage, and pregnancy rates of female fin whales (*Balaenoptera physalus*) in the northeast Atlantic were observed to increase with a concomitant increase in euphausiid prey abundance (Lockyer, 1986).

Understanding the responses of species to their environment is fundamental for determining how populations may be impacted by future climatic variability, and how best to manage those populations and the broader ecosystem under ongoing oceanic change. Nevertheless, the impacts of environmental variability on many marine predators remain poorly understood. Marine mammals are especially challenging to study; their at-sea distribution, often remote and unpredictable study sites, and for cetaceans at-sea breeding behaviour, makes obtaining data logistically difficult.

Subsequently for many long-lived marine mammal species, particularly cetaceans, the extent to which changing environmental conditions will impact energetic intake and population dynamics is difficult to assess. This is particularly so for the Australian and New Zealand regions.

Climate influences on marine productivity in the Southern Hemisphere

Marine ecosystem function across the Australian and New Zealand region is influenced by interannual climate variability related to broad-scale climate and atmospheric patterns, primarily the ENSO, the Indian Ocean Dipole (IOD) and the Southern Annular Mode (SAM) (Salinger et al., 2016). The ENSO and the IOD have more influence across the Australian region, while the ENSO has more influence on climate and oceanographic conditions across the New Zealand region. Climate variability associated with changes in the SAM is more prominent across southern regions. Fluctuations in the phases of broad-scale phenomena influences climate and oceanographic conditions on a regional scale, which are important drivers of marine productivity and the abundance and distribution of prey resources (Stenseth et al., 2002).

Climate variability influences ocean circulation and productivity particularly through changes in SST and wind conditions (Behrenfeld et al., 2006; Stenseth et al., 2002). Higher wind speeds are negatively correlated with SST (Trenberth, 1976), and stronger winds are frequently associated with elevated productivity due to increased vertical mixing through the water column, and changes in surface winds and oceanic currents (Poloczanska et al., 2007). Variability in the annual frequency of strong zonal westerly winds has been correlated with the frequency of cetacean strandings on southeast Australian coastlines, likely due to cetaceans following prey aggregations associated with wind-driven higher coastal productivity into shallow waters (Evans et al., 2005). Relationships between wind strength and recruitment variability of commercially important fish species have been documented in southeast Australian waters (Harris et al., 1988; Thresher, 1994). Physical oceanographic features such as oceanic fronts, upwelling zones and cold or warm core eddies, characterised by SST gradients, are frequently regions of higher primary productivity and subsequently

satellite derived measurements of SST can provide a proxy for locations of increased prey biomass (Bakun, 2006; Bost et al., 2009; Grémillet et al., 2008; Tynan, 1998). Although higher predators are separated from SST 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; Guinet et al., 2001; Pinaud and Weimerskirch, 2007). From the onset of variations in broad-scale climate phases, there may however be a temporal lag and/or spatial separation between wind-driven changes in mixing and SST, the onset of increased productivity, and transfer to higher trophic levels (Jaquet and Whitehead, 1996; Mann and Lazier, 2006).

El Niño-Southern Oscillation

The ENSO 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; Trenberth, 1997). These fluctuations in sea surface temperature occur irregularly on cycles of two to ten years, with varying intensity (Trenberth, 1984; Trenberth and Stepaniak, 2001). The strength of El Niño and La Niña events are measured by the Southern Oscillation Index (SOI), calculated as the mean sea level pressure difference between the east (Tahiti) and west (Darwin) Pacific; strong sustained negative (positive) SOI values below -7 (above $+7$) are indicative of El Niño (La Niña) events. Effects on climate and biological processes have been related to ENSO across broad spatial scales, with pronounced impacts on the availability and nutritive value of prey resources for marine predators such as fish, seabirds and marine mammals during strong El Niño events (Barber and Chavez, 1983). Impacts on marine ecosystems are most obvious in the equatorial/tropical Pacific where El Niño events originate, but effects propagate to the South Pacific, Indian and Southern Oceans via atmospheric teleconnection and oceanic processes (Cai et al., 2011a; Carleton, 2003; Fogt et al., 2011). Effects on circulation, SST, productivity and higher trophic levels due to

ENSO-related physical forcing outside the tropical Pacific vary regionally and temporally (Murphy et al., 2007; Trathan and Murphy, 2002; Trathan et al., 2007).

Environmental variations resulting from changes in the ENSO impact the marine regions of Australia through changes in winds and storm track activity (Ashok et al., 2007; Cai et al., 2011b; Nakamura et al., 2004) and changes in the flow strength and SSTs of the major boundary currents that flow parallel to the Australian coastline: the Leeuwin Current to the west and the East Australian Current to the east (Feng et al., 2003; Holbrook et al., 2009). The ENSO cycle has a strong influence on New Zealand climate, particularly in terms of seasonal wind regimes (Gordon, 1985; Mullan, 1995). During La Niña events New Zealand experiences more northeasterly winds, reduced westerlies and SSTs are generally warmer, while strong El Niño events are associated with increased westerlies and southwesterlies and lower SSTs (Gordon, 1985; Hurst et al., 2012; Mullan, 1995).

Indian Ocean Dipole

The IOD 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 (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 IOD is measured by the dipole mode index (DMI), which generally fluctuates within the range -0.4 to $+0.4$. Positive (negative) IOD events are also associated with a teleconnection off the southwest coast of Australia, resulting in a weakening (strengthening) of westerly winds and storm activity over southern Australia (Ashok et al., 2007; Cai et al., 2011b; Weller et al., 2012). The IOD and ENSO have a complex, in/out of phase relationship; positive (negative) IOD events can co-occur with El Niño (La Niña) events, or develop independently (Meyers et al., 2007; Saji and Yamagata, 2003; Yamagata et al., 2004). The impacts of El Niño and La Niña events are often more pronounced when the IOD and ENSO are in phase (Yamagata et al., 2004).

Phases of the IOD have been associated with shifts in SSTs and in association net primary productivity and the catch rates of yellowfin tuna (*Thunnus albacares*) across the Indian Ocean (Lan et al., 2013). However, the effects of the IOD on the Australian marine environment are not well known, with the majority of studies focused on the influence of the IOD on rainfall across Australia (e.g. Cai et al., 2009; Risbey et al., 2009). Increases and/or directional changes in wind and increased storm activity associated with negative IOD phases are likely to be beneficial to marine predators that utilise fronts and upwelling zones, due to increases in productivity and prey abundance via wind-driven mixing and current transport (Bost et al., 2009; Genin et al., 1988; Murphy, 1995).

Southern Annular Mode

The SAM describes the atmospheric phenomenon of the north-south oscillation of the westerly wind belt surrounding Antarctica (Thompson and Wallace, 2000). The SAM index is defined as the monthly difference in zonal mean sea level pressure between 40°S and 65°S (Gong and Wang, 1999). Seasonal and interannual atmospheric variability in the mid to high southern latitudes is dominated by the SAM, which drives large-scale variability of the Southern Ocean (Hall and Visbeck, 2002; Marshall, 2003). The SAM index generally fluctuates within the range -4 to $+4$ (Marshall, 2016). 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 (Hall and Visbeck, 2002; Thompson and Wallace, 2000). Changes in the meridional position and productivity of Southern Ocean frontal zones are associated with changes in the SAM, and can vary on basin-wide scales (Bostock et al., 2015; Lovenduski and Gruber, 2005; Sallée et al., 2008; 2010). Southern annular mode variability can result in wind-driven shifts in the position of Southern Ocean fronts and currents, changes to mixed layer depths, and associated changes in productivity (Leung et al., 2015; Lovenduski and Gruber, 2005; Sallée et al., 2010). The SAM index has been dominated by an increasingly positive trend (i.e., a shift to the positive phase, highest in austral summer) since the late 20th century, attributed to anthropogenic forcing by greenhouse emissions, with this shift predicted to continue in the future (Marshall, 2003; Thompson et al., 2011).

Oceanographic features of the southern Australian and New Zealand regions

Marine predators are known to exploit regions of high productivity, resulting from bathymetric features or oceanographic factors that concentrate prey biomass, e.g. frontal zones, currents, upwelling systems, eddies, seamounts (Ballance, 2009; Bost et al., 2009; Tynan, 1998). The productivity of the Australian marine environment is dominated by two southward-flowing boundary currents that flow parallel to the west (Indian Ocean) and east (Pacific Ocean) coasts (Ridgway and Dunn, 2003; Ridgway and Condie, 2004; Suthers et al., 2011; Waite et al., 2007). South of Australia and New Zealand, the Southern Ocean is subdivided into distinct circumpolar regions by three major fronts; the subtropical front (STF), the subantarctic front (SAF) and the polar front (PF) (Belkin and Gordon, 1996; Orsi et al., 1995) (see Figure 1.1). New Zealand is an isolated landmass in the western Pacific Ocean surrounded by a complex bathymetry of submarine plateaus and canyons, deep sea trenches, ridge systems, and seamounts (Gordon et al., 2010; Heath, 1985). The interaction of currents and water masses with bathymetric features gives rise to greater productivity in New Zealand waters compared to the relatively oligotrophic surrounding waters of the Pacific Ocean (Gordon et al., 2010). Three major plateaus dominate the region: the Challenger Plateau, the Campbell Plateau in the subantarctic and the Chatham Rise (Figure 1.1).

The Leeuwin Current and southern Australian region

The Leeuwin Current is a warm boundary current that flows south along the West Australian coast and east along the coast of southern Australia (Cresswell and Golding, 1980; Feng et al., 2012; Ridgway and Condie, 2004). The ENSO drives variability in the flow strength and temperature of the Leeuwin Current, which varies seasonally due to changes in coastal wind stresses (Feng et al., 2003; Godfrey and Ridgway, 1985). A strong (weak) Leeuwin Current flow is associated with higher (lower) sea level anomalies along the western coast of Australia and positive (negative) SOI (Feng et al., 2003). The Fremantle coastal sea level (FSL) is a proxy index for the strength of the Leeuwin Current (Feng et al., 2010). The submarine canyons that incise the west and southern Australian shelf regions are known areas of increased upwelling and eddy formation supporting high productivity and

aggregations of large marine predators (Pattiaratchi, 2007; Rennie et al., 2009). On the southern coast highly productive seasonal upwelling along the shelf and shelf break occurs between the eastern side of the Great Australian Bight and western Bass Strait between November and May due to upwelling-favourable winds (Kämpf et al., 2004; Middleton and Bye, 2007).

The East Australian Current, Tasman Sea and New Zealand waters

The EAC flows south from the tropics into the Tasman Sea (Figure 1.1), where high seasonal productivity is driven by eddy separation from the main current flow (Tilburg et al., 2002). Flow strength of the EAC varies seasonally and interannually, and is highest during austral summer and La Niña conditions (Harris et al., 1988; Holbrook et al., 2011; Ridgway and Godfrey, 1997). The EAC separation flows eastward across the Tasman Sea forming the Tasman Front, and the East Auckland and East Cape Currents north of New Zealand (Denham and Crook, 1976; Stanton, 1981; Tilburg et al., 2001). The mesoscale eddy field generated by the Tasman Front separation and currents northeast of New Zealand support high primary productivity through the interaction of warm subtropical and cooler subantarctic waters and current and eddy driven mixing (Bradford et al., 1982; Murphy et al., 2001; Tilburg et al., 2002).

Oceanic fronts south of Australia and New Zealand

South of Australia and New Zealand the STF and the SAF are highly productive due to the convergence of subtropical and subantarctic waters, wind driven upwelling of cooler waters and eddy formation (Sokolov and Rintoul, 2002; Tomczak et al., 2004; Westwood et al., 2011). South of New Zealand the STF is bathymetrically constrained by the Campbell Plateau until it deflects eastwards along the Chatham Rise, where upwelling and frontal mixing results in relatively high productivity (Bradford-Grieve et al., 1999; Heath, 1981; Hopkins et al., 2010). The STF over the Campbell Plateau and Chatham Rise shows greater seasonality in primary productivity than the STF over open waters, with chlorophyll *a* levels highest during the spring bloom (Bradford-Grieve et al., 2003; Nodder et al., 2003). The Campbell Plateau and Chatham Rise regions encompass important foraging zones for marine mammals and

seabirds and commercially important fisheries including squid (Bradford-Grieve et al., 2003; Chilvers, 2008; Jackson et al., 2000; Waugh et al., 1999).

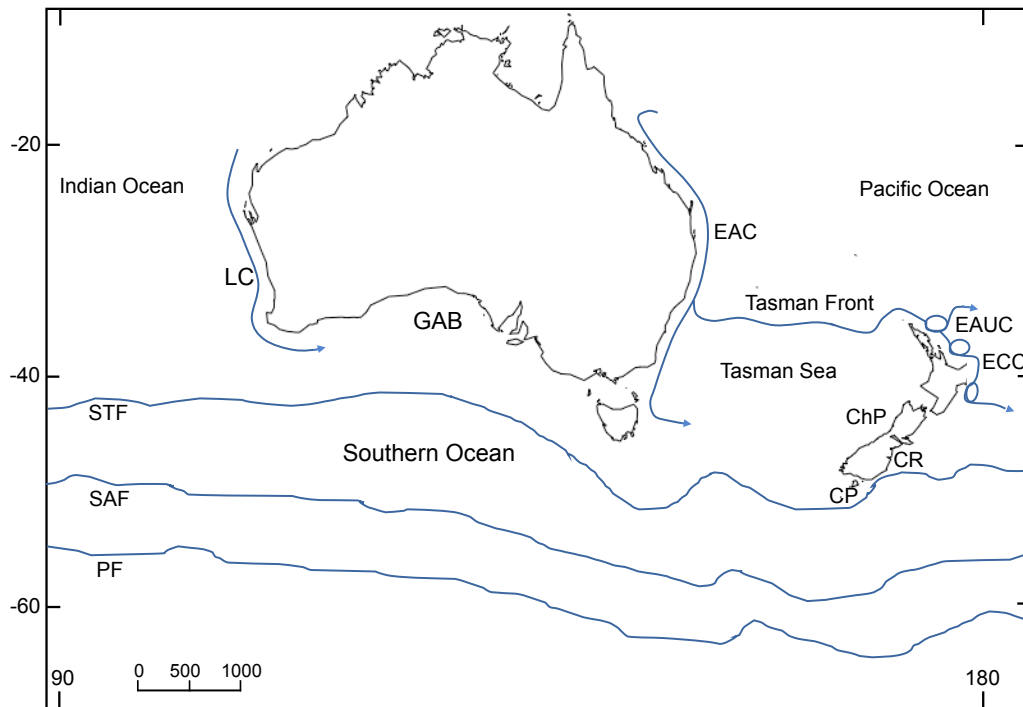


Figure 1.1. Schematic diagram showing the approximate location of major surface currents, oceanic fronts and bathymetric features surrounding Australia and New Zealand. LC: Leeuwin Current, EAC: East Australian Current, GAB: Great Australian Bight, STF: subtropical front, SAF: subantarctic front, PF: polar front, EAUC: East Auckland Current, ECC: East Cape Current, ChP: Challenger Plateau, CP: Campbell Plateau, CR: Chatham Rise.

Teeth as proxy archives of variability in energy budgets

To better understand environmental drivers of foraging behaviour, physiology, survival or reproductive success, datasets of varying lengths are necessary to cover year-to-year or sub-decadal variability and also climatic cycles operating on decadal time scales (Trathan et al., 2007). Obtaining such datasets, particularly long-term, longitudinal datasets for marine mammals that provide a measure of changes in energy budgets and population state has inherent difficulties. The cryptic nature of many species, combined with time and financial constraints make obtaining such

datasets challenging, and is rarely achievable over extended, continuous time periods. There is therefore a need for alternative, time-efficient and cost-effective methods of investigating the effects of environmental variability on marine mammals.

Retrospective studies that encompass past trends and responses to environmental variability can increase understanding of potential future responses (Brown et al., 2011; Chambers et al., 2015). In this regard, high-resolution proxy archives of changes in growth and energy budgets can make a valuable contribution to our knowledge of the impacts of climate variability on marine species (Helama et al., 2006a; Morrongiello et al., 2012). Assessment of historical relationships between the environment and energy budgets of species can increase understanding of past responses to climate variability and change; information that can be used to inform predictive ecosystem models and future management approaches (Chambers et al., 2015; Morrongiello et al., 2012). Proxy archives, such as hard structures that accumulate incremental annual growth are a valuable resource as they can provide a more accessible and rapid (in instances where such samples have been archived) means of gaining insights into the effects of the environment. Such archives can also provide historical perspectives, integrating responses to both short-term (i.e., annual to interdecadal) changes and longer-term (multidecadal) trends and patterns of climate variability (Morrongiello et al., 2012).

Within the teeth of marine mammals, incremental growth layers (known as growth layer groups or 'GLGs') are deposited in the dentine and cementum of each tooth. Each GLG is broadly defined as comprising a pair of layers, one broad and one fine, occurring as a cyclic and repeatable pattern (Perrin and Myrick, 1980). Dentine comprises the bulk of the tooth structure and is a mineral/organic composite: largely inorganic material; primarily calcium phosphate minerals with small amounts of elements, and organic material; mainly collagen (Hillson, 2005; Klevezal', 1996). The incremental layering pattern of dentine results from changes in density due to variations in mineralisation rates and collagen synthesis, influenced by a combination of endogenous rhythms, nutritional supply and environmental or metabolic stress experienced over the deposition period of each GLG (Boyde, 1980; Klevezal', 1996; Langvatn, 1995; Maas, 2009). Growth layer groups are metabolically inert after deposition and because odontocetes are monophyodonts, the number of GLGs within the tooth cementum or dentine can be counted to provide an estimate of an

individual's age (Hohn, 2009; Scheffer and Myrick, 1980). Annual deposition of GLGs has been validated for a number of species, for example, spinner dolphins; *Stenella longirostris* (Myrick et al., 1984) and bottlenose dolphins; *Tursiops truncatus* (Hohn et al., 1989). Based on similar layering structure and biological parameters of odontocetes, GLG deposition is assumed to be annual for those species in which validation of GLGs is impractical (Hohn, 2009).

Energy essential for the metabolic processes associated with GLG deposition are necessarily derived from an individual's diet (Klevezal', 1996; Langvatn, 1995). Factors influencing the deposition of GLGs in teeth will therefore be mediated primarily by prey availability and foraging success, although other factors that affect the amount of energy available for growth can vary with age, sex, condition and reproductive state (Berta et al., 2006; Costa, 2009; Klevezal', 1996; Rosen, 2009). Experimental studies in terrestrial mammals have established that changes in an individual's growth rate are 'recorded' by changes in the growth of teeth (Klevezal', 1980). Inhibition or stimulation of growth in laboratory rats (*Rattus norvegicus*) demonstrated changes in body weight were correlated with changes in dentine thickness (Johannessen, 1964). For marine mammals, relationships between tooth growth and overall body growth and energetic intake have been demonstrated in northern fur seals; *Callorhinus ursinus* (Baker and Fowler, 1990), Antarctic fur seals; *Arctocephalus gazella* (Boyd and Roberts, 1993; Hanson et al., 2009) and polar bears; *Ursus maritimus* (Medill et al., 2010). A reduction in dentinal GLG widths coincided with the decrease in overall body growth rate in bottlenose dolphins (Hohn, 1980). Changes in GLG widths have been linked to the reproductive demands of marine mammals, with reduced GLG deposition during periods of high maternal investment (Medill et al., 2010; Von Biela et al., 2008). Nutritional stress during times of low food availability has been related to the formation of anomalous growth layers in marine mammal teeth including those of dusky dolphins; *Lagerorhynchus obscurus* (Manzanilla, 1989), pilot whales; *Globicephala melas* and *G. macrorhynchus* (Lockyer, 1993a) and dugongs; *Dugong dugon* (Mitchell, 1981). Experimental confirmation of links between overall body growth and tooth growth is impractical in large cetacean species, but there is every reason to assume the mechanisms of tooth formation are the same as in other mammalian species (Klevezal', 1980).

Given that the deposition of annual GLGs can be linked to the overall energy an individual has for metabolic processes, interannual variability in GLG width will reflect the nutritional status or physiological condition of the individual at the time of deposition (Boyd and Roberts, 1993; Hanson et al., 2009; Klevezal', 1996). Consequently, variation in GLG widths can be considered a proxy record for variability in energy budgets, with the growth of each GLG representing energetic intake balanced with energetic outputs (e.g. costs of movement and foraging, maintenance of body functions and condition and reproductive output) for the year (Hamilton et al., 2013; Hanson et al., 2009). A deficit in the individual's annual energy budget due to inadequate nutritional intake and/or physiological stresses will result in 'below average' tooth deposition; i.e., a relatively narrow GLG, whereas high energetic intake due to good conditions of prey availability will manifest as 'above average' tooth deposition; i.e., a relatively wide GLG (Hamilton et al., 2013; Klevezal', 1996; Lockyer, 1993a). Interannual variability in GLG widths can therefore provide a temporally continuous, proxy record for energy budgets throughout the lifetime of an individual, analogous to chronologies of annual tree-ring growth (Bradley et al., 2003; Hamilton et al., 2013; Knox et al., 2014).

To date, a small number of studies have explored relationships between variability in tooth growth and the environment for marine mammal species. Tree-rings and bivalve shell increments represent a direct growth record of variation in size that can be related to extrinsic conditions (Morrongiello et al., 2012; Speer, 2010). Tree-ring growth or the growth of increments in bivalve shells, and to an extent teleost otoliths are more dependent on environmental conditions than are mammalian growth rates (Klevezal', 1996). For mammals, the effect of the environment on energy budgets and tooth growth will be indirect, and driven by factors such as changes in prey density (and energetic intake) rather than climate variability *per se*. The coupling between growth and extrinsic conditions means that exposure to similar environmental conditions for trees in particular, but also bivalves and teleosts, induces common growth responses among individuals within the same region (Black, 2009; Stokes and Smiley, 1996). The 'synchronising' effect of the environment on the growth of individuals is a fundamental requirement for chronology studies, whereby variations in environmental conditions will cause individuals from the same region to manifest similar patterns of narrow and wide growth increments (Black et al., 2005; Fritts,

1976). Individual-level responses will vary (i.e., some level of individual ‘noise’ is to be expected), however the overall regional population signal should reflect relationships between growth and environmental influences (Black et al., 2016; Speer, 2010). Synchrony among individuals in the year of formation of anomalous dentinal layers in teeth of dusky dolphins; *Lagenorhynchus obscurus* (Manzanilla, 1989) and Commerson’s dolphins; *Cephalorhynchus commersonii* (Dellabianca et al., 2012) has been observed. The occurrence of the anomalous layers was then correlated with key Southern Hemisphere climate oscillations (i.e., the SOI, and the SAM). While not directly related to changes in GLG widths, the observed synchrony suggests that climate-driven changes in environmental conditions influence the formation of similar growth layers in the teeth of individuals from the same region.

Previous investigations have identified relationships between time series of GLG widths and environmental variables, such as the SOI (*Arctocephalus* spp.: Boyd and Roberts, 1993; Knox et al., 2014), the SOI and local SST (*A. forsteri*: Wittmann et al., 2016) and SST (*Physeter macrocephalus*: Hamilton et al., 2013). The life span and length of the resultant time series for many species however, particularly pinnipeds and small delphinid species, can restrict the ability to differentiate between short-term variability (i.e., noise) and variability in growth operating on longer time scales. Additionally, studies so far have varied in methodology, generally being developed specific to the particular dataset, with differing approaches to measurement and standardisation of GLG widths, and varying use of individual or population wide responses in comparisons with environmental indices. As a result, the applicability of techniques to other species or regions, and comparability between studies has been limited. Tooth growth chronology development could be improved by the application of proven methods developed for use on other taxa in terrestrial environments, and more recently applied to marine invertebrate and teleost species. Once established, standardised techniques should be applicable to other long-lived marine mammal species, allowing comparisons on a similar basis between regions, species and taxa.

Applying dendrochronology techniques to develop tooth growth chronologies

The use of annually resolved chronologies for establishing relationships between long-term tree-ring growth and environmental drivers was pioneered in the field of dendrochronology (tree-ring science). Robust methods have been developed for producing multidecadal chronologies and isolating regional or population-wide common climatic signals, to enable investigation of relationships between environmental drivers and growth. Dendrochronology techniques have been further expanded to establish relationships between environmental drivers and long-term chronologies of marine species with structures that exhibit incremental growth ('sclerochronology'), such as corals, bivalves and teleost otoliths (e.g. Black, 2009; Carilli et al., 2010; Matta et al., 2010; Rountrey et al., 2014). Chronology development for many marine teleost species requires considerations that are also applicable to marine mammals, such as shorter life spans than trees, the ability to move across regions of differing environmental conditions, and higher levels of individual variability (e.g. Black et al., 2008a; Gillanders et al., 2012; Ong et al., 2015).

Adapting dendrochronology techniques to build annually resolved tooth growth chronologies has the potential to address previous limitations associated with establishing relationships between tooth growth and environmental variability, the research problem herein, and issues specific to marine mammal tooth growth chronologies (such as tooth wear, and that knowledge of birth date is impractical for individuals of most species). Chronologies derived through dendrochronology techniques can be compared to annually resolved climate and oceanographic indices to investigate how changes in environmental factors may affect energy budgets of individuals. The current study builds on Hamilton et al. (2013) through the implementation of dendrochronology methods to establish a standardised and readily repeatable method for tooth growth chronology development. Additionally, the use of crossdating is extended to marine mammal tooth growth chronologies. Crossdating is a fundamental principle of dendrochronology studies, yet has been relatively unexplored for marine mammal teeth to date.

Study species

Testing the efficacy of these methods requires study species with relatively long life spans. As long-lived species, sperm whales (70 – 80 years; Ohsumi, 1966) and pilot whales (35 – 60 years; Bloch et al., 1993) should provide long time series for analysis, and therefore the potential for chronologies to capture climate signals on an appropriate temporal scale. Both sperm whales and pilot whales have strong social bonds. Female sperm whales maintain long-term, multi-year associations in social units averaging 10 – 13 individuals, with other related females, and their immature offspring, as well as unrelated females (Christal and Whitehead, 2001; Christal et al., 1998; Mesnick, 2001). Immature males separate from their natal groups at around four to five years of age, or older, remaining in multi-male ‘bachelor’ groups of 12 – 15 individuals until they reach maturity when they become increasingly solitary (Best, 1979; Rice, 1989; Whitehead, 2009). Pilot whales are highly social animals, travelling in cohesive, multigenerational matrilineal groups of 10 – 50 individuals; however feeding aggregations can number 100s (Amos et al., 1993; Ross, 2006). The social structure of sperm whales (particularly females) and pilot whales means that animals from the same social group should experience similar environmental conditions throughout all, or a portion of their lives, and therefore demonstrate common signals in energy budget responses to environmental variability.

Because sperm whales and pilot whales frequently mass strand, access to reasonable sample sizes sourced from potentially socially connected individuals is possible. Additionally, in the case of sperm whales, archived tooth samples collected during past whaling operations provides the opportunity to explore responses to environmental variability over extended periods of time.

Aims

This project aims to improve understanding of how the energy budgets of long-lived, top predator species are influenced by variability in the marine environment. The project does this by:

- i) Firstly exploring the applicability of dendrochronology techniques to time series of GLG widths measured in odontocete teeth (as proxies for energy budgets), and their potential for improving understanding of the relationships

between marine mammal species and environmental variability. This includes establishing methodologies for generating chronologies of annual tooth growth that are transparent, repeatable and applicable across multiple marine mammal species.

ii) Applying this methodology to the study species: sperm whales and long-finned pilot whales to investigate relationships between variability in tooth growth and a number of climate and environmental indices reflecting variability in the marine environment. Little is known regarding the spatial movements and influence of environmental factors on the foraging success and associated energy budgets in these species within the Southern Hemisphere. As wide-ranging pelagic species foraging across the Southern Ocean, south Indian Ocean and southwest Pacific Ocean, sperm whales and pilot whales are likely to be indirectly affected by multiple climate drivers that influence prey availability and distribution. Spatial variability in relationships are explored by including samples from sperm whales derived from Western Australia (1960s whaling archives) and from Tasmania, Australia (1990s and 2000s strandings) and samples from long-finned pilot whales stranded in New Zealand and Tasmania (Figure 1.2).

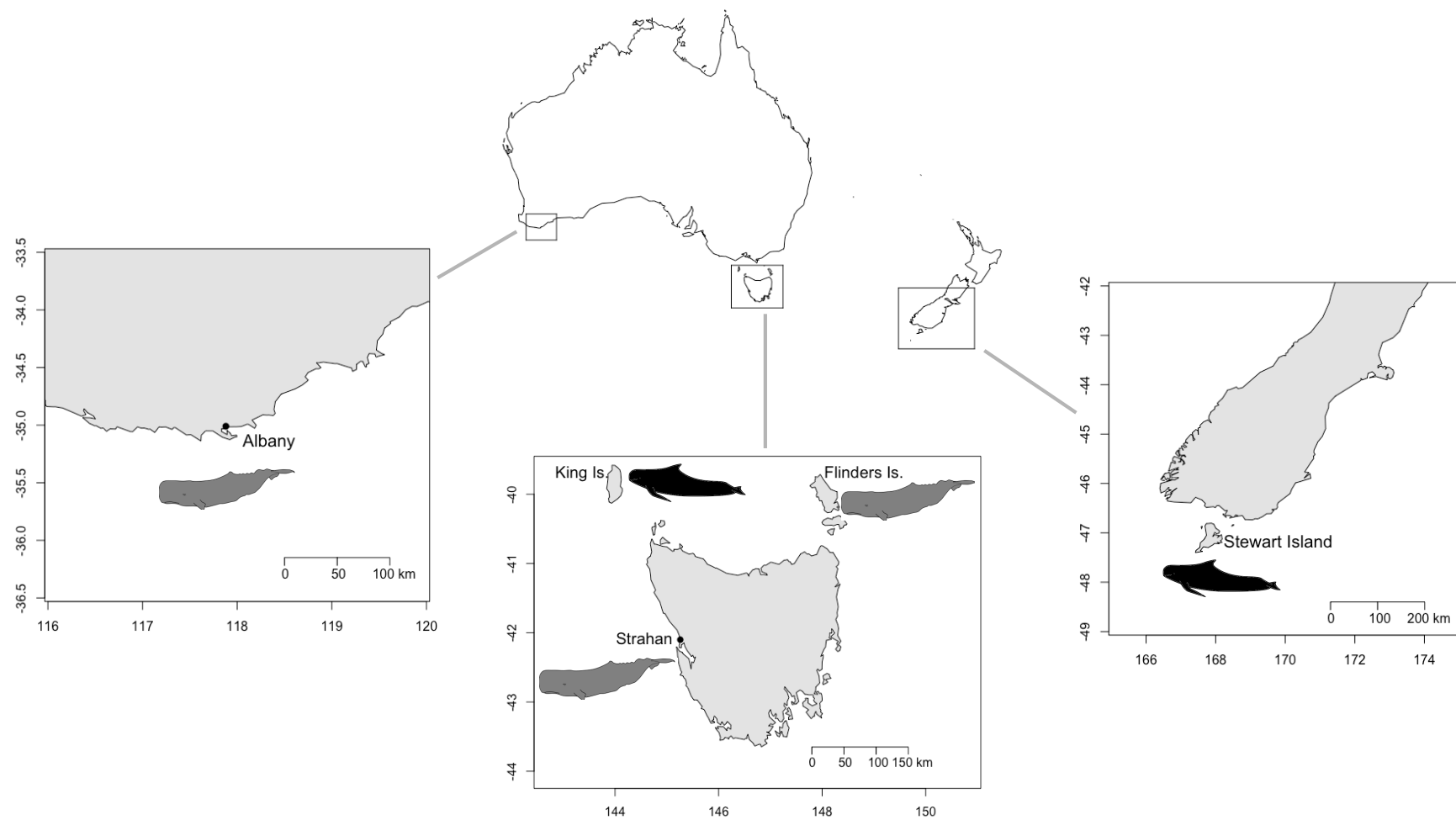


Figure 1.2. Locations of sample sites in Australia and New Zealand from which tooth samples were obtained from sperm whales and long-finned pilot whales.

