Biol. Lett. (2005) 1, 147-150 doi:10.1098/rsbl.2005.0313 Published online 16 May 2005 2005), confused navigation arising from bathymetric conditions (Brabyn & McLean 1992), distraction by activities such as foraging (Wood 1979) and regression to ancient instinctive behaviours (Cordes 1982).

In the Southern Hemisphere, strandings occur irregularly, but at high frequencies on the southernmost areas of land masses (Goodall 1978; Nicol & Croome 1988; Cockcroft & Ross 1991; Brabyn & McLean 1992). In the southeast Australian region, cetacean strandings were first recorded in 1825 in Tasmania and in 1862 in Victoria and have been recorded regularly since, providing a comprehensive record of these events. To examine temporal patterns and investigate potential correlates with stranding events in this region, we undertook a comprehensive survey of all Tasmanian and Victorian strandings and analysed these in association with both climatic and

Periodic variability in cetacean strandings: links to large-scale climate events

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Cetacean strandings elicit much community and scientific interest, but few quantitative analyses have successfully identified environmental correlates to these phenomena. Data spanning 1920-2002, involving a total of 639 stranding events and 39 taxa groups from southeast Australia, were found to demonstrate a clear 11-13- year periodicity in the number of events through time. These data positively correlated with the regional persistence of both zonal (westerly) and meridional (southerly) winds, reflecting general long-term and large-scale shifts in sea-level pressure gradients. Periods of persistent zonal and meridional winds result in colder and presumably nutrient-rich waters being driven closer to southern Australia, resulting in increased biological activity in the water column during the spring months. These observations suggest that large-scale climatic events provide a powerful distal influence on the propensity for whales to strand in this region. These patterns provide a powerful quantitative framework for testing hypotheses regarding environmental links to strandings and provide managers with a potential predictive tool to prepare for years of peak stranding activity.

Keywords: cetacean strandings; southeast Australia; climate; meridional winds; zonal winds; sea-surface temperature

1. INTRODUCTION

Cetaceans are mammals that have evolved and adapted to a completely marine existence. On occasion, however, individuals or groups of whales are found ashore either already perished or, depending on the nature of the stranding event, the size of those individuals involved and the extent of human intervention, they perish soon after. The causes of cetacean strandings remain largely unknown, although many hypotheses have been advanced (e.g. magnetic navigation anomalies (Klinowska 1985; Vanselow & Ricklefs

2. MATERIAL AND METHODS

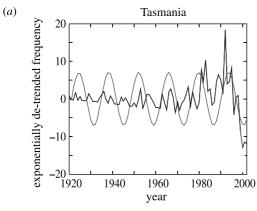
oceanographic variables.

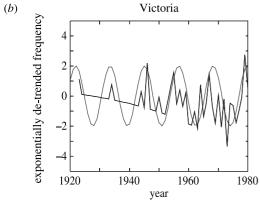
We collated all available data on cetacean strandings in the southeast Australian region from published accounts and unpublished data held by government agencies, museums, the University of Tasmania and from private accounts (see Electronic Appendix). Only those stranding events attributable to the year of the reporting (involving recently deceased or live animals) were included in analyses. Strandings attributed to human activities (e.g. ship strike, shooting) were excluded from analyses. Low numbers of stranding events recorded before the 1920s resulted in analyses focusing on stranding events during the period 1920-2002 (Tasmania) and 1923-2003 (Victoria). Both single strandings and mass strandings were combined for analyses to increase sample sizes and the power of analyses. The Victorian dataset revealed a significant increase in the number of events reported in the period from the late 1980s to the mid-1990s associated with a concerted increase in observer effort (R. M. Warneke, unpublished data), which overwhelmed analyses and the ability to discern any trends underlying in the data. To account for this bias in the stranding record, we analysed only those data from Victoria across the period 1923-1980.

A fast Fourier transform (FFT; Duhamel & Vetterli 1990) was applied to the residuals of an exponential regression of n+1 against time (where n = the number of strandings per year) to estimate the most common integer frequency of peaks over the time-series. The absolute values of the discrete Fourier transform of the detrended time-series data were divided by the integer of half the time-series length (Tasmania = 42; Victoria = 29) and squared. An examination of the first 10 elements in the sorted Fourier series using a semilog 10 plot of the absolute coefficients versus the frequency distribution (Hz) indicates the number of cycles (frequency) over the time-series. To test the significance of these frequencies, a Monte Carlo simulation of the order of the stranding data was calculated over 10 000 randomizations and all frequencies recalculated. The number of times that the randomized frequencies determined for each coefficient were equal to the observed frequencies was used as an estimate of the probability that the observed frequencies were random. In both datasets, the highest coefficients described increases in strandings reports over the time-series, so we tested the significance of subsequent coefficients describing quasidecadal pulses in both datasets.

