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1 **The influence of historical climate changes on Southern Ocean**
2 **marine predator populations: a comparative analysis**

3 **Running head:** Southern Ocean predator palaeoecology

4

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29

30 **Abstract**

31 The Southern Ocean ecosystem is undergoing rapid physical and biological changes that are
32 likely to have profound implications for higher-order predators. Here we compare the long-
33 term, historical responses of Southern Ocean predators to climate change. We examine
34 palaeoecological evidence for changes in the abundance and distribution of seabirds and
35 marine mammals, and place these into context with palaeoclimate records in order to identify
36 key environmental drivers associated with population changes. Our synthesis revealed two
37 key factors underlying Southern Ocean predator population changes; 1) the availability of
38 ice-free ground for breeding, and 2) access to productive foraging grounds. The processes of
39 glaciation and sea ice fluctuation were key; the distributions and abundances of elephant
40 seals, snow petrels, gentoo, chinstrap and Adélie penguins all responded strongly to the
41 emergence of new breeding habitat coincident with deglaciation and reductions in sea ice.
42 Access to productive foraging grounds was another limiting factor, with snow petrels, king
43 and emperor penguins all affected by reduced prey availability in the past. Several species
44 were isolated in glacial refugia and there is evidence that refuge populations were supported
45 by polynyas. While the underlying drivers of population change were similar across most
46 Southern Ocean predators, the individual responses of species to environmental change
47 varied because of species specific factors such as dispersal ability and environmental
48 sensitivity. Such interspecific differences are likely to affect the future climate change
49 responses of Southern Ocean marine predators and should be considered in conservation
50 plans. Comparative palaeoecological studies are a valuable source of long-term data on
51 species' responses to environmental change that can provide important insights into future
52 climate change responses. This synthesis highlights the importance of protecting productive
53 foraging grounds proximate to breeding locations, as well as the potential role of polynyas as
54 future Southern Ocean refugia.

55 **Introduction**

56 Southern Ocean marine ecosystems have undergone rapid physical changes in recent decades,
57 including increases in air and ocean temperatures, changes in the extent and seasonality of
58 sea ice, decreasing salinity, and poleward shifts of oceanographic fronts (Böning *et al.*, 2008,
59 Bracegirdle *et al.*, 2008, Sokolov & Rintoul, 2009, Stammerjohn *et al.*, 2012, Turner *et al.*,
60 2009, 2014). In turn, the changes in the physical environment are driving change in marine
61 biota at all trophic levels, including fish, cephalopods and zooplankton such as Antarctic krill
62 (*Euphausia superba*), all of which are important prey species for higher-order predators such
63 as seabirds and marine mammals (Atkinson *et al.*, 2005, Constable *et al.*, 2014). Further
64 physical changes are projected by climate models into the future (Collins *et al.*, 2013a).
65 Collectively, these changes are likely to have profound implications for Southern Ocean
66 marine predators, with effects varying by both species and location, and expected to impact
67 both breeding habitat and marine foraging grounds (Constable *et al.*, 2014, Smetacek &
68 Nicol, 2005).

69 The ongoing physical and biological changes in the Southern Ocean are the result of a
70 marked shift in the Earth's environmental state (Lewis & Maslin, 2015). This shift is being
71 considered as the dawn of a new epoch, termed the Anthropocene, that is characterised by
72 changes to land, oceans, the atmosphere and evolutionary pressures (Lewis & Maslin, 2015).
73 The extinction rate during this new era is estimated at 100 to 1,000 times greater than in
74 previous epochs and is likely to result in a sixth mass extinction (Barnosky *et al.*, 2011). In
75 order to understand how species might respond to the unprecedented environmental change
76 predicted for the Anthropocene, we must consider not only their recent population trends over
77 decadal timescales, but also how they responded to similar long-term environmental regime
78 shifts in past epochs.

79 Evidence of species' histories can be found in various forms such as fossil remains and
80 genetic data. With the right tools this evidence can be used to build a picture of a species'
81 past ecology, known as palaeoecology, over periods of hundreds to millions of years (Seddon
82 *et al.*, 2014). Such palaeoecological evidence provides long-term insight into how species
83 have coped with environmental change in the past. Reconstructing historical trends in
84 abundance and distribution can provide clues about how specific environmental changes
85 affected populations, thereby increasing our understanding of species' environmental niches.
86 If a species was robust to past climate perturbations we might expect them to have good
87 resilience to future change, depending on the direction and pace of the environmental shift.
88 When combined with information on extant population structure and abundance, information
89 on the past processes that shaped population characteristics may enable predictions of how
90 species will respond as habitat availability and quality changes, and help us to assess the risk
91 of local or widespread extinction (Hoelzel, 2010, Seddon *et al.*, 2014). By comparing trends
92 for different species we can begin to understand which are the most important of these
93 environmental factors.

94 Predators have an integral role in regulating ecosystems via top-down processes (Baum &
95 Worm, 2009, Heithaus *et al.*, 2008); hence how they might respond to environmental change
96 is particularly important. For predators to prosper, productive foraging grounds must exist
97 within reach of suitable breeding habitat. However, what constitutes suitable marine foraging
98 grounds or terrestrial breeding sites varies by species due to differences in their foraging
99 modes and abilities, as well as the required physical characteristics of their breeding sites.
100 Both marine and terrestrial conditions are projected to change across the Southern Ocean, and
101 predator populations in both the sub-Antarctic and Antarctic are likely to be affected.
102 Potential mechanisms for these impacts include, but are not limited to: the loss of breeding
103 habitat in cases where predators use sea ice as a breeding platform; the influence of changing

104 sea ice seasonality on the timing of breeding; the effects of increasing temperatures for
105 species that are highly cold adapted; and changes in prey abundance, distribution and
106 accessibility. Different populations of the same species are likely to experience different
107 impact mechanisms due to regional variation in environmental trends.

