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3   **COMMENT**

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

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20   RPH: Boersch-Supan et al.: Elephant seal dives track prey depth

21   ABSTRACT: McIntyre et al. (2011; Mar Ecol Prog Ser 441:257–272) concluded that climate-

22   change related ocean warming may lead to deeper foraging dives by southern elephant seals as

23   their prey is forced into deeper depths. They further assert that fitness for the seals will be

24   reduced because of greater physiological costs for deep dives and the assumption that deep

25   foraging is less successful. Their conclusions are based on an observed correlation between a

26   temperature index and elephant seal diving depth, but do not include any observations of prey.

27   We recently observed pronounced differences in the vertical distribution of pelagic biota —

28   biota that may well include elephant seal prey — across the same frontal zone considered by

29   McIntyre et al. (2011) and believe that their suggested link between temperature and diving

30   depth is actually a link between predators and distinct prey fields — a reflection of adaptive

31   foraging behaviour in a complex and dynamic pelagic system. As such, the analysis of McIntyre

32   et al. (2011) is uninformative about likely impacts of ocean warming.

33   KEY WORDS: Climate change · Effect size · Prey field · Vertical structure · Southern elephant

34   seal · Foraging ecology · Deep scattering layer

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Introduction

37   McIntyre et al. (2011) studied the diving behaviour of southern elephant seals *Mirounga*

38   *leonina* from Marion Island (southwest Indian Ocean) in relation to a number of hydrographic

39   and biological variables, and observed a significant positive correlation between a temperature

40   index and the diving depth. They concluded that diving behaviour is influenced by ocean

41   temperature, and further, that as the Southern Ocean warms because of climate change, elephant

42   seals will have to dive deeper. However, their analysis and the employed predictors are not

43   suitable to detect effects of climate change for the following reasons: (1) The temperature index

44   they use is likely to be a proxy variable for watermass and not an ocean warming indicator;

45   (2) some statistically significant model results are not biologically meaningful; (3) data on the

46   pelagic environment of the southwest Indian Ocean from recent transects across the subtropical

47   convergence and Subantarctic Front demonstrate step changes in the vertical structure (data

48   presented in this Comment) and community composition of pelagic biota (authors' unpubl. data),

49   indicating distinct prey fields on either side of the frontal zone; (4) several alternative

50   explanations such as seasonal and regional effects on diving depth were not explored in the

51   analysis; and (5) the asserted link between time-at-depth and foraging success is tentative. Here,

52   we address these issues and propose an alternative explanation for dive-depth variability based

53   on prey distribution.

Temperature, frontal zone positions and the use of daily averages

55   The temperature index employed by McIntyre et al. (2011) is the daily average of the maximum

56   temperature recorded below 100 m during a dive ($T_{max}100$). As the thermal watercolumn

57   structure north of the Polar Front is usually characterised by a shallow temperature-maximum

58   and a monotonic decrease in temperature (Belkin & Gordon 1996, Boehme et al. 2008), $T_{max}100$

59   is likely to represent the temperature at, or near 100 m (Fig. 1), a depth that is 300 to 700 m

60   shallower than the mean foraging depths reported by McIntyre et al. (2011; see our Fig. 2B).

61   Given that they base their conclusions on the assumption that the vertical distribution of prey

62   species will change with ocean warming it it would have been more appropriate for their models

63   to be based on the *in situ* temperature at foraging depth.

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

65   Southern Subtropical Front and Subantarctic Front in late 2009 (Rogers et al. 2009), the $T_{max}100$

66   index is closely related to the geographic location of a temperature profile relative to the

67   individual fronts (Fig. 1) and therefore a proxy for watermass. In fact, the temperature at 100 m

68   has been used for the very definition of frontal locations (Belkin & Gordon 1996). In addition to

69    $T_{max}100$, McIntyre et al. (2011) employ a factor in their initial models to indicate the position of

70   a dive relative to the fronts. This predictor is dropped in most of their final models, possibly

71   because of collinearity with the temperature index based on the relationship between $T_{max}100$

72   and watermass. Furthermore, the temperature variation encountered by foraging elephant seals

73   in the frontal zone is likely to be influenced by smaller scale features (days, 10s of km), such as

74   mesoscale eddies (Bailleul et al. 2010, Dragon et al. 2010, 2012), while the location of a dive

75   relative to the fronts would only explain temperature variation on large temporal and spatial

76   scales (months, 100s of km). This scale-dependent temperature variation likely makes $T_{max}100$ a

77   better predictor for any variation in diving behaviour, therefore favouring it during model

78   selection.

