

COMMENT

Elephant seal foraging dives track prey distribution, not temperature: Comment on McIntyre et al. (2011)

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ABSTRACT: McIntyre et al. (2011; Mar Ecol Prog Ser 441:257–272) concluded that climate change-related ocean warming may lead to deeper foraging dives by southern elephant seals as their prey is forced into deeper depths. They further assert that fitness for the seals will be reduced because of greater physiological costs for deep dives and the assumption that deep foraging is less successful. Their conclusions are based on an observed correlation between a temperature index and elephant seal diving depth but do not include any observations of prey. We recently observed pronounced differences in the vertical distribution of pelagic biota—biota that may well include elephant seal prey—across the same frontal zone considered by McIntyre et al. (2011) and believe that their suggested link between temperature and diving depth is actually a link between predators and distinct prey fields—a reflection of adaptive foraging behaviour in a complex and dynamic pelagic system. As such, the analysis of McIntyre et al. (2011) is uninformative about likely impacts of ocean warming.

KEY WORDS: Climate change · Effect size · Prey field · Vertical structure · Southern elephant seal · Foraging ecology · Deep scattering layer

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Introduction

McIntyre et al. (2011) studied the diving behaviour of southern elephant seals *Mirounga leonina* from Marion Island (southwest Indian Ocean) in relation to a number of hydrographic and biological variables, and observed a significant positive correlation between a temperature index and the diving depth. They concluded that diving behaviour is influenced by ocean temperature, and further, that as the Southern Ocean warms because of climate change, elephant seals will have to dive deeper. However, their analysis and the employed predictors are not suitable to detect effects of climate change for the following

reasons: (1) The temperature index they use is likely to be a proxy variable for water mass and not an ocean warming indicator; (2) some statistically significant model results are not biologically meaningful; (3) data on the pelagic environment of the southwest Indian Ocean from recent transects across the subtropical convergence and Subantarctic Front demonstrate step changes in the vertical structure (data presented in this Comment) and community composition of pelagic biota (authors' unpubl. data), indicating distinct prey fields on either side of the frontal zone; (4) several alternative explanations such as seasonal and regional effects on diving depth were not explored in the analysis; and (5) the asserted link

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between time-at-depth and foraging success is speculative. Here, we address these issues and propose an alternative explanation for dive-depth variability based on prey distribution.

Temperature, frontal zone positions and the use of daily averages

The temperature index employed by McIntyre et al. (2011) is the daily average of the maximum temperature recorded below 100 m during a dive ($T_{\max 100}$). As the thermal water column structure north of the Polar Front is usually characterised by a shallow temperature maximum and a monotonic decrease in temperature (Belkin & Gordon 1996, Boehme et al. 2008), $T_{\max 100}$ is likely to represent the temperature at, or near 100 m (Fig. 1), a depth that is 300 to 700 m shallower than the mean foraging depths reported by McIntyre et al. (2011; see our Fig. 2B). Given that they base their conclusions on the assumption that the vertical distribution of prey species will change with ocean warming, it would have been more appropriate for their models to be based on the *in situ* temperature at foraging depth.

Judging from temperature profiles that we collected during a crossing of the Agulhas Front, South-