108 Here, historical changes in populations of Antarctic and sub-Antarctic marine predators,
109 specifically seabirds and mammals, are reviewed, compared and placed into context with past
110 environmental changes. We focus on predators with breeding sites that are distributed in and
111 around mainland Antarctica, its offshore islands and the sub-Antarctic islands, because these
112 species utilise the Southern Ocean for both breeding and foraging. Migratory species that
113 periodically reside in the Southern Ocean, including cetaceans, are excluded. In order to
114 restrict our study to purely environmental driven responses, only changes in predator
115 populations that occurred prior to anthropogenic impacts, defined here as 1610 to coincide
116 with the proposed inception of the Anthropocene (Lewis & Maslin, 2015), are considered.

117 **An overview of Southern Ocean palaeoclimate**

118 The Pleistocene geologic period (2.588 mya to 11.7 kya) (Cohen *et al.*, 2013) was
119 characterized by large-scale global climate oscillations, varying from cold periods of
120 glaciation to warmer interglacial periods (Figure 1) (Jouzel *et al.*, 2007). Changes in the
121 Southern Ocean environment throughout the Pleistocene have been reconstructed using a
122 variety of methods, including ice cores, marine and lake sediment cores, and lithology. The
123 last glacial maximum (LGM, 26 – 19.5 kya) marks the most recent time of maximum ice
124 sheet extent in Antarctica (Clark *et al.*, 2009). During the LGM, air temperatures were *ca.*
125 13°C colder than the present day (Jouzel *et al.*, 2007) and glaciation was extensive, with most
126 of the continental shelf covered by either marine-based ice sheets or thick, perennial sea ice

127 (Figure 2) (Anderson *et al.*, 2002, Bentley *et al.*, 2014, Gersonde *et al.*, 2005). Many sub-
128 Antarctic islands were glaciated (Hodgson *et al.*, 2014) and surrounded by sea ice in the
129 winter (Gersonde *et al.*, 2005). Oceanographic fronts, which are the boundaries between two
130 water masses that tend to be associated with high prey abundance due to both enhanced local
131 primary production and transport of prey to the front by currents (Bost *et al.*, 2009), were
132 displaced northwards by around five degrees of latitude (Figure 2) (Gersonde *et al.*, 2005).

133 The dynamics of Antarctic sea ice are highly complex and can be described in terms of areal
134 extent, concentration, thickness, formation rate and seasonality. Many of these variables are
135 difficult to measure for contemporary sea ice, and reconstructing historical sea ice conditions
136 is an ongoing challenge (Collins *et al.*, 2013b, de Vernal *et al.*, 2013). Fossils of diatom taxa
137 that live in association with sea ice, and have particularly intense blooms at the ice edge, are
138 preserved in marine sediments and can provide an excellent proxy for historical sea ice limits
139 (Allen *et al.*, 2011, Gersonde & Zielinski, 2000). Diatom records are commonly used in
140 Antarctic sea ice reconstructions, often coupled with other evidence such as lithology (Allen
141 *et al.*, 2011), radiolarians (Gersonde *et al.*, 2005), or, more recently, highly branched
142 isoprenoid biomarkers (Collins *et al.*, 2013b). Diatom records indicate that at its maximum
143 extent during the last glacial period the circum-Antarctic winter sea ice field was
144 approximately double its present area, extending to about 50°S (Figure 2) (Allen *et al.*, 2011,
145 Collins *et al.*, 2012, Gersonde *et al.*, 2005). The extent of summer sea ice during the last
146 glacial period is poorly constrained and an area of ongoing study (Collins *et al.*, 2013b),
147 however, the data that are available suggest a northerly expansion to 55°S in some locations
148 (Figure 2) (Allen *et al.*, 2011, Collins *et al.*, 2012, Gersonde *et al.*, 2005). Interestingly, the
149 timing of the maximum extent of sea ice pre-dates the LGM (Allen *et al.*, 2011), with
150 maximum winter and summer extents occurring at 25–23.5 kya and 31–23.5 kya, respectively
151 (Collins *et al.*, 2012).

152 During the LGM, biological productivity south of the Polar Front was greatly reduced
153 (Hillenbrand & Cortese, 2006), with estimates placing primary production at between two
154 and five times less than current values (Kohfeld *et al.*, 2005). This estimate is inferred from
155 export production records in sediment cores, where export production is the portion of
156 primary production that accumulates in sediments (Kohfeld *et al.*, 2005). The low primary
157 productivity during the LGM is likely to have had a regulatory effect on all trophic levels in
158 the Southern Ocean food web by severely limiting the food resources that were available
159 (Thatje *et al.*, 2008).

160 While overall biological productivity of the Southern Ocean was much reduced during the
161 LGM, polynyas may have provided oases of productivity (Thatje *et al.*, 2008) and access
162 points for predators amidst the extensive sea ice field. Polynyas are areas of open water
163 within the sea ice field that are associated with enhanced primary production, due to an
164 earlier spring melting of sea ice and a resultant earlier start in photosynthetic primary
165 production (Martin, 2001). Coastal polynyas are formed by the outflow of katabatic winds
166 that push sea ice away from the coastline, whereas open-ocean polynyas are generally formed
167 by upwelling of warm, deep water associated with submarine geological formations such as
168 seamounts (Comiso & Gordon, 1987, Holland, 2001, Martin, 2001, Thatje *et al.*, 2008).
169 Sediment cores suggest the existence of LGM polynyas in several locations in the northern
170 Weddell and Ross Seas (Figure 2) (Brambati *et al.*, 2002, Mackensen *et al.*, 1994, Smith *et*
171 *al.*, 2010, Sprenk *et al.*, 2014, Thatje *et al.*, 2008). Polynyas could only have existed in the
172 northern sections of the Weddell and Ross Seas because ice sheets covered large portions of
173 these embayments during the LGM (Figure 2) (Anderson *et al.*, 2014, Hillenbrand *et al.*,
174 2014). Polynyas are thought to have been more widespread during the LGM due to a
175 heightened intensity of katabatic winds (Smith *et al.*, 2010, Sprenk *et al.*, 2014), however the

176 sediment core record around Antarctica is sparse, so the locations of other LGM polynyas are
177 currently unknown.