79   In addition to $T_{max}100$ being a watermass proxy rather than an ocean warming indicator, the

80   use of daily temperature averages is prone to confound the relationship between temperature,

81   watermass, relative position of a dive in relation to the fronts, and seal diving behaviour, as

82   elephant seals are capable of travelling over 100 km d^{-1} (Biuw et al. 2003) and forage in a highly

83   variable environment.

84   ### *Effect sizes and variability in predictors and model results*

85   McIntyre et al. (2011) set out to investigate potential effects of ocean warming on elephant seals.

86   Their analysis, however, does not distinguish between climate effects (small, <1°C) and natural

87   environmental variation (large, >10°C) in their study area, especially regarding the magnitude of

88   the effect that these distinct sources of variation have on ocean temperature. Elephant seals

89   forage in extremely diverse habitats where oceanographic and topographic features such as

90   fronts, eddies, seamounts, and shelf breaks influence prey availability on a variety of spatial and

91   temporal scales (Biuw et al. 2007, Charrassin et al. 2008, Simmons et al. 2010, Maxwell et al.

92   2011). While the biophysical coupling associated with these diverse habitats and processes is

93   influenced by climate, the effect of present climate change is very small compared to the

94   environmental variability within and between the habitats.

95   The surface waters around Marion Island have been warming at an approximate rate of

96   0.03°C yr^{-1} in recent decades (Mélice et al. 2003). At intermediate depths (700 to 1000 m),

97   warming rates have been estimated to be in the order of 0.006°C yr^{-1} (Gille 2002). In contrast to

98   this, the $T_{max}100$ index employed by McIntyre et al. (2011) has a range of approximately 10°C

99   across the frontal zone (Fig. 1). It is difficult to see how their model could distinguish a climate

100   signal from environmental variability when the latter is several orders of magnitude greater. In

101   addition, any measurable climate effect on ocean temperature would be within the measurement

102   error of at least one of the two sensor types used by McIntyre et al. (2011). Boehme et al. (2008)

103   show that the temperature accuracy of the CTD satellite-relay data loggers (SRDLs) is between

104   ±0.005°C and ±0.03°C after post-deployment corrections. However, this does not apply to the

105   temperature-only Series 9000 SRDL, which incorporates an uncalibrated thermistor as a

106   temperature probe. The manufacturer (Sea Mammal Research Unit, University of St. Andrews,

107   UK) claims an accuracy of ±0.1°C (www.smru.st-

108   andrews.ac.uk/protected/downloads/SRDL9000X.pdf), but does not quantify the long-term

109   stability of accuracy.

110   Concerning their model results, McIntyre et al. (2011) highlight the statistical significance of

111   the relationship between temperature and diving depths. The biological meaning of this result is,

112   however, not explicitly discussed, and the reporting of log-transformed and untransformed

113   coefficients side-by-side does not help the interpretation of model results. Their estimate for the

114   temperature effect on log-transformed adult male diving depth is reported as 0.03, which

115   approximately translates into a 1 m diving depth increase per 1°C temperature increase. Even

116   under drastic ocean warming, a few metres of difference in diving depth are ecologically

117   meaningless, as oscillations in scattering layer depth of 10s of m are common (cf. Fig 2A,C).

118   The effect is much more pronounced for female seals at approximately 10 m °C^{-1} (McIntyre et

119   al. 2011), but this is also of little biological relevance in the context of minute warming rates.