Thesis structure

This thesis has been written as a series of separate manuscripts and consequently there is some overlap of text and concepts between chapters. The thesis consists of four research chapters; two chapters in which the methodology is established, with the following two chapters detailing the application of the methodology to the study species to investigate relationships between energy budgets and environmental variability. A final discussion chapter brings together key considerations for the broader application of techniques outlined within the thesis, and provides an integrated overview of the modelled relationships and potential future implications under changing environmental conditions. All chapters, with the exception of this introductory chapter and general discussion, consist of manuscripts that are either published papers, or submitted manuscripts. The Candidate was the senior author on all papers; co-authors are listed at the start of each chapter and author contributions are outlined in the Statement of Co-authorship at the front of the thesis. A brief outline of each research chapter is presented below:

Chapter 2 – From the forests to teeth: Visual crossdating to refine age estimates in marine mammals

Using sperm whale teeth as a case study, this chapter describes a modified approach to the dendrochronology technique of visual crossdating, to match synchronous deposition of distinctive GLGs across multiple teeth from each individual whale. The cross-checking process can be used to refine GLG identification and age estimates based on annual tooth growth, resolving confusion between accessory layers and GLGs. Accuracy in annual GLG identification and subsequent assignment to the correct calendar year are important first steps in building chronologies for comparisons with annually resolved climate indices.

Chapter 3 – Establishing biochronologies from marine mammal teeth: A method applicable across species

Chapter 3 describes the methodology developed during this research project for establishing chronologies of tooth growth from time series of measured GLG widths (as a proxy for energy budgets) in teeth of odontocete whales. Based on dendrochronology techniques, a consistent, step-by-step method to chronology

development is described. The method is broadly applicable across species, ensuring comparability across species and different studies, and allows chronologies to be established relatively quickly.

Chapter 4 – Spatial variability in responses to environmental conditions in Southern Hemisphere long-finned pilot whales

The methodology developed in chapters 2 and 3 is used on long-finned pilot whales to investigate the application to time series of tooth growth, and responses to environmental variability. Using annually resolved broad-scale climate indices and spatial measurements of regional oceanic variables (SST and zonal wind speed); models are used to investigate relationships between pilot whale tooth growth chronologies and variability in the ocean environment across two geographic regions in the Southern Hemisphere; New Zealand and Australia.

Chapter 5 – Long in the tooth? Insights into environmental influences on energy budgets in marine mammals

Multidecadal tooth growth chronologies of sperm whales from four spatially and temporally separated sample groups (southwest Australia whaling catches 1965 – 1966 and three Tasmanian strandings between 1998 – 2004) are established in this chapter. Modelled relationships between tooth growth chronologies and broad-scale climate indices and spatial measurements of regional variables (SST, zonal wind speed), are then used to investigate regional variability in relationships among chronologies for sperm whales from different social groups, and potential differences in foraging habitat usage in the southern Australian region.

Chapter 2 From the forests to teeth: Visual crossdating to refine age estimates in marine mammals

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All of the research contained in this chapter has been published as:

Hamilton, V., Evans, K. and Hindell, M.A. 2017. From the forests to teeth: Visual crossdating to refine age estimates in marine mammals. *Marine Mammal Science*, 33: 880-888.

Abstract

Age estimates based on annual growth layer deposits (known as growth layer groups or ‘GLGs’) in marine mammal teeth can contain uncertainties, due to variability in tooth structure, and differences between researchers in their interpretation of GLGs and (subannual) accessory layers. Within teeth some GLGs are distinct in appearance, and can be used to match synchronous growth patterns among multiple teeth from the same individual(s). We describe the tree-ring science technique of visual crossdating using sperm whale teeth, as an aid to improve consistency in GLG identification and thereby refine age estimates based on annual tooth growth.

Introduction

Estimation of the age of individuals is a fundamental parameter for understanding the biology of individuals and ecology of populations. Incremental growth deposits in tooth dentine or cementum, known as growth layer groups (GLGs), have been used to estimate the age of toothed marine mammals (odontocetes, pinnipeds) since the 1950s (Scheffer and Myrick, 1980). In most species, it is assumed that GLGs are deposited annually (Hohn, 2009). Validation of this assumption has only been possible in a small number of marine mammal species (e.g. Bowen et al., 1983; Hohn et al., 1989; Lockyer, 1993a; Myrick et al., 1984; Oosthuizen, 1997), due to impracticalities in obtaining validated ages (Evans et al., 2002a; Hohn, 2009). For species in which validation of age is not possible, absolute age or the accuracy of age estimates cannot be confirmed (Campana, 2001). Further, the precision of estimates (i.e., the closeness of repeat counts from an individual tooth) may not necessarily reflect the best estimate of age and, at present, an objective method to assist with identification of GLGs for age estimation purposes has not been established (Campana and Stewart, 2014; Evans et al., 2002a).

Uncertainties in GLG identification and age estimates can arise due to poor clarity and appearance of GLGs, variability in tooth structure, preparation techniques, and differences between readers in their interpretation of GLGs (Evans et al., 2002a; Evans and Robertson, 2001; Hohn, 2009; Hohn et al., 1989). Standardised terminology and accepted descriptions of GLG appearance for most toothed marine mammal species have been developed to address some of these complications (Perrin and Myrick, 1980). However, while these descriptions provide essential guides to identifying GLGs and ultimately obtaining an age estimate, a considerable element of subjectivity moderated by experience on the part of researchers is still associated with age estimation (Evans et al., 2002a; Hohn, 2009; Perrin and Myrick, 1980). Much of this subjectivity relates to the reader's interpretation of GLGs and other features, such as accessory layers, within a tooth (Evans et al., 2002a; Hohn, 2009).

Within the teeth of individuals, some GLGs are more distinct or vary in appearance relative to surrounding GLGs (Klevezal', 1996; Klevezal' and Myrick, 1984; Lockyer, 1993a; Luque et al., 2013). Similar layering structure and patterns in the occurrence of

distinctive GLGs have been observed within multiple teeth from the same individual for a number of odontocete species including sperm whales (Klevezal', 1996; Mikhalev, 1982), spinner dolphins (Myrick, 1988), bottlenose dolphins (Hohn et al., 1989), harbor porpoises (Luque et al., 2009), long-finned and short-finned pilot whales (Lockyer, 1993a). Conceptually similar to the 'signature years' of relatively narrow or wide layers used for crossdating growth increments in trees and otoliths (Black et al., 2005; Stokes and Smiley, 1996), distinctive layers and variability in GLG widths from marine mammals can potentially be used to match synchronous patterns of GLG growth between multiple teeth from the same individual.

Crossdating is a fundamental principle of dendrochronology (tree-ring science), and is based on the premise that environmental factors that vary over time will influence growth of individuals within a region, resulting in the formation of similar patterns of narrow and wide growth increments among individuals (Fritts, 1976; Stokes and Smiley, 1996). The process of crossdating involves visual comparison of annual increments to confirm that signature years correspond among samples (Black et al., 2005; 2008b). Crossdating noticeably narrow or wide growth increments allows the detection and isolation of possible errors within a sample (Black, 2009; Yamaguchi, 1991). For instance, if a growth increment is missed or falsely added during age estimation, the growth increment pattern from that sample will be offset by a year relative to other samples being cross-matched (Black, 2009; Yamaguchi, 1991). By matching similarities in widths or other morphological features of annual increments, synchronous growth patterns can be identified among samples, and, in association, any errors, increasing confidence in age estimates and assignment of growth increments to the correct calendar year of formation (Black et al., 2005, 2008; Fritts and Speer, 2005).

In a similar process to crossdating, readers may compare the tooth structure of marine mammals to assist identification of GLGs and increase confidence in age estimates. To date, however, a formal description of this technique has not been provided in the literature for the benefit of less experienced researchers. Here we describe the dendrochronology technique of visual crossdating using sperm whale teeth.

Methods

Between two and four mandibular teeth were obtained from each of 15 male sperm whales (total teeth $n = 42$; see Table 2.1) involved in three mass strandings along the coast of Tasmania, Australia, in 2003 (28 November, $n = 9$, Flinders Island 40.10°S, 147.95°E), 2004 (14 June, $n = 3$, Strahan 42.20°S, 145.24°E) and 2007 (7 March, $n = 3$, Strahan 42.21°S 145.23°E). Teeth were prepared according to Evans and Robertson (2001). Etched tooth sections were then photographed following Hamilton et al. (2013) and dentinal GLGs identified on the digital images. Each GLG was defined as comprising a pair of alternating ridges and grooves (Perrin and Myrick, 1980). Growth layer group identification for each tooth was repeated two to three times by a single reader (VH). A final age estimate was derived from the mode of the repeat GLG counts. A single representative image for each tooth was then selected. Identification of GLGs from a subsample of teeth ($n = 16$ teeth from 6 whales) were verified via cross-examination with another experienced reader (KE).

Visual crossdating was performed using the dendrochronology ‘list method’ described in Yamaguchi (1991) and Black et al. (2005). The method was modified slightly from that used on trees and otoliths to increase the likelihood of distinguishing signature GLGs by listing GLGs that were distinctive in both relative width and appearance.

The presence and location of any prominent accessory layers were also noted.

The modified crossdating method included the following steps (in order):

- 1) Using the digital images taken of each tooth from the same individual animal, GLGs identified using standard age estimation methods as described above were assigned a calendar year of deposition by back-counting from the GLG closest to the pulp cavity margin (usually partially formed), which was attributed to the year of death.
- 2) Distinctive or signature GLGs within each tooth were identified and their appearance and year of formation noted. These included GLGs that a) were relatively narrow or wide (compared qualitatively to the width of the adjacent two to three GLGs on either side), or b) following previously published descriptions of distinctive features within GLGs as either ‘marker lines’ or ‘mineralisation interference’; had conspicuous features such as a prominent ridge of the GLG, noticeably narrow or wide ridge or groove components of the GLG, an obvious accessory layer occurring

within the GLG, or paired ridges or ‘double GLGs/laminae’ (Lockyer et al., 2010; Lockyer, 1993a; 1995; Myrick, 1988) (e.g. Figure 2.1).

3) The lists of calendar years assigned to signature GLGs were compared among all teeth from the same individual.

4) If the calendar years assigned to signature GLGs across teeth from the same individual did not match and were offset in one or more teeth, the year in which the offset began was noted. Such an offset indicated the possible occurrence and approximate location of missing (i.e., GLGs misinterpreted as accessory layers) or additional GLGs (i.e., accessory layers misinterpreted as GLGs).

5) Where discrepancies in the calendar year assignment of signature GLGs occurred among teeth from the same individual, the GLGs in questionable year(s) were visually re-examined to identify any potential misinterpretation of GLGs and accessory layers. In most instances, discrepancies were isolated to a single tooth in an individual with the final interpretation (either as a GLG or accessory layer) confirmed by that identified in the rest of the teeth from the same individual. If resolution of GLGs in questionable years was inconclusive among teeth (e.g. in some teeth it had been identified as a GLG, in others it had been identified as an accessory layer), the ultimate decision on GLG identification still remained with the reader, weighted in favour of the section(s) with greatest clarity and proximity to the central axis of the tooth *for that GLG*.

6) If visual examination confirmed that misinterpretation had occurred, adjustments in the identification of GLGs were made and the calendar year assignment (and age estimate) corrected.

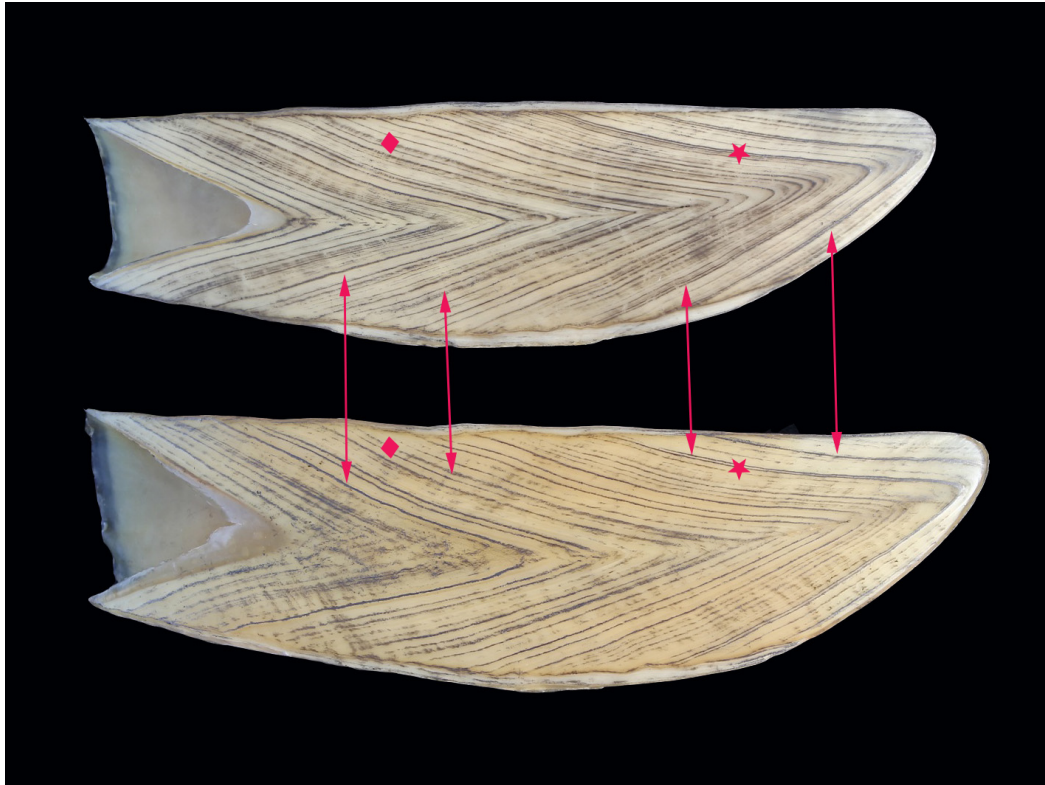


Figure 2.1. Two sectioned teeth from the same individual female sperm whale (ID# 2542) showing distinctive 'signature' GLGs (marked by red arrows) used in visual crossdating. A prominent GLG is marked by ★, 'double GLG' marked by ◆. Specimen #2542 was not used in this analysis, but images are presented here as a representative example displaying different forms of signature GLGs in a single tooth.

Results

Two or more signature GLGs were observed in each tooth examined ($n = 42$), allowing for effective crossdating. After crossdating there was no change to the age estimates of each tooth sampled from six animals (12 teeth, Table 2.1), and no change to age estimates for one to three of the teeth sampled from each of nine animals (16 teeth, Table 2.1). Crossdating revealed discrepancies in the location of signature GLGs in teeth from nine animals, which after adjustment of GLG identification resulted in revision of age estimates ranging from -1 to $+4$ GLGs (14 teeth, Table 2.1). The most discrepancies occurred within teeth of individuals from the Strahan 1 stranding. Variability in the appearance of accessory layers, coupled with differences in etching clarity between teeth from the same individual(s) from Strahan 1, resulted in greater adjustment to GLG identification after crossdating. Re-examination of teeth in which discrepancies occurred highlighted errors including falsely adding a GLG by misidentification of accessory layers as GLGs (13 teeth) and missing a GLG by misidentifying a GLG as an accessory layer (1 tooth). Corrections to GLG identification via crossdating enabled the distribution of age estimates to be tightened, and a consistent bias to overestimation of age by 1 to 2 yr was addressed (Figure 2.2).

Table 2.1. Growth layer group (GLG) estimates established using standard age estimation procedures ('Repeat count estimate') and revised age estimates following crossdating ('Revised estimate') for mandibular teeth from 15 individual male sperm whales. Differences in age estimates derived across teeth from the same individual are due to differential tooth wear across the jaw.

Stranding location	Tooth ID#	Repeat count estimate	Revised estimate	Adjustment after crossdating
Strahan 1	1899-1	26	25	-1
"	1899-2	22	22	0
"	1899-3	24	23	-1
"	1899-4	27	26	-1
"	1900-1	24	22	-2
"	1900-2	22	22	0
"	1900-3	25	25	0
"	1900-4	25	25	0
"	1901-1	20	20	0
"	1901-2	24	20	-4
"	1901-3	23	19	-4
"	1901-4	27	25	-2
Flinders Island	1928-1	30	30	0
"	1928-2	26	26	0
"	1929-1	23	23	0
"	1929-2	22	22	0
"	1930-1	26	26	0
"	1930-2	25	25	0
"	1931-1	23	23	0
"	1931-2	23	23	0
"	1932-1	19	19	0
"	1932-2	18	19	+1
"	1933-1	31	31	0
"	1933-2	29	29	0
"	1934-1	25	25	0
"	1934-2	23	23	0
"	1935-2	26	23	-3
"	1936-1	24	24	0
"	1936-2	23	22	-1

Table 2.1. cont'd

Stranding location	Tooth ID#	Repeat count estimate	Revised estimate	Adjustment after crossdating
Strahan 2	2504-1	18	18	0
"	2504-2	17	17	0
"	2504-3	19	19	0
"	2504-4	18	17	-1
"	2505-1	19	19	0
"	2505-2	18	18	0
"	2505-3	17	17	0
"	2505-4	20	18	-2
"	2506-1	17	17	0
"	2506-2	16	16	0
"	2506-3	17	16	-1
"	2506-4	18	17	-1

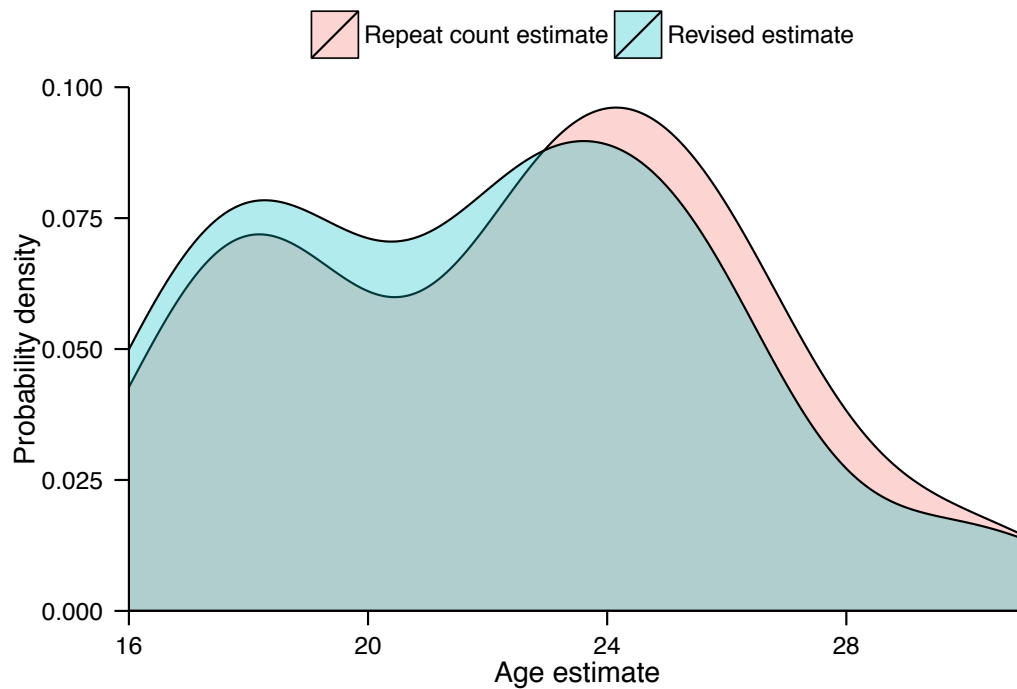


Figure 2.2. Probability density curve of age estimates from sperm whale teeth ($n = 42$) before crossdating ('Repeat count estimate') and following adjustment of age estimates by crossdating ('Revised estimate').

Discussion

It is clear from the results presented here that crossdating based on the occurrence of signature GLGs among teeth from the same individual sperm whale(s) improves consistency in GLG identification by identifying problem GLGs and reducing confusion between GLGs and accessory layers. Crossdating complements age estimation by adding pattern-matching to basic counting of GLGs. Thereby, crossdating allows for refinement of age estimates within individuals and provides estimates that are likely more representative of the true age of the individual. The crossdating method described herein provides a useful tool for GLG identification, particularly for less experienced readers (Black et al., 2008b). Moreover, crossdating provides for a transparent process in GLG identification and refinement of GLG

counts, allowing verification of a reader's ability to consistently identify tooth features. Ultimately this is likely to improve comparability of age estimates for species across multiple studies.

Age estimation routinely involves repeat counts of GLGs within a tooth section, made over multiple sessions or independently by several readers until acceptable repeatability of estimates is obtained, with final age estimates based on the most repeated or the median estimate (Hohn, 2009; Perrin and Myrick, 1980). Using multiple teeth from the same individual, a simplified age estimation technique would comprise 'repeat' estimates consisting of a single GLG count from each tooth, with cross-validation of signature GLGs among teeth from the same individual, allowing for adjustment of GLG identification and refinement of age estimates. This alternative to traditional multiple-count age estimation will depend in part on the clarity of the samples (i.e., repeat estimates may be necessary to arrive at a final estimate for teeth with ambiguity in tooth structure) and also the intended purpose for age estimates. In some cases the end goal of the study may not be age estimates *per se*, but these form a necessary stage in GLG identification. Many investigations require identification of specific GLGs, such as ontogenetic time series of isotopic composition (e.g. Newsome et al., 2010). If multiple teeth from the same individual are used, crossdating could decrease the overall time involved in identifying GLGs by reducing both the need for repeat estimates from each tooth, and time intervals between replicate reading sessions (to avoid reader familiarity with individual sections).

Given that distinctive features occur within the teeth of marine mammals other than sperm whales the method of crossdating presented here should be possible across a wide range of species. Where multiple teeth are available from the same individual(s), we recommend crossdating to assist in identifying problem GLGs and accessory layers, and thereby refining age estimates. One of the foremost purposes of crossdating in tree-ring analysis is the assignment of growth increments to the correct calendar year of formation when constructing growth chronologies (Black et al., 2005; Fritts, 1976). The use of crossdating in marine mammal teeth could assist in this regard, and would enable greater accuracy in comparisons of tooth growth chronologies with annually resolved climate indices, thus aiding assessments of environmental influences on tooth growth in marine mammals.

Acknowledgements

This research was supported by funding from the Winifred Violet Scott Charitable Trust and the Australian Geographic Society. Sperm whale tooth samples were provided by the Department of Primary Industries, Parks, Water and Environment (DPIPWE) Tasmania under permit FA 12276. Kris Carlyon (DPIPWE) is thanked for assistance and access to samples. Sam Thalmann (DPIPWE) is acknowledged for contributing to the preparation of sperm whale teeth. We also thank the Associate Editor, three anonymous reviewers and Christopher Underwood for helpful comments on an earlier version of this manuscript.

Chapter 3 Establishing growth chronologies from marine mammal teeth: A method applicable across species

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All of the research contained in this chapter has been published as:

Hamilton, V. and Evans, K. 2018. Establishing growth chronologies from marine mammal teeth: A method applicable across species. *Journal of Experimental Marine Biology and Ecology*, 505, 24-34. <https://doi.org/10.1016/j.jembe.2018.04.006>

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 utilises 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 standardised growth index were calculated and then averaged into a master chronology for each dataset, maximising 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 modelling studies and compared with annually resolved climate indices to explore sensitivities in tooth growth and associated energy budgets to environmental conditions.

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., 2008a; 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 inert after deposition, and reflect seasonal changes in tooth growth rate and the physiological condition of the animal at time of deposition (Klevezal', 1996; Langvatn, 1995). Nutrients, minerals and the metabolic energy necessary for tooth growth are derived from an individual's dietary intake (Klevezal', 1996; Langvatn, 1995; Medill et al., 2010). Deposition of each GLG will represent 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, 1993a; Medill et al., 2010). As such, time series of measurements of GLG widths provide annually resolved proxies of variability in annual energy 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, standardisation and modelling 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 less than 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 synchronising 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). During crossdating, these patterns of growth are cross-matched among individuals from the same region, wherein any offset in patterns may indicate errors, such as missing or falsely identified increments (Black et al., 2005; Fritts, 1976). The application of crossdating and chronology building techniques pioneered by dendrochronologists remains 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., 2008a; Helama et al., 2006a; 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., 2006a; Rypel et al., 2008) and allow for multi-species comparisons.

Sperm whales (*Physeter macrocephalus*) and long-finned pilot whales (*Globicephala melas*; hereafter referred to as pilot whales) 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. With a longevity of up to 70 – 80 years for sperm whales (Ohsumi, 1966) and 45 – 60 years for pilot whales (Bloch et al., 1993), they have the potential to provide long time series of growth chronologies. The tendency of both species to mass strand also means that tooth samples for developing and testing methodologies are relatively readily available. Here, we detail methods for development of tooth growth chronologies from sperm whales and pilot whales and provide associated guidelines for broader application of the methods to other toothed marine mammals.

Material and methods

Samples and tooth preparation

Past studies involving increments in marine teleost otoliths have found that a minimum of six individuals should be used in chronology development to ensure adequate signal to noise ratios (Gillanders et al., 2012; Matta et al., 2010). Assuming that the degree of environmental signal would be comparable to those in marine teleosts, we sampled between two and four mandibular teeth from each of eight males and ten females from both species. Teeth were sampled from deceased sperm whales involved in mass strandings along the coast of Tasmania, Australia in 2003 (Flinders Island 40.10°S, 147.95°E, Table 3.1) and 2004 (Strahan 42.04°S, 145.24°E; Table 3.1) and from long-finned pilot whales involved in a mass stranding on King Island, Tasmania, Australia in 2012 (39.67°S, 143.83°E; Table 3.1).

Table 3.1. 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	<i>P. macrocephalus</i>	1928 (2)	M	30 (29)	open	low – moderate
28/11/2003	Flinders Island	<i>P. macrocephalus</i>	1929 (2)	M	23 (21)	open	low – moderate
28/11/2003	Flinders Island	<i>P. macrocephalus</i>	1930 (2)	M	26 (24)	open	low – moderate
28/11/2003	Flinders Island	<i>P. macrocephalus</i>	1931 (2)	M	23 (22)	open	low – moderate
28/11/2003	Flinders Island	<i>P. macrocephalus</i>	1932 (2)	M	19 (18)	open	low – moderate
28/11/2003	Flinders Island	<i>P. macrocephalus</i>	1933 (2)	M	31 (29)	open	low
28/11/2003	Flinders Island	<i>P. macrocephalus</i>	1934 (2)	M	25 (22)	open	low – moderate
28/11/2003	Flinders Island	<i>P. macrocephalus</i>	1935 (2)	M	26 (25)	open	low – moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2156 (2)	F	33 (33)	full	low – moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2157 (2)	F	29 (28)	closing	low – moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2158 (4)	F	20 (17)	open	moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2161 (4)	F	29 (27)	open	low – moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2163 (3)	F	26 (17)	open	low – moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2166 (4)	F	21 (18)	open	moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2168 (4)	F	27 (25)	open	low – moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2169 (2)	F	19 (18)	open	moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2172 (4)	F	25 (20)	open	moderate
29/12/2004	Strahan	<i>P. macrocephalus</i>	2174 (3)	F	29 (22)	open	moderate
03/11/2012	King Island	<i>G. melas</i>	KI-GM1	M	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM2	F	9	open	nil

Table 3.1. cont'd

Stranding date	Stranding location	Species	Whale ID#	Sex	Age estimate (T-S length)	Pulp cavity state	Tooth wear
03/11/2012	King Island	<i>G. melas</i>	KI-GM3	F	13	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM4	M	12	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM5	F	9	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM6	F	11	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM7	M	11	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM9	M	15	closing	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM10	M	7	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM11	F	7	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM12	M	13	closing	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM13	F	13	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM14	F	12	closing	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM15	M	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM16	F	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM21	M	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM28	F	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM29	F	13	open	nil

Sperm whale teeth were prepared for GLG identification consistent with methods detailed in Evans and Robertson (2001). Briefly, teeth were sectioned longitudinally using a band saw, sanded to remove saw marks and then the cut surface of one half of each tooth was etched in 15% formic acid for 3 – 8 h to enhance clarity and contrast of GLGs. Pilot whale teeth were prepared following similar methods to those described by Myrick et al. (1983) and Evans and Robertson (2001). The buccal and lingual sides were trimmed from each tooth using a low speed precision saw (Buehler IsoMet, Lake Bluff, IL, USA) to produce a 3 mm wide longitudinal wafer containing the central axis of the tooth. Wafers were decalcified in RDO Rapid Decalcifier solution (Apex Engineering Products, Aurora, IL, USA) for 10 – 21 h. Decalcified wafers were then mounted on 30 mm specimen freezing discs using Tissue-Tek OCT embedding compound (Sakura Finetek, Torrance, CA, USA) and sectioned at 25 – 30 μm thickness using a Leica CM1900 cryostat (Leica Microsystems Nussloch GmbH, Nussloch, Germany). Thin sections were stained using hematoxylin stain (Merck Certistain CI75290, Merck KGaA, Darmstadt, Germany) and permanently mounted onto slides using DPX mountant.

GLG identification

Digital images were taken of the etched sperm whale teeth as per Hamilton et al. (2013). The pilot whale thin sections were digitally imaged at $7.3\times$ magnification using a Canon EOS 5D Mark II camera attached to a Leica M165C stereomicroscope with transmitted-light base. Primary GLG identification for each tooth was undertaken on the digital images by a single reader (VH). Following Perrin and Myrick (1980), annual GLGs were defined as consisting of a pair of alternating ridges and grooves (sperm whale teeth) or a pair of layers of varying staining intensity: one narrow deeply stained layer and a wide lightly stained layer (pilot whale teeth).

Growth layer groups were identified two to three times for each tooth via blind readings of digital images, with the readings in which GLG identification was repeated used to derive a final GLG series for calendar year assignment and measurement of GLG widths. Growth layer group identification for a subsample of teeth (one tooth from each of eight sperm whales and ten pilot whales) was cross-verified by another experienced reader (KE). Any discrepancies in GLG identification

between readers were resolved by joint re-examination of the images of each tooth to achieve consensus.

A modified visual crossdating process, by comparison of ‘signature’ GLGs (i.e., GLGs that were distinctive in appearance) evident in multiple teeth from the same individual following Hamilton et al. (2017) was then used to cross-check GLG identification within individuals. Following this cross-check and any resultant adjustments to GLG identification, a single tooth for each individual was then selected for final calendar year assignment and measurement of GLGs, and all subsequent steps in chronology development. To ensure accuracy in measured GLG widths, the tooth selected from each individual was that with the most central section position and greatest clarity of GLG boundaries (Hohn et al., 1989).

Generally in dendrochronology crossdating to ensure dating accuracy and assignment of growth increments to the correct calendar year is a two-step process. First, similar patterns of relatively narrow and wide growth increments (i.e., GLGs) are visually matched among individuals and aligned according to calendar year *sensu* Fritts (1976). The second step is based on statistical comparisons of individual GLG width time series to check that patterns in GLG widths correlate among samples. Visual inspection of sperm whale and pilot whale samples, however, did not reveal easily observable variability in GLG widths. Therefore we omitted the visual crossdating step prior to calendar year assignment and measurement of GLGs, and proceeded to statistical crossdating thereafter.

Calendar year assignment of GLGs

Each GLG was assigned a calendar year of formation, based on back-counting from the known year of the stranding, commencing with the last formed GLG at the pulp cavity edge. Because the GLG associated with the pulp cavity edge can vary in the degree of completion (from marginally formed to almost completely formed) and depending on the date of the stranding, can therefore be assigned either to the current or previous year, we applied marginal increment analysis (Campana, 2001; Fowler and Short, 1998) to assign a final calendar year (see Supplementary Table S3.1). The last incomplete growth increment is assigned a proportional state of completion

relative to the width of the previous increment, and the presence of an opaque or translucent zone (analogous to the alternating relief or staining intensity of the paired layers comprising a GLG) visible at the structure's edge is noted (Fowler and Short, 1998). The marginal growth is then assigned to the year of the stranding or the previous year, taking into account the known stranding date and an assigned January 'start date' for each GLG (Campana, 2001; Kimura et al., 2007; Morison et al., 1998).

Measurement of GLG widths

Annual GLG widths were measured on the digital images using a plug-in ('IncMeas'; Rountrey, 2009) written for ImageJ, an open source image processing program (version 1.47, National Institutes of Health, USA). For consistency, GLG widths were measured perpendicular to GLG boundaries (Black et al., 2005; Speer, 2010) on the side of each tooth section that was most symmetrical (i.e., no localised thinning of GLG widths) and had the most clearly defined GLGs and GLG boundaries (Myrick et al., 1984) (Figures 3.1 and 3.2).

Differences in GLG deposition patterns relative to the tooth central axis between the two species necessitated modification of the measurement axis position. Dentinal GLGs in sperm whale teeth are deposited at an angle to the longitudinal axis of the tooth (the inclination of deposition angle can flatten as the pulp cavity fills); in addition, sperm whale teeth can exhibit pronounced curvature along the longitudinal axis of each tooth. In contrast, delphinid dentinal GLGs are deposited 'more or less parallel to the longitudinal axis of the tooth' (Perrin and Myrick, 1980). Measurement of GLG widths in sperm whale teeth were subsequently conducted step-wise on one side of the tooth section, anchored along a curved polyline positioned midway between the central axis and the dentine-cementum interface (to avoid thinning of GLG widths at the dentine-cementum interface and distortion in apical GLG widths due to longitudinal growth of the tooth), following the curvature of the tooth central axis (Figure 3.1).