178 Following the LGM, warming temperatures saw the Southern Ocean shift away from glacial
179 conditions and into the warm Holocene (11.7 kya to present, Cohen *et al.*, 2013) (Figure 1).
180 The transition to the Holocene was characterised by retreating ice sheets, rising sea levels,
181 increased seasonality of a decreasing sea ice cover, and increasing primary productivity
182 (Allen *et al.*, 2011, Anderson *et al.*, 2009, Barbara *et al.*, 2010, Bentley *et al.*, 2014, Collins *et*
183 *al.*, 2012, Crosta *et al.*, 2004, 2008, Denis *et al.*, 2009b, Gersonde *et al.*, 2005, Kohfeld *et al.*,
184 2005). These environmental responses to climatic changes happened asynchronously across
185 the Southern Ocean. Throughout the Holocene there have been less dramatic fluctuations in
186 local climate, including shifts in sea level, sea ice cover and some minor readvancement of
187 glaciers.

188 **Palaeoecology of the Southern Ocean**

189 Evidence of palaeoecological processes can be found in a species' physical remains,
190 including bone, tissue, eggshell or guano. Such evidence can be analysed using a combination
191 of genetic, radioisotopic and geochemical methods, in order to study changes in distribution
192 and abundance over thousands of years, identify locations of refugia and assess dietary
193 changes. When combined with palaeoclimatic evidence, such as ice core and sediment
194 records, it is possible to identify potential environmental drivers of population changes. In
195 combination, these varied approaches can build a compelling picture of the past responses of
196 Southern Ocean predators to environmental change.

197 Genetic studies using coalescent modelling allow for the estimation of changes in population
198 size through time. In coalescent Bayesian skyline analysis, sequence data from multiple

199 individuals in a population are used to co-estimate genealogies and the effective population
200 size at different points in time (Drummond *et al.*, 2005, Pybus *et al.*, 2000). If calibrating
201 information such as ancient DNA, (see de Bruyn *et al.* (2011) for a comprehensive review),
202 fossils or a known genetic mutation rate is available, the timings of these changes in
203 abundance can be estimated and correlated with palaeoclimate records. A related method is
204 the pairwise sequentially Markovian coalescent, which is used to estimate past population
205 sizes using whole genome data from a single individual (Li & Durbin, 2011). This method is
206 effective for estimating population sizes over long time scales (i.e. 100 kya to 10 mya), but is
207 less accurate over shorter time scales compared to Bayesian coalescent methods, making
208 these approaches complementary (Sheehan *et al.*, 2013).

209 Genetic data may also identify past refugia (Hewitt, 1996, 2000). Phylogenetic analyses can
210 reveal genetically distinct lineages that may have arisen as a result of past isolation in refugia
211 (Hewitt, 1996, 2000). Again, if the analyses can be calibrated, the timings of these events can
212 be determined and the environmental drivers of isolation in refugia may be thus identified.
213 Telltale patterns of genetic diversity may also be used to pinpoint the locations of past
214 refugia; refugia are typically characterised by a pattern of clinal variation, decreasing with
215 distance from the refuge, arising from founder effects as new areas are colonized following
216 the expansion from the refuge (Hewitt, 1996, 2000).

217 Radiocarbon dating of organic remains, which can survive for thousands of years in the cold,
218 dry Antarctic environment where microbial degradation is inhibited, can provide valuable
219 palaeoecological data. The occupation history of the snow petrel (*Pagodroma nivea*) has been
220 investigated by radiocarbon dating of solidified stomach oil, called mumiyo, which
221 accumulates among rocks in breeding colonies (Hiller *et al.*, 1988). Dating of these deposits
222 can provide a record of occupation at a given site. Radiocarbon dating of excavated penguin

223 guano sediments, called ornithogenic soils, that contain guano, eggshell fragments and bones
224 can likewise be used to investigate occupation history (see Emslie *et al.*, 2014 for a
225 comprehensive review). Such studies may be supplemented with geochemical analyses of
226 typical bio-elements found in penguin guano, which provide a proxy for the abundance of
227 penguins (Sun *et al.*, 2000), and stable isotopic analyses of eggshells and guano can provide
228 an understanding of diet through time (Emslie & Patterson, 2007, Emslie *et al.*, 2013).
229 Finally, radiocarbon dated remains found outside a species' current range can provide clues
230 to their distributions under different climatic regimes (Hall *et al.*, 2006).