120   The female result does, however, become ecologically meaningful when considering the much

121   greater temperature difference between watermasses. Using our temperature data and McIntyre

122   et al.'s (2011) estimate, female southern elephant seals are expected to dive approximately 100 m

123   deeper north of the Subantarctic Front.

124   ### *The vertical structure of pelagic biota across fronts and eddies*

125   We have surveyed the pelagic environment of the southwest Indian Ocean (Rogers et al.

126   2009) and collected data on the distribution and diversity of zooplankton and nekton in the top

127   1000 m of the watercolumn using a calibrated multi-frequency echosounder and a midwater

128   trawl. Our results confirm that the Subantarctic Front is a significant biogeographic boundary

129   (e.g. Pakhomov et al. 1994). The environments on either side of the front are characterised by

130   distinct micronekton assemblages (A. D. Rogers et al. unpubl.) as well as marked differences in

131   the vertical structure of biomass distribution and diel vertical migration behaviour.

132   The environment north of the front is characterized by a thin surface-scattering layer, a very

133   thick deep-scattering layer and moderate amounts of diffuse backscatter at depths below 700 m.

134   The scattering layer structure south of the front is much more complex, featuring at least 4

135   distinct daytime layers at different depths but only weak backscatter in the deepest strata (Fig. 2

136   A,C). Scattering layers on either side of the front follow different patterns of diel vertical

137   migration. North of the front, a substantial proportion of 38 kHz backscatter is located in a non-

138   migratory deep-scattering layer, whereas the main scattering layer at 18 kHz is migratory, rising

139   from 300 m to the surface at night. South of the front the shallower layers show more extensive

140   vertical migration than the deeper ones at both frequencies. The top-most layer ascends from

141   approximately 200 m to 50 m at night while the deepest layer remains stationary.

142   Elephant seals are wide-ranging long-lived animals in a dynamic and heterogeneous

143   environment and must be adapted to large variations in prey availability in time and space (Biuw

144   et al. 2007). Their foraging behaviour is ultimately driven by prey distributions (Hindell et al.

145   2011, Dragon et al. 2012), and elephant seals are able to adapt their diving behaviour seasonally

146   and in differing hydrographic conditions (Bailleul et al. 2007, Biuw et al. 2007, 2010). A direct

147   relationship between observed scattering layer depth and marine mammal foraging behaviour is

148   not always apparent, especially when concurrent *in situ* data are unavailable. Some studies have

149   demonstrated remarkable spatio-temporal overlap between foraging predators and backscatter

150   features (e.g. Fiedler et al. 1998), while in others the correlations are less pronounced (Hazen &

151   Johnston 2010). The mean diving depths reported by McIntyre et al. (2011, their Table 2) do not

152   match exactly any of the echogram features observed by us, which is not surprising considering

153   that the dive data were averaged over 4 yr and thousands of kilometres of seal tracks. The

154   comparison does, however, show that elephant seal foraging depths overlap with pelagic

155   scattering layers on either side of the front (Fig. 2). Furthermore, there are some clues that may

156   explain the observed positive relationship between temperature and diving depth: the dominant

157   18 kHz scattering layer north of the front has its peak intensity at around 300 m (maximum mean

158   volume-backscattering strength, S_v; MacLennan et al. 2002), ca. 100 m deeper than the dominant

159   layer south of the front (maximum S_v at 200 m). In addition to this, mean volume-backscattering

160   strength at both frequencies at depths in excess of 700 m is more than twice as intense north of

161   the front than south of it ($\Delta S_{v;\ 18kHz} = 4.04$ dB re 1 m^{-1}; $\Delta S_{v;\ 38\ kHz} = 3.49$ dB re 1 m^{-1}).

162   Little is known about the vertical structure of pelagic biota in mesoscale eddies in the

163   southwest Indian Ocean, but the foraging of southern elephant seals in eddies in this region has

164   been documented (Bailleul et al. 2010, Dragon et al. 2010, 2012). There is also evidence from

165   the north Atlantic that the vertical distribution of pelagic animals in eddies can be markedly

166   different from that in surrounding waters (Conte et al. 1986), including significant increases of

167   deep (600 to 1200 m) biomass in warm core eddies (Godø et al. 2012).