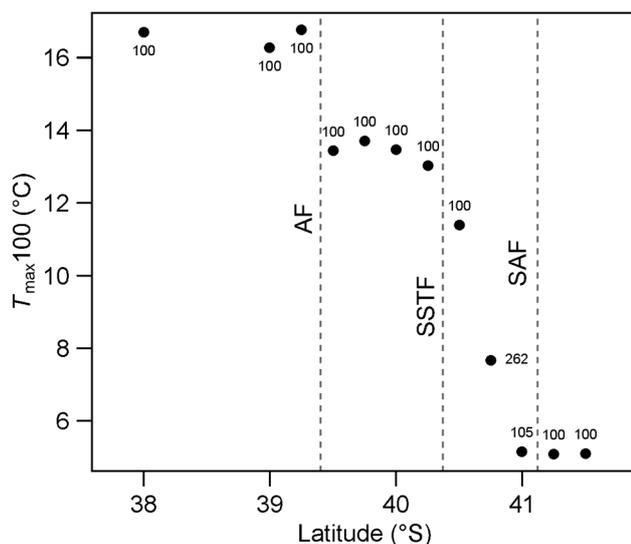


Fig. 1. Relationship between the maximum temperature recorded below 100 m ($T_{\max 100}$), the depth at which $T_{\max 100}$ was recorded ($T_{\max 100}$.depth) and frontal locations for a CTD transect crossing the Subantarctic Frontal zone in the southwest Indian Ocean. Numerals indicate $T_{\max 100}$.depth (m). Dashed lines: front locations (determined from full CTD casts according to criteria from Belkin & Gordon 1996). $T_{\max 100}$ indices were calculated according to McIntyre et al. (2011). AF: Agulhas Front, SSTF: Southern Subtropical Front, SAF: Subantarctic Front

ern Subtropical Front and Subantarctic Front in late 2009 (Rogers et al. 2009), the $T_{\max 100}$ index is closely related to the geographic location of a temperature profile relative to the individual fronts (Fig. 1) and therefore a proxy for water mass. In fact, the temperature at 100 m has been used for the very definition of frontal locations (Belkin & Gordon 1996). In addition to $T_{\max 100}$, McIntyre et al. (2011) employ a factor in their initial models to indicate the position of a dive relative to the fronts. This factor is dropped in most of their final models, possibly because of collinearity with the temperature index based on the relationship between $T_{\max 100}$ and water mass. Furthermore, the temperature variation encountered by foraging elephant seals in the frontal zone is likely to be influenced by smaller scale features (days, 10s of km), such as mesoscale eddies (Bailleul et al. 2010, Dragon et al. 2010, 2012), while the location of a dive relative to the fronts would only explain temperature variation on large temporal and spatial scales (months, 100s of km). This scale-dependent temperature variation likely makes $T_{\max 100}$ a better predictor for any variation in diving behaviour and would explain the result of the model selection procedure.

In addition to $T_{\max 100}$ being a water mass proxy rather than an ocean warming indicator, the use of daily temperature averages is prone to confound the relationship between temperature, water mass, relative position of a dive in relation to the fronts, and seal diving behaviour, as elephant seals are capable of travelling over 100 km d⁻¹ (Biuw et al. 2003) and forage in a highly variable environment.

Effect sizes and variability in predictors and model results

McIntyre et al. (2011) set out to investigate potential effects of ocean warming on elephant seals. Their analysis, however, does not distinguish between climate effects (small, <1°C) and natural environmental variation (large, >10°C) in their study area, especially regarding the magnitude of the effect that these distinct sources of variation have on ocean temperature. Elephant seals forage in extremely diverse habitats where oceanographic and topographic features such as fronts, eddies, seamounts, and shelf breaks influence prey availability on a variety of spatial and temporal scales (Biuw et al. 2007, Charrassin et al. 2008, Simmons et al. 2010, Maxwell et al. 2011). While the biophysical coupling associated with these diverse habitats and processes is influenced by climate, the effect of present climate change is very small com-