231 **Ice-free breeding species – the sub-Antarctic**

232 The sub-Antarctic islands are populated by breeding colonies of many predators, including
233 pinnipeds, penguins, petrels and albatrosses. Of these species, palaeoecological data are
234 currently available for king penguins (*Aptenodytes patagonicus*) and Southern elephant seals
235 (*Mirounga leonina*). Both species congregate in breeding colonies established on coastal ice-
236 free ground; the king penguin breeds exclusively on sub-Antarctic islands between 45° and
237 55° south (Figure 3a) (Bost *et al.*, 2013), while the Southern elephant seal breeds mostly in
238 the sub-Antarctic, with colonies also located in South America, the Antarctic Peninsula and
239 maritime Antarctic islands, and in the Windmill Islands in East Antarctica (Figure 3b)
240 (Heimark & Heimark, 1986, Lewis *et al.*, 2006, Murray, 1981). Both species are meso-
241 predators with wide foraging ranges, extending to the edge of the pack ice in the case of the
242 king penguin (Bost *et al.*, 2004, Moore *et al.*, 1999) and well into the sea ice zone in the case
243 of the elephant seal (Charrassin *et al.*, 2008). Oceanographic fronts are important foraging
244 grounds for both species (Bost *et al.*, 2009, Charrassin *et al.*, 2008). Elephant seals, king
245 penguins and many other sub-Antarctic predators direct their foraging trips toward the Polar

246 Front, the sub-Antarctic Front or the Subtropical Front (Figure 2), as these areas provide a
247 predictable source of prey and good conditions for diving predators (Bost *et al.*, 2009).

248 **King penguins**

249 A genetic coalescent study of king penguins from the Crozet Archipelago revealed a rapid
250 population expansion closely following the end of the LGM (Trucchi *et al.*, 2014). The
251 Crozet king penguin effective population size increased from *ca.* 2,000 during the LGM to
252 *ca.* 170,000 today (Trucchi *et al.*, 2014). While many factors may have contributed to this
253 increase in abundance, the key ecological requirements for king penguins are year-round ice-
254 free breeding habitat and access to productive foraging grounds (Hunt, 1991). There is no
255 definitive evidence that Crozet was glaciated during the LGM, and estimates from sediment
256 core microfossil assemblages place the LGM sea ice field south of Crozet (Figure 3a),
257 although it should be noted that both the glacial history and the microfossil record in this
258 region are poorly resolved (Gersonde *et al.*, 2005, Hall, 2009, Hodgson *et al.*, 2014). Hence,
259 the overall indication is that ice-free breeding habitat was available on Crozet during the
260 LGM. It may therefore have been a lack of productive foraging that limited the size of the
261 king penguin population. As previously mentioned, biological productivity was likely much
262 reduced during the LGM (Hillenbrand & Cortese, 2006, Kohfeld *et al.*, 2005), furthermore,
263 the location of king penguin foraging grounds may have shifted during this time. King
264 penguins currently forage almost exclusively near frontal zones (Bost *et al.*, 2009). Crozet is
265 situated in the Polar Frontal Zone, equidistant (~400 km) from the Polar Front and the sub-
266 Antarctic Front, making it ideally positioned for king penguin foraging (Figure 3a) (Bost *et*
267 *al.*, 2009). However, it is likely that both of these fronts were displaced *ca.* 5-10° northwards
268 during the LGM (Figure 3a) (Gersonde *et al.*, 2005), possibly increasing the travel distance
269 from Crozet. The combination of shifted feeding grounds with lower overall biological

270 productivity may have reduced prey density to a level that was insufficient to support a large
271 population of king penguins. Indeed, given the inherent variability in past population
272 estimates, it is possible that no king penguins were present in the Crozet Archipelago during
273 the LGM, and this colony was subsequently founded during the Holocene once conditions
274 became more favourable. At present, palaeoecological studies of king penguins are limited to
275 genetic coalescent data from a single colony (Table 1). The recovery of sub-fossil remains
276 dating to the LGM would clarify the locations of king penguin colonies during the glacial
277 period, and further genetic studies of other contemporary breeding colonies could indicate
278 whether the Holocene population expansion on Crozet was an isolated trend, or occurred
279 across the species' range.

280 **Southern elephant seals**

281 Southern elephant seals may have undergone a large latitudinal range expansion during the
282 Holocene, taking advantage of emerging ice-free terrestrial habitat on the Victoria Land
283 Coast in the Ross Sea *ca.* 7,000 years ago (de Bruyn *et al.*, 2009, 2014, Hall *et al.*, 2006).
284 There is evidence for a mid-Holocene breeding colony and/or moulting site in the region,
285 based on radiocarbon dated remains and genetic analysis (de Bruyn *et al.*, 2009, 2014, Hall *et*
286 *al.*, 2006). Genetic evidence suggests the remains were most likely the remnants of a
287 breeding colony, founded by individuals originating from Macquarie Island 2,500 km to the
288 north, signifying a long distance colonisation event by a highly mobile species *ca.* 7,000
289 years ago (Figure 3b) (de Bruyn *et al.*, 2009, 2014). Elephant seal numbers then fluctuated in
290 the Ross Sea region, until they eventually abandoned the area completely *ca.* 1,000 years ago,
291 retreating to Macquarie Island (de Bruyn *et al.*, 2009, Hall *et al.*, 2006). However, while the
292 genetic evidence suggests that the Ross Sea elephant seals were the constituents of a breeding
293 population, the recovered remains were predominantly skin and hair, with only two pup

294 carcasses discovered (Hall *et al.*, 2006). Therefore, the possibility that this was a moulting
295 site rather than a breeding colony cannot be discounted, since elephant seal breeding sites
296 tend to contain large numbers of deceased pups, which have not been discovered so far at the
297 Ross Sea.

