

Relationship between long-term environmental fluctuations and diving effort of female Australian fur seals

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ABSTRACT: For predators foraging within spatially and temporally heterogeneous marine ecosystems, environmental fluctuations can alter prey availability. Using the proportion of time spent diving and foraging trip duration as proxies of foraging effort, a multi-year dataset was used to assess the response of 58 female Australian fur seals *Arctocephalus pusillus doriferus* to inter-annual environmental fluctuations. Multiple environmental indices (remotely sensed ocean colour data and numerical weather predictions) were assessed for their influence on inter-annual variations in the proportion of time spent diving and trip duration. Model averaging revealed strong evidence for relationships between 4 indices and the proportion of time spent diving. There was a positive relationship with effort and 2 yr-lagged spring sea-surface temperature, current winter zonal wind and southern oscillation index, while a negative relationship was found with 2 yr-lagged spring zonal wind. Additionally, a positive relationship was found between foraging trip duration and 1 yr-lagged spring surface chlorophyll *a*. These results suggest that environmental fluctuations may influence prey availability by affecting the survival and recruitment of prey at the larval and post-larval phases while also affecting current distribution of adult prey.

KEY WORDS: Benthic diving · Diving behavior · El Niño Southern Oscillation · Sea-surface temperature · Otariid · *Arctocephalus pusillus doriferus*

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INTRODUCTION

Animals foraging within the marine environment encounter a highly dynamic system that is heterogeneous in both space and time. Within this system, the distribution of productivity is driven by numerous climatic events that operate at multiple time scales, from short-term effects (e.g. river discharge after rain over land; Smith & Demaster 1996) to decadal cycles (Chavez et al. 2003). These events can have widespread impacts across multiple ecosystems (Alexander et al. 2002) or be geographically isolated, affecting a relatively small area (e.g. coastal upwelling; Nieblas et al. 2009). The ability of populations to respond to such environmental variation will determine their reproductive success and, ultimately, pop-

ulation demography (Forcada et al. 2012). Understanding how populations respond to such fluctuations is essential if we aim to predict a species' response to current and future environmental change (Costa et al. 2010); however, for many species their behavioural response to environmental fluctuations is currently unknown.

A species' ability to respond to an environmental event will depend on the event's spatial and temporal scale and on the species' physiological, behavioural and life history limitations (Somero 2010). Species that adopt a central-place foraging strategy for all or part of their life cycle may be particularly susceptible to the negative effects brought on by shifting environmental conditions, because they are constrained to forage within a discrete area surrounding their

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colony or home site (Costa 1993). If environmental conditions cause a shift in food availability to areas outside their foraging range, then animals may be limited in their capacity to respond. Individuals will be forced to increase foraging effort to maximise prey encounter rates within the depleted environment, potentially at the loss of personal condition, or abandon the reproductive event to migrate to more productive regions (Costa 2007). For example, at the meso-scale, the westerly trade winds of the Pacific Ocean decrease during El Niño years, leading to a northerly intrusion of warm water up the California coast (Chavez et al. 2002). This leads to a reduction in upwelling intensity and, thus, prey densities within the California Current system (Chavez et al. 2002). During this time, female California sea lions, unable to migrate to more productive regions by their need to provision their young, respond by increasing their foraging effort (measured as the proportion of time spent diving while at sea) within the depleted regions around their colony (Feldkamp et al. 1989).

Juvenile survivorship in fish can be greatly influenced by local environmental conditions, leading to variation in adult recruitment in subsequent years (Hewitt et al. 1985). For example, in red cod *Pseudophycis bachus*, sea-surface temperature (SST) during the early phases of life have been shown to have a significant effect on the recruitment of adult individuals in subsequent years (Beentjes & Renwick 2001). Concurrently in south-eastern Australia, variation in zonal westerly winds have been implicated in the larval survival and subsequent recruitment of King George whiting *Sillaginodes punctatus* and southern rock lobster *Jasus edwardsii* (McGarvey & Matthews 2001, Jenkins 2005). Thus for predators foraging on longer lived prey, environmental conditions during previous seasons may have an effect on prey densities encountered during the current foraging season. Indeed, in Atlantic puffin *Fratercula arctica*, local SST conditions at a 2 yr lag have a strong influence on adult survival during their breeding season, when they are restricted to foraging directly around the nesting colony (Harris et al. 2005).

The Australian fur seal (AUFS) *Arctocephalus pusillus doriferus* is a benthic foraging species that is endemic to the shallow continental shelf re-

gion of Bass Strait in south-eastern Australia (Arnould & Kirkwood 2007, Kirkwood & Arnould 2011). Current estimates give a population size of approx. 120 000, with individuals having an average body mass of 76 and 229 kg for females and males, respectively, making it the largest predator biomass within the Bass Strait region (Arnould & Warneke 2002, Goldsworthy et al. 2003, Kirkwood et al. 2010). Foraging is restricted to on-shelf regions of Bass Strait, a region characterised by a very uniform bathymetry (Fig. 1) (Arnould & Kirkwood 2007, Kirkwood & Arnould 2011). Within this region individuals forage on or near the seafloor at depths ranging between 60 and 80 m, feeding on a large variety of prey types including bony fish, cephalopods and elasmobranchs (Arnould & Hindell 2001, Arnould & Kirkwood 2007, Kirkwood et al. 2008, Deagle et al. 2009). Although benthic foraging species are thought to forage in more stable environments (Costa & Gales 2003), several of the prey species targeted by them commonly exhibit pelagic life histories (Kirkwood et al. 2008). Thus, these prey may be more susceptible to environmental fluctuations when compared with truly benthic species. It has been suggested that within Bass Strait these species are limited in their ability to travel vertically by the region's shallow bathymetry and that AUFS target these species at the benthos (Arnould & Hindell 2001).

