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COMMENT

Comment on "Lagged response of Adélie penguin (*Pygoscelis adeliae*) abundance to environmental variability in the Ross Sea, Antarctica"

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Abstract

Chen et al. (Polar Biology, 43(11):1769–1781) recently reported lagged, region-specific responses of Adélie penguin (Pygoscelis adeliae) abundance to environmental variability in the Ross Sea, Antarctica. Their study suggests that lags are important toward understanding Adélie penguin population change. Though we agree with many of their findings, there are several issues with these authors' hypotheses and consequent interpretation of their results. Generally, the selected environmental variables and the scales analyzed need proper justification, as their reasoning of the causality on penguin abundance at the Ross Sea is not in agreement with previous natural history studies of both the penguins and their prey carried out in this region. Here we provide critically constructive comments on their paper and present alternative initial hypothesis to explain their results. We suggest that the variables analyzed and their scale, should be re-considered in order to reach conclusions that help explain the recent changes in Adélie penguin colonies in the Ross Sea, 'home' to about one-third of the global population.

Keywords Environmental factors · Regional population changes · Lagged efects · Ross Sea · Adélie penguin · Pygoscelis adeliae

Environmental factors operating on wildlife populations do so at different spatial and temporal scales (Newman et al. 2019). Lagged effects, those that operate at some stage of the life cycle of the species and whose impact is measurable later in time, have been detected in numerous wildlife population studies including those in the Antarctic (Wilson et al. 2001; Jenouvrier et al. 2005; Southwell et al. 2015). In their paper, Chen et al. 2020 constructed a generalized additive model (GAM) to investigate the contribution of environmental variables to changes in Adélie Penguin (*Pygoscelis adeliae*) breeding populations in different portions of the Ross Sea, 1982–2013, using data from Lyver et al. (2014) and the Mapping Application for Penguin Populations and Projected Dynamics (MAPPD). They divided what they defined as breeding 'colonies' (= breeding locations separated by uninhabited terrain), numbering 25, into 6 regions that included 1–7 breeding locations. They chose to analyze the lagged effect of chlorophyll (CHL), sea ice concentration (SIC) and sea surface temperature (SST) within a 100 km radius of the colonies. Though we agree with the underlying thesis of Chen et al. that lags are involved in the response of penguin populations to environmental change, justifications for the variables selected by Chen et al. and the spatial scale at which they chose to investigate the effects are not in agreement with previous studies carried out in this region. Moreover, their reasoning of the causality of environmental variables on penguin abundance at the Ross Sea should be justified when considering a different explanation than the current published scientific literature. We believe that their input will benefit the understanding of their conclusions, fostering more rigor of future projections of changes of penguin populations in the Ross Sea region under the effect of climate change.

Chen et al. hypothesized that "Sea surface temperature and chlorophyll concentration might be related to penguin

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abundance by affecting the distribution and availability of prey for penguins in the Ross Sea (Ainley et al. 2015; Davis et al. 2017; Grimaldi et al. 2018)." However, the literature cited does not support this statement. Ainley et al. (2015, 2018) do not indicate a relationship between SST and Chl with the distribution of prey for penguins in the Ross Sea. The Ross Sea is a relatively well-studied ecosystem, with numerous analyses that led to designation of the Ross Sea Region Marine Protected Area (e.g., Smith et al. 2007, 2012, 2014; Ainley et al. 2010; Ballard et al. 2012). Chl and primary production in the Ross Sea can be principally attributed to a non-diatom source, *Phaeocystis antarctica*, that dominates the open waters of the Ross Sea polynyas (Arrigo et al. 2003), and which is largely ungrazed by most meso-zooplankton, the main grazers being pteropods (Smith et al. 2014). Pteropods are not found in Adélie Penguin diets. Contrarily, the penguin-involved food web derives from diatoms grazed by zooplankton such as copepods, larval fish and krill, and it is confined to the polynya marginal ice zone (MIZ) (Smith et al. 2007 and additional references listed above). For example, Dugger et al. (2014) found no relationship between annual variation in CHL and primary production and reproductive effort or success in the Ross-Beaufort penguin metapopulation (Chen et al.'s region #1). Further, the MIZ diatoms are suspected to be undergrazed (Arrigo et al. 2003; Ainley 2007), implying top-down regulation of the penguin-associated food web. Chen et al.'s finding and postulated regulatory effect of CHL on penguin populations is contrary to our current knowledge. Therefore, attempting to relate annual or decadal variation in penguin population dynamics, determined by temporal variation in penguin food, to annual variation in CHL in the Ross Sea should address the known diatom-based food web paths, explain why the purported relationship was not found in previous studies, and clarify how it explains our current understanding of the regulatory mechanisms of the food web. Knowing that Chen et al. might consider a different explanation than the current published structure of the food web and role of phytoplankton in the Ross Sea, we encourage them to share their reasons to suggest an alternative structure than the supported by the established literature. We believe that such input might benefit the current Ross Sea ecosystem knowledge.