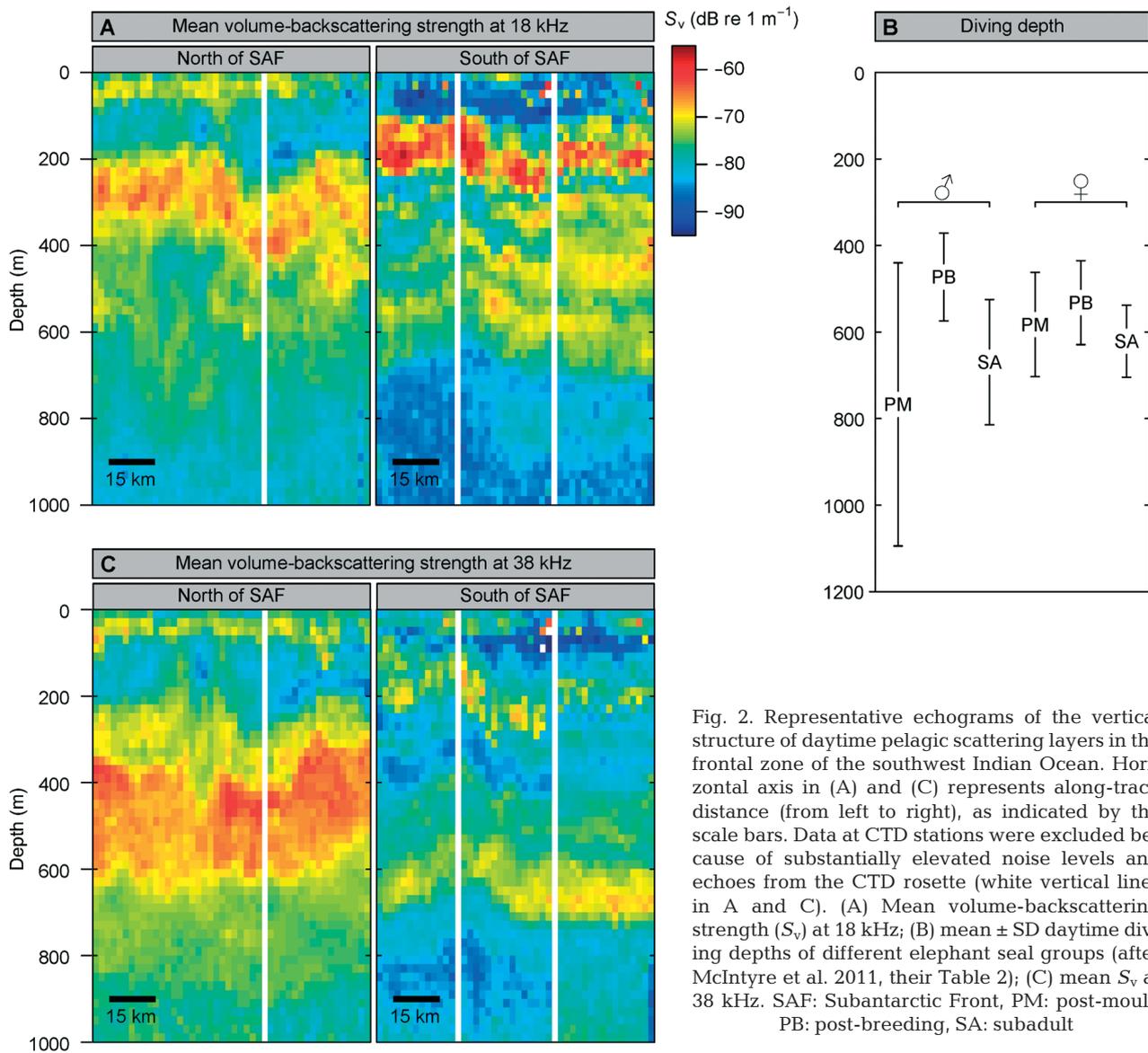


Fig. 2. Representative echograms of the vertical structure of daytime pelagic scattering layers in the frontal zone of the southwest Indian Ocean. Horizontal axis in (A) and (C) represents along-track distance (from left to right), as indicated by the scale bars. Data at CTD stations were excluded because of substantially elevated noise levels and echoes from the CTD rosette (white vertical lines in A and C). (A) Mean volume-backscattering strength (S_v) at 18 kHz; (B) mean \pm SD daytime diving depths of different elephant seal groups (after McIntyre et al. 2011, their Table 2); (C) mean S_v at 38 kHz. SAF: Subantarctic Front, PM: post-moult, PB: post-breeding, SA: subadult

pared to the environmental variability within and between the habitats.

The surface waters around Marion Island have been warming at an approximate rate of $0.03^\circ\text{C yr}^{-1}$ in recent decades (Mélise et al. 2003). At intermediate depths (700 to 1000 m), warming rates have been estimated to be in the order of $0.006^\circ\text{C yr}^{-1}$ (Gille 2002). In contrast to this, the $T_{\text{max}100}$ index employed by McIntyre et al. (2011) has a range of approximately 10°C across the frontal zone (Fig. 1). It is difficult to see how their model could distinguish a climate signal from environmental variability when the latter is several orders of magnitude greater. In addition, any measurable climate effect on ocean temperature would be within the measurement error of at

least 1 of the 2 sensor types used by McIntyre et al. (2011). Boehme et al. (2008) show that the temperature accuracy of the CTD satellite-relay data loggers (SRDLs) is between ± 0.005 and $\pm 0.03^\circ\text{C}$ after post-deployment corrections. However, this does not apply to the temperature-only Series 9000 SRDL, which incorporates an uncalibrated thermistor as a temperature probe. The manufacturer (Sea Mammal Research Unit, University of St. Andrews, UK) claims an accuracy of $\pm 0.1^\circ\text{C}$ (www.smru.st-andrews.ac.uk/protected/downloads/SRDL9000X.pdf) but does not quantify the long-term stability of accuracy.