The Bass Strait region is influenced primarily by 3 separate water bodies (Fig. 1) (Sandery & Kämpf

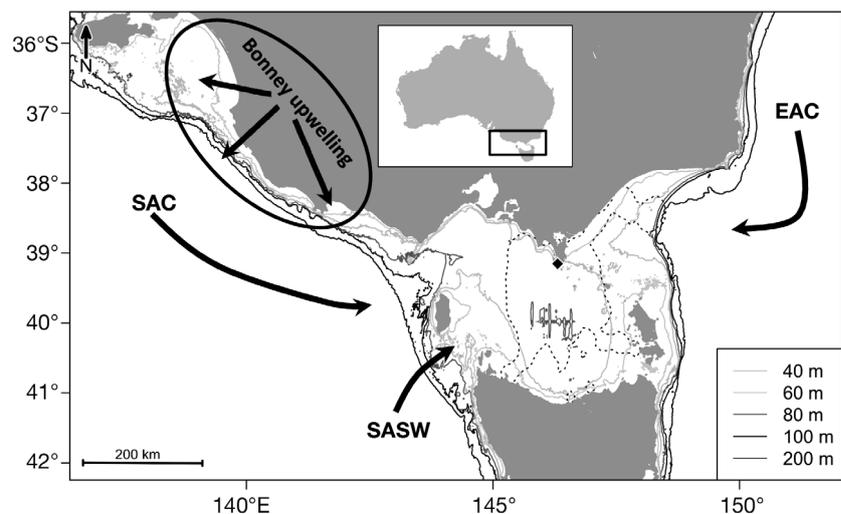


Fig. 1. South-eastern Australian region showing the direction of input from the 3 major water bodies that influence Bass Strait, the location of the Bonney upwelling region, the location of the Kanowna Island study site (◆) and the 95% kernel home range of female Australian fur seals foraging from Kanowna Island (dashed line). Inset map shows the position of the region relative to Australia. SAC: South Australian Current. SASW: Sub-Antarctic Surface Water. EAC: East Australian Current. Foraging home range data taken from Hoskins (2013)

2007). The South Australian Current (SAC) is a warmer water current that is driven along the southern coast of Australia by the region's predominantly westerly winds (Sandery & Kämpf 2007). In winter, the subtropical convergence moves north bringing cool nutrient rich Subantarctic Surface Waters (SASW) into Bass Strait, where they mix with the SAC waters entering from the west (Sandery & Kämpf 2007). During the austral summer, the sub-tropical ridge (a zone of high pressure that is usually located over central Australia) shifts southwards, driving south-easterly winds into Bass Strait (Sandery & Kämpf 2007). This shift allows the nutrient poor East Australian Current (EAC) to extend further south and enter Bass Strait from the east. However, these south-easterly winds also drive greater upwelling of cooler, nutrient rich SASW along the western edge of Bass Strait, including the largest and most predictable upwelling region in Australia (Bonney Upwelling), resulting in an increase in productivity within this region (Nieblas et al. 2009).

Previous studies have suggested that benthic foraging otariids tend to forage nearer to their limits and are, thus, less capable of behaviourally responding to environmental fluctuations (Arnould & Costa 2006). However, recent work on AUFS have revealed that this species is capable of adjusting foraging behaviour/effort at a variety of temporal scales (Hoskins & Arnould 2013), suggesting that they may be capable of responding to environmental fluctuations. Concurrently, studies have already identified relationships with interannual oceanographic variability (in part due to varying influences of these 3 current systems) and changes in the diet, growth and reproductive success of AUFS (Kirkwood et al. 2008, Gibbens & Arnould 2009, Knox et al. 2014). However, it is not known whether or how foraging effort is impacted by interannual environmental fluctuations. The proportion of time spent diving during a foraging trip, as well as foraging trip duration, have been established as good indicators of overall foraging effort in otariids, including this species (Arnould et al. 1996, Costa & Gales 2000, Arnould & Costa 2006, Hoskins & Arnould 2013) and, hence, these indices were used to investigate the relationship between environmental variability and foraging effort in the present study. The aims of this study were to investigate the relationship between interannual variations in environmental conditions and the foraging effort of AUFS by using the proportion of time spent diving and foraging trip duration as proxies of foraging effort.

MATERIALS AND METHODS

Animal handling, data collection and processing

Field work was conducted between April and August of the years 2002 to 2009 at the Kanowna Island (39° 09' S, 146° 18' E) breeding colony in central northern Bass Strait, south-eastern Australia (Fig. 1). Capture and handling techniques varied over the study period. During 2002, individual adult females nursing young were selected at random and captured using a modified hoop net (Fuhrman Diversified) before being manually restrained. Animals were then given an intramuscular injection of the sedative Midazolam (approx. 0.15 mg kg⁻¹, Hypnovel®, Roche Products Pty) and kept in the hoop net for further processing. In subsequent years, individuals were captured in a modified hoop net and given an intramuscular injection of Midazolam (approx. 0.1 mg kg⁻¹); induction of isoflurane gas anaesthesia was then delivered via a portable vaporizer (Gales & Mattlin 1998). Once anaesthetized, individuals were removed from the hoop net and, from 2006 onwards, secured to a board before being weighed on a suspension scale (± 0.5 kg) and measured for straight-line length (± 0.5 cm). Devices were then attached following the methods described above.

Individuals were equipped with a time-depth recorder (one of the following: Mk07, Mk08, Mk09, Mk10; Wildlife Computers) and VHF transmitter (Sirtrack) that were glued in series to the pelage along the dorsal mid-line, just posterior to the scapula, using quick setting epoxy (Accumix 268, Huntsman Advanced Materials Pty). The time-depth recorders (TDRs) were programmed to collect sensor data at 5 or 1 s intervals. Upon completion of at least one foraging trip, animals were captured as previously described and sedated with an intramuscular injection of Midazolam (approx. 0.1 mg kg⁻¹). Data loggers were then removed by cutting the animal's fur beneath them using a scalpel and following completion of the procedure the animals were subsequently released back into the colony.

Downloaded data were corrected for drift in depth readings and subsequently summarised for basic per-dive metrics (dive and post-dive duration, maximum dive depth) using the diveMove package (version 1.3.5; Luque & Fried 2011) within R (version 2.15.1; R Development Core Team 2012). The influence of surface behaviour and differing precisions in depth sensors between models of TDRs was excluded by setting the minimum dive threshold to 5 m. AUFS have been observed to spend periods of several

hours in the waters surrounding the breeding colony for purposes other than foraging (e.g. thermo-regulation; Arnould & Kirkwood 2007, A. J. Hoskins pers. obs). To avoid misclassifying of these non-foraging periods, foraging trips were defined as continuous periods of time spent in water ≥ 6 h. The proportion of time spent diving (per foraging trip) and foraging trip duration were then extracted from TDR records and used as proxies of foraging effort in later analyses.

