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Short Note
Paradigms need hypothesis testing: no evidence for top-down forcing on Adélie and emperor penguin populations

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In their recent review article "Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem?" Ainley *et al.* (2007) questioned why Southern Ocean marine ecologists apparently have shifted to a central paradigm where bottom-up forcing by physics and climate change has become the single most important driver of food web dynamics in the Southern Ocean. Ainley *et al.* (2007) suggest that top-down forcing (forcing by biotic processes) is no longer considered in the interpretation of ecological research results aimed at understanding ecosystem processes of the Southern Ocean. Based on two examples from the literature they suggest that population trends could better be explained by including species interactions in the modelling rather than by changes in climate related physical processes alone. Nicol *et al.* (2007) questioned the paradigm shift proposed by Ainley *et al.* (2007) and made a broad review of the ecological research conducted in the Southern Ocean ecosystems. They concluded that there has been considerable research effort into ecosystem interactions over the last 25 years in the Southern Ocean, and that there seems little evidence that there has been an almost complete shift in paradigms; rather both bottom-up and top-down processes are recognized to govern ecosystems functioning.

Our aim here is to consider more directly one of the two examples proposed by Ainley *et al.* (2007) to support their idea of top-down forcing. This example involves penguins. First, Ainley *et al.* (2007) suggest that the removal of significant numbers of the Antarctic minke whale *Balaenoptera bonaerensis* Burmeister from the Ross Sea area released Adélie penguins *Pygoscelis adeliae* (Hombron & Jacquinot) from trophic competition. Ainley *et al.* (2007) then interpret the increase of Adélie penguins in the Ross Sea area (Wilson *et al.* 2001) as a response to a decrease in competition for food, and the subsequent decrease in penguin numbers as the take of minke whales was severely reduced. However, although strongly suspected (Ainley *et al.* 2006) the intensity of the competition for prey between Adélie penguins and minke whales has, to our knowledge, never been properly quantified, and the effect of the removal of slightly more than 23 000 (~ 20% of 116 600, Ainley *et al.* (2007)) whales in the Ross Sea region on the population dynamics of this species remains unknown - as pointed out by Ainley *et al.* (2007). For example, one might hypothesize that density dependent processes at the scale of the whale population may have impeded the release of Adélie penguins from trophic competition. In addition, the numbers of breeding pairs of Adélie penguins in the Adélie Land sector do not present the same trends as in the Ross Sea, with a major increase starting in ~ 1992 in Adélie Land versus ~ 1975–80 at Cape Royds and Cape Bird in the Ross Sea (see Jenouvrier *et al.* 2006), whereas the numbers of minke whales caught followed the same pattern. This does not mean that the hypothesis proposed by Ainley *et al.* (2007) is false, but it does require further testing with appropriate data and modelling.

Second, Ainley *et al.* (2007) suggest that the mortality event that caused a 50% decline in the population of emperor penguins *Aptenodytes forsteri* Gray in Adélie Land (Barbraud & Weimerskirch 2001) might well have been linked to a major rapid large-scale removal of minke whales by the whaling industry. Ainley *et al.* (2007) suggest that killer whale *Orcinus orca* (L.) type A, the main predator of minke whales, may have switched to alternate prey including emperor penguins to thus explain the massive adult mortality responsible for the population decline. A prediction arising from this hypothesis is the presence of remains of emperor penguins in killer whale stomachs. Ainley *et al.* (2007) give anecdotal evidence for this by citing Prévost (1961). However, this last hypothesis is not supported when considering the killer whale diet database of the International Whaling Commission (IWC). None of the 444 killer whale stomachs analysed during the period 1976–80 (i.e. during the emperor penguin population decline) for the oceanic sector 135°–141°E and 64°–66°S off the coast of Adélie Land, contained remains of emperor penguins. Remains of fishes (51.7%) and minkes (23.1%) were the most frequently encountered, and remains of squid (6.1%), pinnipedia (2.0%) and unidentified remains from whales/pinnipedia/fish/squid were less frequently found in killer whale stomachs. The killer whales were taken in January and February in an area where emperor penguins breeding at Pointe Géologie (Adélie Land) perform pre-moult and pre-breeding foraging trips (Zimmer *et al.* 2008). In addition, none of the 1217 killer whale stomachs collected between 1965 and 1980 around Antarctica from November–May contained remains of emperor penguins. Therefore, these data strongly suggest

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that killer whales did not switch to emperor penguins as their main prey, and thus it is highly unlikely that the decline of this emperor penguin population was caused by such a top-down forcing as suggested by Ainley *et al.* (2007).

As highlighted by Nicol *et al.* (2007), "disentangling causative relationships in the Southern Ocean ecosystem will require the development of well structured hypotheses that incorporate both the biological and physical drivers of ecosystem processes". These hypotheses will, however, be insufficient without the availability of suitable long-term data and modelling that will permit to evaluate the likelihood of the proposed hypotheses.

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