168 *Alternative predictors of diving behaviour*

169   McIntyre et al. (2011) partitioned their dive data to account for differences between the sexes

170   and age classes of elephant seals, as well as diel differences in behaviour, but seasonal and/or

171   regional effects were not sufficiently considered. They briefly discuss the fact that the 'track day'

172   variable is a significant predictor in all of their models for female seals, but no attempt is made

173   to investigate seasonality (e.g. by exploring 'day of the year' as a predictor; see also Biuw et al.

174   2010), even though the data presented for the subadult male individual OO405 indicate a non-

175   random seasonal trend for diving depth, encountered temperature and time-at-depth. The

176   possibility of detecting seasonal effects is further hindered by the restriction to the first 150 d at

177   sea for the females' data. Although the seasonality of the vertical distribution of mesopelagic

178   communities is poorly understood, it has been well established that seasonal processes influence

179   scattering layer structures (e.g. Staby et al. 2011).

180   As we suggest here, spatial effects can play an important role (see also Anderson et al. 2005).

181   The relationship between foraging location and ocean temperature has been discussed in detail

182   in 'Temperature, frontal zone positions and the use of daily averages' above, but foraging

183   location is also important when considering differences between pelagic and benthic dives

184   (Maxwell et al. 2011). A variable for bottom depth was a significant predictor for dive depth in

185   some of McIntyre et al.'s (2011) models. While there is a close relationship between bottom and

186   diving depth for benthic dives, bottom depth is — in our experience — often a poor predictor in

187   pelagic systems where the ecology at foraging depth is largely decoupled from bentho-pelagic

188   processes occurring at depths hundreds to thousands of metres deeper. A factor to distinguish

189   between benthic and pelagic dives might have been more informative both biologically and in

190   terms of predictive value.

191 *Time-at-depth and foraging success*

192   McIntyre et al. (2011) did not assess foraging success or body condition of the seals they

193   studied, but suggest that the shorter time-at-depth during deeper dives points to less successful

194   foraging. In the absence of *in situ* behavioural data, constructing a link between time-at-depth

195   and foraging success is speculative. One could argue by the same token that foraging in warmer

196   water is more efficient, or that the energetic costs of deeper diving are balanced by reduced heat

197   loss in warmer water.

198   Furthermore, a comparison of time-at-depth between watermasses may be confounded by

199   adaptive foraging behaviour for different prey species. Trawl data from our 2009 survey indicate

200   distinct pelagic assemblages for decapod and lophogastrid crustaceans (T. Letessier pers.

201   comm.), cephalopods (V. Laptikhovsky pers. comm.) and fishes (K. Kemp pers. comm.) across

202   the Subantarctic Front. Prey-species specific diving behaviour is poorly understood in southern

203   elephant seals but has been observed in other pinnipeds (e.g. Bowen et al. 2002).

Conclusions

205   Climate change is likely to affect elephant seals in the southern Indian Ocean, for example

206   through the intensification of eddy activity (Meredith & Hogg 2006), which may change the

207   locations and temporal availability of foraging opportunities. However, the correlation between

208   ocean temperature and diving behaviour reported by McIntyre et al. (2011) is likely a

209   demonstration of adaptive foraging behaviour in distinct pelagic biomes rather than a climatic

210   effect. Furthermore, such adaptive behaviours are likely to vary at different scales reflecting

211   scales of patchiness in food availability (Simmons et al. 2010).

212   Simplistic correlative analyses of environmental variables and behavioural responses are of

213   limited usefulness for both studies of climate change and predator–prey interactions, particularly

214   in dynamic pelagic systems. An investigation of climate change effects would require a different

215   modelling framework, most importantly one where temperature data were stratified between

216   watermasses, and seasonal effects were accounted for. Studies of predator–prey interactions

217   should include prey distributions as well as potential indicators of foraging success and prey-

218   specific foraging behaviour (e.g. Biuw et al. 2003, Dragon et al. 2012) rather than just

219   environmental proxies.