Measurement of GLG widths in pilot whale teeth were conducted along a straight polyline transect, perpendicular to the GLG boundaries, from just above the base of the neonatal line to the innermost GLG, or pulp cavity margin (Figure 3.2). In teeth

where a single transect would not encompass all GLGs from the neonatal line to the pulp cavity, or where the angle of GLG deposition deviated from parallel with the tooth central axis, GLG width measurements were continued along a second transect placed further down the tooth limb, towards the pulp cavity.

In both species, the width of each GLG was measured from the distal edge of the etched ‘ridge’ (sperm whale) or deeply stained layer (pilot whale) of the previous year’s GLG to the distal edge of the next GLG’s ridge or deeply stained layer (Figures 3.1 and 3.2). Incomplete GLGs at the pulp cavity margin were not measured.

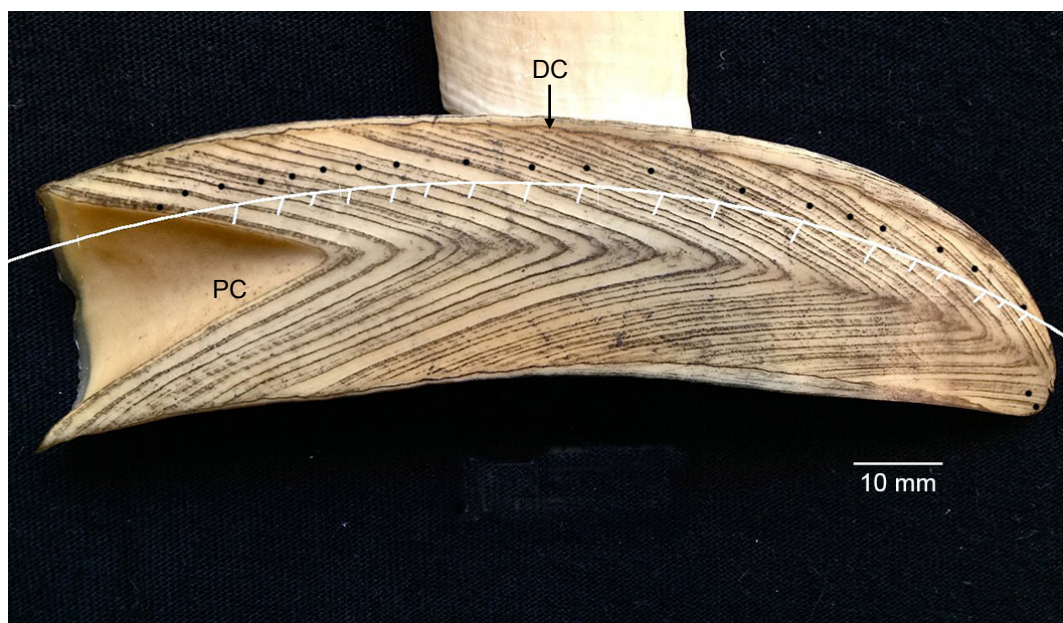


Figure 3.1. Image of etched tooth section from female sperm whale ID# 2166 showing i) position of polyline for measurement of growth layer group (GLG) widths (curved white line) and step-wise GLG width measurements (white lines perpendicular to GLG boundaries), and ii) example of assessment of the marginal GLG at the pulp cavity (PC) edge (equivalent to category 2: see Supplementary Table S3.1). DC = dentine-cementum interface. Black dots indicate GLGs.

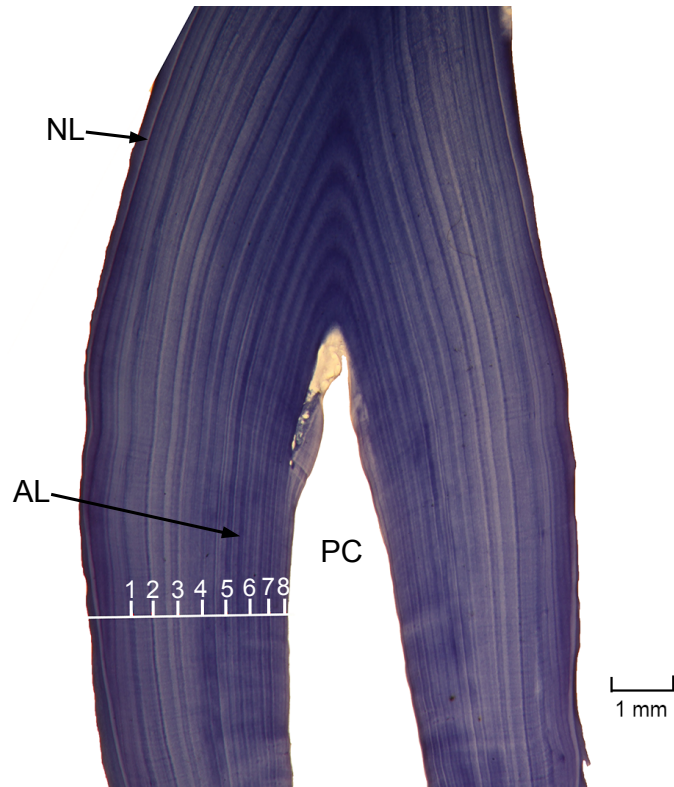


Figure 3.2. Magnified image of tooth thin section from female pilot whale ID# KI-GM16 showing measurement transect (white line) for growth layer group (GLG) widths. PC = pulp cavity, NL = neonatal line, AL = accessory layer (subannual layer within GLG). GLGs numbered 1 – 8.

Statistical crossdating among individuals

Statistical crossdating of individual GLG width time series within each stranding group was used to check GLG width measurements corresponded among samples. Comparing high frequency, year-to-year variability is more effective for crossdating than low frequency variability (Black et al., 2005; Wigley et al., 1987). Therefore, high frequency variability in each GLG width time series was first enhanced by fitting an autoregressive ('AR') model to the data and considering only the residuals from the fitted model: a procedure known as 'prewhitening' (Bunn, 2010; Wigley et al., 1987). Prewhitening removes autocorrelation from the time series, distributing variance more evenly across the frequency range and reducing low frequency

variability (Wigley et al., 1987). Each GLG width time series was prewhitened using either a first-order process autoregressive model AR(1):

$$y_t = \phi y_{t-1} + \epsilon_t$$

or an extended model AR(p), where p indicates the order of the autoregressive model:

$$y_t = \sum_{i=1}^p \phi_i y_{t-i} + \epsilon_t$$

where y is a measure of growth (i.e., GLG width) and $t = 1 \dots n$, ϕ is a coefficient ranging from -1 to 1 , and ϵ represents other growth processes (e.g. related to physiology or climate). The order of the model ($p \leq 4$) was selected using the Akaike Information Criterion (Bunn, 2010; Bunn et al., 2013).

Each prewhitened GLG width time series was split into overlapping segments to assist in locating the approximate position of potential dating errors in the time series. A recommended guideline for selection of segment length is approximately half that of the average length of the individual time series (Grissino-Mayer, 2001). Therefore the prewhitened GLG width time series were broken into 12 year segments that overlapped by 6 years for the sperm whale data and 8 year segments overlapped by 4 years for the pilot whale data (e.g. Flinders Island sperm whales: 1978 – 1990, 1984 – 1996, 1990 – 2002). It should be noted that crossdating using segment lengths < 30 years increases the probability of spurious correlations (Grissino-Mayer, 2001; Wigley et al., 1987) and therefore any dating uncertainties in the GLG width time series require cautious interpretation. Correlations were then calculated serially using Spearman's correlation coefficient ($p \leq 0.05$) between each prewhitened time series and a mean time series calculated as the average of all other prewhitened GLG width time series in the stranding group using Tukey's biweight robust mean. Tukey's biweight robust mean allows for a reduction of the influence of suspected outliers or extreme values (Bunn, 2008; Cook et al., 1990). If a prewhitened GLG width time series had low correlation with the mean time series, indicating a potential error in calendar year assignment, the prewhitened time series was lagged by $\pm 1 - 2$ yr against the mean time series to assess if such an offset would result in a higher correlation. If a higher correlation value occurred, the tooth the time series was derived from was

visually re-examined and corrections were made to the GLG width time series only if an error in GLG identification could be verified on the original image of the tooth. If a GLG width time series did not correlate well, but no obvious errors in GLG identification or measurement were identified, the original GLG width time series was retained and accepted as exhibiting variability in GLG widths specific to that individual.

The interseries correlation, that is the average of the correlations between each prewhitened GLG width time series and the mean time series for each stranding group (Speer 2010), was calculated prior to crossdating and after corrections resulting from investigation of offsets to assess crossdating efficacy.

Detrending of GLG width time series to produce individual chronologies

Raw GLG width time series require standardisation or detrending into a dimensionless index to remove variability specific to each individual (such as differences in age or life stage, or tooth size and morphology), allowing for direct comparisons of time series while still preserving a common population-wide environmental signal (Cook et al., 1990; Fritts, 1976). The most commonly used detrending methods in dendrochronology include simple linear regression, modified negative exponential curves, or cubic smoothing splines. Linear models and negative exponential curves are deterministic and most appropriate for modelling simple growth trends that follow a known mathematical form or to account for strong juvenile growth commonly encountered in tree-ring width time series (Cook et al., 1990; Fritts, 1976). Cubic smoothing splines (symmetrical low-pass digital filters with a centrally weighted moving average) are empirical standardisation methods that can be applied to a wide range of growth trends, and take into consideration autocorrelation in the data (Cook et al., 1990; Cook and Peters, 1981). Empirical models are preferable to deterministic models where there is no clear (i.e., age related) growth trend (Cook et al., 1990).

A linear model is fit as follows:

$$G_t = b_0 + b_1 t$$

where the growth trend G_t is estimated as function of time, b_0 and b_1 are the intercept and slope (Bunn, 2008; Cook et al., 1990).

The negative exponential curve is modelled as:

$$G_t = ae^{-bt} + k$$

where G_t is estimated as function of time t with the coefficients a , b and k (Bunn, 2008; Cook et al., 1990).

The smoothing spline approach calculates G_t as a spline with a frequency response of 50% at a wavelength of n years (Bunn, 2008; Cook and Peters, 1981). The ability to control the flexibility of cubic smoothing splines allows customisation of the standardisation process to the requirements of the data, (Cook and Peters, 1981; Speer, 2010). A highly flexible spline (lower n years) closely follows individual data points in the time series and the most rigid spline approximates a straight line. Some care should be taken in the selection and use of cubic smoothing splines, as different amounts of variance will be removed at differing timescales or wavelengths (Cook and Peters, 1981; Speer, 2010). Over-fitting the spline will remove too much variance in the time series, while under-fitting will retain anomalies (noise) that could be misinterpreted (Cook and Peters, 1981). Determining the best fit to the data is usually done through experimentation with a variety of spline flexibilities, with smoothing expressed in terms of the wavelength at which 50% of the variance is removed (Black et al., 2005; Cook et al., 1990).

To determine the most appropriate detrending function for the GLG width time series from sperm whale and pilot whale teeth, all three detrending methods were applied to the crossdated GLG width time series of individuals. Diagnostic plots of residuals were used to check adherence to model assumptions of normality and homogeneity. Residual diagnostics and visual assessment of the fit of the detrending function superimposed on each individual's GLG width time series were then used to select the detrending function that provided the best fit (Black et al., 2005), quantitatively supported by the highest \bar{r} value as an indication of the strength of the common signal among individuals (Nguyen et al., 2015), for each stranding group (see *Chronology statistics*, p. 49). When applying cubic smoothing splines to each GLG width time series a range of spline flexibilities, including those commonly used in

dendrochronology, were trialled to determine the optimum spline flexibility (Bunn, 2008; Cook et al., 1990; Helama et al., 2004). Splines used included:

- i) spline rigidities of 8, 12, 16 and 22 years for sperm whales (due to time series lengths of < 30 years) and 8 and 12 years for pilot whales (due to time series lengths of < 16 years) with 50% frequency cut-off,
- ii) a 67%*n* spline with 50% frequency cut-off; i.e., half the amplitude of variations with wavelength of 67% of the series length is preserved in the resulting indices,
- iii) a *n*-year/2 spline with 50% frequency cut-off; i.e., half the variance with wavelength of half the series length is preserved.

Conversion to indices by division (ratio detrending) is preferred in most cases because any trend in variance that might accompany trend in mean is removed by the ratio operation (Cook et al., 1990; Fritts, 1976). The GLG width time series for each individual was therefore standardised by dividing the measured GLG width for each year by the value predicted from the selected detrending function, that is:

$$\text{Growth Index (GI)} = R_t / G_t$$

where R_t and G_t are the actual (measured) and predicted GLG widths at year t , respectively. Standardisation resulted in a growth index (GI) with mean of 1 (values >1 suggest above average annual growth, values <1 suggest below average annual growth) and relatively homogenous variance across the time series (Black et al., 2005; Cook et al., 1990; Fritts, 1976; Helama et al., 2006a).

Master chronology development

Individual indexed chronologies can be averaged with respect to calendar year to produce a composite (referred to as a ‘master’) chronology. This will average out individual noise while maintaining interannual variability, thereby allowing the identification of common signals (Cook and Pederson, 2011; Fritts, 1976; Fritts and Speer, 2005).

To build a master chronology for each stranding, the GIs derived from individuals in each stranding were averaged within each year, using Tukey's biweight robust mean. Variability in individual chronology lengths resulted in fewer individuals contributing to the earlier years of the chronology. Therefore the master chronology for each stranding was truncated at the calendar year in which six or more individuals contributed to the chronology, to ensure individual variability did not obscure the overall signal (Matta et al., 2010).

Chronology statistics

Descriptive statistics of chronology properties were calculated to provide a quantitative measure of the strength of the common signal (synchrony) and chronology quality. These included:

- i) \bar{r} ('rbar') calculated as the mean of all pairwise correlations between individual chronologies (Briffa and Jones, 1990; Cook and Pederson, 2011; Wigley et al., 1984) and;
- ii) the expressed population signal (EPS) as an indicator of how well the chronology derived from the sample site represents an 'ideal' chronology from the theoretical population where a common forcing signal is fully represented. The EPS measures fractional variance among series and is dependent on sample depth where $EPS = n\bar{r}/(1 + (n - 1)\bar{r})$ (Briffa and Jones, 1990; Wigley et al., 1984). A threshold EPS value of 0.85 is typically applied in dendrochronology (Black et al., 2016).

Statistical crossdating, detrending analyses and chronology building were conducted using the Dendrochronology Program Library in R package 'dplR' (Bunn, 2008, 2010), an open-source package used within the R statistical programming environment (version 3.0.2, R Core Team, 2013).

Results

GLG identification and associated length of individual GLG width time series

The number of GLG widths measured per individual sperm whale ranged 18 – 29 for the Flinders Island stranding and 17 – 33 for the Strahan stranding, resulting in

individual GLG width time series spanning 1974 – 2003 and 1972 – 2004, respectively (Table 3.1). The number of GLGs measured for each pilot whale ranged 7 – 15, resulting in individual GLG width time series spanning 1997 – 2012 (Table 3.1).

Adjustment to GLG identification via modified visual crossdating within individuals
Cross-checks of distinctive GLGs among teeth from the same individuals resulted in GLG adjustments of –5 to +5 GLGs in 23 teeth from 11 sperm whales and adjustments of –1 to +3 GLGs in a single tooth from each of seven pilot whales (see Supplementary Table S3.2). The modal GLG adjustment for sperm whales was –1 GLG and was associated with falsely adding a GLG by misidentifying an accessory layer as a GLG, and +1 GLG for pilot whales, associated with missing a GLG by misidentification of a GLG as an accessory layer. The modified visual crossdating process also assisted in the identification of GLG boundaries including that associated with the pulp cavity margin.

Statistical crossdating among individuals

Seven pilot whale time series were not sufficient in length (≤ 8 GLGS) to effectively correlate back to the pilot whale mean time series and so crossdating was not carried out on these individuals. Six time series for Flinders Island sperm whales, nine time series for Strahan sperm whales and eight time series for pilot whales returned poor correlation values ($p \geq 0.05$) and were re-examined for potential errors. Interseries correlation values for each stranding ranged 0.043 – 0.464 before crossdating (Table 3.2).

Errors in GLG identification were located and corrected for one sperm whale GLG width time series from Flinders Island (an accessory layer misidentified as a GLG) and three sperm whale GLG width time series from Strahan (one time series had two GLGs misidentified as accessory layers, and in two time series, GLGs at the pulp cavity margin had been misidentified as incomplete). Two pilot whale GLG width time series contained an error in GLG identification (falsely added GLGs).

After correction of errors, poor correlations ($p \geq 0.05$) remained for six sperm whale time series from Flinders Island, seven time series from the Strahan stranding and four pilot whale time series. The interseries correlation values for each stranding improved overall, reflecting the corrections made, ranging from 0.177 – 0.523 (Table 3.2). The lower interseries correlation value for the Flinders Island stranding was related to individual variability and the smaller sample size for this stranding, rather than difficulty in GLG identification and measurement.

Table 3.2. Interseries correlation values (a measure of crossdating strength among individuals) calculated for sperm and long-finned pilot whales before and after statistical crossdating of GLG width time series.

Stranding	Interseries correlation	
	Before crossdating	After crossdating
Flinders Island	0.094	0.177
Strahan	0.043	0.312
King Island	0.44	0.523

Detrending

Linear models and negative exponential curves did not provide a good fit to the sperm whale time series as the majority of samples did not exhibit a strong age-related decline in GLG widths. This was likely due to the high proportion of teeth from younger individuals (with open pulp cavities) and tooth wear in older individual sperm whales precluding the earliest (and possibly wider) GLGs from time series. Some linear regressions exhibited zero or positive slopes, related to shorter time series of younger animals being dominated by year-to-year fluctuations. Growth curves resulting from the negative exponential model deviated little from the linear model in many cases, resulting in minimal differences in the calculated indices (Figure 3.3). Measured GLG widths showed considerable variability over the time series for a number of individual sperm whales (e.g. relatively extremely wide GLGs in the middle of the time series, related to curvature of the tooth, see Figure 3.3). For these

time series, the more flexible fit of the cubic smoothing spline provided the best model for growth variation over time, by reducing the influence of short-term variations in growth increments likely associated with changes in tooth morphology (e.g. varying degrees of curvature of teeth).

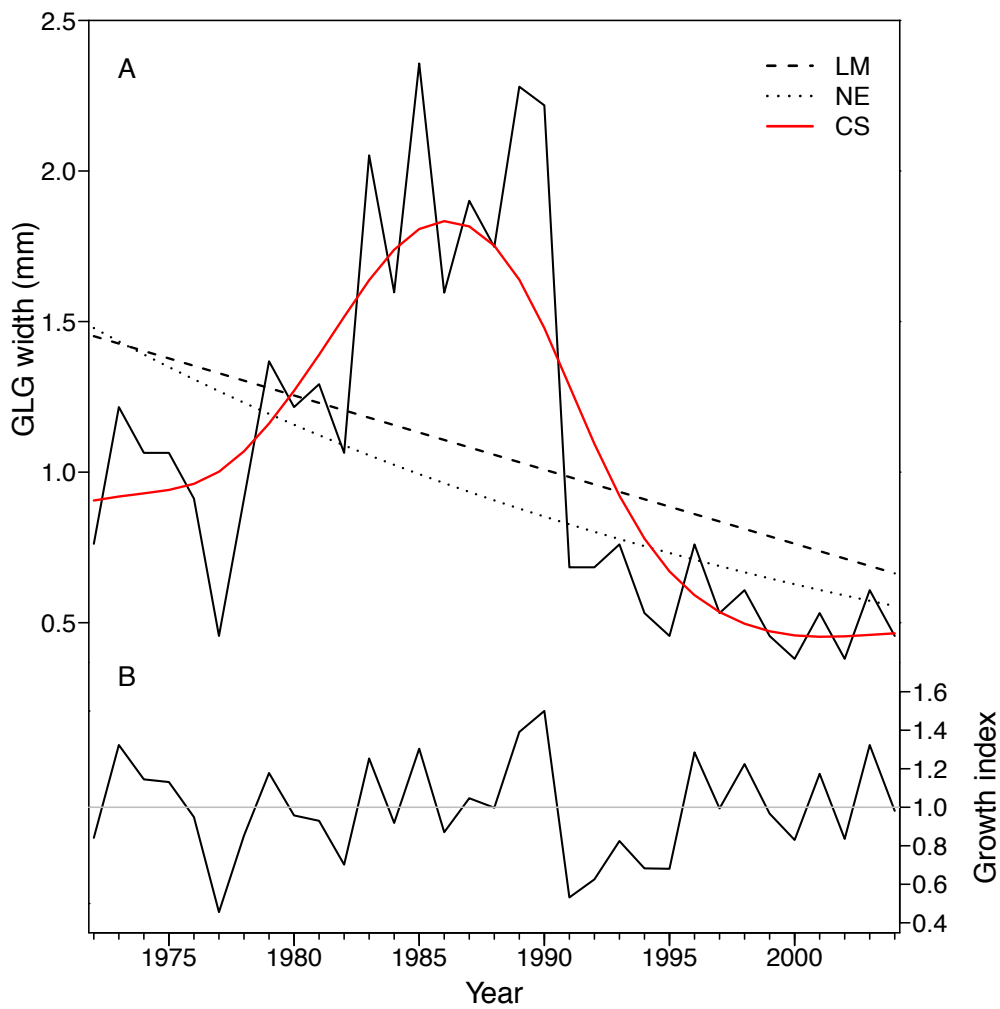


Figure 3.3. (A) Detrending functions fit to the raw GLG width time series (solid line) of female sperm whale ID# 2156. Linear model (LM), Negative exponential curve (NE) and Cubic smoothing spline (CS). (B) Growth Index calculated from the same time series detrended using a cubic smoothing spline at a 50% frequency cut-off of $67\%n$ years. Horizontal grey line represents the mean (1.0).

A decreasing trend in GLG widths was observed in the pilot whale time series, resulting in a good fit of negative linear or negative exponential curves to the early portions of individual time series. Departures from the exponential model in the latter parts of time series were best fit by cubic smoothing splines. Subsequently a ‘double detrending’ method as described by Cook (1985) was used for pilot whales, in which GLG width time series were first detrended by negative exponential curves or negative linear regression models and then the indexed time series were detrended once more using cubic smoothing splines.

Different flexibilities of cubic smoothing splines applied to both the sperm whale and pilot whale time series varied in their ability to enhance a common signal. Cubic smoothing splines with a frequency response of 50% at a wavelength of eight years for the Flinders Island data and wavelength of 67% the length of each individual series ($67\%n$) for the Strahan sperm whale data provided the highest \bar{r} value and the best detrending fits (Table 3.3). Cubic smoothing splines with a frequency response of 50% at a wavelength of 12 years provided the highest \bar{r} value and the best fit to the pilot whale data after initial detrending using negative exponential models (Table 3.3).

Table 3.3. Comparison of \bar{r} (the average of pairwise correlations between detrended time series) chronology statistic calculated for sperm whale GLG width time series detrended using cubic smoothing splines with a 50% frequency cut-off at differing spline flexibilities: 8, 12, 16 and 22 years, $67\%n$ years spline and n -years/2 spline (n = time series length) and the same smoothing splines applied to long-finned pilot whale GLG width time series after initial detrending with negative exponential curves. (16 and 22 year splines not applied to pilot whales as all pilot whale time series < 16 years)

Spline	Sperm whale Flinders Is.	Sperm whale Strahan	Pilot whale
8 year	0.115	0.033	0.004
12 year	-0.003	0.093	0.038
16 year	0.085	0.046	–
22 year	0.064	0.07	–
$67\%n$ years	0.001	0.104	-0.02
n -years/2	0.048	0.048	-0.012

Chronology statistics

Individual chronology lengths developed for sperm whales ranged 17 – 33 years and 7 – 15 years for pilot whales. Chronologies showed considerable variation in GIs among individuals, yet some synchrony in growth was evident among individuals and reflected in the master chronology (Figure 3.4). Growth indices varied 0.41 – 1.7 for sperm whales and varied 0.63 – 1.47 for pilot whales. Master chronology lengths were 21 years (spanning 1982 – 2002) for Flinders Island sperm whales, 20 years (spanning 1984 – 2003) for the Strahan sperm whale stranding and 8 years (spanning 2003 – 2011) for pilot whales. Master chronology index values ranged 0.72 – 1.24 and 0.8 – 1.17 for Flinders Island and Strahan sperm whales, respectively, and 0.89 – 1.1 for pilot whales. The \bar{r} values for each stranding were 0.115 and 0.104 for the Flinders Island and Strahan sperm whales, respectively, and 0.038 for pilot whales. The EPS values for each chronology were 0.511, 0.537 for the Flinders Island and Strahan sperm whales, respectively, and 0.415 for pilot whales.

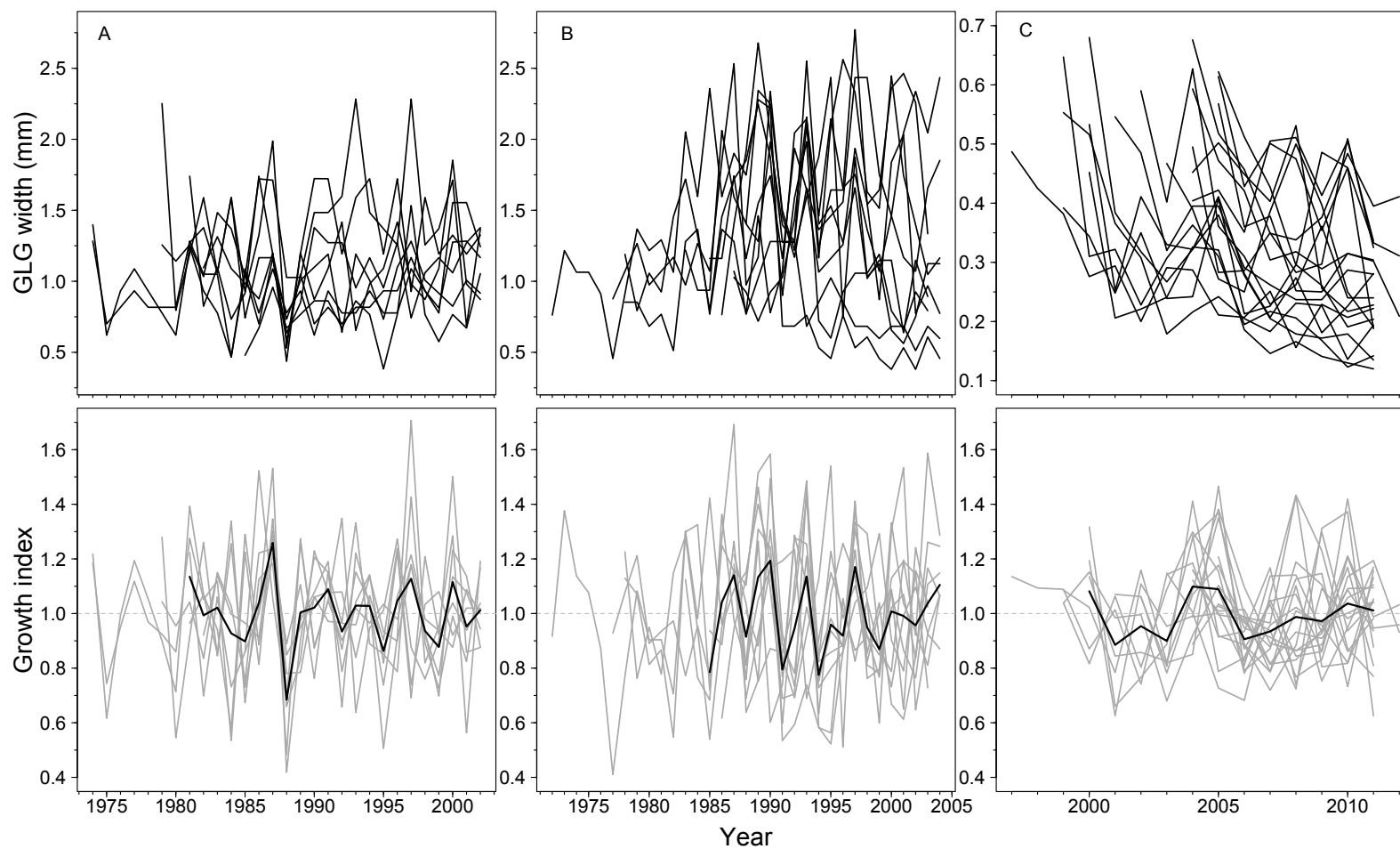


Figure 3.4. Raw GLG measurement time series (upper) and individual indexed chronologies (grey lines) with master chronology (black line) (lower) for (A) sperm whales, Flinders Island stranding ($n = 8$), (B) sperm whales, Strahan stranding ($n = 10$) and (C) long-finned pilot whales, King Island stranding ($n = 18$).

Discussion

The main tenets of dendrochronology are accurate annual resolution of growth increments achieved through crossdating and replication of samples to maximise a common growth signal among samples that might be related to environmental conditions (Cook and Kairiukstis, 1990; Fritts, 1971; Hughes, 2011). Attaining these objectives is an innovative and active research field, building on well tested principles and protocols and the development of statistically robust methods of analysis (Cook et al., 1990; Hughes, 2011; Speer, 2010). The application of dendrochronology techniques to the measurement and standardisation of time series of marine mammal GLG widths as carried out here, was successful in building individual chronologies of odontocete tooth growth and in association allowed for the detection of a common signal among samples.

Approaches to analysing interactions between the environment and increment growth chronologies derived from marine species developed to date (reviewed in Morrongiello et al., 2012) can be statistically complex (e.g. mixed-effect modelling), and subsequently can be difficult to replicate on similar terms across studies (Bolker et al., 2009; Morrongiello et al., 2012). Furthermore, growth index standardisation methods that rely on the presence of the first formed increment or known age of the individual have limited usage for marine mammal species. The process of tooth formation (new GLGs form adjacent to the pulp cavity), and tooth wear (which can remove the enamel, neonatal line and early deposited GLGs in teeth) restricts the ability to consistently identify the neonatal line, and ‘age zero’ or birth year cannot always be established. Subsequently, the method described circumvents two common issues within marine mammal taxa of tooth wear and lack of an identifiable birthdate (particularly for odontocetes). The method described here should be equally applicable for GLG width measurements of both dentine and cementum, taking into consideration determination of best measurement position, as cementum thickness can vary across the tooth root (e.g. Medill et al., 2009; Wittmann et al., 2016). In addition, given similarities in tooth morphology and deposition of GLGs in other species of marine mammals, the method should be consistently appropriate across species.

The recommendations outlined herein offer a number of advantages. Foremost, the guidelines provided in dendrochronology analysis offer established techniques, trialled across many different species, in both terrestrial and aquatic environments. Chronology development is essentially a relatively simple, step-by-step process, and is also highly repeatable, allowing

direct comparisons between similarly developed chronologies from different species or regions.

The application of both visual and statistical crossdating offers further advantages to enhance development of tooth growth chronologies. Although visual crossdating was not possible for this dataset, this step may have potential for other species that exhibit greater interannual variability in GLG widths. Crossdating is an integral precursor to chronology development within dendrochronology studies, and aims to reduce the occurrence of errors introduced through inaccuracy in calendar year assignment within individual chronologies. Such errors could suppress the interannual signal by spreading (and effectively ‘cancelling out’) high and low index values across multiple years when individual chronologies are averaged into a master chronology (Black et al., 2016; Fritts and Swetnam, 1989; Helama et al., 2006a; Hendy et al., 2003). Some care, however should be exercised when applying statistical crossdating methods to time series that are relatively short (< 20 years). When time series are short, and in particular when fewer individuals contribute to the mean time series, accidental or false correlations can occur, resulting in misleading interpretation of errors indicated by crossdating (Bunn, 2010; Grissino-Mayer, 2001; Wigley et al., 1987). Reader subjectivity has the potential to introduce errors in calendar year assignment through misidentification of GLGs (e.g. falsely adding or missing a GLG), which will affect the accuracy of individual and master chronologies. While crossdating cannot eliminate reader subjectivity and provide absolute dating at the level routinely accepted for tree-rings, it can assist in the detection of GLG identification errors, and the effect of remaining errors in GLG identification can be further mitigated through increasing the number of individuals contributing to the master chronology (Black et al., 2016).