Calculation of environmental variables

To investigate the influence of interannual environmental variations on the foraging effort of female AUFS, relationships between diving behaviour and several environmental variables were analysed (Table 1). All selected variables were chosen for their potential to affect local prey densities and/or describe fluctuations in productivity of the Bass Strait region. Gibbens & Arnould (2009) previously reported mean winter (June–August) SST and westerly zonal wind component within central Bass Strait (39° – 41° S, 144° – 148° E) to affect female body condition and pup production at the study colony, and thus, these variables were included in the present study (Table 1). In addition, although Gibbens & Arnould (2009) found winter surface chlorophyll *a* (chl *a*) concentrations did not have an effect on pup production and female body condition, it was included in the current study because chl *a* concentrations are a

strong indicator of the primary productivity within a region (Table 1; Falkowski & Kiefer 1985). The El Niño Southern Oscillation (ENSO) cycle is a major driver of productivity within the southern Australian region; as such, the Southern Oscillation Index (SOI; Troup 1967), an indicator of the state of the ENSO cycle, was included in the current study.

The primary spawning time for many of the prey species consumed by AUFS, including the main AUFS fish prey (e.g. redbait *Emmelichthys nitidus*, a species of jack mackerel [*Trachurus declivis*] and red cod *Pseudophycis bachus*), occurs during the Austral spring (September–November) (Hewitt et al. 1985, Kirkwood et al. 2008, Neira et al. 2008, Kemp et al. 2012). In fish, juvenile survivorship can greatly influence the densities of adults within a population in subsequent years (Beentjes & Renwick 2001). AUFS feed on a variety of prey which mature between 0.5 and 4 yr; however, many of these prey are consumed when immature (Kirkwood et al. 2008). Thus to examine the relationship between AUFS foraging effort and lagged environmental conditions, the mean Bass Strait SST, chl *a* and zonal wind component during the 2 previous springs was investigated in the present study (Table 1).

The upwelling that occurs along the Bonney Coast is a significant source of productivity for the region and has been positively linked to pup production in AUFS (Gibbens & Arnould 2009). Therefore, to investigate the influence of this oceanographic feature on foraging effort, the upwelling index developed by Nieblas et al. (2009) was calculated (Table 1). Con-

Table 1. Environmental variables considered to have a potential influence on the foraging effort of female Australian fur seals at the interannual and intra-trip time scales. chl *a*: chlorophyll *a*; SST: sea-surface temperature

Interannual environmental variables	Unit	Abbreviation	Predicted mechanism of effect
SST (winter)	$^{\circ}\text{C}$	SST _{win}	Indicative of influence of different water bodies
Surface chl <i>a</i> (winter)	mg m^{-3}	Chl- <i>a</i> _{win}	Source of primary productivity
West–east wind component (winter)	m s^{-1}	windU _{win}	Primary driver of flow into Bass Strait
SST (summer)	$^{\circ}\text{C}$	SST _{sum}	As for SST _{win} but during peak upwelling period
Surface chl <i>a</i> (summer)	mg m^{-3}	Chl- <i>a</i> _{sum}	As for Chl- <i>a</i> _{win} but during peak upwelling period
West–east wind component (summer)	m s^{-1}	windU _{sum}	As for windU _{win} but during peak upwelling period
SST (previous spring, 1 year lag)	$^{\circ}\text{C}$	SST _{spr1}	As for SST _{win} but during prey spawning period
Surface chl <i>a</i> (previous spring, 1 yr lag)	mg m^{-3}	Chl- <i>a</i> _{spr1}	As for Chl- <i>a</i> _{win} but during prey spawning period
West–east wind component (previous spring, 1 yr lag)	m s^{-1}	windU _{spr1}	As for windU _{win} but during prey spawning period
SST (spring, 2 yr lag)	$^{\circ}\text{C}$	SST _{spr2}	As for SST _{win} but during prey spawning period
Surface chl <i>a</i> (spring, 2 yr lag)	mg m^{-3}	Chl- <i>a</i> _{spr2}	As for Chl- <i>a</i> _{win} but during prey spawning period
West–east wind component (spring, 2 yr lag)	m s^{-1}	windU _{spr2}	As for windU _{win} but during prey spawning period
Southern oscillation index		SOI	Major driver of weather within the region
Bonney upwelling index	$\text{mg m}^{-3} \text{ km}^{-2} \text{ d}^{-1}$	Chl- <i>a</i> _i	Major source of productivity for the region

currently, to give an indication of the oceanic conditions within Bass Strait during these summer months, the mean SST, chl *a* and zonal wind component were also calculated and included in analysis (Table 1).

For all the above parameters, monthly means of SST and chl *a* were derived from satellite based ocean color imagery taken by the AVHRR pathfinder and SeaWiFS satellites, respectively (resolution—SST: 4 km; chl *a*: 9 km). Level-3 data products were accessed via the NASA ocean color website (<http://oceancolor.gsfc.nasa.gov/>) and processed using the SeaWiFS Data Analysis System (SeaDAS 6.4, SeaWiFS – GSFC, NASA, Greenbelt, MD, USA). Monthly means of SOI were downloaded from the Australian Bureau of Meteorology (www.bom.gov.au/climate/current/soihtm1.shtml) and converted to yearly means. The Zonal U wind component was extracted as 6 hourly readings from the NCEP-NCAR reanalysis project database (Kanamitsu et al. 2002) using the RNCEP package within R (version 1.0.5). The mean seasonal (winter and spring) west–east zonal wind component was then calculated from these 6 hourly readings.