Concerning their model results, McIntyre et al. (2011) highlight the statistical significance of the relationship between temperature and diving depths.

The biological meaning of this result is, however, not explicitly discussed, and the reporting of log-transformed and untransformed coefficients side-by-side does not help the interpretation of model results. Their estimate for the temperature effect on log-transformed adult male diving depth is reported as 0.03, which approximately translates into a 1 m diving depth increase per 1°C temperature increase. Even under drastic ocean warming, a few metres of difference in diving depth are ecologically meaningless, as oscillations in scattering layer depth of 10s of metres are common (cf. Fig. 2A,C). The effect is much more pronounced for female seals at approximately 10 m °C⁻¹ (McIntyre et al. 2011), but this is also of little biological relevance in the context of minute warming rates. The female result does, however, become ecologically meaningful when considering the much greater temperature difference between water masses. Using our temperature data and McIntyre et al.'s (2011) estimate, female southern elephant seals are expected to dive approximately 100 m deeper north of the Subantarctic Front.

Vertical structure of pelagic biota across fronts and eddies

We have surveyed the pelagic environment of the southwest Indian Ocean (Rogers et al. 2009) and collected data on the distribution and diversity of zooplankton and nekton in the top 1000 m of the water column using a calibrated multi-frequency echosounder and a midwater trawl. Our results confirm that the Subantarctic Front is a significant biogeographic boundary (e.g. Pakhomov et al. 1994). The environments on either side of the front are characterised by distinct micronekton assemblages (A. D. Rogers et al. unpubl.) as well as marked differences in the vertical structure of biomass distribution and diel vertical migration behaviour.

The environment north of the front is characterized by a thin surface-scattering layer, a very thick deep-scattering layer and moderate amounts of diffuse backscatter at depths below 700 m. The scattering layer structure south of the front is much more complex, featuring at least 4 distinct daytime layers at different depths but only weak backscatter in the deepest strata (Fig. 2 A,C). Scattering layers on either side of the front follow different patterns of diel vertical migration. North of the front, a substantial proportion of 38 kHz backscatter is located in a non-migratory deep-scattering layer, whereas the main scattering layer at 18 kHz is migratory, rising from

300 m to the surface at night. South of the front the shallower layers show more extensive vertical migration than the deeper ones at both frequencies. The top-most layer ascends from approximately 200 to 50 m at night while the deepest layer remains stationary.

Elephant seals are wide-ranging long-lived animals in a dynamic and heterogeneous environment and must be adapted to large variations in prey availability in time and space (Biuw et al. 2007). Their foraging behaviour is ultimately driven by prey distributions (Hindell et al. 2011, Dragon et al. 2012), and elephant seals are able to adapt their diving behaviour seasonally and in differing hydrographic conditions (Bailleul et al. 2007, Biuw et al. 2007, 2010). A direct relationship between observed scattering layer depth and marine mammal foraging behaviour is not always apparent, especially when concurrent *in situ* data are unavailable. Some studies have demonstrated remarkable spatio-temporal overlap between foraging predators and backscatter features (e.g. Fiedler et al. 1998), while in others the correlations are less pronounced (Hazen & Johnston 2010). The mean diving depths reported by McIntyre et al. (2011, their Table 2) do not match exactly any of the echogram features observed by us, which is not surprising considering that the dive data were averaged over 4 yr and 1000s of km of seal tracks. The comparison does, however, show that elephant seal foraging depths overlap with pelagic scattering layers on either side of the front (Fig. 2). Furthermore, there are some clues that may explain the observed positive relationship between temperature and diving depth: the dominant 18 kHz scattering layer north of the front has its peak intensity at around 300 m (maximum mean volume backscattering strength, S_v ; MacLennan et al. 2002), ca. 100 m deeper than the dominant layer south of the front (maximum S_v at 200 m). In addition to this, mean S_v at both frequencies at depths in excess of 700 m is more than twice as intense north of the front than south of it ($\Delta S_{v; 18 \text{ kHz}} = 4.04 \text{ dB re } 1 \text{ m}^{-1}$; $\Delta S_{v; 38 \text{ kHz}} = 3.49 \text{ dB re } 1 \text{ m}^{-1}$).