Uncertainties regarding the underlying physiological influences on GLG growth, however, coupled with higher levels of variability among individuals and shorter time series lengths than that usually accepted for crossdating growth-rings in trees means the process may not be as straightforward or robust in application to marine mammals. The increasing use of animal species with shorter lifespans (relative to time series derived from trees), greater mobility (and therefore potential to move across different climate conditions throughout their lifetime) and potential lower sensitivity to environmental conditions means that currently accepted levels of correlation used in crossdating may not be appropriate for such time series (Black et al., 2016; Ong et al., 2015). This will require further testing of datasets from marine mammals across a

number of species and regions in order to determine the most appropriate values and subsequent adaptation of crossdating protocols.

Detrending aims to remove noise (related to age, tooth morphology or individual variability), while retaining as much signal (related to climate) as possible (Cook et al., 1990; Speer, 2010). Choice of detrending method can affect the resultant chronology; no single method is applicable to all situations and requires site- and species-specific consideration with a range of detrending functions tested (Cook et al., 1990; Sullivan et al., 2016). Given regional and species-specific variations in tooth clarity and structure (Hohn, 2009; Klevezal', 1996), there is every reason to expect that different detrending approaches may be required within marine mammal species. Linear models describing changes in GLG width over time may be suitable for approximating short-term growth series (e.g. Boyd and Roberts, 1993; Knox et al., 2014), or growth patterns that do not follow a negative exponential curve (Cook and Holmes, 1986). Using a predetermined mathematical model for describing growth trends may be too restrictive for addressing relatively short or medium term fluctuations in growth occurring within longer measurement series (Cook et al., 1990) such as that demonstrated by marine mammals.

Negative exponential models are able to account for the strong age-related growth trends observed in many of the time series generated from tree-rings, bivalve shells or teleost otoliths; that is rapid juvenile growth followed by progressive thinning of rings due to new material being added to an increasing circumference each year (Black et al., 2005; Hughes, 2011; Speer, 2010). Although the GLGs in marine mammal teeth often show a decreasing trend in widths as the animal ages, particularly as the pulp cavity fills and compresses GLGs, this trend is neither as distinctive nor consistent as that demonstrated by growth in trees. Further, any positive trends or fluctuations in the time series will not be represented with negative exponential growth models (Helama et al., 2004).

Goodness-of-fit of the detrending model can vary over the time series, and therefore the degree to which noise-related variance is removed or retained during the standardisation process may also vary (Cook et al., 1990). Cubic smoothing splines provide a more flexible, data-adaptive approach for standardising measurement time series, particularly when the trend is not linear, or monotonically increasing or decreasing over time (Cook and Peters, 1981). There is a risk of over-fitting to the data with cubic splines, as a too flexible spline could

remove low frequency variability related to climate signals (Cook et al., 1990). Low frequency variability in dendrochronology studies is usually interpreted as that occurring over timescales of several decades or more, as opposed to higher frequency, interannual to decadal variability (Briffa et al., 1996). The intended purpose of the chronologies and time scales over which variability is to be investigated should be considered when determining spline flexibility and the amount of variance (and ‘signal’) to be preserved (Cook et al., 1990; Speer, 2010). Given the lengths of tooth growth chronologies in this study (< 30 years), the detrending models used should retain variability at relevant timescales (interannual to decadal).

While cubic smoothing splines were applicable to both sperm whales and pilot whales, each stranding dataset was best described by models with different spline flexibilities (based on visual inspection of spline fit and \bar{r} values). The Strahan sperm whale dataset, comprising time series of 17 – 33 years, and teeth exhibiting varying degrees of wear (suggesting that the actual ages for many of these animals were likely much higher) was best described by a spline of 67%*n* years. In contrast, the Flinders Island sperm whale data, comprising time series of 18 – 29 years, and teeth with minimal wear was best described by a fixed 8-year smoothing spline. The degree of tooth wear is likely to have an effect on the fit of the detrending function to the data, wherein the loss of GLGs at the tooth tip may alter or, if large enough, obscure any age-related trend in GLG widths. In such cases, forcing all time series in a dataset to be fit by the same fixed length spline could result in indices unrepresentative of the actual variability in growth. Instead, the use of variable spline flexibilities (such as the 67%*n* spline) allows for alterations to growth curves caused by factors such as tooth wear to be more robustly estimated. The double detrending process applied to the pilot whale time series may provide a judicious method, particularly in animals where there is no tooth wear. The process allows for the accounting of early age-related trends in GLG width, while still retaining the flexibility of a spline fit to accommodate later variability in time series due to other individual processes and low frequency variation (Cook et al., 1990). As these detrending methods are extended to other marine mammal species experimentation with both deterministic and empirical detrending functions is recommended.

Crossdating quality and signal strength measures calculated for the data were, for the most part, low compared to values from other species reflecting high degrees of synchrony among samples such as those derived from tree-rings (Carrer et al., 2007), and otoliths (e.g. Black et

al., 2008a; Gillanders et al., 2012). They were, however, on a comparable level with those obtained for otolith chronologies exhibiting high individual variability such as western blue groper (*Achoerodus gouldii*) off Western Australia (Rountrey et al., 2014) and mangrove jack (*Lutjanus argentimaculatus*) from tropical northwest Australia (Ong et al., 2015). Expressed population signal values obtained for sperm whales and pilot whales (0.415 – 0.537) were below the EPS threshold of 0.85 typically accepted for dendrochronology studies. However, the EPS threshold is somewhat subjective, with no specific minimum accepted value (Briffa and Jones, 1990). For other species with lower \bar{r} (synchrony) and smaller sample sizes, lower EPS thresholds could be considered appropriate. In a multi-species chronology study Ong et al. (2018) applied a threshold of $\text{EPS} > 0.50$ to marine teleost otolith chronologies, which were then correlated with environmental variables. An EPS value below 0.85 suggests the chronology may be dominated by individual noise rather than a clear population-level signal (Speer, 2010), but does not necessarily mean the chronology is unacceptable for correlation with environmental parameters (Briffa and Jones, 1990; Buras, 2017). More exactly, the EPS provides an indication of the predictive power of the sample, rather than the strength of the signal, which in many cases may be improved by a larger sample size, as low EPS values are often indicative of small sample sizes and/or low \bar{r} (Buras, 2017). Large sample sizes and relatively high \bar{r} are a common feature of tree-ring and some teleost otolith datasets (particularly those associated with commercial fisheries), which will often have sample sizes up to or exceeding 50 individuals. Subsequently, increased sample size and time series length could be expected to improve both crossdating quality and chronology confidence for sperm whales and pilot whales.

Conclusions

A consolidated and consistent approach to growth increment chronology development such as the method described here provides for comparisons of multidecadal annually resolved proxies of growth at overlapping temporal and spatial scales that can be applied across multiple species (Black, 2009; Black et al., 2008a). The use of GLGs in marine mammal teeth to estimate age has been in practice since the 1950s (Scheffer and Myrick, 1980). Consequently extensive archived collections of teeth from many species worldwide, already prepared and aged, are in existence, including known age collections or descriptive models of GLG appearance for some species (e.g. Frie et al., 2011; Hohn et al., 1989; Medill et al., 2009; Pinedo and Hohn, 2000). Access to such collections would allow comparison of

alternative detrending approaches, while ensuring consistency in GLG identification and measurement between readers/studies and reduce potential errors in calendar year assignment. Further, historical samples with known collection dates provide an opportunity to establish chronologies for different species relatively quickly, to extend existing chronologies, and to integrate marine mammal chronologies with existing chronologies from other taxa. A large number of species form annual growth increments, with many chronologies already developed following dendrochronology methods for different species, taxa and geographic regions (Black, 2009; Black et al., 2009; Gillanders et al., 2012; Matta et al., 2010; Ong et al., 2016). Once established, chronologies can be applied to modelling studies investigating biological, physiological and environmental drivers of variability, which is the next research step for the chronologies developed in this study. Such applications will progress understanding of the effects of changing environmental conditions on the energy budgets of individuals.

Acknowledgements

Sperm whale tooth samples were provided by the Marine Conservation Program, Department of Primary Industries, Parks, Water and Environment (DPIPWE) Tasmania under permit FA 12276. Kris Carlyon (DPIPWE) is thanked for assistance and access to samples. Sam Thalmann (DPIPWE) is acknowledged for contributing to the preparation of sperm whale teeth. Pilot whale tooth samples were collected under DPIPWE permit FA12255; we thank Kris Carlyon (DPIPWE) and Shelley Graham (Ranger in Charge, King Island, Parks and Wildlife Service Tasmania) for assistance. Ben Arthur, Owen Daniel and Delphi Ward provided valuable assistance in the field. Catherine Kemper (Marine Mammal Ageing Facility, South Australian Museum) is gratefully thanked for assistance with preparation of pilot whale teeth and access to facilities. Dirk Welsford, Gabrielle Nowara and Bryn Farmer (Australian Antarctic Division) are thanked for laboratory access and assistance. We thank two anonymous reviewers for helpful comments that improved this manuscript. This research was supported by funding from the Winifred Violet Scott Charitable Trust, the Ethel Mary Read Research Grant and the Australian Geographic Society. VH was supported through an Australian Government Research Training Program Scholarship.

Supplementary information

Supplementary Table S3.1. Calendar year assignment of the marginal GLG of the teeth of sperm whales and long-finned pilot whales. GLG categories: 1. a full layer of a GLG representing the groove in etched teeth or the wide lightly stained layer in thin sectioned teeth is present and the ridge or deeply stained layer is visible at pulp cavity edge, 2. slight growth of groove or lightly stained layer visible at pulp cavity edge beyond last ridge or deeply stained layer, 3. a groove or lightly stained layer at pulp cavity edge, proportional to $\frac{1}{4}$ – $\frac{1}{2}$ of the width of the previous GLG's groove or lightly stained layer, 4. a groove or lightly stained layer at pulp cavity edge, proportional to $\frac{1}{2}$ to the full width of the previous GLG's groove or lightly stained layer (adapted from Kimura et al., 2007).

Marginal GLG category	Time of collection	Calendar year assignment
1	Jan – Aug	Previous year
1	Sep – Dec	Year of collection
2	Jan – Aug	Year of collection
2	Sep – Dec	Following year
3	Jan – Aug	Year of collection
3	Sep – Dec	Following year
4	Jan – Apr	Previous year
4	May – Dec	Year of collection

Supplementary Table S3.2

Growth layer group (GLG) estimates established using standard repeat count age estimation procedures ('Initial estimate') and revised age estimates following modified visual crossdating ('Revised estimate') for two – four mandibular teeth from each individual sperm whale(s) ($n = 18$) and for two teeth from each pilot whale(s) ($n = 18$). Differences in age estimates derived across teeth from the same individual sperm whale are due to differential tooth wear across the jaw.

Stranding location	Tooth ID#	Initial estimate	Revised estimate	Adjustment
Flinders Island	1928-1	30	30	0
“	1928-2	26	26	0
“	1929-1	23	23	0
“	1929-2	22	22	0
“	1930-1	26	26	0
“	1930-2	25	25	0
“	1931-1	23	23	0
“	1931-2	23	23	0
“	1932-1	19	19	0
“	1932-2	18	19	+1
“	1933-1	31	31	0
“	1933-2	29	29	0
“	1934-1	25	25	0
“	1934-2	23	23	0
“	1935-1	26	26	0
“	1935-2	26	23	-3
Strahan	2156-1	35	30	-5
“	2156-2	34	33	-1
“	2157-1	35	30	-5
“	2157-2	30	29	-1
“	2158-1	18	17	-1
“	2158-2	24	24	0
“	2158-3	20	20	0
“	2158-4	24	24	0
“	2161-1	23	24	+1
“	2161-2	29	29	0
“	2161-3	33	31	-2
“	2161-4	26	29	+3
“	2163-1	21	25	+4
“	2163-2	26	26	0
“	2163-3	22	26	+4

Supplementary Table S3.2. cont'd

Stranding location	Tooth ID#	Initial estimate	Revised estimate	Adjustment
Strahan	2166-1	20	19	-1
"	2166-2	21	21	0
"	2166-3	21	20	-1
"	2166-4	19	20	+1
"	2168-1	23	23	0
"	2168-2	27	25	-2
"	2168-3	24	24	0
"	2168-4	30	30	0
"	2169-1	20	19	-1
"	2169-2	21	21	0
"	2172-1	20	21	+1
"	2172-2	26	25	-1
"	2172-3	22	22	0
"	2172-4	16	17	+1
"	2174-1	29	28	-1
"	2174-2	27	29	+2
"	2174-3	24	29	+5
King Island	KI-GM1-1	8	8	0
"	KI-GM1-2	8	8	0
"	KI-GM2-1	9	9	0
"	KI-GM2-2	8	9	+1
"	KI-GM3-1	13	13	0
"	KI-GM3-2	13	13	0
"	KI-GM4-1	12	12	0
"	KI-GM4-2	12	12	0
"	KI-GM5-1	10	10	0
"	KI-GM5-2	9	10	+1
"	KI-GM6-1	11	11	0
"	KI-GM6-2	11	11	0
"	KI-GM7-1	10	10	0
"	KI-GM7-2	7	10	+3
"	KI-GM9-1	17	16	-1
"	KI-GM9-2	16	16	0
"	KI-GM10-1	6	6	0
"	KI-GM10-2	6	6	0

Supplementary Table S3.2. cont'd

Stranding location	Tooth ID#	Initial estimate	Revised estimate	Adjustment
King Island	KI-GM11-1	7	7	0
"	KI-GM11-2	6	7	+1
"	KI-GM12-1	14	14	0
"	KI-GM12-2	14	14	0
"	KI-GM13-1	12	14	+2
"	KI-GM13-2	14	14	0
"	KI-GM14-1	12	12	0
"	KI-GM14-2	12	12	0
"	KI-GM15-1	8	8	0
"	KI-GM15-2	9	8	-1
"	KI-GM16-1	8	8	0
"	KI-GM16-2	8	8	0
"	KI-GM21-1	8	8	0
"	KI-GM21-1	8	8	0
"	KI-GM28-1	8	8	0
"	KI-GM28-1	8	8	0
"	KI-GM29-1	13	13	0
"	KI-GM29-2	13	13	0

Chapter 4 Spatial variability in responses to environmental conditions in Southern Hemisphere long-finned pilot whales

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All of the research contained in this chapter has been submitted to Marine Ecology Progress Series as ‘Hamilton, V., Evans, K., Raymond, B., Betty, E. and Hindell, M.A. Spatial variability in responses to environmental conditions in Southern Hemisphere long-finned pilot whales.’

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 Tasmania, Australia (2012), we investigated relationships between tooth growth chronologies, as a proxy for energy budgets, and interannual variations in broad-scale climate indices (Southern Oscillation Index: SOI, Indian Ocean Dipole: IOD, and the Southern Annular Mode: SAM) and spatially explicit, seasonally averaged environmental variables (sea surface temperature: SST, and zonal wind speed). Tooth growth 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 only, but at a one year 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 the Australian tooth growth chronology and SST revealed spatial consistencies in areas associated with higher tooth growth across seasons. In contrast, pilot whales utilising New Zealand waters demonstrated greater spatial variability in relationships suggesting differences in habitat utilisation between the two regional groups. Results suggest that pilot whales from Australia associated with the subtropical and subantarctic fronts south of Tasmania while those from New Zealand associated with a number of regions of seasonally enhanced productivity closer to New Zealand. This study is the first to provide insights into environmental conditions influencing pilot whale populations in the region.

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 (Schumann et al., 2013; Trathan et al., 2007). Fluctuations in broad-scale climate modes can result in changes in sea surface temperature, wind and ocean currents that influence the marine environment at differing spatial and temporal scales (Behrenfeld et al., 2006; Stenseth et al., 2002). Resultant changes in productivity and the location and abundance of prey species will have flow-on effects on the energy budgets of higher trophic level species (Learmonth et al., 2006). Responses to short-term natural variability in oscillating climate signals (e.g. such as the El Niño-Southern Oscillation: ENSO) and environmental parameters (e.g. sea surface temperatures), 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 the response to environmental variation 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 the largely underwater, remote and wide-ranging habitats of many pelagic species.

Time series of annual growth increment widths in 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 and physiological condition for their rate of formation over each year (Boyd and Roberts, 1993; Klevezal', 1996; Langvatn, 1995; Medill et al., 2010). As a result, interannual variation in GLG widths will reflect variability in energy budgets (Hamilton et al., 2013; Hanson et al., 2009; Klevezal', 1996). Similarly 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. Boyd and Roberts, 1993; Hanson et al., 2009; 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 annual return

to rookeries. Additionally, varying methodology has limited the repeatability and comparability of studies, and only one study 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. 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 other species (Hamilton and Evans, 2018).

Long-finned pilot whales (*Globicephala melas*; hereafter referred to as pilot whales) are long-lived (> 60 years for females and 35 – 45 years 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. Pilot whales form 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; Ottensmeyer and Whitehead, 2003). This social structure means animals from the same social unit should have experienced similar environmental conditions. 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, the long-finned pilot whale is thought to inhabit temperate and subantarctic deep oceanic waters and areas of high productivity along the continental slope (Ross, 2006). Nonetheless, 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. Genetic studies suggest population differentiation of pilot whales from the geographically adjacent regions of New Zealand and Tasmania, Australia (Oremus et al., 2009) and imply that the two populations may have distinct foraging ranges. Given the potential suitability of pilot whales for chronology studies, the paucity of information on the species in the region and the availability of samples from strandings; here we apply novel modified dendrochronology techniques to teeth collected from pilot whales stranded in New Zealand and Australia to:

- i) investigate responses 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),
- ii) investigate spatial variability in relationships between tooth growth and spatially explicit, gridded environmental variables (sea surface temperature: SST, wind speed) as a guide to potential foraging areas of pilot whales in the Australian/New Zealand region, and
- iii) assess any differences in the responses of pilot whales from the two geographic regions.

Methods

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 stranding of 107 animals) in 2011 and King Island, Tasmania, Australia (39.67°S, 143.83°E, $n = 18$ from stranding of 44 animals) in 2012 (Table 4.1); sites separated by a distance of ~2000 km.

Tooth preparation and GLG identification

Teeth were decalcified, thin sectioned, stained and mounted on slides before being digitally imaged following methods detailed in Hamilton and 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 and Myrick, 1980). Growth layer groups were identified two to three times for each tooth via blind readings of digital images by VH and a sub-sample of teeth ($n = 12$) was cross-verified by another experienced reader (KE). 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 cross-check GLG identification within each individual (Hamilton et al., 2017). Following any adjustments made to the GLG time series as a result of cross-checking (see Supplementary Table S4.1), the tooth with the most central section position and greatest clarity of GLG boundaries was selected for GLG width measurement and chronology development.

Table 4.1. Details of individual long-finned pilot whales, tooth state and growth layer group (GLG) width time series (T-S length) included in tooth growth chronologies.

Stranding date	Stranding location	Species	Whale ID #	Sex	Age estimate (T-S length)	Pulp cavity state	Tooth wear
20/02/2011	Rakiura	<i>G. melas</i>	R-GM1	M	13	closing	low
20/02/2011	Rakiura	<i>G. melas</i>	R-GM2	M	13	open	low
20/02/2011	Rakiura	<i>G. melas</i>	R-GM3	F	12	closing	nil
20/02/2011	Rakiura	<i>G. melas</i>	R-GM4	M	9	open	low – moderate
20/02/2011	Rakiura	<i>G. melas</i>	R-GM5	M	8	open	nil
20/02/2011	Rakiura	<i>G. melas</i>	R-GM6	M	10	open	low
20/02/2011	Rakiura	<i>G. melas</i>	R-GM7	M	11	open	nil
20/02/2011	Rakiura	<i>G. melas</i>	R-GM8	M	7	open	nil
20/02/2011	Rakiura	<i>G. melas</i>	R-GM9	M	7	open	low – moderate
20/02/2011	Rakiura	<i>G. melas</i>	R-GM10	M	10	open	nil
20/02/2011	Rakiura	<i>G. melas</i>	R-GM11	M	6	open	nil
20/02/2011	Rakiura	<i>G. melas</i>	R-GM12	M	11	open	low
03/11/2012	King Island	<i>G. melas</i>	KI-GM1	M	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM2	F	9	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM3	F	13	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM4	M	12	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM5	F	9	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM6	F	11	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM7	M	11	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM9	M	15	closing	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM10	M	7	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM11	F	7	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM12	M	13	closing	nil

Table 4.1. cont.d

03/11/2012	King Island	<i>G. melas</i>	KI-GM13	F	13	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM14	F	12	closing	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM15	M	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM16	F	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM21	M	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM28	F	8	open	nil
03/11/2012	King Island	<i>G. melas</i>	KI-GM29	F	13	open	nil

Chronology development

Measurement of GLG widths, adjustments to GLG identification via statistical crossdating and detrending to produce tooth growth chronologies for each individual followed the methods detailed in Hamilton and Evans (2018). The short length (≤ 8 years) of four time series from New Zealand and seven time series from Australia did not allow sufficient numbers of GLGs overlapping in time for statistical crossdating (Fritts and Speer, 2005). As a result, some residual errors in GLG identification and calendar year assignment may have remained for those individuals. Individual GLG width time series from New Zealand whales were detrended using a cubic smoothing spline with 50% frequency cut-off at $n\text{-years}/2$ (i.e., a wavelength of half the series length). Because time series from Australian individuals exhibited a more obvious age-related decline in GLG widths they 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 in the early portions of the time series. The resulting indexed time series were then detrended once more using cubic smoothing splines at a 50% frequency cut-off of 12 years to accommodate departures from the exponential model due to growth variations in the latter parts of the time series. Although a decreasing trend in GLG widths was also observed in the New Zealand pilot whale time series, negative exponential curves did not provide a good fit to all individual time series, resulting in ‘end effects’ for time series (i.e., poor fits at either end of the individual time series, leading to inflated indices when converted to standardised measurements). The poor fit of negative exponential curves for the New Zealand time series was likely related to varying degrees of tooth wear removing the earliest GLGs from some time series. Additional crossdating and detrending details can be found in the supplementary material.

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 therefore be exposed to similar environmental conditions for large portions of their lives. Combining multiple chronologies from individuals 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 (Bunn, 2008; Cook et al., 1990). Master chronologies for each of the stranding groups comprised years in which there was a minimum of six 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 $EPS = n\bar{r}/(1 + (n - 1)\bar{r})$ (Briffa and Jones, 1990; Wigley et al., 1984).

Environmental analyses

Generalised additive models (GAMs; Wood, 2006) with a Gaussian error distribution and identity link function were used to investigate relationships between the two master chronologies and indices of broad-scale climate-ocean interactions (see Supplementary Table S4.2). The SOI, IOD and SAM were selected as they are recognised as important determinants of interannual environmental and biological variability in the Australian and New Zealand regions (Salinger et al., 2016). 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 a temporal lag could potentially occur as changes in productivity propagate through trophic levels (Forcada et al., 2005; Weimerskirch et al., 2003). Pilot whales feed primarily on cephalopods, which typically have a relatively short life cycle of 1 – 2 years, and respond rapidly to fluctuations in their environment (Boyle and Rodhouse, 2005; Clarke, 1996). With this knowledge of prey dynamics in mind, climate indices were therefore included in the models both concurrently with the chronologies and at a lag of 1 year. 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 and 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; Tynan, 1998; Wilson and Adamec, 2002). Gridded measurements of SST and zonal near-surface wind speed (Supplementary Table S4.2) 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 bounded by 30°S – 60°S, 110°E – 190°E to identify regions associated with increased tooth growth. The spatial domain covered areas of assumed long-finned pilot whale distribution in the southern Australian/New Zealand region, based on pilot whale sighting and stranding records (Woinarski et al., 2014).

Annual GLG widths were measured using a plug-in ('IncMeas'; Rountrey, 2009) written for ImageJ, an open source image processing program (version 1.47, National Institutes of Health, USA). 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, 2010) was used for crossdating, detrending and chronology building and GAMs were implemented using the R package 'mcgv' (Wood, 2004, 2011).

Results

Chronologies

The number of GLGs measured for each individual ranged 6 – 13 years, spanning 1998 – 2010 for pilot whales from New Zealand, and 7 – 15 years, spanning 1997 – 2011 for pilot whales from Australia (Table 4.1). Master chronology lengths were 10 and 12 years for the New Zealand and Australian strandings, respectively.

Chronologies of individuals from each of the strandings varied with Pearson's correlation coefficients ranging –0.86 – 0.88 and –0.85 – 0.91 for the New Zealand and Australian chronologies respectively (Supplementary Figure S4.1). The strength of the common signal

(\bar{r}) and expressed population signal values reflected this variability being 0.069 and 0.475 for the New Zealand chronology and 0.038 and 0.415 for the Australian chronology. Despite this high variability, individuals did show some synchrony, which was reflected in the master chronologies (Figure 4.1). This included above average (> 1.0) growth across most individuals from New Zealand in 2004, and across most individuals from the Australian stranding in 2004 and 2005 (Figure 4. 1). Most individuals from New Zealand had below average (< 1.0) growth in 2003 and 2005 and those from Australia had below average growth in 2003 and 2006 (Figure 4.1). Little correlation was evident between the New Zealand and Australian master chronologies (Pearson's $r = -0.09$).

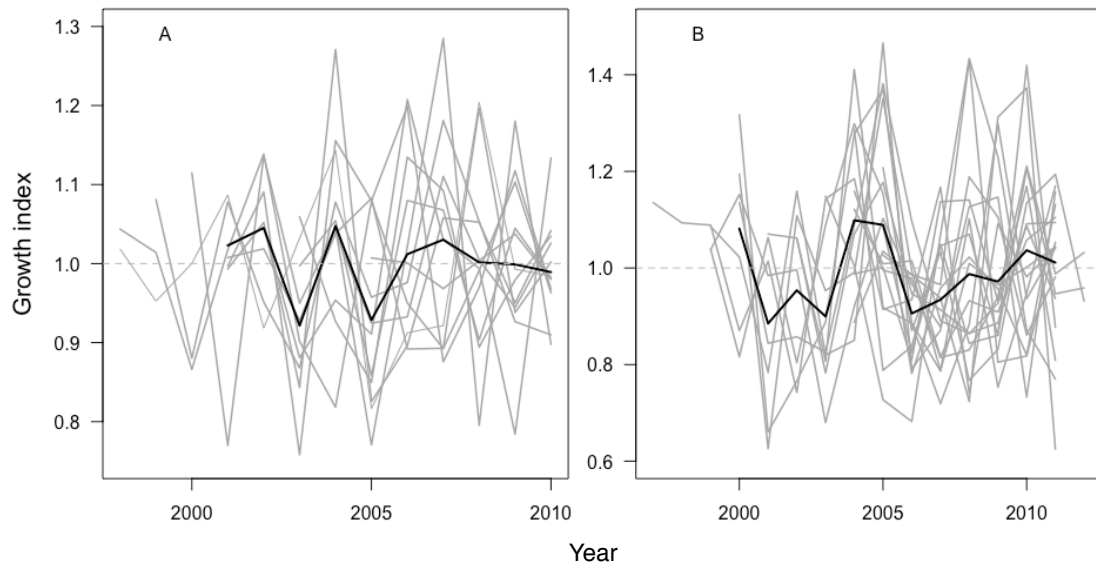


Figure 4.1. Tooth growth chronologies of individuals (grey lines) and master chronologies (black line) for long-finned pilot whales from (A) New Zealand ($n = 12$) and (B) Australia ($n = 18$). The dashed horizontal line is the mean.

Relationships with broad-scale climate indices

The highest scoring model (AIC_c) for the New Zealand chronology included the SOI with a one year lag only and explained 50.8% of the deviance in the data (Table 4.2). Below average tooth growth was associated with SOI values less than approximately -2 and above average tooth growth was associated with SOI values greater than -2 (Figure 4.2A). The highest scoring model (AIC_c) for the Australian chronology included both the SOI and the IOD and explained 40.1% of the deviance in the data (Table 4.2). 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 tooth growth associated with IOD values of $0 - 0.25$, above which tooth growth was below average (Figure 4.2B).

Table 4.2. Outputs from the top ranked generalised additive models fitted to New Zealand and Australian long-finned pilot whale tooth growth chronologies and climate indices. GI = Chronology, SOI = Southern Oscillation Index, IOD = Indian Ocean Dipole, SAM = Southern Annular Mode. Lagged covariates are indicated by lag1. The accepted model is highlighted in bold.

Candidate models	AIC_c	% Deviance explained
<i>New Zealand</i>		
1. GI ~ SOI_{lag1}	-23.944	50.8%
2. GI ~ SAM	-19.364	43.6%
<i>Australia</i>		
1. GI ~ SOI + IOD	-20.470	40.1%
2. GI ~ SOI + SAM _{lag1}	-16.047	24.1%

AIC_c , Akaike's (second order) Information Criterion

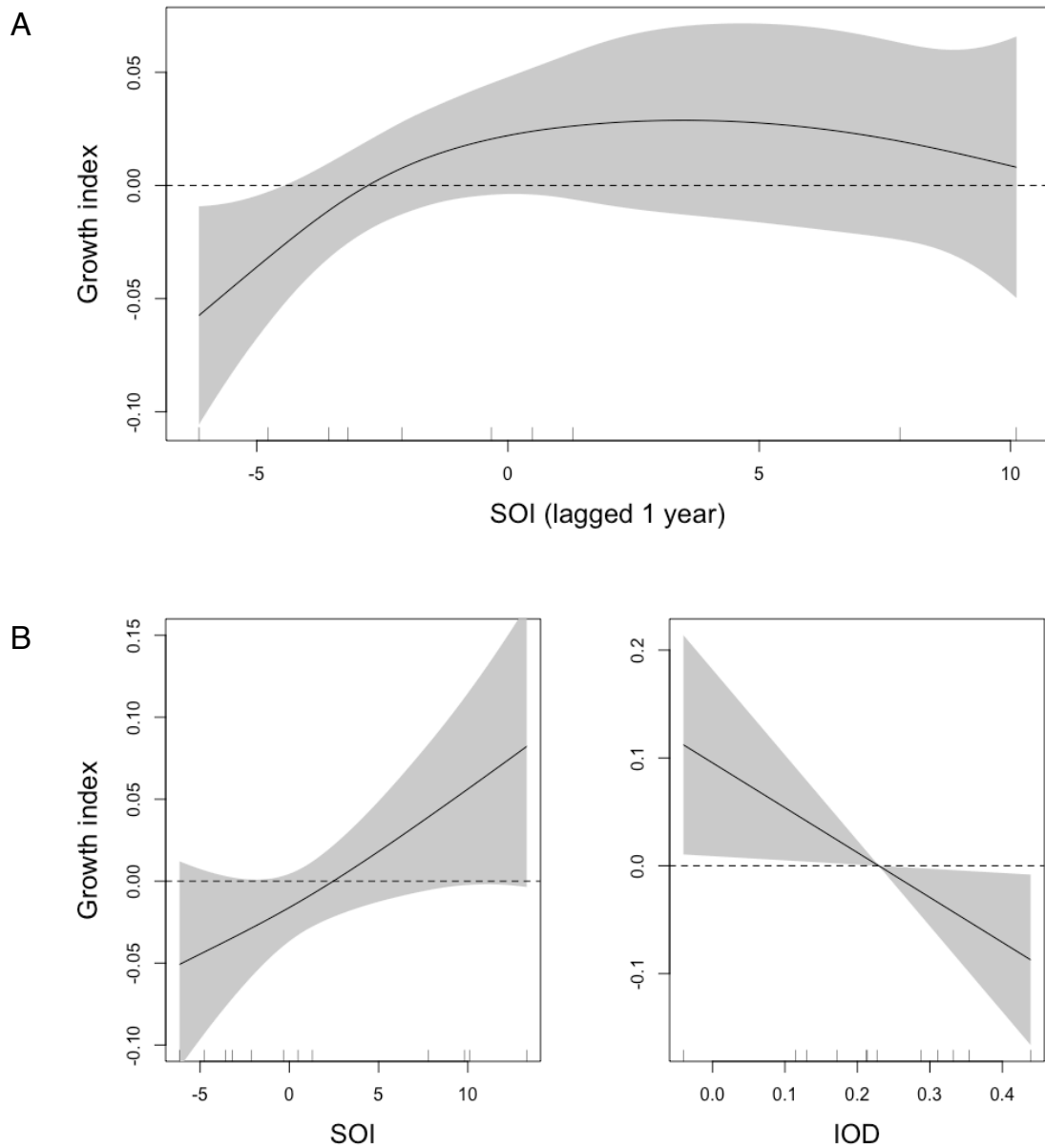


Figure 4.2. Results of generalised additive models for predicted tooth growth in relation to broad-scale climate indices: the Southern Oscillation Index (SOI) and the Indian Ocean Dipole (IOD) in long-finned pilot whales from (A) New Zealand and (B) Australia. Shading represents the 95% confidence limits and the horizontal dashed line is the mean.