298 It has been postulated that the availability of ice-free breeding habitat, as determined by
299 glaciation, sea ice extent and seasonality, was the major limiting factor of elephant seal
300 distribution during the Holocene (de Bruyn *et al.*, 2009, Hall *et al.*, 2006). Elephant seals
301 currently maintain several small colonies on ice-free areas of the Antarctic Peninsula and
302 continent; however, no breeding or moulting sites exist within the Ross Sea region today,
303 with the Victoria Land Coast presently bounded by fast ice for the majority of the year,
304 thereby precluding the establishment of breeding colonies (Hall *et al.*, 2006). Beaches free of
305 glacial ice were probably released on the Victoria Land Coast between 8,000 and 7,500 years
306 ago, based on the grounding-line retreat of the Ross Sea ice sheet (Conway *et al.*, 1999).
307 Taylor Dome ice core records also indicate warmer conditions coincident with elephant seal
308 occupation of the Ross Sea (Monnin *et al.*, 2004), with these conditions possibly resulting in
309 reduced sea ice concentration in the area and therefore open water adjacent to the shore (Hall
310 *et al.*, 2006). Around 1,000 years ago, coeval with the final abandonment of the region by
311 elephant seals, glacial advance began to overrun the Holocene beaches (Baroni & Hall, 2004,
312 Baroni & Orombelli, 1991, 1994b) and methanesulfonic acid records from nearby Newall
313 Glacier indicate an increase in sea ice extent (Mayewski *et al.*, 1995). A contemporary study
314 of elephant seals from Macquarie Island indicated that increases in sea ice duration within the
315 seals' foraging range can have a negative influence on their abundance (van den Hoff *et al.*,
316 2014), therefore, the late Holocene increases in sea ice (Mayewski *et al.*, 1995) may have
317 directly contributed to elephant seals abandoning the Ross Sea. It is unlikely that prey
318 distribution was a factor limiting the occupation of the Ross Sea by elephant seals during the

319 late Holocene, as they forage in this region today but return to the sub-Antarctic to breed and
320 moult (Hall *et al.*, 2006).

321 If ice-free breeding habitat suitable for elephant seals was available during the mid to late
322 Holocene in the Ross Sea, then it may have also been suitable for king penguin occupation.
323 However, no king penguin remains have been discovered in the region. The most probable
324 explanation is that king penguins did not venture into the Ross Sea for foraging, and therefore
325 did not have the opportunity to discover emergent breeding habitat in the region. Today, king
326 penguins from Macquarie Island forage almost exclusively in the Polar Frontal Zone, well
327 north of the Ross Sea (Sokolov *et al.*, 2006). While Macquarie Island elephant seals often
328 forage in the Polar Frontal Zone, they also forage much further south over the Antarctic
329 continental shelf and in the Ross Sea (Bradshaw *et al.*, 2003, Charrassin *et al.*, 2008, Hindell
330 *et al.*, 1991). It appears that the wide-ranging foraging habits of the elephant seal may convey
331 an advantage in discovering newly available breeding habitat.

332 Given that many of the sub-Antarctic islands that are currently host to elephant seal breeding
333 colonies were probably glaciated and/or surrounded by sea ice during the LGM (Gersonde *et al.*
334 *et al.*, 2005, Hodgson *et al.*, 2014), it is likely that elephant seal populations were either reduced
335 in size or displaced northwards, possibly to continental South America, which is currently
336 home to several Southern elephant seal breeding colonies (Lewis *et al.*, 2006, Thatje *et al.*,
337 2008) and may have been occupied by the species during the Middle Pleistocene, based on
338 limited fossil evidence (Valenzuela-Toro *et al.*, 2015). The population sizes of other elephant
339 seal colonies during the LGM could be investigated in the future using genetic coalescent
340 methods, as has been done successfully for king penguins (Trucchi *et al.*, 2014).

341 **Ice-free breeding species – the *Pygoscelis* penguins**

342 The three *Pygoscelis* penguins are the chinstrap (*Pygoscelis antarctica*), the gentoo
343 (*Pygoscelis papua*) and the Adélie (*Pygoscelis adeliae*). Chinstraps and gentoos currently
344 breed in colonies on sub-Antarctic islands, the Antarctic Peninsula and maritime Antarctic
345 islands (Figure 3c,d) (Borboroglu & Boersma, 2013), while the Adélie has a circumpolar
346 distribution with breeding colonies located at ice-free areas of the Antarctic continent, the
347 Antarctic Peninsula and some maritime Antarctic islands (Figure 3e) (Emslie *et al.*, 2003,
348 Lynch & LaRue, 2014, Schwaller *et al.*, 2013). All three *Pygoscelis* species require ice-free
349 ground for nesting (Williams, 1995). They arrive at their breeding colonies when the sea ice
350 is most extensive (Emmerson *et al.*, 2011) and build nests out of small rocks (Williams,
351 1995). This reliance on ice-free ground suggests that Pygoscelids experienced a restriction of
352 their breeding habitat during the LGM and may have retreated into glacial refugia or range-
353 shifted to lower latitudes, at least for breeding purposes. Given that sea levels were lower
354 during the LGM than now, it is possible that many LGM breeding sites are now submerged,
355 making the discovery of physical evidence of these sites unlikely. The palaeoecology of the
356 Pygoscelids has been very well studied relative to other Southern Ocean predators, with a
357 wealth of evidence available concerning their distributions and abundances throughout the
358 Holocene.

359 A common occurrence for all three Pygoscelid penguins throughout the Holocene is the
360 regular shifting of colony sites (often local altitudinal shifts) in response to fluctuating sea
361 levels and changing coastlines (Tatur *et al.*, 1997). A clear distinction must be made between
362 the effects of climatic changes, such as changes in sea ice conditions, glaciation, prey
363 availability or predation, as opposed to local geologic changes, such as fluctuating sea levels
364 (Tatur *et al.*, 1997). In the first scenario, climate change may result in changes to the overall

365 numbers of penguins and their ranges, whereas in the second scenario, individual nesting
366 sites could be locally relocated or abandoned even when the population is of constant size
367 and the overall range is unchanged (Tatur *et al.*, 1997). There is evidence for local shifts of
368 Pygoscelid colonies in response to sea level changes across their distributions (Baroni &
369 Orombelli, 1994b, Emslie & McDaniel, 2002, Emslie *et al.*, 1998, Emslie & Woehler, 2005,
370 Myrcha & Tatur, 1991, Stonehouse, 1970b, Tatur *et al.*, 1997). However, here we will focus
371 on changes in the overall abundance and distribution of these species in response to large-
372 scale climate changes.