Little is known about the vertical structure of pelagic biota in mesoscale eddies in the southwest Indian Ocean, but the foraging of southern elephant seals in eddies in this region has been documented (Bailleul et al. 2010, Dragon et al. 2010, 2012). There is also evidence from the north Atlantic that the vertical distribution of pelagic animals in eddies can be markedly different from that in surrounding waters (Conte et al. 1986), including significant increases in deep (600 to 1200 m) biomass in warm core eddies (Godø et al. 2012).

Alternative predictors of diving behaviour

McIntyre et al. (2011) partitioned their dive data to account for differences between the sexes and age classes of elephant seals, as well as diel differences in behaviour, but seasonal and/or regional effects were not sufficiently considered. They briefly discuss the fact that the 'track day' variable is a significant predictor in all of their models for female seals, but no attempt is made to investigate seasonality (e.g. by exploring 'day of the year' as a predictor; see also Biuw et al. 2010), even though the data presented for the subadult male individual OO405 indicate a non-random seasonal trend for diving depth, encountered temperature and time-at-depth. The possibility of detecting seasonal effects is further hindered by the restriction to the first 150 d at sea for the females' data. Although the seasonality of the vertical distribution of mesopelagic communities is poorly understood, it has been well established that seasonal processes influence scattering layer structures (e.g. Staby et al. 2011).

As we suggest here, spatial effects can play an important role (see also Anderson et al. 2005). The relationship between foraging location and ocean temperature has been discussed in detail in 'Temperature, frontal zone positions and the use of daily averages' above, but foraging location is also important when considering differences between pelagic and benthic dives (Maxwell et al. 2011). A variable for bottom depth was a significant predictor for dive depth in some of McIntyre et al.'s (2011) models. While there is a close relationship between bottom and diving depth for benthic dives, bottom depth is—in our experience—often a poor predictor in pelagic systems where the ecology at foraging depth is largely decoupled from benthic-pelagic processes occurring at depths hundreds to thousands of metres deeper. A factor to distinguish between benthic and pelagic dives might have been more informative both biologically and in terms of predictive value.

Time-at-depth and foraging success

McIntyre et al. (2011) did not assess foraging success or body condition of the seals they studied but suggest that the shorter time-at-depth during deeper dives points to less successful foraging. In the absence of *in situ* behavioural data, constructing a link between time-at-depth and foraging success is speculative. One could argue by the same token that foraging in warmer water is more efficient, or that the

energetic costs of deeper diving are balanced by reduced heat loss in warmer water.

Furthermore, a comparison of time-at-depth between water masses may be confounded by adaptive foraging behaviour for different prey species. Trawl data from our 2009 survey indicate distinct pelagic assemblages for decapod and lophogastrid crustaceans (T. Letessier pers. comm.), cephalopods (V. Laptikhovsky pers. comm.) and fishes (K. Kemp pers. comm.) across the Subantarctic Front. Prey species-specific diving behaviour is poorly understood in southern elephant seals but has been observed in other pinnipeds (e.g. Bowen et al. 2002).

Conclusions

Climate change is likely to affect elephant seals in the southern Indian Ocean, for example through the intensification of eddy activity (Meredith & Hogg 2006), which may change the locations and temporal availability of foraging opportunities. However, the correlation between ocean temperature and diving behaviour reported by McIntyre et al. (2011) is likely a demonstration of adaptive foraging behaviour in distinct pelagic biomes rather than a climatic effect. Furthermore, such adaptive behaviours are likely to vary at different scales reflecting scales of patchiness in food availability (Simmons et al. 2010).

Simplistic correlative analyses of environmental variables and behavioural responses are of limited usefulness for both studies of climate change and predator-prey interactions, particularly in dynamic pelagic systems. An investigation of climate change effects would require a different modelling framework, most importantly one where temperature data were stratified between water masses, and seasonal effects were accounted for. Studies of predator-prey interactions should include prey distributions as well as potential indicators of foraging success and prey-specific foraging behaviour (e.g. Biuw et al. 2003, Dragon et al. 2012) rather than just environmental proxies.

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