Statistical analysis

A regression modelling approach was used to assess the effect of the environmental variables on the proportion of time spent diving and foraging trip duration of AUFS. Due to the nested nature of the data, linear mixed effects models (LME) were used with month of foraging trip and individual seal held as nested random effects (individual seal nested within month). Inspection of residuals revealed patterns (heteroscedasticity), which were corrected for using an exponential variance structure. LMEs were fit to the data using the R package nlme (version 3.1-105)

Interannual variations in environmental conditions were assessed using the previously discussed environmental variables (Table 1) and the foraging effort calculated at the level of individual foraging trips. LMEs were fit to the data but, as no single model was found to satisfactorily explain the variation within the data, a multi-model inference framework with model averaging (Grueber et al. 2011, Symonds & Moussalli 2011) was adopted to best describe the relationships in the data. To avoid overfitting of models, a candidate set of models was constructed using combinations of up to 10 environmental variables. Collinearity between predictor variables was assessed, and where a pair of variables had a correlation ≥ 0.6 , models containing these pairs were excluded from the

candidate set. Models were compared using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and the difference in AIC_c (ΔAIC_c). A subset of the most likely models was then taken ($\Delta AIC_c < 4$; Burnham & Anderson 2002), and model-averaged coefficient estimates were calculated from these using the AICcmodavg (version 1.33) package in R. Due to the high number of predictor variables and the need to not overfit models, goodness of fit was not calculated on a full model (Symonds & Moussalli 2011), rather a final model containing all variables assessed as having a relationship with the response variables was constructed and used. Goodness of fit was assessed using conditional R^2 as described in Nakagawa & Schielzeth (2013).

RESULTS

A total of 58 individual female AUFS were captured and instrumented for the current study. Where mass and length data were available (2006–2009), ANOVAs were fitted to identify if interannual variance in these measures existed and no interannual variation was found in the sample population (mass: $F_{3,38} = 0.86$, $p = 0.46$; length: $F_{3,38} = 1.63$, $p = 0.19$). Deployment durations ranged between 3.9 and 125.4 d (mean \pm SD: 31.5 ± 35.0 d) with individuals performing an average of 8.05 ± 9.10 foraging trips (Table S1 in the Supplement at www.int-res.com/articles/suppl/m511p285_supp.pdf). During deployments a total of 467 foraging trips were recorded with trips ranging between 0.5 and 13.0 d, individuals performed an average of 201.5 ± 62.5 dives per day and spent an average of $40.1 \pm 13.6\%$ of their time spent diving (Table S1). Individuals achieved an average modal dive depth of 70.7 ± 21.1 m, with no variation in dive depth found between years (mixed-effects ANOVA; $F_{7,50} = 0.52$, $p = 0.81$). A LME on the proportion of time spent diving per foraging trip by individuals found it to vary between years ($F_{2,32} = 42.16$, $p < 0.0001$) while also varying with the duration of a foraging trip ($F_{62} = 5.52$, $p = 0.0001$). This suggests that, when variation caused by different foraging trip durations are held fixed, annual variations in foraging conditions still have an effect on the proportion of time spent diving per foraging trip. As such, to account for the effect of trip duration on foraging effort, foraging trip duration was included as a fixed effect in all models used to assess the effects of interannual environmental variations on foraging effort.

Table 2. Model averaged parameter estimates ($\bar{\beta} \pm SE(\bar{\beta})$) for the effects of interannual environmental variation (see Table 1 for abbreviations) on the foraging effort of female Australian fur seals. **Bold** parameter estimates represent those whose 95 % unconditional confidence intervals did not cross zero

Interannual environmental variables	Prop. of time spent diving	Foraging trip duration (h)
Trip duration	-0.03 ± 0.01	
SST _{win}	0.04 ± 0.07	-0.83 ± 0.74
Chl- <i>a</i> _{win}	1.06 ± 0.69	-4.37 ± 4.18
windU _{win}	0.02 ± 0.01	0.15 ± 0.14
SST _{sum}	0.00 ± 0.04	-0.44 ± 0.40
Chl- <i>a</i> _{sum}	0.19 ± 0.84	-4.97 ± 5.10
windU _{sum}	-0.02 ± 0.03	0.11 ± 0.23
SST _{spr1}	0.02 ± 0.04	0.53 ± 0.44
Chl- <i>a</i> _{spr1}	-0.17 ± 0.33	10.56 ± 3.92
windU _{spr1}	-0.01 ± 0.02	-0.14 ± 0.12
SST _{spr2}	0.10 ± 0.03	-0.12 ± 0.36
Chl- <i>a</i> _{spr2}	-0.07 ± 0.95	-13.20 ± 6.74
windU _{spr2}	-0.04 ± 0.01	0.15 ± 0.19
SOI	0.01 ± 0.001	-0.03 ± 0.02
Chl- <i>a</i> _i	-0.17 ± 3.09	25.35 ± 48.20

Interannual variation was observed in all of the environmental variables assessed (Table S1). When investigating the relationship between the proportion of time spent diving and interannual environmental fluctuations, model averaging of parameter estimates determined that the strongest relationships (attributes with unconditional 95 % confidence intervals that exclude 0; Burnham & Anderson 2002) were observed with 4 of the parameters investigated (wind U_{win}, wind U_{spr2}, SST_{spr2} and SOI; Table 2). All 4 of these variables had a strong presence within the final candidate model set (proportion of models containing windU_{win}: 91 %, SOI: 75 %, windU_{spr2}: 54 % and SST_{spr2}: 35 %), providing further evidence of their relationship with the proportion of time spent diving (Table 3A). The model containing all 4 influential environmental predictor variables, as well as foraging trip duration, had a conditional R² of 0.44, suggesting a moderate explanation of the variation within the data.