373 **Chinstrap penguins**

374 A genetic coalescent study of chinstrap penguins from the Scotia Arc (West Antarctic
375 Peninsula, South Shetland Islands, South Orkney Islands and South Sandwich Islands; Figure
376 3c), representing almost the entire global population of chinstrap penguins, detected a
377 dramatic increase in chinstrap abundance during the Holocene (Clucas *et al.*, 2014). From an
378 LGM female effective population size of *ca.* 2,000 birds, the population began to increase
379 gradually around 10 kya and then rapidly around 7 kya, eventually reaching an effective
380 female population size of almost 100,000 individuals, equating to a 50-fold increase in
381 abundance (Clucas *et al.*, 2014). The increase occurred coeval with deglaciation of the
382 species current range; deglaciation of the South Shetland Islands was underway by *ca.* 14
383 kya, with open marine conditions present in Maxwell Bay (adjacent to current colonies) by
384 10 kya (Ó Cofaigh *et al.*, 2014, Hodgson *et al.*, 2014), facilitating the initial range-expansion
385 and gradual increase in abundance. Deglaciation of the South Orkney Islands and the
386 Antarctic Peninsula occurred by *ca.* 7.5 kya and 6.8 kya, respectively (Ó Cofaigh *et al.*, 2014,
387 Hodgson *et al.*, 2014), opening up further chinstrap habitat and facilitating the rapid increase
388 in abundance from *ca.* 7 kya.

389 The evidence suggests that chinstrap penguins rapidly colonised new breeding habitat as it
390 became available during deglaciation. The locations of chinstrap colonies during the LGM
391 are unknown, but the species was most likely distributed further north than they are now, as
392 their current breeding locations were glaciated at that time. Future recovery of sub-fossil
393 remains dating to the early Holocene or LGM may shed light on the chinstrap penguin's past
394 distribution; currently only genetic coalescent data are available for this period (Table 1).

395 **Gentoo penguins**

396 Modern gentoo penguins are split into two sub-species, the northern (*Pygoscelis papua*
397 *papua*) and southern (*Pygoscelis papua ellsworthii*) gentoos, which are currently distributed
398 on either side of the Polar Front (Figure 3d) (Stonehouse, 1970a). Phylogenetic analyses
399 indicate that the two sub-species diverged either during the LGM or just after it, with their
400 most recent common ancestor dated at between 11 and 59 kya (Clucas *et al.*, 2014). There are
401 two possible scenarios for how the sub-species arose. Firstly, if the divergence occurred
402 during the LGM it is likely that the two sub-species represent two glacial refuge populations
403 that were geographically isolated during the LGM for long enough to diverge genetically
404 (Clucas *et al.*, 2014). In the second scenario, that of divergence following the end of the
405 LGM, penguins originating from a single LGM gentoo population in the north may have
406 colonised new areas south of the Polar Front as more breeding habitat became available
407 following deglaciation, thus forming the southern gentoo sub-species (Clucas *et al.*, 2014).
408 The second scenario is the more likely, as the current breeding habitat of the northern gentoo
409 penguins on the Falkland Islands was not glaciated during the LGM (Hodgson *et al.*, 2014)
410 and was also north of the maximum sea ice extent (Allen *et al.*, 2011, Collins *et al.*, 2012),
411 suggesting that it was ice-free and probably suitable for nesting. The Falkland Islands could
412 therefore have supported an LGM population of gentoos (Figure 3d), which were able to

413 expand south following the deglaciation of their current range from *ca.* 14 kya (for Maxwell
414 Bay, South Shetland Islands) (Ó Cofaigh *et al.*, 2014). This scenario is supported by genetic
415 coalescent analyses which indicate that while both sub-species increased in number during
416 the Holocene, the size of the northern gentoo population gradually increased by
417 approximately three-fold from *ca.* 9 kya (Clucas *et al.*, 2014), while the southern gentoos
418 increased far more rapidly, by about 70-fold commencing *ca.* 13 kya, consistent with
419 expansion into new habitat (Clucas *et al.*, 2014, Peña *et al.*, 2014). Gentoo penguin bones
420 dated at *ca.* 4.5 kya have been discovered on King George Island in the South Shetlands,
421 indicating that the island may have been occupied at this time, however, the remains were
422 adult skeletons only, therefore it is unclear whether breeding colonies were present (Del Valle
423 *et al.*, 2002). The slight increase in the northern gentoo population can probably be attributed
424 to increasing biological productivity in the Southern Ocean at this time (Anderson *et al.*,
425 2009, Denis *et al.*, 2009b, Kohfeld *et al.*, 2005).

426 **Adélie penguins**

427 The palaeoecology of Adélie penguins has been very well studied, more so than any other
428 Southern Ocean predator. Accumulations of the weathered remains of Adélie penguins were
429 first noted in the Ross Sea during the *Carsten Borkgreivink Southern Cross* expedition in 1899
430 (Emslie *et al.*, 2014), and the first radiocarbon dating of sub-fossil remains was performed in
431 the 1950s (Harrington & McKellar, 1958). Many studies on the relationship between Adélie
432 penguins and climate changes followed and the topic has been recently reviewed by Emslie *et*
433 *al.* (2014), Millar *et al.* (2012) and Sun *et al.* (2013). In light of this, we will give only a brief
434 overview of Adélie penguin population changes in relation to historical climate change.