To confirm the results of the FFT, the residuals were also submitted to lag analysis which tested for auto-correlations at lags ranging from 1 to 20 years. Using lag analysis, periodicity in the time-series is indicated by significant negative correlations at half wavelengths (peaks correlating with prior and subsequent troughs) and positive correlations at full wavelengths (troughs correlating with troughs and peaks with peaks; Finerty 1980).

Mean sea-level pressure (MSLP) gradient is regarded as representative of the strength and persistence of circulation (winds) across the region (Das 1956; Trenberth 1976; White & Peterson 1996; Hartmann & Lo 1998). An index of winter zonal (westerly) winds for the month of August was determined for the Victorian region from the difference in MSLP between Devonport, Tasmania and Melbourne, Victoria and for the Tasmanian region from the difference between Maatsuyker Island and Devonport, Tasmania. Winter meridional (southerly) winds were determined from the difference in MSLP during August from Eddystone Point and





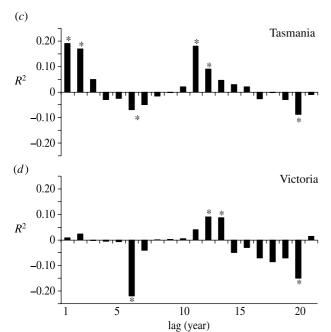


Figure 1. Frequency of stranding events (a) for Tasmania (1920–2002) and (b) Victoria (1920–1980) in relation to FFT coefficients at 11.9 years (Tasmania) and 11.6 years (Victoria) and results of lag analysis demonstrating positive correlations at lags of (c) 11 and 12 years (Tasmania) and (d) 12 years (Victoria). Asterisks represent significant correlations at the 95% level.

Marrawah, Tasmania. MSLP data were obtained from the Australian Bureau of Meteorology. De-trended strandings data were then regressed against winter meridional and zonal wind indices and mean summer sea-surface temperatures (SSTs) collected from Maria Island, Tasmania to determine potential relationships.

3. RESULTS

In Tasmania, 399 stranding events were recorded between 1920 and 2002, which included stranding

date (to at least month and year) and number of individuals. These comprised 85 mass strandings (greater than or equal to two individuals, excluding mother/calf pairs) and 314 individual strandings. A total of 232 stranding events were recorded for the same period in Victoria, of which seven were mass strandings. A total of 39 taxa groups comprised the stranding record, 30 of which were identified to species. The most common species stranded were sperm whales, common dolphins, long-finned pilot whales, bottlenose dolphins and pygmy right whales. The number of stranding events that occurred per year ranged from 0 to 29, increased exponentially over time and was characterized by considerable inter-annual variability. Strandings occurred throughout the year, with a tendency to be more frequent in the austral summer months.

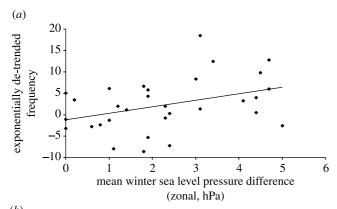
Stranding events in southeast Australia are highly periodic (figure 1). A FFT of the strandings data indicated a significant periodicity at quasi-decadal time-scales, producing integer frequencies of 6 and 7 in strandings over the Tasmanian data series and 5 across the Victorian data. These represented periodicities of 13.8 (i.e. 83 years/6) and 11.9 (83 years/7) years, and 11.6 (58 years/5) years, respectively (figure 1). Monte Carlo analysis of the random ordering of the FFT over 10 000 randomizations confirmed quasidecadal periodicity in both datasets, producing coefficients significant at the periods identified in the FFT (Tasmania: third- and fourth-highest coefficients, p < 0.001; Victoria: third-highest coefficient, p=0.05). Lag analysis of the de-trended data also showed significant positive correlations at lags of 11 (Tasmania: $r^2 = 0.18$, p < 0.001) and 12 years (Tasmania: $r^2 = 0.09$, p = 0.01; Victoria: $r^2 = 0.09$, p=0.03) and negative correlations at lags of 6 (Tasmania: $r^2 = 0.07$, p = 0.02; Victoria: $r^2 = 0.22$, p = 0.003) and 19 years (Tasmania: $r^2 = 0.09$, p = 0.02; Victoria: $r^2 = 0.2$, p = 0.01), indicating a periodicity positive at full wavelength and negative at half wavelength (figure 1).

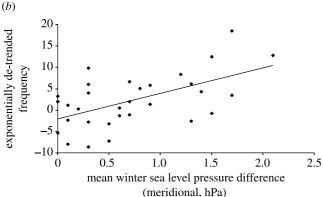
Stranding events from 1970 to 2002 (earlier records from the Tasmanian and Victorian datasets were too sparse to be included in the analyses) were observed to correlate positively with both zonal $(F_{1,29}=4.9,\ p=0.03)$ and meridional $(F_{1,29}=13.8,\ p=0.01)$ MSLP gradients throughout the winter prior to the summer peak in strandings (figure 2) and correlated negatively with summer SSTs off eastern Tasmania $(F_{1,32}=5.5,\ p=0.02;$ figure 2).