There was a positive relationship with the mean zonal wind component during winter and the proportion of time spent diving recorded at the same time (estimated increase of 8 % of time spent diving dur-

Table 3. Most likely models, in descending order, to explain the relationship between variations in either (A) the proportion of time spent diving during a foraging trip or (B) foraging trip duration of female Australian fur seals, and interannual fluctuations in environmental conditions. In (B) only top 10 models are shown; model averaged parameter estimates have been derived from a candidate set containing 177 models. K: number of parameter estimates per model; LogLik: log-likelihood of the models; AIC_c Wt = weight of Akaike's information criterion corrected for small sample sizes for each model; ER: evidence ratio. Further abbreviations as in Table 1

Candidate models	K	LogLik	AIC _c	ΔAIC _c	AIC _c Wt	ER
(A) Proportion of time spent diving						
SOI + windU _{win} + windU _{spr2} + trip duration	8	362.86	-709.25	0.00	0.08	1.00
SOI + windU _{win} + Chl- <i>a</i> _i + windU _{spr2} + trip duration	9	363.10	-707.61	1.64	0.03	2.26
SOI + windU _{win} + windU _{spr2} + windU _{sum} + trip duration	9	363.02	-707.44	1.81	0.03	2.47
SOI + windU _{win} + SST _{win} + windU _{spr2} + trip duration	9	362.97	-707.35	1.90	0.03	2.58
SOI + windU _{win} + windU _{spr1} + windU _{spr2} + trip duration	9	362.97	-707.35	1.90	0.03	2.59
SOI + windU _{win} + SST _{spr1} + windU _{spr2} + trip duration	9	362.96	-707.33	1.92	0.03	2.61
SOI + windU _{win} + SST _{spr2} + Chl- <i>a</i> _{spr2} + trip duration	9	362.95	-707.32	1.93	0.03	2.63
SOI + windU _{win} + SST _{win} + SST _{spr2} + trip duration	9	362.92	-707.24	2.01	0.03	2.73
SOI + windU _{win} + windU _{spr2} + SST _{sum} + trip duration	9	362.88	-707.17	2.08	0.03	2.83
SOI + windU _{win} + Chl- <i>a</i> _{spr1} + windU _{spr2} + trip duration	9	362.88	-707.16	2.09	0.03	2.84
(B) Foraging trip duration						
SOI + Chl- <i>a</i> _{spr1} + windU _{spr1}	7	-360.31	734.99	0.00	0.02	1.00
SOI + SST _{spr1} + Chl- <i>a</i> _{spr1}	7	-360.46	735.29	0.30	0.02	1.16
windU _{win} + SST _{win} + Chl- <i>a</i> _i	7	-360.50	735.36	0.37	0.02	1.20
SST _{spr1} + Chl- <i>a</i> _{spr1} + Chl- <i>a</i> _{sum}	7	-360.56	735.49	0.50	0.02	1.28
Chl- <i>a</i> _{win} + cclag1 + SST _{sum}	7	-360.63	735.62	0.63	0.02	1.37
Chl- <i>a</i> _{spr1} + windU _{sum}	6	-361.90	736.07	1.08	0.01	1.72
SOI + Chl- <i>a</i> _{spr1}	6	-361.98	736.24	1.25	0.01	1.87
Chl- <i>a</i> _{spr1} + windU _{spr1} + Chl- <i>a</i> _{sum}	7	-360.95	736.27	1.28	0.01	1.89
SST _{spr1} + Chl- <i>a</i> _{spr1} + SST _{sum}	7	-360.97	736.31	1.32	0.01	1.93
Chl- <i>a</i> _{spr1} + Chl- <i>a</i> _{sum}	6	-362.04	736.35	1.36	0.01	1.97

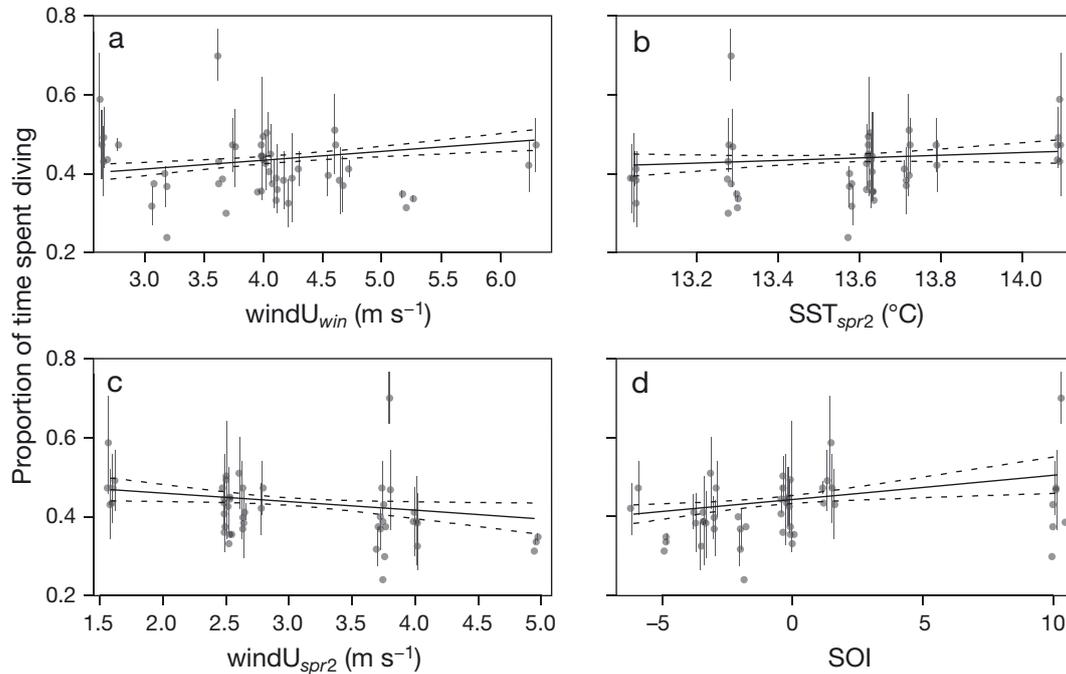


Fig. 2. Predicted response of the proportion of time spent diving in Australian fur seals *Arctocephalus pusillus doriferus* to interannual variations in (a) winter zonal wind ($\text{windU}_{\text{win}}$), (b) 2 yr-lagged springtime sea-surface temperature (SST_{spr2}), (c) 2 yr-lagged springtime zonal wind ($\text{windU}_{\text{spr2}}$) and (d) southern oscillation index (SOI). Solid black lines: model averaged global prediction; dashed lines: corresponding 95% unconditional confidence intervals; grey points with vertical grey lines: average proportion ($\pm\text{SD}$) of time spent diving per individual

ing a foraging trip across the range of $\text{windU}_{\text{win}}$ encountered; Fig. 2a). Relationships between spring conditions lagged by 2 yr and the proportion of time spent diving during winter were also seen (Fig. 2b,c). Proportion of time spent diving was reduced during years where the 2 yr-lagged spring conditions in Bass Strait were cooler (estimated increase of 3% of time spent diving during a foraging trip across the range of SST_{spr2} recorded) and had overall increased westerly winds (estimated decrease of 7% of time spent diving during a foraging trip across the range of $\text{windU}_{\text{spr2}}$ recorded). In addition, mean annual SOI was found to positively influence the proportion of time spent diving in the current year (estimated increase of 10% of time spent diving during a foraging trip across the range of SOI recorded; Fig. 2d).