435 A pairwise sequentially Markovian coalescent analysis of an Adélie penguin genome from
436 the Ross Sea revealed a gradual increase in Adélie numbers from *ca.* 1 mya, followed by a

437 rapid increase commencing *ca.* 150 kya (Li *et al.*, 2014), in the heart of the penultimate
438 glacial period (Jouzel *et al.*, 2007). The onset of an Adélie penguin population expansion
439 during a glacial period is unexpected, as much of their contemporary Antarctic breeding
440 habitat would have been glaciated at that time. A possible explanation is that the Adélie
441 penguin breeding distribution was located further north in the past, for example on sub-
442 Antarctic islands, however, until sub-fossil remains dated to this period are discovered this
443 possibility remains necessarily speculative. The oldest remains so far discovered are *ca.*
444 45,000 years old and recovered in the Ross Sea (Emslie *et al.*, 2007).

445 The abundance of Adélie penguins then declined *ca.* 60 kya during a cold period (Figure 1),
446 corresponding with reduced ice-free ground available for nesting (Li *et al.*, 2014).
447 Radiocarbon dating of remains has shown that Adélies were present in the Ross Sea as early
448 as *ca.* 45 kya, however, despite extensive radiocarbon dating from the Ross Sea, there are no
449 records of occupation during the LGM (Emslie *et al.*, 2007), suggesting that the species was
450 displaced to the north and/or LGM colony sites are now submerged. Phylogenetic studies
451 found evidence of two genetic lineages that are suggestive of two refuge populations dating
452 to the LGM (Clucas *et al.*, 2014, Lambert *et al.*, 2002, Ritchie *et al.*, 2004). One of these
453 lineages was comprised solely of individuals from modern Ross Sea colonies suggesting that,
454 although no physical evidence has been discovered so far, an LGM refuge may have been
455 situated in the vicinity of the Ross Sea (Ritchie *et al.*, 2004).

456 The radiocarbon record so far indicates that Terra Nova Bay, which is located just north of
457 the Drygalski Ice Tongue, was the first area within the Ross Sea to be occupied by Adélie
458 penguins following the LGM, with colonies dated at *ca.* 8 kya (Emslie *et al.*, 2007).
459 Colonisation followed very closely after deglaciation of the area, with the Ross Sea ice sheet
460 retreating from Terra Nova Bay shortly prior to 8 kya (Baroni & Hall, 2004). While

461 deglaciation provided the ice-free nesting habitat that Adélie penguins require, they would
462 also have needed open water access amidst the sea ice, which is thought to have been
463 provided by the Terra Nova Bay polynya (Berkman *et al.*, 1998, Emslie *et al.*, 2007). The
464 polynya is currently an area of high productivity (Saggiomo *et al.*, 2002), and Terra Nova
465 Bay is home to the only Adélie colony in the Ross Sea with a demonstrated record of
466 continuous occupation over the past 7,000 years (Emslie *et al.*, 2007), suggesting that the
467 locale is particularly favourable for Adélie penguins. Sediment core records indicate that the
468 Terra Nova Bay polynya has been present since the mid Holocene, although dating the time
469 of inception has proven difficult (Krissek, 1988). Sediments from outside the current polynya
470 limits also show that the polynya was much larger during the mid Holocene (Cunningham *et*
471 *al.*, 1999, Krissek, 1988). There was also a peak in productivity in Terra Nova Bay from 7.1–
472 3.2 kya (Cunningham *et al.*, 1999) which could have further facilitated Adélie penguin
473 occupation by increasing local prey resources. Dietary analysis showed that between 7.2 and
474 2 kya Adélie penguins in Terra Nova Bay consumed higher-trophic level prey, predominantly
475 Antarctic silverfish (*Pleuragramma antarcticum*), before shifting towards more krill
476 consumption after 2 kya (Lorenzini *et al.*, 2009, 2010).

477 A genetic coalescent study of Adélie penguin populations from the Antarctic Peninsula and
478 Scotia Arc (Figure 3e) indicated an LGM effective population size roughly one tenth of the
479 current population size (Clucas *et al.*, 2014). The increase in abundance began *ca.* 16 kya
480 (Clucas *et al.*, 2014), following the end of the LGM and coinciding with deglaciation of the
481 region (Ó Cofaigh *et al.*, 2014, Hodgson *et al.*, 2014). It is likely that Adélie penguins in this
482 region were displaced north during the LGM and then underwent a latitudinal range-shift and
483 population expansion as habitat became available to the south, similar to gentoo and chinstrap
484 penguins in the same region (Clucas *et al.*, 2014). It is interesting to note that the expansion
485 of Adélie penguins predates that of the other Pygoscelid penguins by a few thousand years

486 (Clucas *et al.*, 2014). A possible explanation for this is that the Adélie penguin's enhanced
487 proclivity for sea ice compared to the other two Pygoscelid species allowed it to colonise
488 southerly habitat at an earlier stage of sea ice retreat.