Relationships with gridded spatially explicit environmental variables

The spatial distribution of correlations between the New Zealand chronology and seasonally averaged SST varied across seasons (Figure 4.3A). During the austral autumn areas of higher tooth growth in association with lower SSTs occurred to the east and north of New Zealand ($30^{\circ}\text{S} - 40^{\circ}\text{S}$, $175^{\circ}\text{E} - 190^{\circ}\text{E}$). Similar correlations occurred in the eastern area of the Great Australian Bight during the winter while in spring they occurred in a region southeast of New Zealand in the region of the Campbell Plateau ($45^{\circ}\text{S} - 55^{\circ}\text{S}$, $160^{\circ}\text{E} - 190^{\circ}\text{E}$). Areas of higher tooth growth in association with higher SSTs occurred to the east of New Zealand ($35^{\circ}\text{S} - 45^{\circ}\text{S}$, $175 - 190^{\circ}\text{E}$) during summer, shifting progressively west and south across autumn and winter until in the spring they occurred in a region to the south of western parts of Australia (Figure 4.3A).

In contrast, the spatial distribution of correlations between the Australian chronology and SST indicating regions of higher tooth growth was seasonally consistent. Higher tooth growth in association with lower SSTs occurred in a region south of Tasmania ($45^{\circ}\text{S} - 55^{\circ}\text{S}$, $130^{\circ}\text{E} - 160^{\circ}\text{E}$) across all seasons with correlations strongest in autumn and winter (Figure 4.3B). Regions of higher tooth growth in association with higher SSTs occurred consistently to the east of Australia in the Tasman Sea ($30^{\circ}\text{S} - 40^{\circ}\text{S}$, $152^{\circ}\text{E} - 165^{\circ}\text{E}$) across all seasons, being strongest in autumn and spring. Similar correlations with higher SSTs 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 (see Supplementary Figure S4.2).

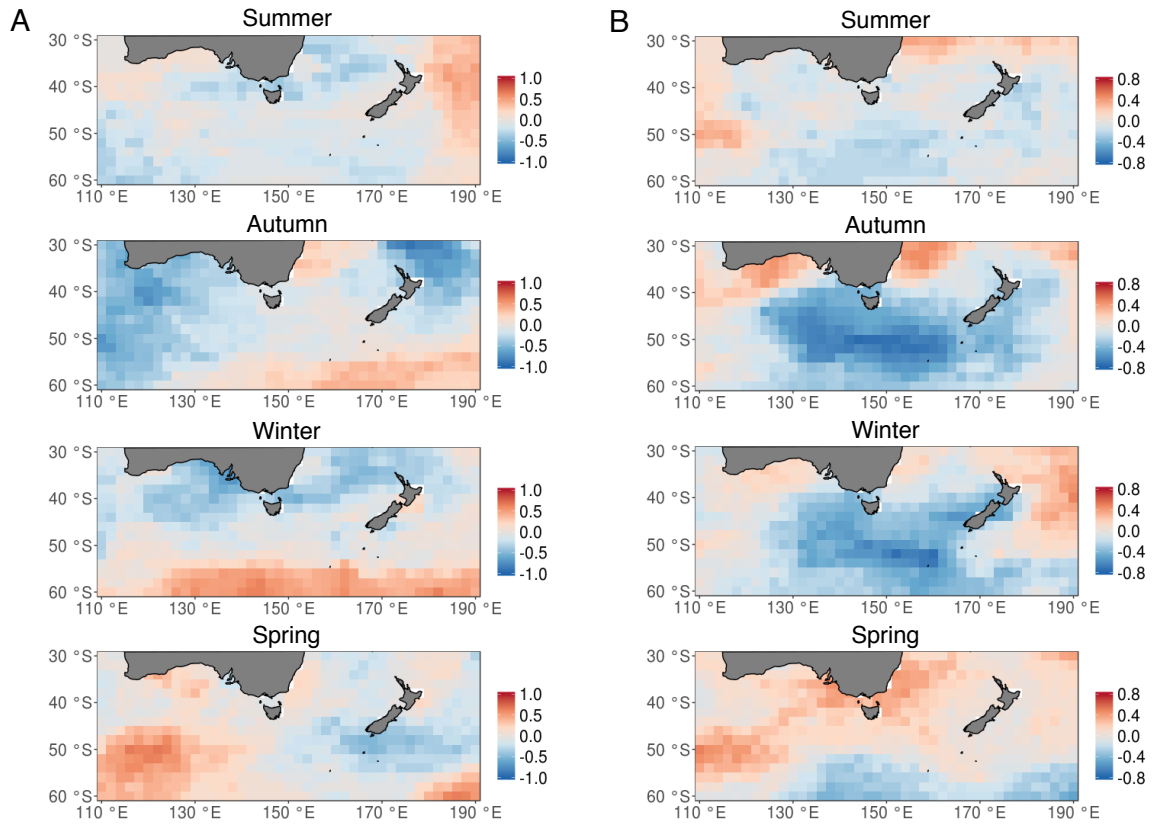


Figure 4.3. Spatial maps of correlations between gridded seasonal averages (austral Summer: Dec, Jan, Feb; Autumn: Mar, Apr, May; Winter: Jun, Jul, Aug and Spring: Sep, Oct, Nov) of sea surface temperature (SST) and long-finned pilot whale tooth growth chronologies from (A) New Zealand (2001 – 2010) and (B) Australia (2000 – 2011). Red shades represent positive correlations and blue shades represent negative correlations.

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. Synchrony across individual chronologies from each stranding was relatively low compared to chronologies established for tree species or marine species with limited ranges such as bivalves (e.g. 0.3 – 0.4; Brocas et al., 2013; Frank and Esper, 2005). Synchrony was however comparable with values reported for highly mobile teleosts; e.g. *Achoerodus gouldii*; 0.019 (Rountrey et al., 2014) and *Lutjanus argentimaculatus*; 0.153 (Ong et al., 2015), likely reflecting the ability of individuals to move more widely among regions of varying environmental conditions. These teleost chronologies demonstrated similar levels of individual variability to that observed for pilot whales, and common signals related to climate and environmental indices were able to be determined. Variations in synchrony across individual chronologies is to be expected, particularly in higher trophic level species (e.g. see Matta et al., 2010; Nguyen et al., 2015; Ong et al., 2015; van der Sleen et al., 2016) and can result from a number of sources. Given the size of both of the stranding groups, those individuals from which samples were derived may not have been part of the same matriline or social unit, rather the strandings may have comprised feeding or mating associations formed of multiple social units (Oremus et al., 2013; Ottensmeyer and Whitehead, 2003). Subsequently, the environmental conditions and prey resources experienced by different social units may vary, resulting in differing energy budget responses. Further, individuals within social groups are capable of making independent foraging decisions, thereby varying in their foraging success and nutritive intake. 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 (Costa, 2009; Lockyer, 2007).

Age estimation and GLG identification is a subjective process, and misidentification of GLGs and subsequent errors in calendar year assignment could also affect alignment of time series. Such errors are more likely in cases where crossdating is restricted due to short time series lengths, because time series will not be long enough to confidently match patterns among individuals (Black et al., 2016). Many of the individual time series in this study were relatively short in length, and so could potentially be prone to these errors. The occurrence of

synchronous growth amongst the majority of individuals in some years (e.g. 2003 and 2004) suggests any potential misalignment of GLGs in the latter parts of the time series dampened, rather than completely obscured common signals.

The ENSO was an important predictor of tooth growth for both sample groups with increases in tooth growth associated with increasing SOI values. While this relationship occurred concurrently with the Australian chronology, the relationship with the New Zealand chronology occurred at a one year lag. Environmental conditions associated with ENSO 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 (Ashok et al., 2007; Cai et al., 2011b; Gordon, 1986). 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). Storm activity can assist with mixing and supply of nutrients from depth or coastal sources, resulting in regional increases in productivity (Rennie et al., 2009). Warmer SSTs and increases in SST gradients can influence the timing of spawning, growth and survival or distribution of prey species (Chambers et al., 2011; Pecl and Jackson, 2008).

Little is known regarding the spatial distribution and habitat preferences of pilot whales in the Australian and New Zealand regions. There are no existing photo-identification studies and satellite telemetry studies have been conducted on only five individuals released post-stranding on the Tasmanian coastline in 2008, and within the tagging timeframe these individuals travelled a limited range; remaining in the waters of Bass Strait (Gales et al., 2012). Similarly, there have been few dietary investigations, and those focused on stomach contents of small sample numbers of stranded individuals (Beatson et al., 2007a; 2007b; Beatson and O'Shea, 2009; Gales et al., 1992). This lack of information on diet and distribution makes it difficult to assess what may be driving differences in relationships of energy budgets with ENSO for the New Zealand and Australian pilot whales. However, lagged responses to environmental variability are not uncommon in higher trophic predators, as effects on primary productivity and food web transfer will vary regionally (Mann and Lazier, 2006; Trathan et al., 2007). Combining stable isotope analysis of dentinal GLGs with chronology studies may assist in determining if differences in responses to climate indices reflect spatial variation in foraging habitats or differences in prey preferences of regional populations.

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. The influence of the IOD on climate is strongest across the Indian Ocean basin and southern Australian region (Saji et al., 1999). The inclusion of the IOD in the preferred model for the Australian pilot whales suggests that the Australian pilot whales spend more time in regions influenced by the IOD than the New Zealand pilot whales. Positive (negative) IOD events are associated with a weakening (strengthening) of westerly winds and storm activity during winter off Australia (Ashok et al., 2007). Biological responses to variability in the IOD in the Australian marine environment are not well known; however, decreases in wind-driven mixing associated with higher positive IOD may depress productivity by reducing nutrient supply to the photic zone (Bakun, 1996; Rennie et al., 2009). Increases in regional wind conditions and strengthened storm activity associated with neutral or lower IOD and/or positive ENSO phases are likely to increase wind-driven 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 (Bost et al., 2009; Genin et al., 1988; Murphy, 1995). Such 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.

Correlations between the chronologies and SST demonstrated temporal-spatial variability. 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 (Gowans and Whitehead, 1995; Hooker et al., 1999; Zachariassen, 1993), likely reflecting seasonal or temperature regulated movements of prey species (Fullard et al., 2000). On this basis, we therefore considered regions of above average tooth growth in relation to cooler SSTs (negative correlations) and warmer SSTs (positive correlations) to be equally relevant. Association with such varying oceanographic conditions most likely reflects some flexibility in prey preferences by pilot whales. This is supported by what is known of the diet of pilot whales in the southern Australian and New Zealand regions, with a variety of cephalopod species consumed (Beatson et al., 2007a; 2007b; Beatson and O'Shea, 2009; Gales et al., 1992).

The greater spatial variability of correlations between the New Zealand chronology and SST across seasons suggests that the New Zealand pilot whales are likely associating with more highly dispersed foraging habitats than the Australian whales. 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. Catches of sperm whales (*Physeter macrocephalus*; also cephalopod predators) by whaling vessels across the Tasman Sea and New Zealand region tended to occur 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, potentially reflecting utilisation of relatively stable areas of high productivity. Variability or stability in oceanographic conditions and subsequently the location and availability of prey resources can drive differing foraging strategies in higher predators. In less temporally stable environments predators may time their foraging movements to take advantage of regions of seasonally-high productivity (e.g. Baylis et al., 2008). Alternatively, individuals or groups may consistently rely on regions of predictable prey resources (Bost et al., 2009; Weimerskirch, 2007).

The frontal regions south of Tasmania and New Zealand associated with the subtropical and subantarctic fronts are highly productive due to the convergence of subtropical and subantarctic waters, wind-driven upwelling of cooler waters and eddy formation (Sokolov and Rintoul, 2002; Tomczak et al., 2004; Westwood et al., 2011). South of New Zealand the subtropical front is bathymetrically constrained by the Campbell Plateau, and bounded along the southeast coast by the north-flowing Southland Current until it deflects eastwards along the Chatham Rise (see Figure 1.1) (Bradford-Grieve et al., 1999; Heath, 1981; Hopkins et al., 2010). Productivity is elevated along the front, due to mixing of iron-enriched subtropical waters with cold nutrient-rich subantarctic waters transported by the Southland Current (Boyd et al., 1999; Butler et al., 1992). The region south and southeast of New Zealand encompasses important foraging zones for marine mammals and seabirds and commercially important fisheries including squid (Bradford-Grieve et al., 2003; Chilvers, 2008; Jackson et al., 2000; Waugh et al., 1999). Correlations with SST suggest an association with the Campbell Plateau and Chatham Rise regions for New Zealand pilot whales during the austral spring. This is consistent with observations of relatively high levels of chlorophyll a in the region, and a high spring bloom (Bradford-Grieve et al., 2003; Murphy et al., 2001; Nodder 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 (Godfrey et al., 1980; Rowden et al., 2005; Tilburg et al., 2001; 2002). The East Australian Current (EAC) flows south along the continental shelf of Australia (see Figure 1.1), with eddy separation from the main flow of the EAC forming a region of upwelling and downwelling (Ridgway and Dunn, 2003; Tilburg et al., 2002). Outflow from the EAC forms the Tasman Front, an eastward flowing zonal jet that passes to the north of New Zealand, connecting the EAC to the East Auckland and East Cape Currents (Stanton, 1981; Tilburg et al., 2001). A series of three permanent warm core eddies occur along the offshore side of the East Auckland Current, providing localised productivity and prey aggregations (Bradford et al., 1982; Ridgway and Dunn, 2003; Roemmich and Sutton, 1998).

The productivity of the Tasman Sea and waters to the north and east of New Zealand supports a number of high value pelagic finfish fisheries (Ministry for Primary Industries, 2017; Stewardson et al., 2016), suggesting the region provides consistent prey resources for higher trophic levels, and may therefore be an important foraging region for pilot whales. Flow strength of the EAC varies seasonally and interannually, and is highest in association with positive ENSO (La Niña) conditions (Holbrook et al., 2011; Ridgway and Godfrey, 1997). Periods of higher EAC flow are associated with increased mesoscale eddy activity and enhanced transport across the Tasman Front (Ridgway and Godfrey, 1997; Sprintall et al., 1995). Both the model results and spatial patterns in correlations suggest that the Tasman Sea and northern New Zealand waters may represent foraging regions of elevated localised prey resources important to pilot whales, particularly when conditions are associated with positive ENSO phases.

Conclusions

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 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 years, 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 environmental variability under a wide range of conditions and climate interactions to be established.

Acknowledgements

Rakiura (Stewart Island) pilot whale tooth samples were collected under permit DOCDM-324868, issued to EB by the New Zealand Department of Conservation (DOC). We thank the many individuals involved with the New Zealand Rakiura stranding, including representatives from Ngāi Tahu iwi, Brent Beaven and Sharon Pascoe (DOC Rakiura Field Centre), and Rakiura Helicopters. Severine Hannam, Nik Hannam, Jessie Williams and Jeanie Fay are thanked for assistance with field sampling. King Island pilot whale tooth samples were collected under permit FA12255, provided by the Marine Conservation Program, Department of Primary Industries, Parks, Water and Environment (DPIPWE); we thank Kris Carlyon (DPIPWE) and Shelley Graham (Ranger in Charge, King Island, Parks and Wildlife Service Tasmania) for assistance. Ben Arthur, Owen Daniel and Delphi Ward provided valuable assistance in the field. Dirk Welsford, Gabrielle Nowara and Bryn Farmer (Australian Antarctic Division) are thanked for laboratory access and assistance. Catherine Kemper (Marine Mammal Ageing Facility, South Australian Museum) is gratefully thanked for assistance with preparation of pilot whale teeth and access to facilities. This research was supported by funding from the Winifred Violet Scott Charitable Trust and the Ethel Mary Read Research Grant (RZSNSW). VH was supported through an Australian Government Research Training Program Scholarship.

Supplementary Information

Adjustment to GLG identification via modified visual crossdating within individuals

Cross-checks of distinctive growth layer groups (GLGs) among teeth from the same individuals resulted in GLG adjustments of -1 to +3 GLGs in a single tooth from each of 14 pilot whales (see Supplementary Table S4.1). The modal GLG adjustment was +1 GLG, associated with missing a GLG by misidentification of a GLG as an accessory layer. The modified visual crossdating process also assisted in the identification of GLG boundaries including that associated with the pulp cavity margin.

Statistical crossdating among individuals

GLG width time series were statistically crossdated following Hamilton and Evans (2018) to check similar patterns of GLG widths correlated among samples, as an additional step to aid correct calendar year assignment of GLGs. If potential errors in GLG width time series were identified during the crossdating process, the tooth image the time series was derived from was visually re-examined and corrections were made to the GLG width time series only if an error in GLG identification could be verified on the original image of the tooth.

Four New Zealand time series and seven Australian pilot whale time series were not sufficient in length (≤ 8 GLGS) to effectively correlate back to the pilot whale mean time series for each stranding group, and so crossdating was not carried out on these individuals. Six New Zealand pilot whale time series and eight time series for Australian pilot whales returned poor correlation values ($p \geq 0.05$) and were re-examined for potential errors. Interseries correlation values for each stranding were 0.529 for New Zealand and 0.464 for Australian pilot whales before crossdating. Errors in GLG identification were located and corrected for one pilot whale GLG width time series from New Zealand (GLG at the pulp cavity margin had been misidentified as incomplete) and two pilot whale GLG width time series from Australia contained an error in GLG identification (falsely added GLGs). After correction of errors, poor correlations ($p \geq 0.05$) remained for five New Zealand pilot whale time series and four Australian pilot whale time series. The interseries correlation values for each stranding improved overall, reflecting the corrections made, 0.621 for New Zealand and 0.523 for Australian pilot whales.

After crossdating checks and any adjustments to GLG identification, the raw GLG width time series were detrended to remove age-related trends in GLG width time series or variability specific to an individual, thereby enhancing detection of a common, population-wide signal (Cook et al., 1990; Fritts, 1976).

Detrending

Linear models, negative exponential curves and different flexibilities of cubic smoothing splines were applied to both the New Zealand and Australian pilot whale time series to determine the best detrending method to standardise GLG width time series and enhance a common signal for each stranding group. A decreasing trend in GLG widths was observed in the Australian pilot whale time series, resulting in a good fit of negative linear or negative exponential curves to the early portions of individual time series. Departures from the exponential model in the latter parts of time series were best fit by cubic smoothing splines. Subsequently a ‘double detrending’ method as described by Cook (1985) was used for pilot whales from Australia, in which GLG width time series were first detrended by negative exponential curves or negative linear regression models and then the indexed time series were detrended once more using cubic smoothing splines. Although negative exponential detrending returned a higher \bar{r} value for New Zealand pilot whale time series, visual inspection revealed that cubic smoothing splines with a frequency response of 50% at a wavelength of $n\text{-years}/2$ provided a better fit to the data (second highest \bar{r} value).

Supplementary Table S4.1. Growth layer group (GLG) estimates established using standard repeat count age estimation procedures ('Initial estimate') and revised age estimates following modified visual crossdating ('Revised estimate') for two teeth from each pilot whale(s) ($n = 30$).

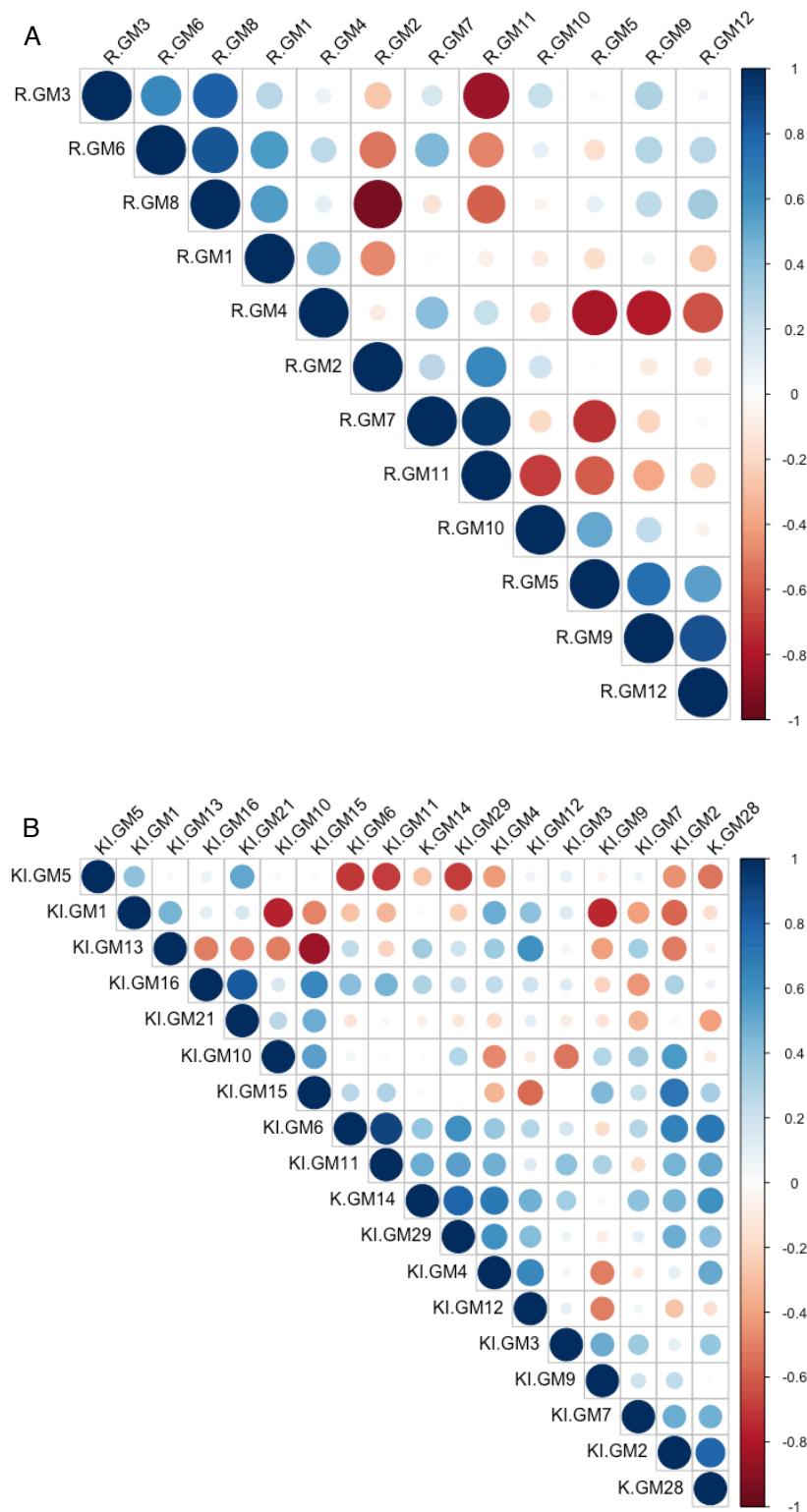
Stranding location	Tooth ID#	Initial estimate	Revised estimate	Adjustment
Rakiura	R-GM1-1	13	13	0
"	R-GM1-2	12	13	+1
"	R-GM2-3	13	13	0
"	R-GM2-4	14	13	-1
"	R-GM3-3	12	12	0
"	R-GM3-4	12	12	0
"	R-GM4-2	9	9	0
"	R-GM4-3	10	9	-1
"	R-GM5-1	8	8	0
"	R-GM5-2	8	8	0
"	R-GM6-1	10	10	0
"	R-GM6-2	10	10	0
"	R-GM7-1	11	11	0
"	R-GM7-3	10	11	+1
"	R-GM8-2	7	7	0
"	R-GM8-3	6	7	+1
"	R-GM9-2	7	7	0
"	R-GM9-3	7	7	0
"	R-GM10-1	12	12	0
"	R-GM10-4	10	12	+2
"	R-GM11-3	6	6	0
"	R-GM11-4	6	6	0
"	R-GM12-1	11	11	0
"	R-GM12-4	10	11	+1
King Island	KI-GM1-1	8	8	0
"	KI-GM1-2	8	8	0
"	KI-GM2-1	9	9	0
"	KI-GM2-2	8	9	+1
"	KI-GM3-1	13	13	0
"	KI-GM3-2	13	13	0
"	KI-GM4-1	12	12	0
"	KI-GM4-2	12	12	0

Table S4.1. cont.d

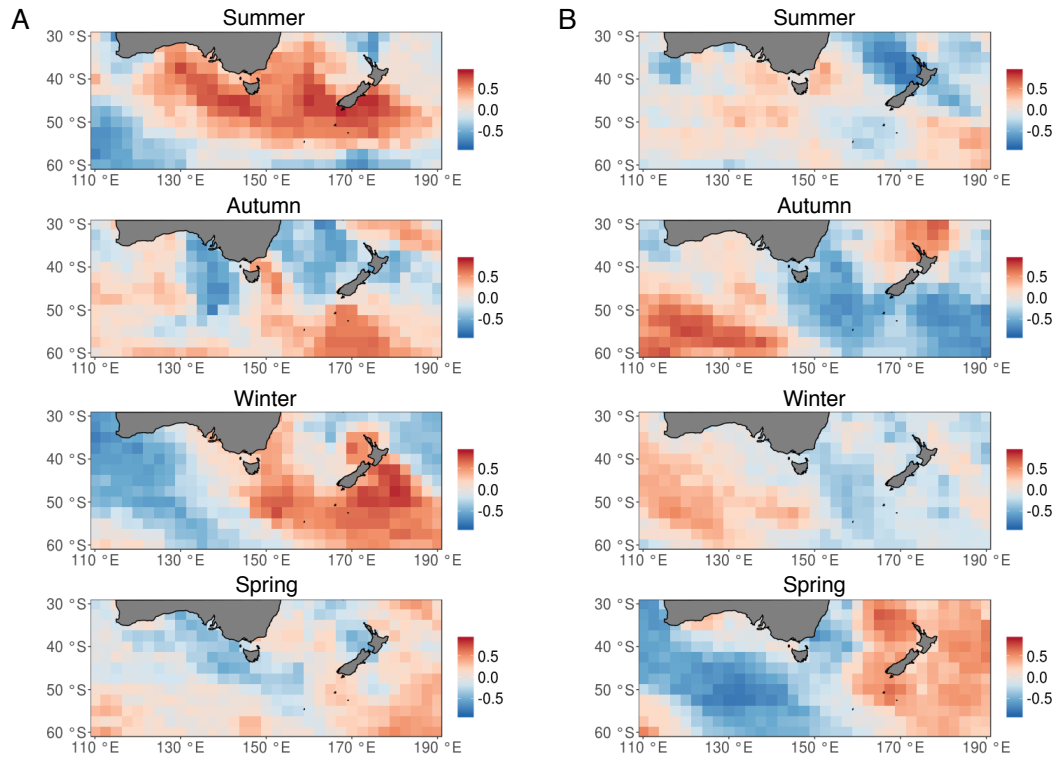
Stranding location	Tooth ID#	Initial estimate	Revised estimate	Adjustment
King Island	KI-GM5-1	10	10	0
"	KI-GM5-2	9	10	+1
"	KI-GM6-1	11	11	0
"	KI-GM6-2	11	11	0
"	KI-GM7-1	10	10	0
"	KI-GM7-2	7	10	+3
"	KI-GM9-1	17	16	-1
"	KI-GM9-2	16	16	0
"	KI-GM10-1	6	6	0
"	KI-GM10-2	6	6	0
"	KI-GM11-1	7	7	0
"	KI-GM11-2	6	7	+1
"	KI-GM12-1	14	14	0
"	KI-GM12-2	14	14	0
"	KI-GM13-1	12	14	+2
"	KI-GM13-2	14	14	0
"	KI-GM14-1	12	12	0
"	KI-GM14-2	12	12	0
"	KI-GM15-1	8	8	0
"	KI-GM15-2	9	8	-1
"	KI-GM16-1	8	8	0
"	KI-GM16-2	8	8	0
"	KI-GM21-1	8	8	0
"	KI-GM21-1	8	8	0
"	KI-GM28-1	8	8	0
"	KI-GM28-1	8	8	0
"	KI-GM29-1	13	13	0
"	KI-GM29-2	13	13	0

Supplementary Table S4.2. Environmental data used in models and spatial correlations.

Climate index/environmental variable	Time period	Source	Resolution
Southern Annular Mode Index (SAM)	2000 – 2011	https://climatedataguide.ucar.edu/climate-data/marshall-southern-annular-mode-sam-index-station-based (Marshall, 2003, 2016)	Annual values
Southern Oscillation Index (SOI)	2000 – 2011	Australian Bureau of Meteorology (http://www.bom.gov.au/climate/current/soi2.shtml)	Annual means calculated from the monthly values
Indian Ocean Dipole (IOD)	2000 – 2011	https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/DMI/ (http://www.jamstec.go.jp/frcgc/research/d1/iod/e/iod/about_iod.html)	Annual means calculated from the monthly values
Sea surface temperature (SST, °C), NOAA ERSST v5	2000 – 2011	https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.v5.html	Seasonal averages calculated from monthly values, 2° spatial resolution
Zonal wind speed, NCEP/NCAR Reanalysis	2000 – 2011	https://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.surface.html	Seasonal averages calculated from monthly values, 2.5° spatial resolution



Supplementary Figure S4.1. Correlation matrix (Pearson's) comparing individual tooth growth chronologies of long-finned pilot whales from (A) New Zealand and (B) Australia. The colour (legend at right) and size (larger circle = higher correlation value) of circles are proportional to the correlation coefficient values. Positive correlations are displayed in blue and negative correlations in red.



Supplementary Figure S4.2. Spatial maps of correlations between gridded seasonal averages (austral Summer: Dec, Jan, Feb; Autumn: Mar, Apr, May; Winter: Jun, Jul, Aug and Spring: Sep, Oct, Nov) of zonal wind speed and long-finned pilot whale tooth growth chronologies from (A) New Zealand (2001 – 2010) and (B) Australia (2000 – 2011). Red shades represent positive correlations and blue shades represent negative correlations.

Chapter 5 Long in the tooth? Insights into environmental influences of energy budgets in marine mammals

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All of the research contained in this chapter has been written and formatted for submission to *Nature Ecology & Evolution*, with the Methods section placed at the end of the chapter. Consequently there is some overlap of text between the Results and Methods to aid interpretation.

Abstract

In a changing climate, determining the environmental influences on energy budgets (which underpin population state) is fundamental for informing how populations may fare under future conditions. For most marine mammals this is inherently challenging, due to the difficulty of physical access to animals and their potentially far-ranging spatial movements. We developed time series of energy budgets for southern Australian sperm whales from measurements of annual tooth growth spanning 70 years (1935 – 2004). Using these chronologies, multidecadal energetic responses to broad-scale climate and ocean indices are demonstrated for the first time for a toothed whale species. Positive phases of the El Niño-Southern Oscillation and the Southern Annular Mode, negative phases of the Indian Ocean Dipole and cooler sea surface temperatures positively influenced tooth growth. The relationships varied among groups of whales, with variability likely associated with spatial differences in foraging patterns and in association, environmentally-driven variability in the trophodynamics of foraging regions.

Introduction

Studying long-lived marine mammals is inherently difficult. Their underwater habitat, far-ranging movements, and the difficulty of physical access to animals present challenging obstacles to collecting information on individuals and population status. In a changing climate, determining the environmental influences on energy budgets, (which underpin population state), is fundamental for informing how populations may fare under future conditions (Berteaux et al., 2006; Murphy et al., 2007). For wide-ranging pelagic species, the time and financial investment necessary for obtaining long time series datasets is particularly problematic. Datasets of changes in life history parameters spanning decades are often required to reliably assess responses to environmental variability on time scales relevant to long-lived species (Musick, 1999); unfortunately, such datasets are extremely rare.

The use of long-term chronologies of tooth growth, as proxy records for variability in energy budgets of individuals, can provide information on past responses of marine mammal species to variability in their environment (Boyd and Roberts, 1993; Hanson et al., 2009). Growth layers (termed growth layer groups: ‘GLGs’) are laid down annually in the teeth of marine mammals. Because the growth of each GLG is dependent on the nutritional intake and physiological condition of the individual, the width of each GLG is influenced by the metabolic energy available for the deposition of the structures associated with each (Boyd and Roberts, 1993; Klevezal', 1996; Langvatn, 1995). Tooth growth chronologies of long-lived odontocetes (toothed whales) therefore can provide multidecadal individual records of biological responses. Individual chronologies spanning overlapping temporal periods can be combined to produce even longer chronologies, in a similar manner to studies of climate-growth responses recorded in tree-rings (Fritts and Speer, 2005; Hughes, 2002). Studies so far however, have been limited to pinnipeds rather than odontocetes, used varying methodologies and focused on species with relatively short life spans (e.g. pinnipeds: Boyd and Roberts, 1993; Knox et al., 2014; Wittmann et al., 2016).