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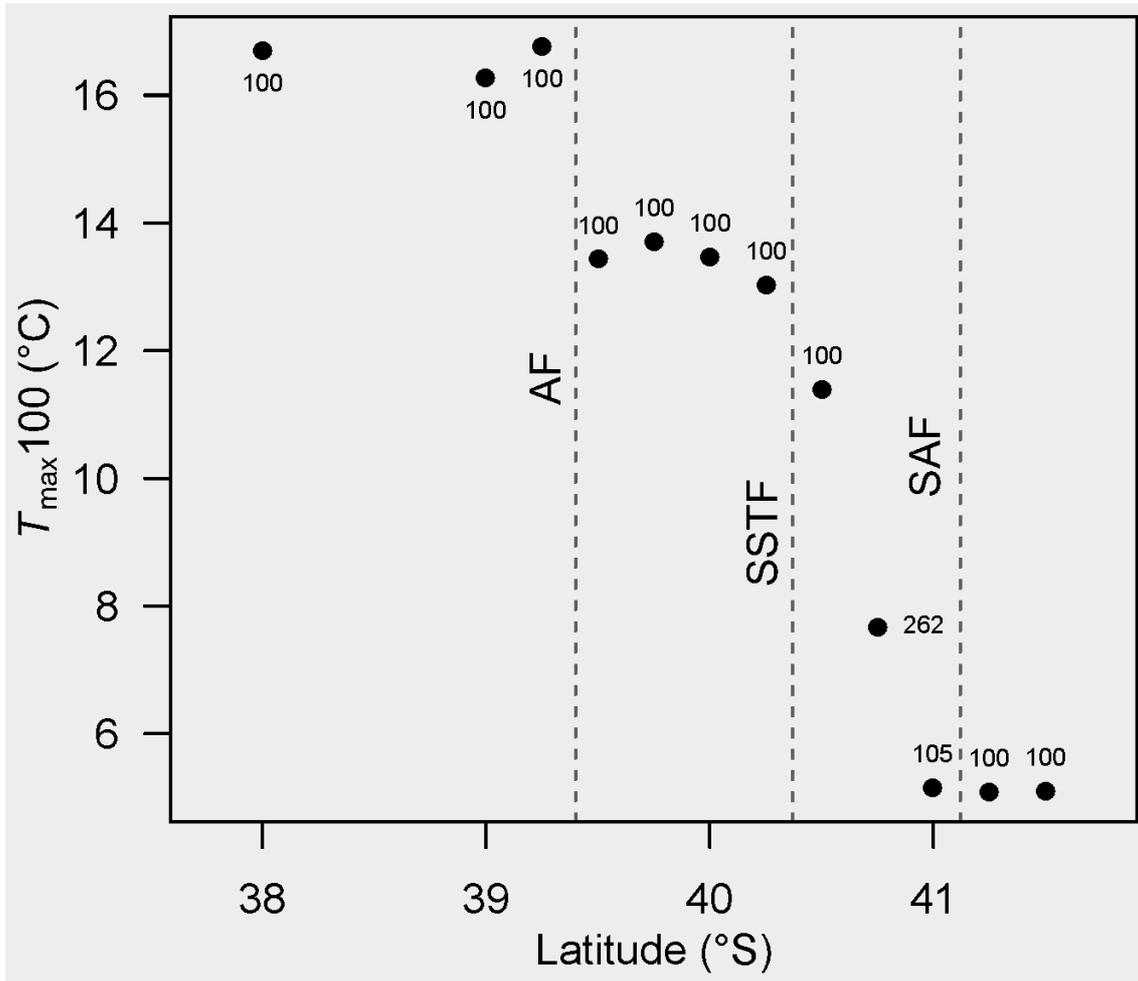
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312   Fig. 1. Relationship between $T_{max}100$, $T_{max}100$.depth and frontal locations for a CTD