When assessing the relationship between foraging trip duration and interannual environmental variation, model averaging determined a strong relationship between foraging trip duration and $\text{Chl-}a_{\text{spr1}}$ (Table 2). Further evidence was seen in the strong presence of $\text{Chl-}a_{\text{spr1}}$ within the final candidate set with 79% of models containing this variable (Table 3B). The model containing $\text{Chl-}a_{\text{spr1}}$ as a predictor had a conditional R^2 of 0.51, suggesting a moderate explanation of the variation within

the data. Across the recorded range of $\text{Chl-}a_{\text{spr1}}$ (0.43 to 0.55 mg m^{-3}), foraging trip duration was estimated to increase by 57.2 h with increasing $\text{Chl-}a_{\text{spr1}}$ (Fig. 3).

DISCUSSION

Comparing foraging effort between years can give an indication of the variation in the foraging conditions that individuals experience (Costa et al. 1989, Costa 2007, Boyd 1999, Petersen et al. 2006). interannual fluctuations in environmental conditions have been found to affect the foraging conditions, and thus foraging effort, of many marine species (e.g. Costa 2007). In the present study, relationships were found between the proportion of time spent diving and foraging trip duration (proxies of foraging effort) and environmental fluctuations during the current year, as well as in previous years.

Relationships were found with interannual variations in foraging effort and differences in environmental conditions (SST and zonal wind strength) present during the spring months at a lag of 2 yr. Concurrently, a relationship between foraging trip duration and spring chl *a* concentrations at a lag of

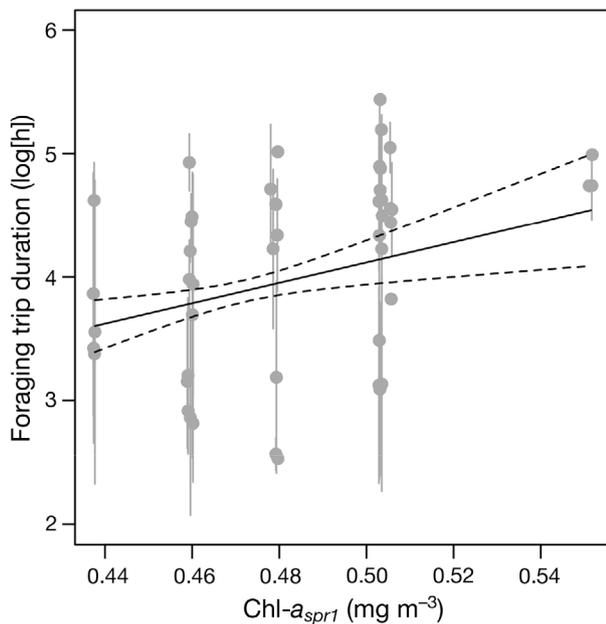


Fig. 3. Predicted response of foraging trip duration in Australian fur seals *Arctocephalus pusillus doriferus* to interannual variations in 1 yr-lagged spring chlorophyll *a* concentrations. Solid black lines: model averaged global prediction; dashed lines: corresponding 95% unconditional confidence intervals; grey points with vertical grey lines: average proportion (\pm SD) of foraging trip duration per individual

one year was also found. In fish, sub-optimal environmental conditions during the initial phase of life (spawning until the conclusion of the larval phase) can have a significant effect on the survival and future mass of individuals within their cohort (McCormick & Molony 1995, Houde 1997). Spring is the primary spawning time for many of the prey species consumed by Australian fur seals (AUFS) (Hewitt et al. 1985, Neira et al. 2008, Kemp et al. 2012). The relationships between lagged spring environmental conditions and the proportion of time spent diving/foraging trip duration, suggest that conditions influencing the larval and/or post-larval phases of AUFS prey, may be impacting their availability or profitability to AUFS females in later years.

Zonal westerly wind and SOI during the year of the data logger deployments were also found to have an effect on the foraging effort of AUFS. AUFS generally consume fish prey of age one year or greater (Kirkwood et al. 2008), thus, environmental conditions at the time of data collection are unlikely to affect fish resource availability through mechanisms affecting the survival and recruitment of larval and post-larval fish. However, AUFS also consume sev-

eral species of cephalopods (Kirkwood et al. 2008), many of which have very short (<12 mo) life cycles (Jackson et al. 2003). The zonal westerly wind and SOI during the current year may have an influence on the growth and/or survival of these species, leading to greater prey resources being available for AUFS.

The majority of prey species consumed by AUFS live for multiple years (Kirkwood et al. 2008) and, once mature, many would be adapted to surviving through all but the most extreme of environmental changes. Consequently, rather than affecting the survivability of prey species, the relationships between unlagged environmental indices and the proportion of time spent diving, may be the result of environmental fluctuations causing prey species to migrate into/out of the foraging range of AUFS. ENSO conditions have been implicated in the changing migratory patterns/spatial distribution of many species of marine fish (e.g. Gutierrez et al. 2007), including a species of jack mackerel (*Trachurus murphyi*) found off the coast of Chile (Arcos et al. 2001). Furthermore, it is possible that interannual differences in zonal wind and ENSO conditions lead to prey species having varying body conditions, and thus varying energy densities, in different years (Ballón et al. 2008). Consequentially, individual seals may have to expend greater effort during years where prey condition is poor to acquire similar resources as in years when prey are in a better condition. However, the interannual differences in diet detected by Kirkwood et al. (2008) suggest a mechanistic link between availability of adult prey types and the current environmental conditions, supporting the initial supposition of prey species migrating into/out of the foraging range of AUFS.