Sperm whales (*Physeter macrocephalus*) are long-lived (70 – 80 years; Ohsumi, 1966) and because they were subjected to commercial whaling, samples that span extended temporal scales are attainable. Female sperm whales also demonstrate strong

social bonds; females and their young travel in semi-stable matrilineal groups, with sub-adult males continuing to form loosely affiliated groups once leaving these matrilineal groups (Best, 1979; Christal and Whitehead, 2001; Mesnick, 2001). This social structure, coupled with their tendency to mass strand, means that it is possible to sample multiple individuals potentially exposed to similar environmental conditions for a large portion of their lives.

As large, wide-ranging mesopelagic predators, the influence of environmental variability on energy budgets is poorly understood for sperm whales, particularly in the Australian region. Using modified dendrochronology (tree-ring science) techniques, Hamilton and Evans (2018) developed standardised methodology for establishing chronologies of tooth growth in marine mammals. Here, we apply this methodology to:

- i) establish long-term multidecadal chronologies of energy budgets in sperm whales from the southern Australian region, and
- ii) using these chronologies, we then investigate the potential responses of these large apex predators to indices reflecting broad-scale environmental variability in the region (El Niño-Southern Oscillation: ENSO, measured by the Southern Oscillation Index: SOI; the Southern Annular Mode: SAM and the Indian Ocean Dipole: IOD), and spatial variability using spatially explicit, gridded environmental variables (sea surface temperature: SST, wind speed).

In doing so, we provide a step change in our ability to quantify how ongoing climate change might influence populations of these long-lived marine mammals.

Results

Chronologies

Teeth were obtained from four sample groups: sperm whales caught in whaling operations off the southwest of Western Australia during 1965 – 1966 and sperm whales involved in three mass strandings in Tasmania, Australia in 1998, 2003 and 2004. Time series of GLG widths ranged from 16 – 48 years and collectively spanned the years 1927 – 2004 (Table 5.1). The composite master chronology, constructed by

averaging the standardised values within each calendar year for all individual chronologies combined was 70 years in length, spanning 1935 – 2004 (Supplementary Figure S5.1). Subsequent environmental analyses indicated poor relationships between the composite master chronology and environmental covariates when included in generalised additive models and as a result this chronology was not considered further. To investigate if sample site differences were responsible, separate master chronologies were constructed for each sample site, and all following investigations were conducted using these sample site chronologies. Sample site chronologies spanned 1935 – 1965 for the southwest Australia dataset, 1960 – 1997 for the 1998 Strahan stranding dataset, 1981 – 2002 for the Flinders Island stranding dataset and 1985 – 2004 for the 2004 Strahan stranding dataset.

Table 5.1. Details of individual sperm whales, tooth state and growth layer group (GLG) width time series (T-S length) included in this study. TL: total length. Note total length of whales from southwest Australia were converted from feet to cm.

Collection date	Location	Whale ID #	TL (cm)	Sex	Age estimate (T-S length)	Pulp cavity state	Tooth wear
1966	Southwest Aus.	16A66	1433	M	23 (22)	open	low
1966	Southwest Aus.	19A66	1463	M	26 (20)	open	low (nil)
1966	Southwest Aus.	44A66	1494	M	32 (31)	open	low
1966	Southwest Aus.	59A66	1433	M	25 (25)	open	low – moderate
1966	Southwest Aus.	96A66	1280	M	25 (24)	open	low
1966	Southwest Aus.	107A66	1433	M	28 (27)	open	low
1966	Southwest Aus.	109A66	1494	M	28 (28)	open	low – moderate
1966	Southwest Aus.	113A66	1494	M	25 (23)	open	low
1966	Southwest Aus.	147A66	1524	M	39 (38)	full	moderate
1966	Southwest Aus.	148A66	1463	M	28 (27)	open	low
1966	Southwest Aus.	25A66	1067	F	23 (18)	open	low (nil)
1966	Southwest Aus.	54A66	1097	F	30 (29)	open	low
1965	Southwest Aus.	224A65	1128	F	37 (32)	full	low
1965	Southwest Aus.	368A65	1090	F	42 (38)	closing	low
1965	Southwest Aus.	388A65	1060	F	29 (29)	open	low
1965	Southwest Aus.	C31A65	1006	F	38 (37)	full	low
1965	Southwest Aus.	C14A65	1014	F	23 (19)	open	low
1965	Southwest Aus.	G7A65	1014	F	35 (32)	full	low – moderate
1965	Southwest Aus.	G18A65	1014	F	26 (25)	open	low
1965	Southwest Aus.	G31A65	991	F	27 (20)	open	low

Table 5.1. cont.d

Collection date	Location	Whale ID #	TL (cm)	Sex	Age estimate (T-S length)	Pulp cavity state	Tooth wear
04/02/1998	Strahan	STR6	1108	F	23 (23)	open	low – moderate
04/02/1998	Strahan	STR7	1080	F	38 (37)	open	moderate
04/02/1998	Strahan	STR8	1083	F	26 (26)	open	moderate
04/02/1998	Strahan	STR11	1125	F	27 (24)	open	moderate
04/02/1998	Strahan	STR13	1127	F	49 (48)	full	moderate
04/02/1998	Strahan	STR19	1116	F	40 (39)	full	low – moderate
04/02/1998	Strahan	STR21	1162	F	38 (37)	open	moderate
04/02/1998	Strahan	STR22	1124	F	36 (35)	open	low – moderate
04/02/1998	Strahan	STR23	1144	F	33 (33)	open	high
04/02/1998	Strahan	STR31	1138	F	27 (25)	open	low
04/02/1998	Strahan	STR34	1122	F	31 (31)	open	moderate
04/02/1998	Strahan	STR35	1120	F	33 (32)	open	high
04/02/1998	Strahan	STR36	1110	F	25 (24)	open	low – moderate
04/02/1998	Strahan	STR41	1060	F	39 (39)	full	moderate
04/02/1998	Strahan	STR44	1110	F	26 (26)	open	moderate
04/02/1998	Strahan	STR49	1100	F	22 (21)	open	moderate – high
04/02/1998	Strahan	STR51	1110	F	42 (40)	full	high
04/02/1998	Strahan	STR52	1110	F	37 (36)	open	low – moderate
04/02/1998	Strahan	STR56	1127	F	32 (31)	open	moderate – high
04/02/1998	Strahan	STR60	1078	F	39 (38)	closing	moderate – high
28/11/2003	Flinders Island	1928	1259	M	30 (29)	open	low – moderate

Table 5.1. cont.d

Collection date	Location	Whale ID #	TL (cm)	Sex	Age estimate (T-S length)	Pulp cavity state	Tooth wear
28/11/2003	Flinders Island	1929	1130	M	23 (21)	open	low – moderate
28/11/2003	Flinders Island	1930	1234	M	26 (24)	open	low – moderate
28/11/2003	Flinders Island	1931	1184	M	23 (22)	open	low – moderate
28/11/2003	Flinders Island	1932	1099	M	19 (18)	open	low – moderate
28/11/2003	Flinders Island	1933	1196	M	31 (29)	open	low
28/11/2003	Flinders Island	1934	1192	M	25 (22)	open	low – moderate
28/11/2003	Flinders Island	1935	1232	M	26 (25)	open	low – moderate
28/11/2003	Flinders Island	1936	1135	M	23 (22)	open	low
29/12/2004	Strahan	2156	1085	F	33 (33)	full	low – moderate
29/12/2004	Strahan	2157	1060	F	29 (28)	closing	low – moderate
29/12/2004	Strahan	2158	1130	F	20 (17)	open	moderate
29/12/2004	Strahan	2160	1080	F	16 (13)	open	moderate
29/12/2004	Strahan	2161	1120	F	29 (27)	open	low – moderate
29/12/2004	Strahan	2163	1130	F	26 (17)	open	low – moderate
29/12/2004	Strahan	2164	1100	F	18 (16)	open	low – moderate
29/12/2004	Strahan	2166	1140	F	21 (18)	open	moderate
29/12/2004	Strahan	2168	1140	F	27 (25)	open	low – moderate
29/12/2004	Strahan	2169	1080	F	19 (18)	open	moderate
29/12/2004	Strahan	2171	1140	F	20 (16)	closing	moderate
29/12/2004	Strahan	2172	1060	F	25 (20)	open	moderate
29/12/2004	Strahan	2174	1130	F	29 (22)	open	moderate

Chronology synchrony

Synchrony among individuals within sample sites was evident in particular years (Figure 5.1). For example, the majority of individuals demonstrated above average tooth growth in 1987 and below average tooth growth in 1988 for the Flinders Island sample site (Figure 5.1C), and tooth growth was below average in 1991 and above average in 1997 for the majority of individuals in the 2004 Strahan sample site (Figure 5.1D). Pairwise correlation (Pearson's) of individual chronologies within each sample site group ranged from -0.77 – 0.87 , reflecting variability in the strength of the common signal and chronology quality (Supplementary Figures S5.2 – S5.5). High similarity (Pearson's $r > 0.7$, amongst individual tooth growth chronologies occurred within the Flinders Island and 2004 Strahan sample sites, although moderate ($r = 0.3$ – 0.7) to high negative correlations also occurred within these sample sites. Low ($r < 0.3$) to moderate similarities between chronologies occurred amongst individuals in the southwest Australia and 1998 Strahan sample sites.

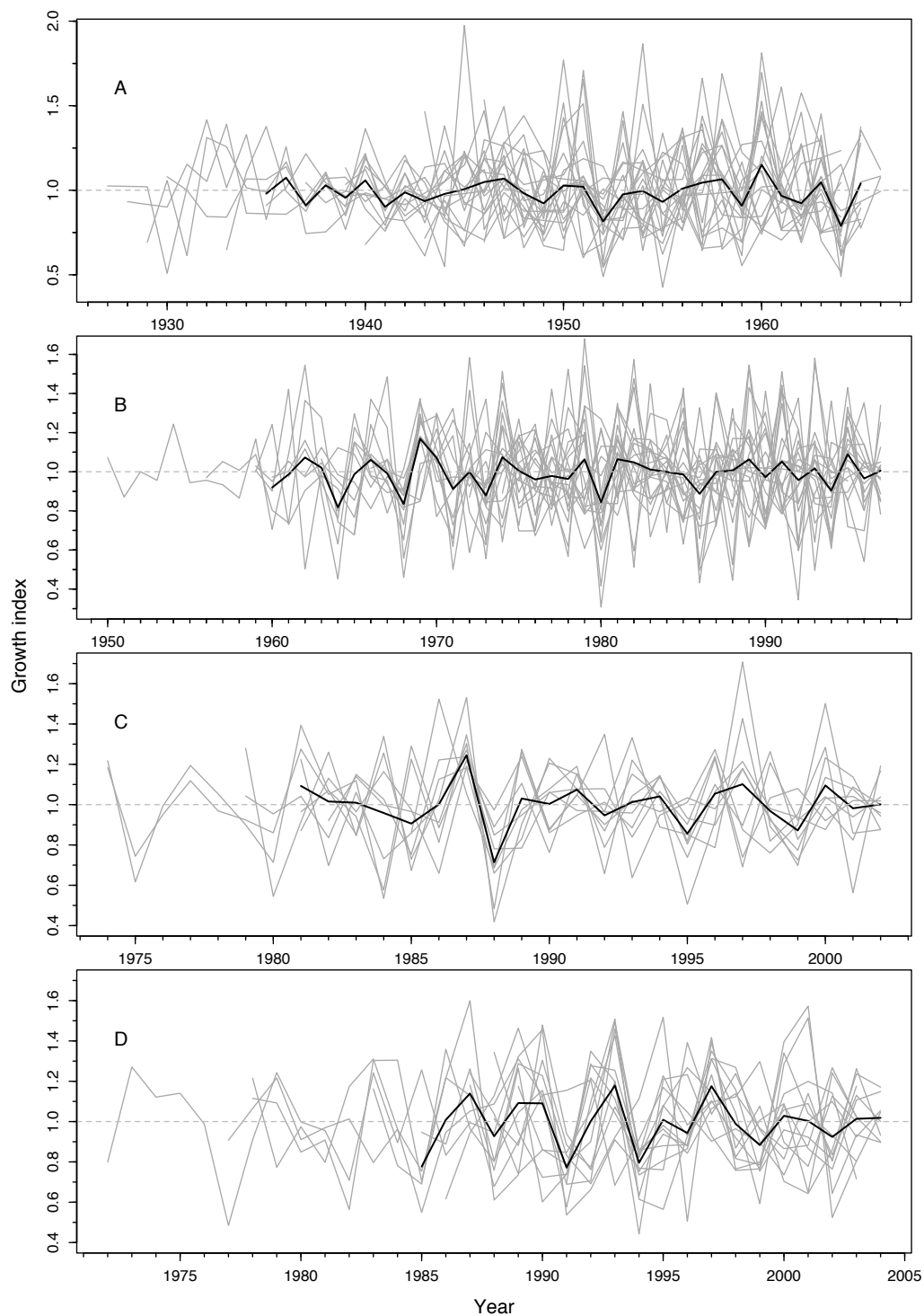


Figure 5.1. Tooth growth chronologies for sperm whales from the southern Australian region. Chronologies for individual animals (grey lines) with sample site master chronology (black line) for (A) southwest Australia dataset ($n = 20$), (B) 1998 Strahan stranding ($n = 20$), (C) Flinders Island stranding ($n = 9$) and (D) 2004 Strahan stranding ($n = 13$). Growth index is standardised to a mean of 1.0 (horizontal line). Each master chronology is truncated at the year in which six or more individuals contributed (Matta et al., 2010).

The strength of the common signal for each sample site was quantitatively assessed by \bar{r} ; calculated as the average of all pairwise correlations between individual chronologies in each sample group. Chronology quality was assessed using the expressed population signal (EPS), which takes both \bar{r} and sample depth (i.e., the number of individuals contributing to the chronology) into account, to indicate how well the chronology represents a hypothetical population where a common signal is fully represented. Signal strength (\bar{r}) ranged from 0.061 – 0.121 across sample site chronologies and EPS values ranged from 0.491 – 0.642 (Supplementary Table S5.4), reflecting the high variability introduced to sample site chronologies by individuals. Signal strength for the Flinders Island and 2004 Strahan sample site chronologies was higher than that for the southwest Australia and 1998 Strahan sample site groups. The Flinders Island sample site chronology EPS value was lower than that of the other three sample site chronologies. This is most likely related to the lower sample size of this dataset, as calculations of EPS values are strongly influenced by sample size.

Relationships with broad-scale climate indices

The highest ranking models used to explore relationships between the sample site chronologies and climate indices explained 23.4 – 54.0% of deviance in the data (Table 5.2). Models identified that tooth growth in whales from the southwest Australia sample site was influenced most by the IOD at a lag of 1 year; below average tooth growth was associated with IOD values above 0.2 but not particularly affected by values less than this with tooth growth close to average (Figure 5.2A). The 1998 Strahan sample site chronology was most influenced by the SAM. Below average tooth growth was associated with SAM values less than –2. Above values of –2 tooth growth was not particularly influenced by the SAM, being close to average (Figure 5.2B). The highest ranking model including the Flinders Island sample site chronology identified that this chronology was most influenced by the IOD at a lag of 1 year and the SAM. Below average tooth growth was associated with SAM index values below –1, beyond which tooth growth was above average before declining to below average at SAM index values of approximately 1.5. The relationship between tooth growth and the IOD was linear and negative with above average tooth growth associated with IOD values less than 0.2 and below average tooth growth at IOD values greater than 0.2 (Figure 5.2C). The 2004 Strahan sample site chronology was

most influenced by the IOD and the SOI, both at a lag of 1 year. Tooth growth was above average at values of the IOD less than -0.1 , below average from -0.1 and 0.3 and above average at values higher than 0.3 . The relationship with the SOI was linear and positive with below average tooth growth associated with SOI values less than -1 and above average at values greater than -1 (Figure 5.2D).

Table 5.2. Summary of the highest ranking/top 3 generalised additive model (GAM) comparisons examining the relationship between tooth growth and environmental covariates for the regional chronologies from each sample site: Southwest Australia, 1998 Strahan, Flinders Island and 2004 Strahan. GI = Chronology, SOI = Southern Oscillation Index, IOD = Indian Ocean Dipole, SAM = Southern Annular Mode, FSL = Fremantle sea level (proxy for strength of Leeuwin Current). Lagged covariates are indicated by lag1. The accepted model is highlighted in bold.

Candidate models	AIC _c	ΔAIC	wAIC	% Dev. Exp.
<i>Southwest Australia</i>				
1. GI ~ IOD_{lag1}	-69.147	0	0.892	23.4
2. GI ~ IOD _{lag1} + FSL _{lag1}	-64.578	4.569	0.091	30.8
3. GI ~ IOD _{lag1} + FSL _{lag1} + SOI _{lag1}	-61.248	4.892	0.017	37.3
<i>Strahan 1998</i>				
1. GI ~ SAM	-89.424	0	0.537	25.1
2. GI ~ SAM + IOD	-88.689	0.735	0.372	32.1
3. GI ~ SAM + IOD + SOI	-85.886	3.538	0.092	32.4
<i>Flinders Island</i>				
1. GI ~ SAM	-34.952	0.797	0.342	42.6
2. GI ~ SAM + SOI _{lag1}	-33.275	2.474	0.148	54.3
3. GI ~ SAM + IOD_{lag1}	-35.749	0	0.510	54.0
<i>Strahan 2004</i>				
1. GI ~ IOD _{lag1}	-23.481	0	0.079	22.3
2. GI ~ IOD_{lag1} + SOI_{lag1}	-22.914	0.567	0.525	43.6
3. GI ~ IOD _{lag1} + SOI _{lag1} + FSL _{lag1}	-19.695	3.219	0.396	58.7

AIC_c, Akaike's (second order) Information Criterion; ΔAIC, difference in AIC from that of the best fitting model; wAIC, AIC weight; % Dev. Exp.; percentage deviance explained by the model

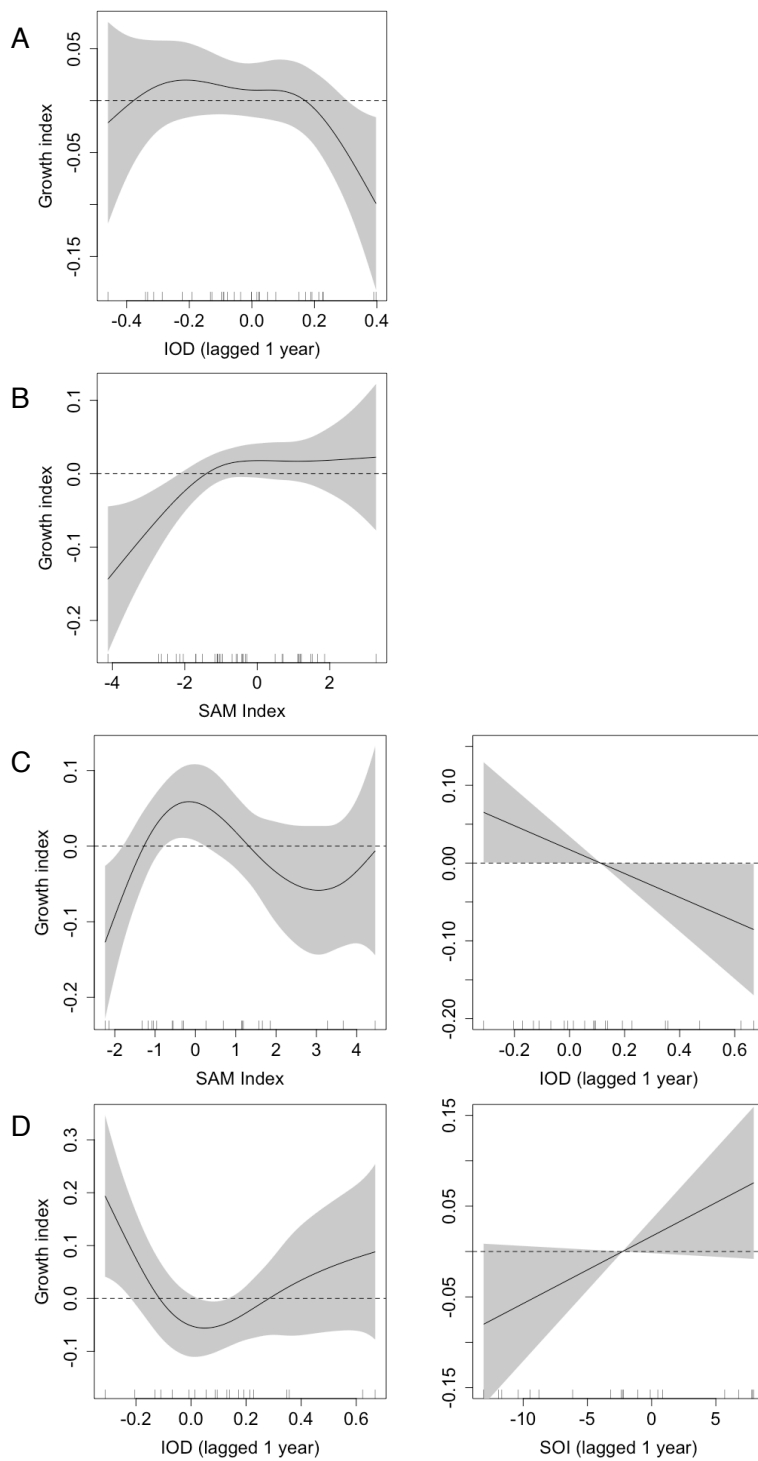


Figure 5.2. Predicted growth indices in relation to environmental variables for sample site tooth growth chronologies of sperm whales. (A) Southwest Australia, (B) 1998 Strahan, (C) Flinders Island and (D) 2004 Strahan. Lines show the prediction of a GAM fit to a Gaussian error distribution for each chronology with broad-scale climate indices: the Indian Ocean Dipole (IOD), the Southern Annular Mode (SAM) and the Southern Oscillation Index (SOI). Shading represents the 95% confidence interval for predictions. Horizontal line is the mean.

Relationships with gridded spatially explicit environmental variables

Spatial correlations between the sample site chronologies and SST across seasons varied between the four datasets, although some seasonal consistencies were evident (Figure 5.3). In particular, the southwest Australia, Flinders Island and 2004 Strahan sample site chronologies showed similar spatial patterns in negative correlations with SSTs during the austral winter across a region southwest of Western Australia, at approximately 30°S – 50°S, 105°E – 130°E (Figure 5.3). This was a region of consistent negative correlations between SSTs and the 2004 Strahan sample site chronology extending into the autumn and spring. Other spatial consistencies also occurred around the northern New Zealand region between SSTs and the Flinders Island and 2004 Strahan sample site chronologies during the summer (Figures 5.3C and 5.3D). This was a region of consistent negative correlations between SSTs and the Flinders Island sample site chronology across all months, with the region of negative correlations extending into the Tasman Sea and south of Tasmania during summer and autumn (Figure 5.3C).

Other regions in which negative correlations occurred included an area broadly south of Australia (45°S – 55°S, 95 – 140°E), where SSTs were negatively correlated with the Flinders Island sample site chronology across the austral autumn and winter and a region south – southeast of the South Island of New Zealand where SSTs were negatively correlated with the 2004 Strahan sample site chronology during autumn. Negative correlations between SST and the 1998 Strahan chronology occurred across a region south of 50°S, 120°E – 180°E, consistently across all seasons, with the strongest correlations occurring in autumn (Figure 5.3B).

The spatial distribution of positive and negative correlations between the sample site chronologies and seasonally averaged zonal wind speed did not reveal any biologically meaningful patterns, and so were not considered further (Supplementary Figure S5.6).

Details for results of the preliminary chronology development steps, including identification and measurement of GLGs, statistical crossdating and detrending of individual chronologies can be found in the Supplementary information.

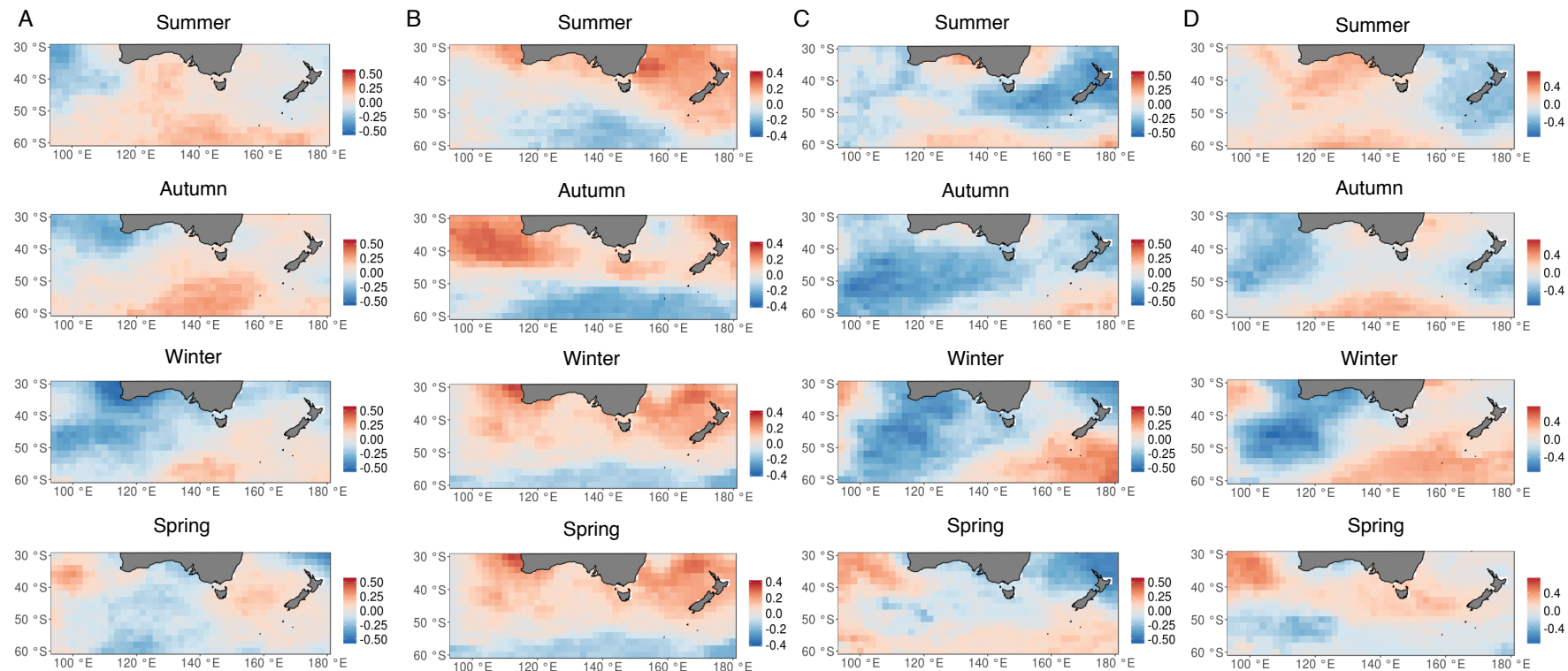


Figure 5.3. Spatial maps of correlations between gridded seasonal averages (austral Summer: Dec, Jan, Feb; Autumn: Mar, Apr, May; Winter: Jun, Jul, Aug and Spring: Sep, Oct, Nov) of sea surface temperature (SST) and sperm whale tooth growth chronologies from (A) Southwest Australia (1935 – 1965), (B) 1998 Strahan (1960 – 1997), (C) Flinders Island (1981 – 2002) and (D) 2004 Strahan (1985 – 2004). Red shades represent positive correlations and blue shades represent negative correlations.

Discussion

This study is the first to develop extended multidecadal growth chronologies for a marine mammal species and then relate those chronologies to climate/environmental drivers. These chronologies are directly related to the energy budgets of the animals in question and so provide a clear means by which the energetic responses of marine mammals to their environment can be established. Differing relationships with climate drivers and spatially resolved SST support hypotheses relating to key foraging areas formulated from the distribution of whaling catches. Further, these relationships suggest previously unrecognised potential foraging areas across the southern Australian/New Zealand region. Variability in conditions driven by broad-scale climate processes have been related to changes in diet, condition and breeding performance of higher trophic level predators across the region, as a result of changes in productivity and flow on effects to prey abundance and distribution (e.g. Hoskins and Arnould, 2014; McMahon and Burton, 2005).

Common signals (\bar{r}) for each sample site chronology were low relative to studies of trees and bivalves in environments exerting strong limiting conditions, or teleosts with restricted ranges (e.g. 0.3 – 0.4: Brocas et al., 2013; Frank and Esper, 2005).

Synchrony within sperm whale groups was, however, comparable with more mobile teleost species, for which common responses to environmental conditions have been demonstrated (e.g. *Lutjanus argentimaculatus*: Ong et al., 2015; *Achoerodus gouldii*: Rountrey et al., 2014). Individual variability among chronologies is to be expected, particularly in higher trophic organisms that are influenced indirectly by environmental conditions. Individual otolith chronologies contributing to master chronologies of marine teleosts characteristically demonstrate similar levels of individual variability as the sperm whale chronologies herein (e.g. see: Matta et al., 2010; Ong et al., 2016; van der Sleen et al., 2016). A number of factors can contribute to this variability. Higher mobility enables movement across varying environmental gradients, influencing individual foraging decisions and potentially reducing synchrony among individuals. Differences in foraging success and differing energetic demands associated with reproductive state (e.g. pregnancy, lactation) will also influence individual energy budgets (Boyd, 2002; Lockyer, 2007).

Synchrony was lowest in the southwest Australia (samples from whaling activities) and 1998 Strahan chronologies (samples from a large stranding of whales). The samples derived from whaling activities included in this study are likely to have come from dispersed groups of whales and potentially different social groups. They may therefore comprise individuals with potentially little environmental history in common. Similarly, samples taken from larger stranding groups likely comprised of multiple social units could have an equally disparate social and environmental history. Despite these limiting factors, \bar{r} and EPS values for sperm whale chronologies were comparable with teleost otolith chronology studies (e.g. Ong et al., 2018), providing confidence in sample site chronologies and observed relationships with climate and environmental indices.

Given the broad foraging ranges of sperm whales, it is not surprising that relationships of the four sample site chronologies with climate phenomena varied and in some cases included multiple climate factors, as they are likely foraging in regions where the influence of multiple climate modes overlap or vary. Female sperm whale social groups in the Northern Hemisphere have been estimated to have large home ranges (e.g. 1000 – 3000 km; Jaquet et al., 2003) with males ranging over even broader regions. Based on whaling, aerial survey and stranding records (Bannister, 1968; Bannister et al., 1996; Evans et al., 2005; Woinarski et al., 2014) sperm whales are thought to forage in waters across the entire southern Australian marine region year round. The effect and relative contributions to variability in environmental conditions of combined climate drivers may vary by region and season and will have differing regional impacts on prey availability and distribution, with flow-on effects to energy budgets (Pui et al., 2012; Risbey et al., 2009; Trathan et al., 2007).

The IOD, a coupled ocean-atmosphere interaction of the Indian Ocean basin, was an important predictor of tooth growth in the chronologies of three of the four sampling site groups. This suggests that whales from the southwest Australia, Flinders Island and 2004 Strahan sample site groups potentially foraged at least part of the time in regions of IOD influence. Our results suggest conditions associated with negative IOD (at a one year lag), result in more positive energy budget responses for sperm whales. During a negative (positive) IOD phase, SSTs are cooler (warmer) in the

tropical western Indian Ocean relative to the east (Saji et al., 1999). A teleconnection in the southern Indian Ocean results in a strengthening (weakening) of westerly winds and storm activity and cooler (warmer) SSTs off the southwest of Australia during negative (positive) IOD events (Ashok et al., 2007; Cai et al., 2011b; England et al., 2006; Weller et al., 2012). Increases in winds and storm activity enhance productivity in frontal regions and upwelling zones, through mixing and upwelling of cooler nutrient rich waters (Bakun, 2006; Falkowski et al., 1998). The lagged relationship is not unexpected; the response of predators to environmental conditions can occur at a lag as a result of the time taken for energy transfer through trophic food webs (Frederiksen et al., 2006; Poloczanska et al., 2007). Sperm whales feed primarily on squid, which are highly mobile, typically have a relatively short life cycle of 1 – 2 years and respond rapidly to fluctuations in their environment (Boyle and Rodhouse, 2005; Clarke, 1996).