313   transect crossing the Subantarctic Frontal zone in the southwest Indian Ocean. Numerals

314   indicate $T_{max}100$.depth (m). Dashed lines: front locations (determined from full CTD

315   casts according to criteria from Belkin & Gordon [1996]). $T_{max}100$ indices were

316   calculated according to McIntyre et al. (2011). AF: Agulhas Front, SSTF: Southern

317   Subtropical Front, SAF: Subantarctic Front

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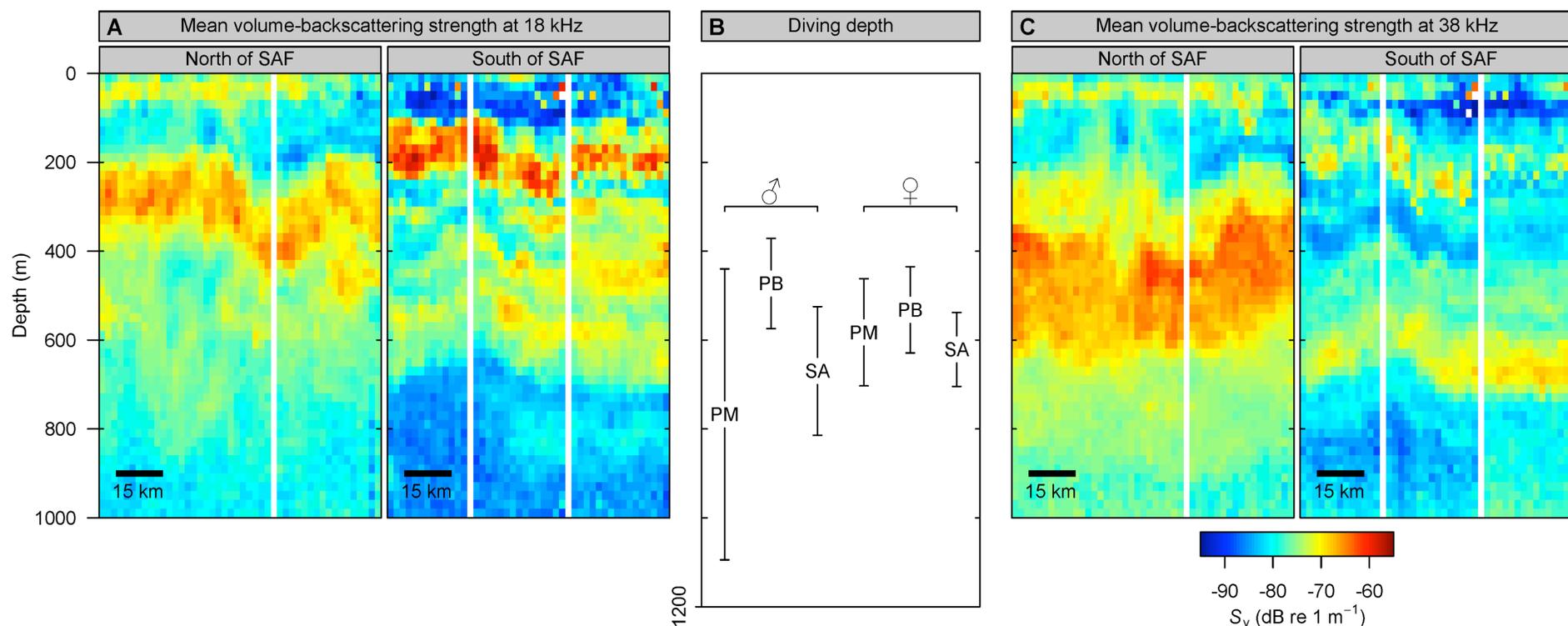
Fig. 2. Representative echograms of the vertical structure of daytime pelagic scattering layers in the frontal zone of the southwest Indian Ocean. The horizontal axis in panels A and C represents along-track distance (from left to right), as indicated by the scale-bars. Data at CTD stations were excluded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