We also think the following arguments from Chen et al. deserve examination. They hypothesize that "…CHL might be related to penguin abundance by affecting penguin breeding performance through the food web. These findings confirmed the lagged effects of environmental factors on penguin population." If in fact penguins' prey did respond to variation in CHL or some other variable colinear with CHL, the lag should not be 5 years as Chen et al. reported but rather 7–9 years, because Ross Sea penguins consume krill that are older than one year, and fish that are 2–3 years of age (Ainley et al. 1998, 2003). Those values then need to be added to the mean age of recruitment of the penguins, 4–5 years (Wilson et al. 2001).

The statement is made by Chen et al. that **"**For each colony [breeding location], we spatially averaged SIC, SST and CHL data within a 100 km radius of the colonies by considering the foraging range of Adélie penguins (Ainley et al. 2015)." This may be a consequential oversimplification of current knowledge without an adequate justification. During the decades analyzed by Chen et al. (Lyver et al. 2014), the colonies studied included two that were > 200,000 breeding pairs, one > 100,000, two > 50,000, five > 25,000, and the remainder between 150 and 20,000 breeding pairs (5 colonies < 2,000 pairs). To note, the data in Lyver et al. (2014, not actually shown in Ainley et al. 2015) combine breeding locations within a 5-nautical mile (8 km) radius as a demographic unit, i.e., a colony, based on demographic analysis (Ainley 2002). Santora et al. (2020), using that same 8-km definition of colony, show that the foraging range of Adélie Penguins during the chick crèche stage, when penguins are exerting the greatest pressure on their prey, expands as a function of colony size: $y = 0.280x^{0.54}$, with those of 2000 pairs foraging within 15 km and those of > 150,000 foraging an order of magnitude larger distances, to 180 km. Thus, the appropriate radius on the basis of colony size should be considered in order to determine the spatial scale for relating population change to ocean variables. This may be a consequential improvement to their model.

We also found Chen et al.'s proposed relationship between penguin numbers, SIC and SST lacking a proper justification, given the spatial scale they used. Contrary to results obtained at larger scales, at a smaller colony-specific scale, foraging success and ultimately change in colony size might well be predicted by changes in SIC (Ainley 2002), but not necessarily SST. Relating change in penguin numbers to SST in the Ross Sea environment, a region covered in sea ice for much of year, is especially problematic given the influence of SIC on SST (more ice, lower temperature); furthermore, SST at the Ross Sea scale varies very little on an annual basis (Arrigo et al. 2015). Chen et al. found a relationship to SST only for the five breeding locations in the vicinity of Cape Adare (their region #6). Those colonies are sustained by the open water of the Ross Passage Polynya (Thatje et al. 2008), a sensible-heat polynya formed by upwelling of warmer-than-surface-water Circumpolar Deep Water (Jacobs and Comiso 1989; Dinniman et al. 2011). The link thus may be more one of access to prey, rather than temperature affecting prey abundance.

Finally, Chen et al. included the annual values of environmental variables using the mean value of monthly data in the breeding season. We believe that winter co-variables should have been also included when analyzing lagged effects of environmental variables. The lagged effect of a breeding season variable is expected to affect the recruitment of penguins ~ 5 years later, but recruitment depends on both a change in the amount of chicks fledged and their subsequent survival, which presumably is mainly affected by winter conditions.

With this comment, we hope to engage in a productive dialogue with Chen et al. to debate the basis for their hypotheses and the potential interpretation of their results, thus benefitting the current knowledge about the Ross Sea ecosystem. We concur with them that there might be lags that optimal environmental conditions for Adélie penguin population might exist, and we welcome more ideas and findings in these regards.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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Consent to participate This manuscript did not include research with human participants.

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