4. DISCUSSION

Temporal increases in the number of strandings reported through time are likely to be due to long-term changes in observer effort as a result of increasing public interest in whales, expanding human habitation and coastal activities, and changes in government policies concerning strandings. Seasonal variability in observer effort may in part explain the reduction in reported strandings during the winter months.

Similar periodicity to both Tasmanian and Victorian stranding frequencies has been reported in the recruitment of Tasmanian trumpeter and rock lobster





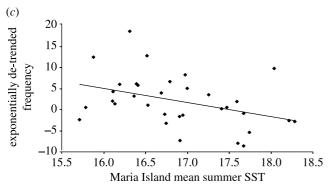


Figure 2. Relationship between stranding events and (a) an annual index of zonal (westerly) wind strength ($R^2 = 0.2$; y=1.5x-1.2); (b) an annual index of meridional (southerly) wind strength ($R^2 = 0.3$; y = 6.0x - 2.1); (c) mean summer sea-surface temperatures collected from Maria Island, Tasmania ($R^2 = 0.2$; y = 58.4 - 3.3x).

as well as spring phytoplankton blooms in the southeast Australian region and these have been correlated to both zonal winds and SSTs (Harris et al. 1988; Thresher 1994, 2002). Both zonal winds and SSTs cycle across quasi-decadal time-scales (Kidson 1925) and trends in wind strength are negatively related to sea-surface temperatures (Trenberth 1976).

Quasi-decadal variability in zonal winds appears to be hemispheric (Tyson 1986), and may be associated proximally with expansion and contraction of the Antarctic Circumpolar Vortex (Haigh 1999; Thresher 2002). Periods of strong zonal winds are associated with higher northward Ekman transport of sub-Antarctic colder water (Oke & England 2004; see Electronic Appendix), as well as mid-latitude intermediate water depths associated with sub-Antarctic mode water and Antarctic intermediate water (Gillie 2002). Meridional winds may serve to enhance this northward movement of colder sub-Antarctic waters. More generally, strong winds are well documented to increase coastal productivity owing to effects on nutrient dynamics (Harris et al. 1988) and are a feature of lowpressure weather fronts throughout this region in winter.

The cyclic behaviour of stranding events in Tasmania and Victoria, coupled with evidence of its persistence since at least 1920, suggests that the periodicity in stranding events is not a function of regular variability in observer effort. The findings presented here offer two possible hypotheses regarding the relationship between cetacean stranding events and climate in this region. Firstly, strong and persistent storm events may in themselves cause strandings through disorientation or additional energetic costs. Secondly, higher coastal productivity generated either by the injection of northerly extensions of colder, sub-Antarctic water masses in years of strong meridional and zonal winds, or the effects of more frequent turnover of the coastal water column, may result in a net movement of cetaceans following their prey northward into southeast Australian waters, particularly those associated with the continental shelf, thereby increasing the number of whales available to strand in the region. We feel that this is the most likely interpretation given the correlation between stranding event numbers and MSLP gradients measured in the preceding winter (figure 2).

Our identification of a long-term pattern in stranding events from this region, and climatic and oceanographic correlates, is a major advance in the understanding of this phenomenon. At one level, it allows for the development and testing of more focused hypotheses regarding correlates with strandings, and thereby a greater understanding of the proximate causes of these events. This study highlights the significance of long-term ecological data and the importance of integration of these with similar oceanographic and climatic datasets to identify ecosystem-level patterns. Integrated ecological investigations involving regular surveys for cetaceans in the region would provide means by which the shifts in abundance and distribution of cetaceans hypothesized here can be investigated. Additionally, collaborative projects integrating stranding datasets from agencies located in regions elsewhere in the Southern Hemisphere would allow the investigation of the potential hemispheric nature of the observed periodicity in cetacean strandings. At another level, the results presented here may help managers to predict periods of increased numbers of stranding events. They may also provide an important guide for potentially disturbing activities (e.g. those involving seismic or sonar operations) to be scheduled for periods of lower potential abundance of cetaceans in the region.

We thank the Department of Primary Industries, Water and Environment, Tasmania, the University of Tasmania, the Australian Antarctic Division and all volunteers for their support at strandings. We thank two anonymous referees for their useful comments on an earlier draft of this manuscript.

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The supplementary Electronic Appendix is available at http://dx.doi.org/10.1098/rsbl.2005.0313 or via http://www.journals.royalsoc.ac.uk.