Knowledge of sperm whale association with bathymetric and oceanographic features in the region (Bannister, 1968; Gill et al., 2015; Hann et al., 2016), combined with existing understanding of the influence of broad-scale drivers on oceanographic processes in the Australian/New Zealand region suggested that negative correlations with SST (higher tooth growth associated with cooler SSTs) were more biologically relevant. Spatial correlations between three of the four sample site chronologies and SSTs indicated an association with cooler SSTs in a region to the southwest of Australia that was strongest in austral winter. This is consistent with observations of increases in westerly winds and storm activity in the region in winter, when IOD events usually develop (Ashok et al., 2007; Cai et al., 2011b). Increased storm activity and cooler SSTs off the southwest Australian region associated with negative IOD phases may increase surface mixing resulting in higher regional productivity and associated prey resources, leading to increased foraging success for sperm whales. The southwest Australian region also encompasses the Perth and Albany submarine canyon systems that incise the west and southern Australian continental shelf. These canyon regions are recognised as areas of increased upwelling and eddy formation and in association are regions of high productivity that are recognised habitat for sperm whales and other large marine predators (Pattiaratchi, 2007; Rennie et al., 2009; Wellard et al., 2016). This habitat and associated localised abundance of sperm

whales was a major reason for establishing a coastal whaling industry off Albany, Western Australia (Bannister et al., 1996).

Model results suggest that whales from both the Flinders Island and 1998 Strahan sample site groups spent more time foraging across regions where the SAM is influential on environmental conditions. However relationships varied across the two groups. While below average tooth growth was associated with negative SAM for both groups, positive SAM influenced growth in varying ways. Positive (negative) SAM results in a strengthening (weakening) of winds between 45°S – 60°S, across regions encompassing the subtropical, subantarctic and polar front zones (Hall and Visbeck, 2002; Lovenduski and Gruber, 2005; Marshall, 2003). South of Australia and New Zealand, these frontal zones are important foraging regions for wide-ranging marine predators in the southern Australian region such as seabirds and marine mammals (Bost et al., 2009; Scales et al., 2014). Increased productivity as a result of wind-driven upwelling of nutrient-enriched water to the photic zone (Lovenduski and Gruber, 2005) is likely to positively influence energy budgets of predators, such as sperm whales, that may forage in these regions.

In the Australian/New Zealand region, sperm whales are known to associate with the subtropical and subantarctic fronts, and spatial correlations for both the 1998 Strahan and Flinders Island groups were consistent with potential utilisation of these regions. The differences in responses to the SAM between these groups may relate to spatial variability in foraging movements. The 1998 Strahan sample site group was exclusively female (see: Evans et al., 2002b). Sperm whale female social groups typically inhabit waters in latitudes less than approximately 40° in both hemispheres (Rice, 1989), although they have been reported as far south as 50°S in the New Zealand region (Gaskin, 1973). The Flinders Island group was exclusively males and demonstrated greater variability in spatial correlations, between New Zealand, the southwest of Australia and frontal regions south of Australia, suggesting greater movements among foraging regions. This is consistent with our knowledge of the foraging patterns of male sperm whales (Best, 1979; Rice, 1989). The Flinders Island group also demonstrated a relationship with the IOD, suggesting these animals foraged across broader regions influenced by both climate drivers. Within the

southern Australian region, differences in diet between sexes and stranding groups suggest differences in foraging habitat which may be related to individual foraging behavior or the social structure of groups (Evans and Hindell, 2004b).

The 2004 Strahan sample site group was the only group in which models identified the ENSO was influencing tooth growth, in combination with the IOD. These results potentially reflect the covarying interaction between the IOD and ENSO over the time period of the chronology. Positive SOI conditions are associated with increases in storm activity and changes in wind strength and direction in the Australian/New Zealand region (Ashok et al., 2007; Cai et al., 2011b; Gordon, 1986). The IOD has a complex, in/out of phase relationship with ENSO. Positive (negative) IOD events can co-occur with El Niño (La Niña) events, or develop independently (Saji and Yamagata, 2003; Yamagata et al., 2004). In the Australian region the climate impacts of El Niño (negative SOI) and La Niña events (positive SOI) are often more pronounced when the IOD and ENSO are in phase (Cai et al., 2011b). However, the combined effects of ENSO and the IOD on marine productivity in the southern Australian region are not well known.

The relationships observed with the 2004 Strahan chronology are overall consistent with the interaction of a positive SOI concurrent with negative IOD (known as an ‘in phase’ relationship, Ménard et al., 2007). The energy budget responses to environmental conditions may be strongest when these drivers act in tandem. The model results could however, also be driven by varying dominance of the climate indices, as annual values of climate-atmosphere processes are a product of seasonal oscillations around the mean state (Kidston et al., 2009). Patterns in spatial correlations suggest potential foraging regions dispersed across areas influenced by both climate phenomena, with seasonal variability occurring in regions associated with New Zealand (influenced by ENSO) and southwest of Australia (influenced by the IOD). This suggests these animals potentially made large-scale movements between the two regions.

Here we have demonstrated that tooth growth chronologies can provide multidecadal longitudinal records of energy budgets for marine mammals that are difficult to obtain

by other methods. The results indicate that climate indices of relevance for the region impart differing intra-specific influences on the energy budgets of sperm whales, with varying combinations of climate phenomena contributing to variability among sample site chronologies. Spatial variability is likely due to region-to-region variability in food webs and differing impacts on energy budgets. This finding suggests that sperm whale groups across the southern Australian region utilise distinct foraging areas and are subject to differing regional effects of climate-driven variability. This study therefore represents an important step in understanding potential areas of foraging significance for sperm whales that inhabit southern Australian waters, and a means by which we can begin to quantify the effects of ongoing climate change on populations of this species. Further studies may provide insight into whether regional variability in the influence of environmental drivers on the energetic responses of sperm whale groups reflect differences in foraging habitats between sexes, social groups or sampling regions.

Methods

Samples

Two teeth (mandibular and maxillary) were sampled from 20 sperm whales caught in whaling operations off the southwest of Western Australia during 1965 – 1966 (Bannister, 1969). Between one and four mandibular teeth were sampled from deceased sperm whales involved in three mass strandings in Tasmania, Australia in 1998 (Strahan; 42.3°S, 145.27°E, $n = 20$ from stranding of 66 animals), 2003 (Flinders Island; 40.10°S, 147.95°E, $n = 9$ from stranding of 11 animals) and 2004 (Strahan; 42.04°S, 145.24°E, $n = 13$ from stranding of 19 animals) (Table 1: Bannister, 1969; Evans and Hindell, 2004a). Teeth were prepared for age estimation using methods detailed in Bow and Purday (1966) for the southwest Australian and Evans and Robertson (2001) for the Tasmanian samples. The resulting etched tooth sections were digitally imaged following Hamilton et al. (2013) and GLGs identified by VH following Evans and Robertson (2001).

Crossdating and chronology development

A modified visual crossdating process (Hamilton et al., 2017) was used to cross-check GLG identification within each individual for which multiple teeth were available (Supplementary Table S5.2). Growth layer groups in the maxillary teeth of five individuals from southwest Australia lacked clarity and were therefore unsuitable for the cross-checking process. For these individuals, cross-verification of GLG identification was carried out by another experienced reader (KE), in addition to a sub-sample of teeth from the overall sample set (a total of one tooth from each of 17 individuals). Following cross-checking and any resultant adjustments to GLG identification, a single tooth for each individual was then selected for final calendar year assignment, measurement of GLGs, and all subsequent steps in chronology development. Measurement of GLG widths, statistical crossdating and detrending of GLG width time series to develop individual chronologies and master chronology development followed methods detailed in Hamilton and Evans (2018), and additional details can be found in the Supplementary information.

Chronology synchrony

Similarities among individual chronologies for each sample site were compared using Pearson's correlation coefficient. Strength of the common signal (synchrony) for each sample site master chronology was compared quantitatively using \bar{r} : the mean of all pairwise correlations between individual chronologies. Chronology quality was compared using the expressed population signal ($EPS = n\bar{r}/(1 + (n - 1)\bar{r})$): a measure of how well the chronology represents an 'ideal' chronology from the theoretical population where a common forcing signal is fully represented (Briffa and Jones, 1990; Wigley et al., 1984).

Relationships with broad-scale climate indices

Based on whaling data and current understanding of sperm whale genetics in the southeast Australian region, individuals occurring across southern Australia are considered to comprise a single stock (Bannister, 1969; Mesnick, 2001; Mesnick et al., 2003). In light of this assumption, as a first step we developed an overall master chronology (hereafter referred to as the composite chronology) built as the average of

each year's index value from all individual chronologies from all sample sites (following Hamilton and Evans, 2018).

Using Generalised Additive Models (GAMs) with a Gaussian error distribution and identity link function, we then explored relationships between this composite chronology and a number of broad-scale climate indices. These included: the Indian Ocean Dipole (IOD), the Southern Oscillation Index (SOI), a measure of the strength of El Niño-Southern Oscillation (ENSO) events, and the Southern Annular Mode (SAM). Additionally, the Fremantle coastal sea level (FSL; a proxy for the strength of the Leeuwin Current, the southward flowing boundary current off Western Australia) was included in models. Indices of broad-scale ocean-atmosphere interactions (see Supplementary Table S5.1 for data sources) were chosen *a priori* for inclusion in models, based on understanding of important drivers of marine ecosystem variability in the Australian region (Salinger et al., 2016). Model covariates were tested for autocorrelation and residual diagnostics were checked to confirm adherence to assumptions of normality and homogeneity of variance. Regressions between the chronology index and each climate index were used to check for collinearity (covariates retained if $r < 0.7$).

As higher trophic level predators, responses to physical conditions could occur at a lag as a result of the time taken for environmentally-driven variability to propagate through the food web (Poloczanska et al., 2007; Weimerskirch et al., 2003). The primary prey of sperm whales are squid, which have relatively short generation and growth times; for many species up to 1 – 2 years (Boyle and Rodhouse, 2005; Clarke, 1996). Consequently sperm whales might be expected to show a relatively short lagged response to changes in environmental conditions that influence productivity and prey resources. Climate indices were therefore included in the GAMs concurrent with the chronologies and also at a lag of 1 year. Covariates were means-centred prior to smoothing to account for differing measurement scales. Degree of smoothing for model terms were estimated using the restricted maximum likelihood (REML) approach, which provides greater resistance to overfitting the smoother to the data and less variability in smoothing parameter estimates (Wood, 2011). Models were built by first including a single covariate as the predictor variable, and then additional covariates were sequentially added to trial models that included multiple predictor

covariates. Models were compared using model-fit residual diagnostics, the percentage deviance in the data explained by the model and information criteria (Aikaike's). Final model selection was based on ranking of models by minimisation of the second-order Aikaike's Information Criterion (AIC_c) scores, which accounts for small sample sizes, and Aikaike Weights (w_i) where AIC differences (ΔAIC) indicated similar support for candidate models ($\Delta AIC < 2$) (Burnham and Anderson, 2002).

Models including the composite chronology performed poorly, with covariates observed to have very little explanatory power (see Supplementary Figure S5.1). As a result, master chronologies for each sample site were developed, to investigate if regional differences in the effects of environmental conditions on tooth growth were driving the low explanatory power of the composite master chronology. We then re-ran GAMs including individual sample site master chronologies and all subsequent investigations were conducted with these sample site master chronologies.

Because indices associated with the SAM only span as far back as 1957, models investigating the relationships between indices of the SAM and sample site chronologies were only constructed for the 1998 Strahan, Flinders Island and 2004 Strahan chronologies.

Relationships with gridded spatially explicit environmental variables

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; Tynan, 1998; Wilson and Adamec, 2002). Gridded spatial SST and zonal near-surface wind speed (Supplementary Table S5.1) were aggregated within each year into seasonal averages for the austral summer (December, January, February), autumn (March, April, May), winter (June, July, August) and spring (September, October, November). The sample site chronologies were then correlated (Spearman's rank) with the seasonal SST/wind averages in each cell of a $2.0^\circ/2.5^\circ$ degree grid within a spatial domain bound by $30^\circ\text{S} - 60^\circ\text{S}$, $94^\circ\text{E} - 180^\circ\text{E}$. The spatial domain was derived from historical and contemporary records of known or assumed sperm whale distribution in the southern Australian region (Bannister et al., 1983; Kirkwood and Bannister, 1980). Spatial maps of correlations produced were

then used to identify regions of positive or negative correlations, as a guide to potential foraging regions of sperm whales.

Annual GLG widths were measured on the digital images using a plug-in ('IncMeas'; Rountrey, 2009) written for ImageJ, an open source image processing program (version 1.47, National Institutes of Health, USA). Statistical analyses were conducted within the R statistical programming environment (version 3.0.2, R Core Team, 2013). Statistical crossdating, detrending and chronology building was conducted using the Dendrochronology Program Library in the 'dplR' package (Bunn, 2008, 2010) and GAMs were implemented using the R package 'mgcv' (Wood, 2004, 2011).

Acknowledgements

This work builds upon the efforts of those involved in the collection of samples from the strandings and whaling operations and we acknowledge the time and effort of the many individuals involved. Flinders Island and Strahan 2004 samples were provided by the Marine Conservation Program, DPIPWE, Tasmania (permit FA 12276). Southwest Australian samples were archived by the CSIRO and provided by the National Archives of Australia (Records Authority RA 2013/00618960). Funding was provided by the Winifred Violet Scott Charitable Trust and the Australian Geographic Society. VH was supported through an Australian Government Research Training Program Scholarship. Concepts in this paper are motivated in part by discussions had as part of the IMBeR Climate Impacts on Top Predators (CLIOTOP) regional programme.

Supplementary Information

Supplementary Table S5.1. Environmental data used in models and spatial correlations.

Climate index/environmental variable	Time period	Source	Resolution
Southern Annular Mode Index (SAM)	1957 – 2004	https://climatedataguide.ucar.edu/climate-data/marshall-southern-annular-mode-sam-index-station-based (Marshall, 2003, 2016).	Annual values
Southern Oscillation Index (SOI)	1935 – 2004	Australian Bureau of Meteorology (http://www.bom.gov.au/climate/current/soi2.shtml)	Annual means calculated from the monthly values
Indian Ocean Dipole (IOD)	1935 – 2004	https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/DMI/ (http://www.jamstec.go.jp/frcgc/research/d1/iod/e/iod/about_iod.html)	Annual means calculated from the monthly values
Fremantle sea level (FSL, in mm)	1935 – 2004	Permanent Service for Mean Sea Level Database (Holgate et al., 2013; PSMSL, 2018). http://www.pmsl.org/data/obtaining/stations/111.php	Annual values
Sea surface temperature (SST, °C), NOAA ERSST v5	1935 – 2004	https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.v5.html	Seasonal averages calculated from monthly values, 2° spatial resolution
Zonal wind speed, NCEP/NCAR Reanalysis	1935 – 2004	https://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis.derived.surface.html	Seasonal averages calculated from monthly values, 2.5° spatial resolution

Adjustment to GLG identification via modified visual crossdating within individuals

Cross-checks of distinctive GLGs among teeth from the same individuals resulted in GLG adjustments of -5 to $+5$ GLGs in 50 teeth from 28 sperm whales (Supplementary Table S5.2). The modal GLG adjustment was -1 GLG and was associated with falsely adding a GLG by misidentifying an accessory layer as a GLG. Maxillary teeth for five individuals from the southwest Australia dataset had poor clarity of GLGs and were unsuitable for the cross-checking process.

Statistical crossdating

Errors in GLG identification were identified and corrected for four GLG width time series for sperm whales from southwest Australia (one GLG misidentified as an accessory layer, one accessory layer misidentified as a GLG and two time series with ambiguity at the pulp cavity margin requiring a lag of ± 1 GLG to compensate for non-specific month of death in marginal GLG assessment). Errors were identified and corrected for six time series from the 1998 Strahan dataset (four associated with incorrect calendar year assignment of the final GLG at the pulp cavity margin due to compacted pulp cavities, one time series had two errors: an accessory layer misidentified as GLG and a GLG misidentified as an accessory layer, and one time series had an error in GLG boundary identification, resulting in a measurement error). Errors in GLG identification were identified and corrected for two sperm whales from Flinders Island (accessory layer misidentified as a GLG in both individuals) and four sperm whales from the 2004 Strahan dataset (one time series had two GLGs misidentified as accessory layers, accessory layer misidentified as a GLG for one time series, and in two time series, GLGs at the pulp cavity margin had been misidentified as incomplete). Interseries correlation values ranged $-0.003 - 0.094$ before statistical crossdating and improved after crossdating, ranging $0.164 - 0.344$ (Supplementary Table 5S.3).

Detrending

Cubic smoothing splines with a frequency response of 50% were applied to all of the GLG width time series with a wavelength of 22 years providing the highest \bar{r} value and the best detrending fit for the southwest Australia dataset, a wavelength of eight years providing the best fit for the 1998 Strahan and Flinders Island datasets and a

wavelength of 12 years providing the best fit for the 2004 Strahan dataset (Supplementary Table S5.4).

Supplementary Table S5.2. Growth layer group (GLG) estimates established using standard repeat count age estimation procedures ('Initial estimate') and revised age estimates following modified visual crossdating ('Revised estimate') for two – four mandibular teeth from each individual sperm whale(s). Differences in age estimates derived across teeth from the same individual sperm whale are due to differential tooth wear across the jaw.

Sample site	Tooth ID#	Initial estimate	Revised estimate	Adjustment
Southwest Australia	16A66-1	23	23	0
"	16A66-2	32	27	-5
"	19A66-1	25	26	1
"	19A66-2	31	31	0
"	44A66-1	32	32	0
"	44A66-2	35	33	-2
"	59A66-1	30	25	-5
"	59A66-2	41	40	-1
"	96A66-1	25	25	0
"	96A66-2	27	26	-1
"	107A66-1	28	28	0
"	107A66-2	33	28	-5
"	109A66-1	33	28	-5
"	109A66-2	34	32	-2
"	113A66-1	27	25	-2
"	113A66-2	35	30	-5
"	147A66-1	42	39	-3
"	147A66-2	44	43	-1
"	148A66-1	28	28	0
"	148A66-2	34	29	-5
"	25A66-1	23	-	-
"	25A66-2	Maxillary unsuitable	-	-
"	54A66-1	30	30	0
"	54A66-2	29	29	0
"	224A65-1	37	-	-
"	224A65-2	Maxillary unsuitable	-	-
"	368A65-1	39	-	-
"	368A65-2	Maxillary unsuitable	-	-
"	388A65-1	29	29	0
"	388A65-2	29	29	0
"	C14A65-1	23	-	-

Table S5.2. cont.d

Sample site	Tooth ID#	Initial estimate	Revised estimate	Adjustment
Southwest Australia	C14A65-2	Maxillary unsuitable	-	-
"	C31A65-1	38	38	0
"	C31A65-2	42	37	-5
"	G7A65-1	34	35	+1
"	G7A65-2	39	36	-3
"	G18A65-1	26	-	-
"	G18A65-2	Maxillary unsuitable	-	-
"	G31A65-1	27	27	0
"	G31A65-2	31	32	1
Flinders Island	1928-1	30	30	0
"	1928-2	26	26	0
"	1929-1	23	23	0
"	1929-2	22	22	0
"	1930-1	26	26	0
"	1930-2	25	25	0
"	1931-1	23	23	0
"	1931-2	23	23	0
"	1932-1	19	19	0
"	1932-2	18	19	+1
"	1933-1	31	31	0
"	1933-2	29	29	0
"	1934-1	25	25	0
"	1934-2	23	23	0
"	1935-1	26	26	0
"	1935-2	26	23	-3
"	1936-1	24	24	0
"	1936-2	23	22	-1
2004 Strahan	2156-1	35	30	-5
"	2156-2	34	33	-1
"	2157-1	35	30	-5
"	2157-2	30	29	-1
"	2158-1	18	17	-1
"	2158-2	24	24	0
"	2158-3	20	20	0
"	2158-4	24	24	0

Table S5.2. cont.d

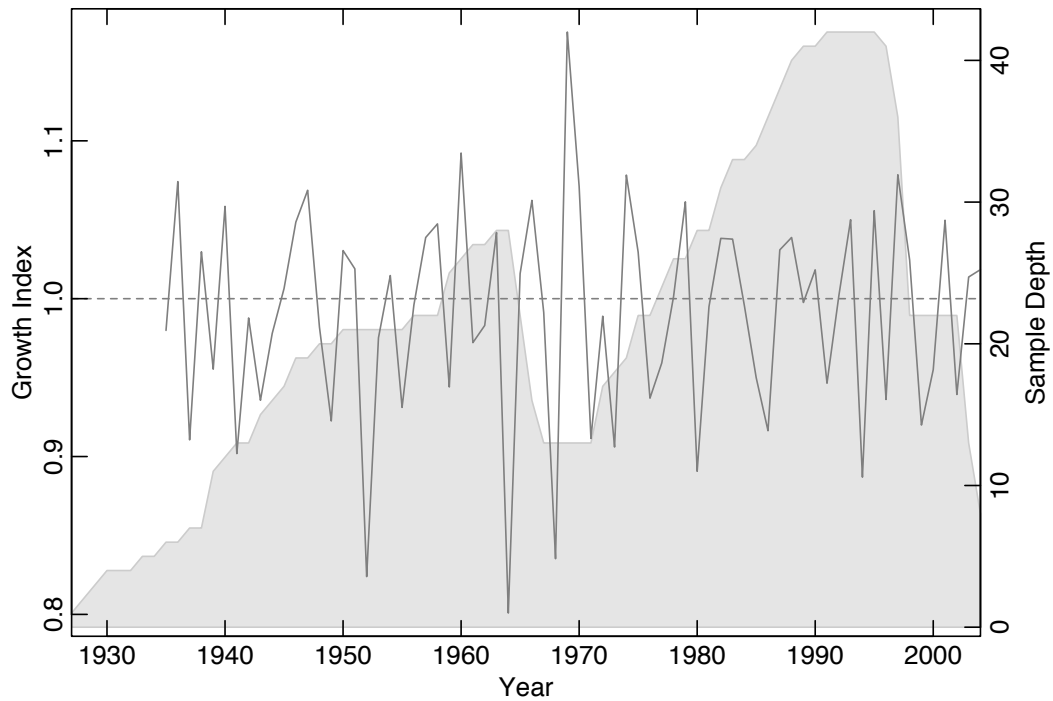
Sample site	Tooth ID#	Initial estimate	Revised estimate	Adjustment
2004 Strahan	2160-1	20	17	-3
"	2160-2	16	16	0
"	2160-3	24	20	-4
"	2160-4	25	20	-5
"	2161-1	23	24	1
"	2161-2	29	29	0
"	2161-3	33	31	-2
"	2161-4	26	29	+3
"	2163-1	21	25	+4
"	2163-2	26	26	0
"	2163-3	22	26	+4
"	2164-1	17	17	0
"	2164-2	22	17	-5
"	2164-3	21	18	-3
"	2164-4	19	18	-1
"	2166-1	20	19	-1
"	2166-2	21	21	0
"	2166-3	21	20	-1
"	2166-4	19	20	+1
"	2168-1	23	23	0
"	2168-2	27	25	-2
"	2168-3	24	24	0
"	2168-4	30	30	0
"	2169-1	20	19	-1
"	2169-2	21	21	0
"	2171-1	19	21	+2
"	2171-2	22	21	-1
"	2171-3	25	21	-4
"	2172-1	20	21	+1
"	2172-2	26	25	-1
"	2172-3	22	22	0
"	2172-4	16	17	+1
"	2174-1	29	28	-1
"	2174-2	27	29	+2
"	2174-3	24	29	+5

Supplementary Table S5.3. Interseries correlation values (measure of crossdating strength among individuals) calculated for sperm whales before and after statistical crossdating of GLG width time series.

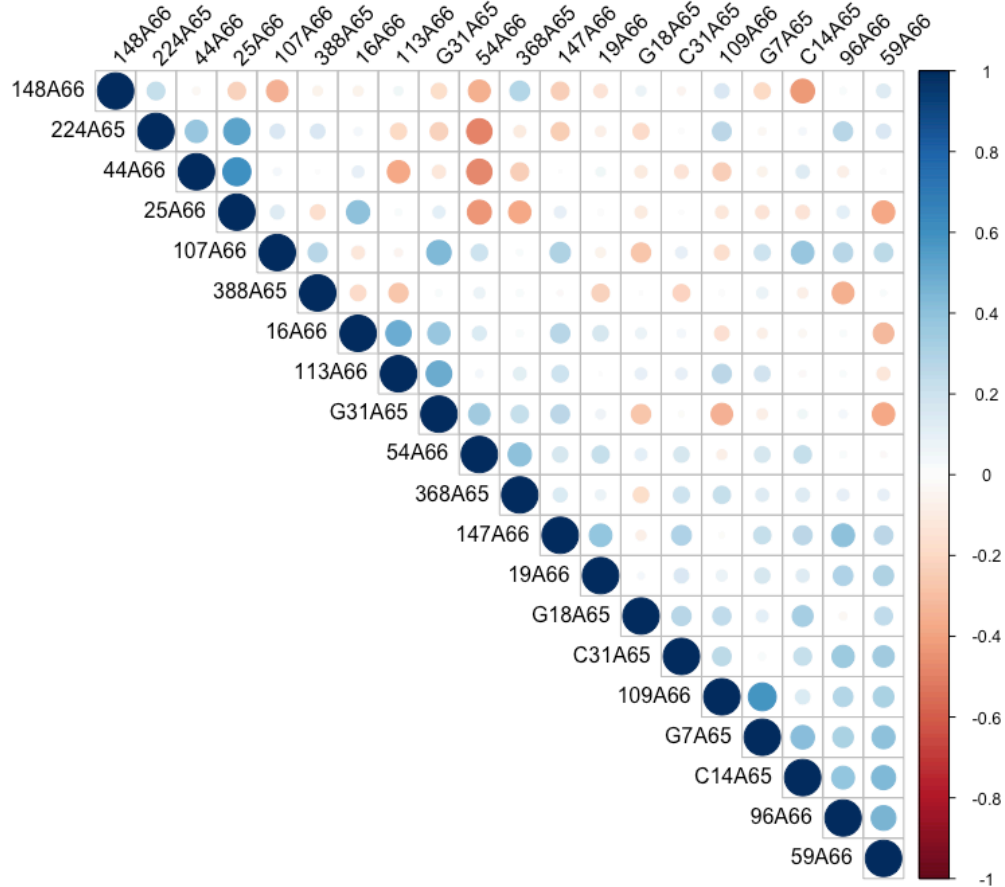
Sample site	Series intercorrelation	
	Before crossdating	After crossdating
Southwest Australia	0.059	0.195
Strahan 1998	−0.003	0.164
Flinders Island	0.094	0.168
Strahan 2004	0.043	0.344

Supplementary Table S5.4. Sperm whale GLG growth chronology properties where n is the number of time series used to develop each chronology and the time period is the range of years spanned by the master chronology where $n \geq 6$.

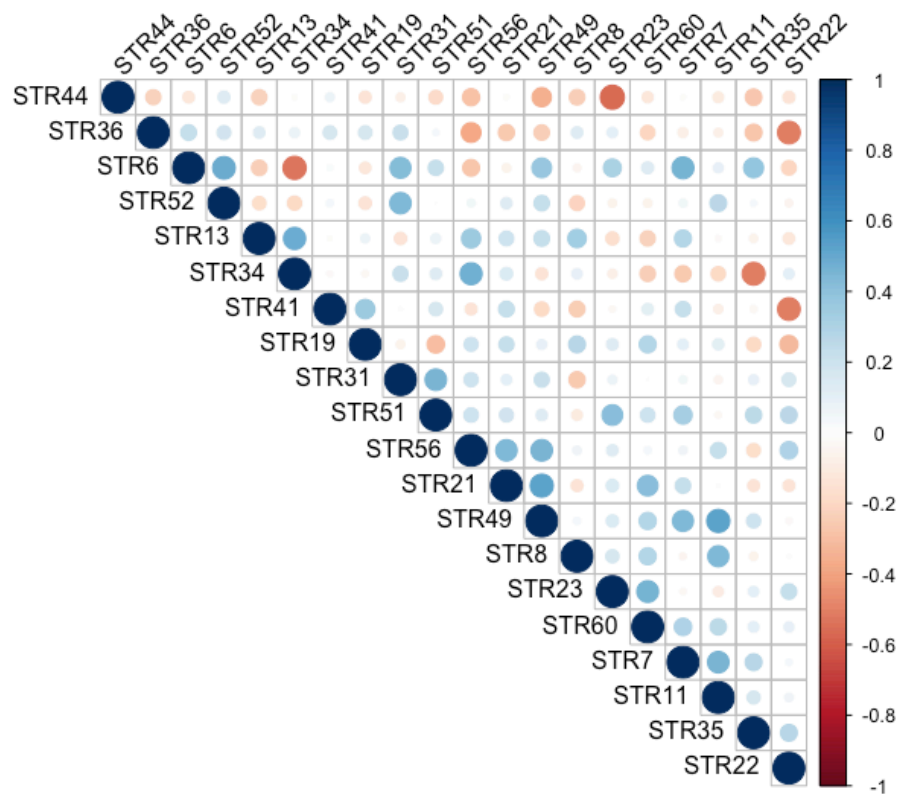
Chronology	n	Time period	\bar{r}	EPS
Composite	62	1935 – 2004	0.029	0.353
Southwest Aus.	20	1935 – 1965	0.061	0.541
Strahan 1998	20	1960 – 1997	0.068	0.593
Flinders Is.	9	1981 – 2002	0.097	0.491
Strahan 2004	13	1985 – 2004	0.121	0.642



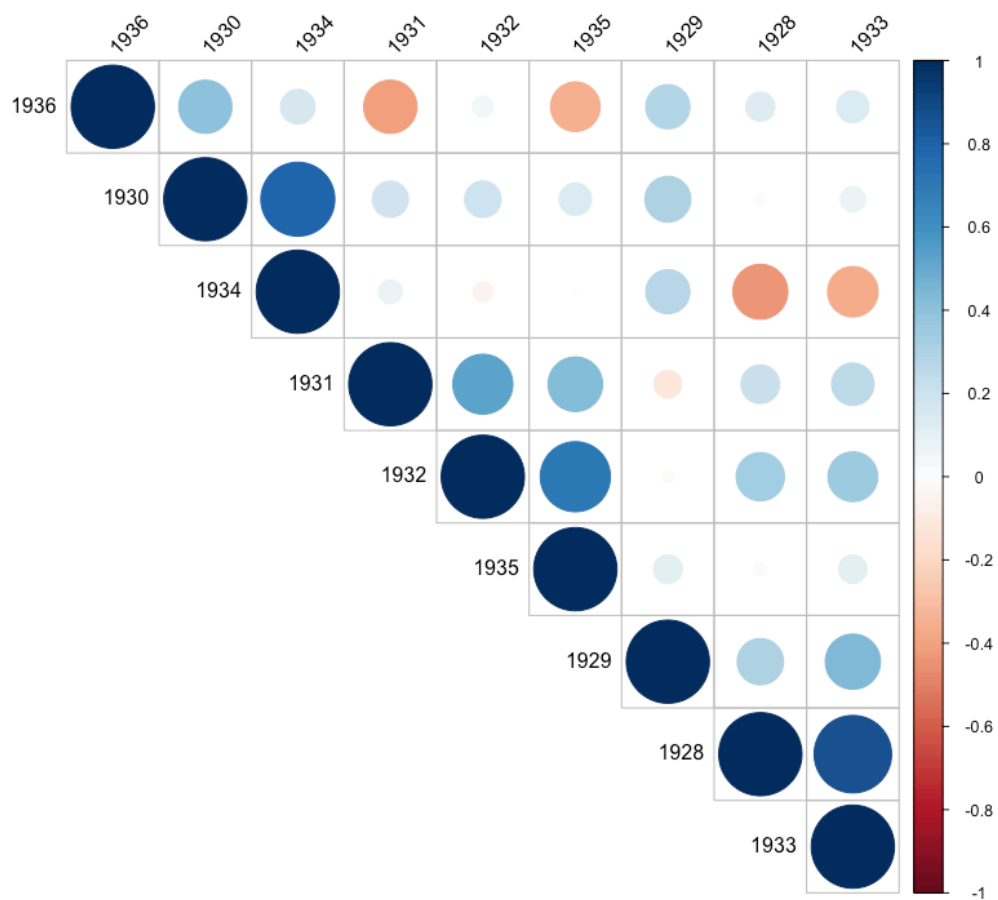
Supplementary Figure S5.1. Composite tooth growth chronology for sperm whales ($n = 62$) from the southern Australian region (1935 – 2004). Shaded region indicates number of individuals contributing to the master chronology (axis on left). The chronology is truncated at the year in which six or more individuals contributed (Matta et al., 2010).