The effects of interannual environmental fluctuations on foraging effort identified in the present study varied between 3 and 10% across the ranges of environmental conditions recorded and may, in some cases, not represent biologically significant effects (e.g. 3% for 2 yr-lagged spring SST). However, the presence of more than a single influential variable at this time lag suggests that, although the predicted response of time spent diving to SST_{spr2} is quite small, the significance of this small response may be compounded when viewed in conjunction with the predicted response to zonal wind during the same 2 yr lagged spring period. Furthermore, benthic foraging Otariids are known to be foraging at close to their physiological capacity such that their ability to increase overall effort may be restricted (Costa & Gales 2000, 2003, Arnould & Costa 2006). Within the lacta-

tion period, female AUFS have been found to alter foraging effort at a variety of different temporal scales (Hoskins & Arnould 2013). However, small alterations in overall foraging effort beyond this (i.e. in response to interannual environmental fluctuations) may be all that these species are able to achieve and, consequently, be biologically significant.

This study did not assess foraging areas, and it is possible that individuals were foraging in different regions during different years of the study. However, prior tracking studies covering 6 years (2002–2003 and 2006–2009) of the current study have consistently shown the Bass Strait basin (Fig. 1) to be the primary foraging area for AUFS from Kanowna Island (Arnould & Kirkwood 2007, Kirkwood & Arnould 2011, Hoskins 2013). Additionally, individuals from the present study were found to be foraging at similar depths between years, suggesting similar foraging regions, though without definitive tracking information for individuals from 2005–2006, the use of different foraging zones cannot be completely discounted. The interannual variations in foraging effort seen in the present study may also have resulted from sampling of different age/size classed individuals in different years. However, where these data were available (2006–2009) no difference was found in body size between individuals from different years, suggesting that body size/age sampling between years was consistent.

In summary, the present study identified relationships between the foraging effort of female AUFS and a number of different environmental factors that likely affect both the survival of prey at their larval and post-larval stages (at the interannual scale) and the distribution of prey within AUFS's foraging. Climate change has already been shown to have had a significant affect on the composition and distribution of fish assemblages within the southeastern Australian region, including Bass Strait (Last et al. 2011) and the results of the present study show the potential for AUFS to adapt their behaviour to shifts in environmental conditions. However, the degree to which they will be able to compensate to continuing change is still uncertain.

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LITERATURE CITED

- Alexander MA, Bladé I, Newman M, Lanzante JR, Lau NC, Scott JD (2002) The atmospheric bridge: the influence of ENSO teleconnections on air–sea interaction over the global oceans. *J Phys Oceanogr* 15:2205–2231
- Arcos DF, Cubillos LA, Núñez SP (2001) The jack mackerel fishery and El Niño 1997–98 effects off Chile. *Prog Oceanogr* 49:597–617
- Arnould JPY, Costa DP (2006) Sea lions in drag, fur seals incognito: insights from the otariid deviants. In: Trites AW, Atkinson SK, DeMaster DP, Fritz LW, Gelatt TS, Rea LD, Wynne KM (eds) Sea lions of the world—conservation and research in the 21st century. Proc 22nd Wakefield Fisheries Symp, Alaska Sea Grant, Fairbanks, AK, p 309–324
- Arnould JPY, Hindell MA (2001) Dive behaviour, foraging locations, and maternal-attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). *Can J Zool* 79:35–48
- Arnould JPY, Kirkwood R (2007) Habitat selection by female Australian fur seals (*Arctocephalus pusillus doriferus*). *Aquat Conserv* 17:S53–S67
- Arnould JPY, Warneke M (2002) Growth and condition in Australian fur seals (*Arctocephalus pusillus doriferus*) (Carnivora: Pinnipedia). *Aust J Zool* 50:53–66
- Arnould JPY, Boyd IL, Speakman JR (1996) The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *J Zool* 239:769–782
- Ballón M, Wosnitza-Mendo C, Guevara-Carrasco R, Bertrand A (2008) The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, *Merluccius gayi peruanus*. *Prog Oceanogr* 79:300–307
- Beentjes MP, Renwick JA (2001) The relationship between red cod, *Pseudophycis bachus*, recruitment and environmental variables in New Zealand. *Environ Biol Fishes* 61:315–328
- Boyd IL (1996) Temporal scales of foraging in a marine predator. *Ecology* 77:426–434
- Boyd IL (1999) Foraging and provisioning in Antarctic fur seals interannual variability in time-energy budgets. *Behav Ecol* 10:198–208
- Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY
- Chavez FP, Pennington JT, Castro CG, Ryan JP and others (2002) Biological and chemical consequences of the 1997–1998 El Niño in central California waters. *Prog Oceanogr* 54:205–232
- Chavez FP, Ryan J, Lluch-Cota SE, Niquen M (2003) From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299:217–221
- Costa DP (1993) The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. In: Boyd IL (ed) Marine mammals: advances in behavioural and population biology. Oxford University