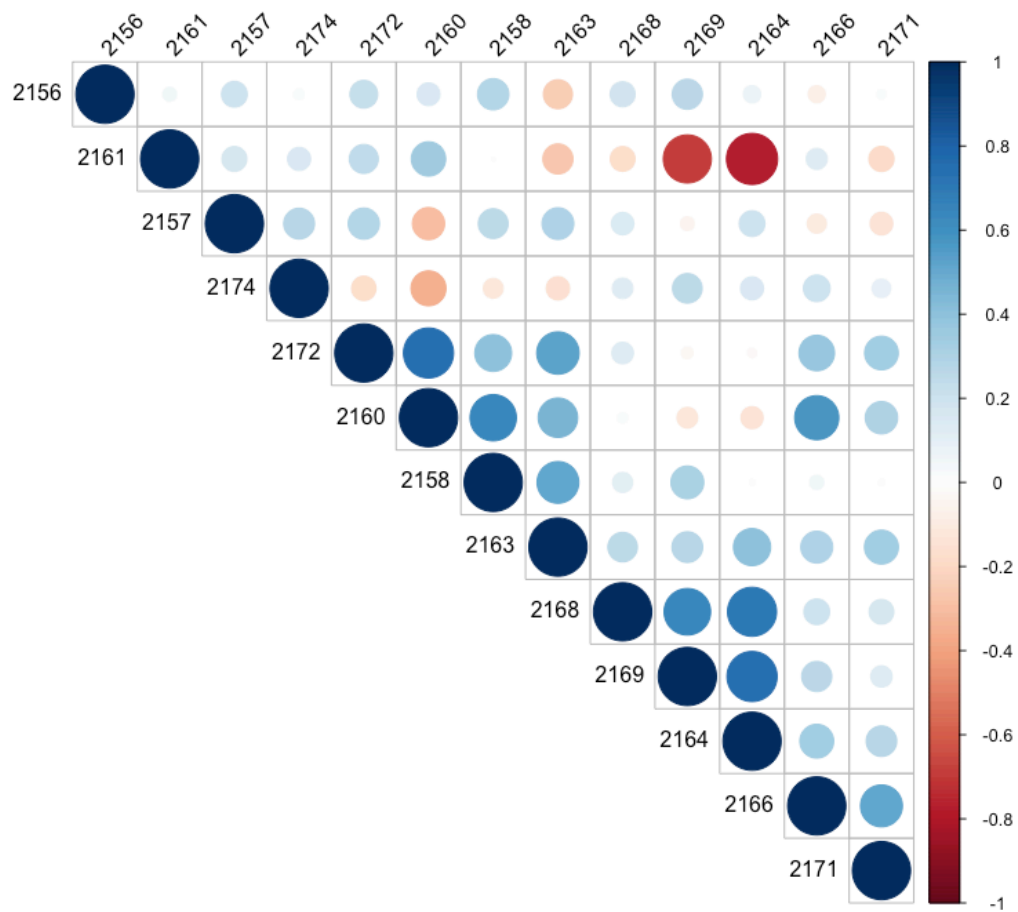
Supplementary Figure S5.2. Correlation matrix (Pearson's pairwise correlation) comparing individual tooth growth chronologies of sperm whales from southwest Australia ($n = 20$). Colour intensity (legend at right) and size (larger circle = higher correlation value) of circles are proportional to the correlation coefficient values. Positive correlations are displayed in blue and negative correlations in red.



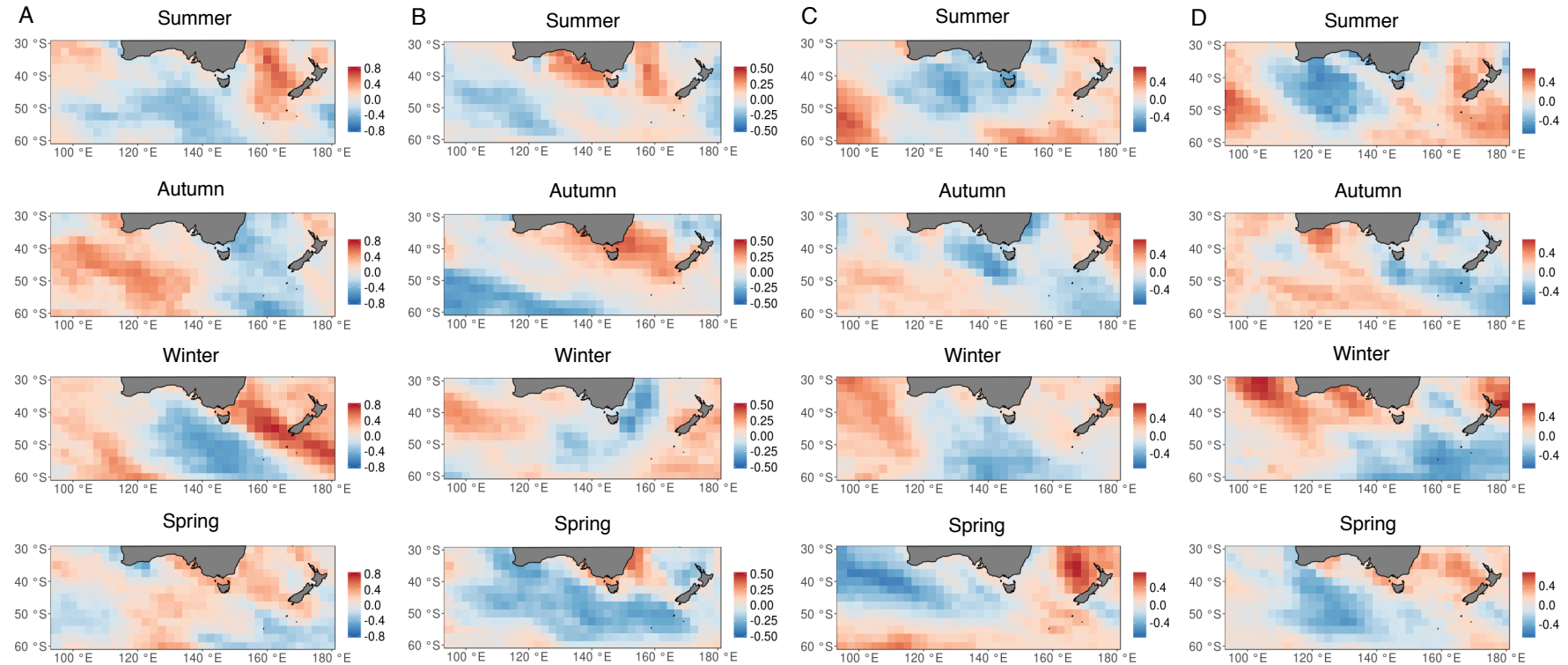
Supplementary Figure S5.3. Correlation matrix (Pearson's pairwise correlation) comparing individual tooth growth chronologies of female sperm whales from the 1998 Strahan stranding ($n = 20$). Colour intensity (legend at right) and size (larger circle = higher correlation value) of circles are proportional to the correlation coefficient values. Positive correlations are displayed in blue and negative correlations in red.



Supplementary Figure S5.4. Correlation matrix (Pearson's pairwise correlation) comparing individual tooth growth chronologies of male sperm whales from the Flinders Island stranding ($n = 9$). Colour intensity (legend at right) and size (larger circle = higher correlation value) of circles are proportional to the correlation coefficient values. Positive correlations are displayed in blue and negative correlations in red.



Supplementary Figure S5.5. Correlation matrix (Pearson's pairwise correlation) comparing individual tooth growth chronologies of female sperm whales from the 2004 Strahan stranding ($n = 13$). Colour intensity (legend at right) and size (larger circle = higher correlation value) of circles are proportional to the correlation coefficient values. Positive correlations are displayed in blue and negative correlations in red.



Supplementary Figure S5.6. Spatial maps of correlations between gridded seasonal averages (austral Summer: Dec, Jan, Feb; Autumn: Mar, Apr, May; Winter: Jun, Jul, Aug and Spring: Sep, Oct, Nov) of zonal wind speed and sperm whale tooth growth chronologies from (A) Southwest Australia (1935 – 1965), (B) 1998 Strahan (1960 – 1997), (C) Flinders Island (1981 – 2002) and (D) 2004 Strahan (1985 – 2004). Red shades represent positive correlations and blue shades represent negative correlations.

Chapter 6 General Discussion

This thesis aimed to develop standardised indices reflecting variability in energy budgets of marine mammals, and once established, use those indices to explore environmental relationships with variability in energy budgets. By adapting dendrochronology techniques to generate chronologies of annual tooth growth (as proxies for energy budgets) in sperm whales and long-finned pilot whales, a method that is transparent and repeatable, with broader applications across other marine mammal species has been developed. Using this methodology, relationships between climate and ocean indices and energy budgets have been identified for the first time in Southern Hemisphere cetaceans. The outputs from this study provide a means by which understanding of the ecology and physiology of marine mammal species can be progressed in a relatively simple and consistent manner. This discussion will provide a comparative synthesis of the main findings and potential applicability of chronology studies to future investigations of the effects of a changing climate on marine mammal species.

Development of methodology

In chapters 2 and 3, using teeth of sperm whales and long-finned pilot whales, standardised methods for generating annually resolved, replicated growth chronologies were developed by modifying dendrochronology techniques. Although the width of GLGs in teeth can be considered analogous to the growth layers that occur in trees, teeth grow in a different manner to trees. A key difference is that new increments are deposited on the inside of a tooth, rather than added to the outside surface, as in tree growth. Because the external surface of the teeth of marine mammals can wear through time as a result of use, for many marine mammals birth year or ‘age zero’ may not be determinable, and anchoring the time series at a calendar year can only be achieved by knowledge of the year of collection. Previous standardisation methods have relied on a number of approaches including standardising individual GLG widths relative to an age-specific GLG width within a population (e.g. Medill et al., 2010; Wittmann et al., 2016). This requires knowledge

of the absolute age of each individual, and identification of the neonatal line to anchor the individual time series at birth year: parameters that are not always available. Other approaches have applied linear growth models to GLG width time series (e.g. Boyd and Roberts, 1993; Hanson et al., 2009). Such approaches do not take into account any curvilinear age-related declines in GLG widths, or variations relating to differing morphology or curvature of teeth. A poor fit of the growth model to the data in some parts or across all of an individual's time series can produce excessively large indices after standardisation (Rypel, 2009).

Crossdating has been little utilised in tooth growth chronology studies, however the improvement in alignment of GLG width time series confirms the value of this process. Crossdating is a fundamental principle of dendrochronology studies, and ensures accuracy in assignment of tree-ring widths to the correct calendar year of growth (Fritts, 1976; Speer, 2010). As a means to reduce the introduction of GLG identification errors, and in association obtain the best estimate of calendar year of deposition for each GLG, in chapter 2 a modified visual crossdating process based on the dendrochronology 'list method' was utilised to assist GLG identification. Consequently, calendar year assignment of GLGs was improved, providing an important precursor step to chronology development in chapter 3.

The application of statistical crossdating in chapters 3 – 5 improved synchrony among individuals within each sample group, and consequently, the strength of the common signal when individual chronologies were consolidated into master chronologies. The extent to which statistical crossdating could be utilised in chapters 3 and 4 was somewhat limited due to the shorter time series available from pilot whale samples. This is because statistical crossdating of short time series (less than 20 – 30 years) may result in spurious correlations (Black et al., 2016; Grissino-Mayer, 2001). It is emphasised here that crossdating can provide a useful aid to improving GLG identification and correct alignment of GLG width time series, however, any potential errors in GLG identification suggested by correlations should always be confirmed on the actual sample.

Standard dendrochronology detrending methods include deterministic (linear and negative exponential models, that follow a known geometric formula and account for

the strong age-related trend in growth related to the increasing circumference of the tree) and empirical methods (cubic smoothing splines). Both are commonly used detrending methods in dendrochronology studies; their suitability depends on the species or region (Cook and Briffa, 1990). The majority of published sclerochronology studies involving bivalves and otoliths have used deterministic models for detrending; because bivalve and otolith growth occurs radially outwards, a strong age-related growth trend can be evident (e.g. Black, 2009; Black et al., 2011; Matta et al., 2010). In contrast, where there is no clear (i.e., age or morphology related) growth trend, empirical models are preferable to deterministic models (Cook et al., 1990; Helama et al., 2006b). Because there was no *a priori* knowledge regarding appropriate models for estimating marine mammal tooth growth, it was necessary to determine optimal detrending functions for marine mammal species and sample groups by experimentation. Chapter 3 found that in many cases the use of deterministic models would have produced unreasonably large growth indices, or the goodness of fit to the data would have varied over the time series, causing noise to be retained in some parts of the standardised series, but not others. Cubic smoothing splines, at a wavelength tailored to each sample group were found to provide the most flexible option for sperm whale and pilot whale tooth growth. In particular they were able to account for relatively abrupt and/or short-term fluctuations in tooth growth that may result from changes in tooth curvature, commonly observed in sperm whale teeth.

Because the teeth of pilot whales from Australia demonstrated a modest age-related decline in GLG widths (which the sperm whale and the New Zealand pilot whale teeth did not), detrending involved not only the use of cubic smoothing splines but also a negative exponential model - known as 'double detrending' (as per Cook, 1985). This approach ensured that any 'end effects'; where a small error in fit to narrow increment widths at the beginnings and ends of the time series can produce unreasonably large indices, were minimised. Similar investigation of various detrending models and their ability to not only isolate the common signal but also minimise end effects is recommended when developing chronologies for other marine mammal species.

Detection of synchronous growth signals

Prior to this study it was unclear if long-lived, upper trophic level, highly mobile marine mammals exhibit synchronous growth among individuals. A synchronous growth response to variations in environmental conditions is fundamental to dendrochronology studies, and is manifest as similar patterns of narrow and wide growth increments among individuals within a region or population (Fritts, 1971; Stokes and Smiley, 1996). It is this synchrony that enables crossdating, and detection of a regional or population-wide response to climate signals. Measures of common signal strength/synchrony (\bar{r}) and chronology quality (expressed population signal: EPS) were understandably not as high for odontocetes as that observed in tree-ring chronologies, or for marine species such as bivalves and teleosts with restricted habitat ranges. For such species synchrony can be relatively high, as regional environmental conditions will exert a strong influence on growth, either through variability in localised food resources, or as a direct response to extrinsic conditions (Black, 2009; Black et al., 2008a). In this study, reasonably high variability among individual chronologies contributing to sample site master chronologies for sperm whales and pilot whales was observed (Figures 4.1 and 5.1). However, similarly high individual variability is also observed among individual chronologies of tree or marine species (e.g. see: Matta et al., 2010; Ong et al., 2016; Seiler et al., 2017; van der Sleen et al., 2016; Wilczyński and Feliksik, 2007), and similar levels of synchrony among individuals have been documented in teleost species with wide habitat ranges (e.g. Ong et al., 2015; Rountrey et al., 2014). The methodology developed in this study was effective for determining common climate signals in energy budgets of pelagic, highly mobile odontocete species. The existence of some degree of synchrony among these animals, and that chronologies derived from teeth can subsequently be used to learn more about the responses of these species to variability in their environment is an important finding of this study.

Chronology quality or confidence can be assessed through the EPS, however while EPS values are useful for assessing how well the sampled chronology represents the population signal, low EPS values are often indicative of low \bar{r} and more importantly, low sample size (Briffa and Jones, 1990; Buras, 2017). Synchrony amongst individuals from a common region can vary throughout the chronology time period,

as environmental conditions influencing growth (or other factors such as individual physiology) will vary over time (Fritts and Speer, 2005; Speer, 2010). Expressed population signal values can also vary through time with variation in sample size/series replication (Briffa and Jones, 1990). For long-term chronologies the EPS can be assessed in segments (e.g. 15 year segments; Rountrey et al., 2014) and those time periods with EPS values considered high enough to represent acceptable chronology quality cited and/or used in environmental comparisons (Briffa and Jones, 1990).

Dendrochronology studies typically apply an EPS threshold value of 0.85, above which tree-ring chronologies are considered acceptable for climate reconstructions (Speer, 2010; Wigley et al., 1984). Some otolith chronology studies have also applied this threshold (e.g. Black et al., 2009; Gillanders et al., 2012), but more recent studies have used lower thresholds (Nguyen et al., 2015; Ong et al., 2018). There is no specific minimum EPS level that guarantees a chronology is adequate for use in climate analyses, and lower EPS values may or may not necessarily mean lower predictive power (Briffa and Jones, 1990; Buras, 2017). The use of a pre-defined threshold, however provides a statistical point of reference for comparisons between chronologies and an acceptable level of chronology confidence (Briffa and Jones, 1990).

Considering the differences between trees and teleosts and marine mammals in their physiology and dependence on extrinsic conditions for growth, a reappraisal of acceptable guidelines for statistical assessment of chronologies may be necessary. In a multi-species study, Ong et al. (2018) applied an EPS threshold of 0.5 and $\bar{r} > 0$ to chronologies derived from marine teleost otoliths from different climatic zones across Western Australia. Calculated values of EPS and \bar{r} for sperm whales and pilot whales were above or very close to these values. Although the Flinders Island sperm whale chronology had an EPS of 0.491, Figure 5.1C clearly indicates that there was reasonable synchrony among individual chronologies. The Flinders Island sample size was relatively low ($n = 9$). Had an increased sample size been available, the EPS value would likely have been higher, as the master chronology will be more representative of the population signal when more individual series are used (Briffa and Jones, 1990). Likewise, estimates of the population signal will be more

representative with longer time series for analysis (Briffa and Jones, 1990). The New Zealand and Australian pilot whale chronologies also fell slightly below an EPS of 0.5, however the pilot whale chronologies were shorter in length than those derived from sperm whale teeth. In the absence of comparable marine mammal chronology studies that utilised similar methodology or provided a quantitative assessment of measures of signal strength and chronology quality, an EPS approaching or above 0.5, and $\bar{r} > 0$ as per Ong et al. (2018), and observed herein for pilot and sperm whales provides a conservative estimate of chronology confidence, given that marine mammals are likely to exhibit higher levels of individual variability than fish. Future tooth growth chronology studies involving marine mammal species will serve to inform future guidelines on acceptable levels of chronology confidence for environmental comparisons.

Much of the variability in levels of synchrony within this, and other studies can be attributed to inter-individual variability. Variability in energy budgets amongst individual whales is not unexpected, given documented variability in energy stores, diet and foraging success between individuals and sexes (Evans and Hindell, 2004b; Evans et al., 2003; Lockyer, 1993b). Additionally, females of both study species have asynchronous breeding cycles. Mature female sperm whales have a calving interval of four to six years, with a 14 – 16 month gestation and prolonged lactation period (Whitehead, 2009). The reproductive cycle for female pilot whales is over three years duration (Bernard and Reilly, 1999). Male pilot whales rely on energy stores to meet energetic demands of seasonal reproductive activities (Lockyer, 2007). Individuals would therefore be expected to differ in physiological demands on energy budgets. Lower synchrony among individuals is also likely in part a result of the ability of these species to make independent foraging decisions and to move among regions of differing environmental conditions. Although these factors may introduce noise into master chronologies, the common signal (in terms of response to environmental factors) was not completely obscured.

The impact of individual variability (or ‘noise’) on master chronologies for trees, bivalves and teleosts from a common region is typically offset by larger sample sizes, which usually exceed 30 – 50 samples (e.g. Black, 2009; Cook et al., 2000; Esper et al., 2002; Rountrey et al., 2014). Sample replication is an important consideration in

dendrochronology studies, to remove the individual tree variability when developing a master chronology (Speer, 2010). Increasing sample replication can enhance the signal to noise ratio, and reduce the ‘dampening’ effect of individual variability on common signals when averaged into master chronologies (Fritts and Speer, 2005; Rountrey et al., 2014).

Conversely, chapters 4 and 5 found that measures of the strength of the common signal within sample group chronologies were higher for samples derived from the sperm whale stranding groups comprised of fewer individuals. In contrast, the groups that could be considered random samples of individuals (whaling samples from southwest Australia) and subsamples from the larger strandings (pilot whales and 1998 Strahan sperm whale stranding) showed lower signal strength. This suggests that the Flinders Island and 2004 Strahan sperm whale groups may have represented higher percentages of socially connected individuals. Female sperm whale social units tend to comprise related and unrelated individuals and dependent young (Christal et al., 1998; Mesnick et al., 2003). The strong social bonds of female sperm whales are purportedly based on co-operative care and protection for offspring (Whitehead, 2003). Prolonged maternal investment buffers offspring against variability in environmental conditions and is ultimately linked to the reproductive success of the mother (Jeglinski et al., 2012). Groups of male sperm whales are thought to represent loose associations with no strong bonds formed after males leave their natal group, and as males age they gradually become more solitary (Best, 1979; Lettevall et al., 2002; Whitehead, 2003). Long-term companions would be more likely to show similar responses to regional environmental variability than individuals from different foraging regions. The synchrony observed in the group of sperm whales from Flinders Island comprised of only males, suggests that these animals to at least a degree experienced similar environmental conditions, and may have either spent time affiliated with each other or foraging in the same broad-scale region.

Pilot whale social groups are reported to represent matrilineally related individuals that spend a large portion of their lives together (Amos et al., 1993; Fullard et al., 2000; Ottensmeyer and Whitehead, 2003). Male offspring potentially remain with their natal kin for life, leaving for short periods for reproductive activities (Amos et al., 1993; Fullard et al., 2000). The propensity for pilot whales to strand in large

numbers means that multiple matrilineal groups can be present within a stranding group. Given the potential fluidity of some sperm whale and pilot whale social groups, and feeding or mating aggregations of multiple social units (Christal et al., 1998; Mesnick, 2001; Oremus et al., 2013), samples derived from stranding groups may not represent individuals that all share a common environmental history. Additionally, sampling time restrictions in the case of very large strandings may result in selective/incidental sampling of individuals from unrelated groups. For species that do not have strong social structure, or where there are uncertainties regarding the structure of stranding groups, sampling animals from defined regions should allow common responses to regional signals to be determined.

High pairwise correlations between individual chronologies within pilot whale and sperm whale sample groups (Supplementary figures S4.1, S5.2 – S5.5) suggest these animals had been foraging together for a large portion of their lives, while low correlations suggest those animals had not been foraging together. Genetic studies to determine potential relatedness among individuals from the same sample groups could allow insight into whether high synchrony in environmental responses is more likely among related individuals, which are more likely to represent long-term foraging companions. Further, this would allow determination of how much ‘noise’ may actually be introduced into master chronologies by chronologies of non-related individuals.

Application of methodology

Chapters 4 and 5 established variability in energy budgets and relationships with environmental indices in both pilot whales and sperm whales, demonstrating the efficacy of the methods established in chapters 2 and 3. In doing so, this study has provided new information regarding the movements and responses to environmental variability of pilot whales and sperm whales.

Sperm whales and pilot whales are highly mobile marine predators, foraging over broad ranges. Sperm whale female groups are reported to forage over large home ranges of 1000 – 2000 km, generally in temperate and tropical waters, with greater

movements of individuals also reported (Jaquet et al., 2003; Mizroch and Rice, 2013; Rice, 1989; Whitehead, 2003). Male sperm whales move even more widely, dispersing across broader latitudinal ranges into subpolar – polar regions as they mature (Rice, 1989). Long-finned pilot whales are generally thought to be nomadic within temperate and sub-polar waters, moving seasonally to follow the distribution of prey resources (Bernard and Reilly, 1999; Ross, 2006). This high mobility means that sperm whales and pilot whales potentially encounter a range of environmental conditions.

Resources in the marine environment are spatially and temporally heterogeneous (Steele, 1978; Stevick et al., 2002). Environmental variation at different temporal and spatial scales determines the distribution of primary productivity and prey resources (Behrenfeld et al., 2006; Mann and Lazier, 2006). Chapters 4 and 5 demonstrated that the energy budgets of pilot whales and sperm whales are influenced by broad-scale climate and oceanographic processes across the southern Australian/New Zealand region. Sperm whales and pilot whales are long-lived cetaceans, with slow maturation and low reproductive rates, and therefore cannot respond to variability in their environment by changing growth or reproductive rates (Bowen et al., 2002). Their evolutionary history has led to adaptations allowing these marine predators to survive environmental variability within their lifetimes and foraging ranges (Whitehead, 1996). Sperm whales and pilot whales undertake wide-ranging movements to follow prey resources. In doing so, they are able to buffer against environmentally mediated localised changes in prey availability to some extent (Bowen et al., 2002; Whitehead, 1996, 2003). Foraging movements and behaviour are shaped by an individual's life history characteristics, evolutionary environment and energy requirements (Berta et al., 2006; Bowen et al., 2002; Spitz et al., 2012).

Overall, the responses to broad-scale climate drivers suggests that sperm whales and pilot whales are subject to common regional climate variability. This result is not surprising, given that there are some similarities in life history, diet and foraging habitats and movements of these pelagic predators. Sperm whales and pilot whales primarily feed on pelagic, mesopelagic and bathypelagic cephalopods and have evolved to take advantage of this abundant and diverse resource, allowing considerable flexibility in diet and foraging behavior (Clarke, 1996; Evans and

Hindell, 2004b). A broad range of variability has been observed in size and species composition of prey, likely related to seasonal availability and abundance, and foraging behaviour (Clarke, 1996; Evans and Hindell, 2004b; Gales et al., 1992). Sperm whales are generally deeper divers than pilot whales; diving to average depths of 500 m, but can dive > 1000 – 2000 m for larger pelagic squid (Watwood et al., 2006). Pilot whales dive to > 100m, and can dive to > 500 m, with maximum dive depths of 600 – 830 m recorded (Baird et al., 2002; Heide-Jørgensen et al., 2002). Sperm whales and pilot whales associate with a variety of oceanographic and bathymetric features, such as oceanic fronts, the continental slope, submarine canyons and seamounts; features that promote primary productivity or aggregate prey (e.g. Bannister, 1968; Gannier and Praca, 2007; Gill et al., 2015; Hamazaki, 2002; Hann et al., 2016).

Regional differences in responses to environmental drivers among groups were observed in both sperm whales and pilot whales, highlighting a need for consideration of potential regional differences when generating master chronologies from what might be disparate or spatially dispersed samples. Because sperm whales in the southern Australian region are thought to represent a single stock (Bannister, 1969), as an initial exploratory analysis all individual chronologies were combined into a single master chronology (the ‘composite’ chronology). The explanatory power of environmental covariates when the composite chronology was included in models was extremely poor and subsequent investigations revealed differing responses of sample groups to broad-scale drivers. In light of these results, it is recommended that when undertaking similar investigations chronologies should be developed from samples of individuals derived from defined regions and/or the same stranding group. The differences among sample groups in the relationships with broad-scale indices suggests spatial variability in the movements of sperm whale and pilot whale groups, across regions under the influence of differing climate phenomena, likely driven by spatial variability in prey and foraging preferences. The Flinders Island and 2004 Strahan sperm whale groups and Australian pilot whale group influenced by a combination of drivers may have moved more broadly across regions where the influence and dominance of climate drivers vary.

The Indian Ocean Dipole (IOD) and Southern Oscillation Index (SOI): a measure of the El Niño-Southern Oscillation (ENSO), were important predictors of tooth growth, and therefore energy budgets, for all sperm whale and pilot whale groups, except the 1998 Strahan sample group, for which the Southern Annular Mode (SAM) was an important influence. This is broadly consistent with what is known about the influence and interaction of these broad-scale phenomena on climatic conditions within the Australian/New Zealand region. The IOD is a basin-scale pattern of sea surface and subsurface temperatures that affects climate in the Indian Ocean (Saji et al., 1999). The influence of the IOD on biological productivity, particularly in the eastern Indian Ocean region is poorly known. However relationships with the IOD for both sperm whales and pilot whales from Australia suggest that conditions associated with the IOD have a strong regional influence on energy budgets of higher predators. The effects of ENSO are strongest in the Pacific (Clarke, 2008), however teleconnections into adjoining ocean basins result in the influence of the ENSO extending across the globe. The influence of ENSO varies regionally, with effects on sea surface temperature (SST) and wind activity leading to alterations in primary productivity (Barber and Chavez, 1983; Clarke, 2008; Lehodey, 2001). As changes in productivity propagate through the food web, the abundance and distribution of prey species will be affected, with flow-on effects to the energy budgets of higher predators. The influence of the SAM on energy budgets varied across sperm whales and model results suggest that it had little influence on the energy budgets of pilot whales. This suggests that these animals spent little time in regions where the SAM influences conditions important to the development and distribution of prey resources (south of 45°S).

Spatial maps derived from correlations with spatially resolved SST in chapters 4 and 5 provided indicative guides to regions associated with higher tooth growth, and potential foraging regions. Regions identified by correlations were consistent with areas of historical and contemporary occurrence of these species and other marine predators in the Australian and New Zealand regions and where oceanographic or bathymetric features associated with high productivity are known to occur. High correlations consistently occurred across austral autumn and winter for sperm whale groups, southwest of Western Australia in the region of the Perth and Albany submarine canyon systems (Exon et al., 2005). This suggests that this region may

represent important foraging habitat for sperm whales, which has remained relatively consistent over an extended time period. The region southwest of Western Australia is influenced by a teleconnection of the IOD, whereby negative IOD events are associated with increased storm activity and a dipole of lower SSTs in the region, strongest in austral winter (Ashok et al., 2007; England et al., 2006). These conditions are likely to increase productivity in the region, with positive effects on energy budgets of sperm whales. Correlations in regions associated with oceanic frontal zones south of Australia; the subtropical, subantarctic and polar fronts (Sokolov and Rintoul, 2007) and regions north of New Zealand, where mesoscale eddies and seamounts occur (Hann et al., 2016) were common to sample groups of both species. Comparison of spatial correlations suggests potential overlap of seasonal utilisation of areas by different sperm whale groups (e.g. the region southwest of Western Australia), and also between sperm whales and pilot whales (e.g. north of New Zealand and frontal zones south of Australia).

Spatial correlations suggest differing foraging strategies within and between species; with some groups potentially moving among differing regions across seasons, while other groups may have utilised regions relatively consistently. Differing movement strategies or foraging habitats have been reported among sperm whale groups in the Northern Hemisphere (Pace et al., 2018; Whitehead et al., 2012; Whitehead and Rendell, 2004). These differences may be driven by variability in prey resources and the need to fulfill nutritional requirements. In regions where food resources are less temporally stable or more dispersed, animals may need to move among different areas in order to meet energetic requirements. In regions of relatively consistent high productivity, remaining in, or returning to the same region (supported by long-term memory of profitable foraging regions) may provide a more energetically efficient foraging strategy (Arthur et al., 2015; Calambokidis et al., 2001). Further research using samples derived from other strandings of sperm whales and pilot whales in the Australian/New Zealand region may reveal if differences are specific to groups, or are representative of a range of foraging strategies.

Perspectives

This thesis demonstrates the utility of tooth growth chronologies to provide proxy records of energy budgets and describes methods that are widely applicable to other toothed marine mammal species. A large archive of teeth samples from many marine mammal species exists within numerous research institutions and museums. Many of these samples are already prepared for age estimation and subsequently provide an ideal, cost-effective resource for chronology studies. This study forms a first step in creating a broader-based study in which chronologies developed using similar methodology for marine mammal species and other taxa from the southern Australian region could be integrated. Multi-taxa chronology studies have already proved effective in providing broader-based approaches to investigations of climate influences on ecosystems, whereby chronologies developed from bivalves or corals and teleost otoliths have been integrated with tree-ring chronologies of coastal species (e.g. Black, 2009; Black et al., 2011; Ong et al., 2016).

A multi-proxy approach has the potential to provide complementary information to variability in energy budgets of individuals and may yield greater insight into physiological and ecological links between species and variability in their environment. Changes in the biochemical composition of teeth of individuals have been used to investigate variability in habitat, movement and distribution, diet/trophic level and ontogenetic changes in marine mammals (e.g. Matthews and Ferguson, 2014; Matthews et al., 2016; Mendes et al., 2007). Sequential sampling of dentinal GLGs derived from teeth of individuals can yield time series of interannual variability in isotopic composition, providing information on spatial variation in the foraging habitats of marine mammals (Matthews et al., 2016; Newsome et al., 2010). Use of these proxies in conjunction with tooth growth chronologies and environmental indices could increase understanding of the drivers of distribution and population state of species over multiple spatial and temporal scales.

This study is the first to identify relationships between variability in annual GLG widths and broad-scale climate indices in two species of Southern Hemisphere cetaceans. In doing so, this thesis has provided new insights into the energy budget responses of marine mammals to environmental variability, which will have broader

applicability for understanding how individuals and populations may respond to changing environmental conditions in the future.

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