- Press, Symposium Zoological Society of London, London, p 293–314
- Costa DP (2007) A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. *Aquat Conserv* 17:S44–S52
- Costa DP, Gales NJ (2000) Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. *J Exp Biol* 203:3655–3665
- Costa DP, Gales NJ (2003) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol Monogr* 73:27–43
- Costa DP, Croxall JP, Duck CD (1989) Foraging energetics of antarctic fur seals in relation to changes in prey availability. *Ecology* 70:596–606
- Costa DP, Huckstadt LA, Crocker DE, McDonald BI, Goebel ME, Fedak MA (2010) Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. *Integr Comp Biol* 50:1018–1030
- Deagle BE, Kirkwood R, Jarman SN (2009) Analysis of Australian fur seal diet by pyrosequencing prey DNA in faeces. *Mol Ecol* 18:2022–2038
- Falkowski P, Kiefer DA (1985) Chlorophyll a fluorescence in phytoplankton: relationship to photosynthesis and biomass. *J Plankton Res* 7:715–731
- Feldkamp SD, DeLong RL, Antonelis GA (1989) Diving patterns of California sea lions, *Zalophus californianus*. *Can J Zool* 67:872–883
- Forcada J, Trathan PN, Boveng PL, Boyd IL and others (2012) Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. *Biol Conserv* 149:40–50
- Gales NJ, Mattlin RH (1998) Fast, safe, field-portable gas anesthesia for otariids. *Mar Mamm Sci* 14:355–361
- Gibbens J, Arnould JPY (2009) Interannual variation in pup production and the timing of breeding in benthic foraging Australian fur seals. *Mar Mamm Sci* 25:573–587
- Goldsworthy S, Bulman C, He X, Larcome J, Littan C (2003) Trophic interactions between marine mammals and Australian fisheries: an ecosystem approach. In: Gales N, Hindell M, Kirkwood R (eds) *Marine mammals: fisheries, tourism and management issues*. CSIRO Publishing, Collingwood, p 62–99
- Grémillet D, Pichegru L, Siorat F, Georges JY (2006) Conservation implications of the apparent mismatch between population dynamics and foraging effort in French northern gannets from the English Channel. *Mar Ecol Prog Ser* 319:15–25
- Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. *J Evol Biol* 24:699–711
- Gutierrez M, Swartzman G, Bertrand A, Bertrand S (2007) Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983–2003. *Fish Oceanogr* 16:155–168
- Harris MP, Anker-Nilssen T, McCleery RH, Erikstad KE, Shaw DN, Grosbois V (2005) Effect of wintering area and climate on the survival of adult Atlantic puffins *Fratercula arctica* in the eastern Atlantic. *Mar Ecol Prog Ser* 297:283–296
- Hewitt RP, Theilacker GH, Lo NCH (1985) Causes of mortality in young jack mackerel. *Mar Ecol Prog Ser* 26:1–10
- Hoskins AJ (2013) Factors influencing the foraging behaviour of female Australian fur seals. PhD thesis, Deakin University, Burwood
- Hoskins AJ, Arnould JPY (2013) Temporal allocation of foraging effort in female Australian fur seals (*Arctocephalus pusillus doriferus*). *PLoS ONE* 8:e79484
- Houde D (1997) Patterns and trends in larval-stage growth and mortality of teleost fish. *J Fish Biol* 51:52–83
- Jackson GD, McGrath Steer B, Wotherspoon S, Hobday AJ (2003) Variation in age, growth and maturity in the Australian arrow squid *Nototodarus gouldi* over time and space—What is the pattern? *Mar Ecol Prog Ser* 264: 57–71
- Jenkins GP (2005) The influence of climate on the fishery recruitment of a temperate, seagrass-associated fish, the King George whiting *Sillaginodes punctata*. *Mar Ecol Prog Ser* 288:263–271
- Kanamitsu M, Ebisuzaki W, Woollen J, Yang SK, Hnilo JJ, Fiorino M, Potter GL (2002) NCEP-DOE AMIP-II Reanalysis (R-2). *Bull Am Meteorol Soc* 83:1631–1644
- Kemp J, Jenkins GP, Swearer SE (2012) The reproductive strategy of red cod, *Pseudophycis bachus*, a key prey species for high trophic-level predators. *Fish Res* 125-126:161–172
- Kirkwood R, Arnould JPY (2011) Foraging trip strategies and habitat use during late pup rearing by lactating Australian fur seals. *Aust J Zool* 59:216–226
- Kirkwood R, Hume F, Hindell M (2008) Sea temperature variations mediate annual changes in the diet of Australian fur seals in Bass Strait. *Mar Ecol Prog Ser* 369: 297–309
- Kirkwood R, Pemberton D, Gales R, Hoskins AJ, Mitchell T, Shaughnessy PD, Arnould JPY (2010) Continued population recovery by Australian fur seals. *Mar Freshw Res* 61: 695–701
- Knox TC, Stuart-Williams H, Warneke RM, Hoskins AJ, Arnould JPY (2014) Analysis of growth and stable isotopes in teeth of male Australian fur seals reveals inter-annual variability in prey resources. *Mar Mamm Sci* 30: 763–781
- Last PR, White WT, Gledhill DC, Hobday AJ, Brown R, Edgar GJ, Pecl G (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Glob Ecol Biogeogr* 20:58–72
- Luque SP, Fried R (2011) Recursive filtering for zero offset correction of diving depth time series with GNU R package diveMove. *PLoS ONE* 6:e15850
- McCormick MI, Molony BW (1995) Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. *Mar Ecol Prog Ser* 118:59–68
- McGarvey R, Matthews JM (2001) Incorporating numbers harvested in dynamic estimation of yearly recruitment: onshore wind in interannual variation of South Australian rock lobster (*Jasus edwardsii*). *ICES J Mar Sci* 58: 1092–1099
- Nakagawa S, Schielzeth H (2013) A general and simple method of obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- Neira FJ, Keane JP, Lyle JM, Tracey SR (2008) Development of eggs and larvae of *Emmelichthys nitidus* (*Percoidei: Emmelichthyidae*) in south-eastern Australia, including a temperature-dependent egg incubation model. *Estuar Coast Shelf Sci* 79:35–44
- Nieblas AE, Sloyan BM, Hobday AJ, Coleman R, Richardson AJ (2009) Variability of biological production in

- low wind-forced regional upwelling systems: a case study off southeastern Australia. *Limnol Oceanogr* 54: 1548–1558
- Petersen SL, Ryan PG, Gremillet D (2006) Is food availability limiting African penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* 148:14–26
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org
- Sandery PA, Kämpf J (2007) Transport timescales for identifying seasonal variation in Bass Strait, south-eastern Australia. *Estuar Coast Shelf Sci* 74:684–696
- Smith W Jr, Demaster DJ (1996) Phytoplankton biomass and productivity in the Amazon River plume: correlation with seasonal river discharge. *Cont Shelf Res* 16:291–319
- Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J Exp Biol* 213:912–920
- Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* 65:13–21
- Troup AJ (1967) Opposition of anomalies of upper tropospheric winds at Singapore and Canton Island. *Aust Meteorol Mag* 15:32–37

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