489 Adélie penguin nesting locations and local abundances have fluctuated regularly throughout
490 the Holocene as glaciation and sea ice cover changed (Baroni & Orombelli, 1994b, Emslie *et*
491 *al.*, 1998, 2003, 2007, Emslie & McDaniel, 2002, Emslie & Woehler, 2005, Huang *et al.*,
492 2009, Millar *et al.*, 2012). The extensive breeding distribution of Adélie penguins has
493 resulted in regional variation in their ecological responses, with notable differences between
494 the Antarctic Peninsula compared to continental Antarctica, owing to the different
495 environmental conditions of these regions (i.e. the Antarctica Peninsula is relatively warm
496 and moist compared to the cold, dry climate of continental Antarctica). A common finding of
497 many of the Holocene studies is of an Adélie penguin "optimum" in continental Antarctica
498 during the mid Holocene (*ca.* 2–5 kya), corresponding to a time of maximum Adélie penguin
499 numbers in the Ross Sea (Baroni & Orombelli, 1994b, Emslie *et al.*, 2003, 2007), Windmill
500 Islands (Emslie & Woehler, 2005) and Vestfold Hills (Huang *et al.*, 2009). The timing of the
501 Adélie penguin optimum is coincident with a warm period indicated by the ice core record
502 (Jouzel *et al.*, 2007), and it is possible that reduced concentrations of sea ice were the driver
503 for increased penguin occupation (Emslie *et al.*, 2003). The species is thought to occupy a
504 narrow habitat optimum between too much sea ice (insufficient nesting habitat and access to
505 foraging grounds) and too little sea ice (insufficient foraging habitat) (Ainley, 2002, Fraser *et*
506 *al.*, 1992).

507 Studies of Adélie penguin diet through time and space show a remarkable flexibility in prey
508 species consumed (Emslie & Patterson, 2007). On the Antarctic Peninsula, a study of diet
509 since *ca.* 6 kya using physical prey remains recovered from ornithogenic soils showed that

510 Antarctic silverfish were preferentially consumed during cool periods, while squid
511 (*Psychroteuthis glacialis*) were exploited more during warmer periods (Emslie & McDaniel,
512 2002). Similar patterns were observed at the Windmill Islands, East Antarctica, with
513 recovered prey type fluctuating over the 9 kyr occupation period, and a notable abundance of
514 squid remains during the mid-Holocene warm period (Emslie & Woehler, 2005). Stable
515 isotopic analyses at the Vestfold Hills, East Antarctica, are consistent with these findings,
516 with elevated consumption of higher-trophic level prey during warm periods, compared to
517 more krill consumption in colder periods (Huang *et al.*, 2013). In the Ross Sea, stable
518 isotopic analyses suggested a preference for higher-trophic level prey until 2 kya, after which
519 time there was a shift towards more krill consumption (Lorenzini *et al.*, 2010). The Adélie
520 penguin “optimum” coincided with periods of higher-trophic level prey consumption in East
521 Antarctica (Huang *et al.*, 2013) and the Ross Sea (Lorenzini *et al.*, 2010). Whether an
522 increased availability of higher-trophic level prey was a driver for Adélie penguin population
523 expansion, or warmer climate and reduced sea ice cover drove increases in both Adélie
524 penguins and Antarctic silverfish, is currently unclear. However, the ability of Adélie
525 penguins to adapt their diet according to prey availability may have aided in the species’
526 capacity to adapt to changing environmental conditions, as reflected by their widespread
527 persistence around most of Antarctica throughout the Holocene.

528 **Ice-free breeding species – flying seabirds of the Antarctic continent**

529 Antarctica is home to breeding populations of several flying seabird species that nest at ice-
530 free sites along the Antarctic coastline and offshore islands. However, historical population
531 data are only available for the snow petrel; as such, the population trends of Antarctic flying
532 seabirds in relation to past climate change is an area warranting much further study, given
533 that seabirds are particularly vulnerable to projected climate change (Jenouvrier, 2013).

534 **Snow petrels**

535 Snow petrels require ice-free rock for their colony sites and typically establish nests in
536 cavities created by large boulders on nunataks, rocky hills or mountains, located anywhere
537 from the coast to up to several hundreds of kilometres inland (Figure 3f) (Ainley *et al.*, 2006,
538 Goldsworthy & Thomson, 2000, Verkulich & Hiller, 1994). The locations of snow petrel
539 nesting sites are governed by the availability of suitable cavities with access to productive
540 feeding locations, usually within a day's flight of the sea ice field (Ainley *et al.*, 2006, Fraser
541 & Ainley, 1986, Hiller *et al.*, 1988).

542 Snow petrel occupation histories are available for several locations based on radiocarbon
543 dating of mumiyo deposits. Snow petrels have been present in Dronning Maud Land from at
544 least *ca.* 37 kya (Figure 3f) and were widely distributed in the region throughout the LGM
545 (Hiller *et al.*, 1988, 1995, Steele & Hiller, 1997, Thor & Low, 2011). Interestingly, snow
546 petrels only colonised the ice-free Bunger Hills region *ca.* 10 kya (Figure 3f), after which
547 time they were continuously present in the area, with periods of rapid population expansion
548 between 6 and 8 kya and again from 2 kya (Verkulich & Hiller, 1994). The timing of the
549 initial colonisation of the region is noteworthy, as the inner region of the Bunger Hills was
550 partially deglaciated both prior to and during the LGM (Gore *et al.*, 2001, Mackintosh *et al.*,
551 2014), indicating that ice-free nesting sites were probably available and, therefore, that
552 alternative factors may have prevented snow petrel colonisation of this area prior to 10 kya.

553 Access to feeding grounds may have limited the locations of snow petrel colonies during the
554 glacial period and early Holocene, when a combination of the East Antarctic Ice Sheet
555 expansion (Mackintosh *et al.*, 2011) and greater sea ice extent (Gersonde *et al.*, 2005) placed
556 open water further from terrestrial nesting sites (Figure 1). At the Bunger Hills, mumiyo
557 deposits spanning the last *ca.* 10 kyr have been analysed for stable isotopes and compared

558 with the isotopic variation in a nearby marine sediment core within the snow petrels' foraging
559 range (Ainley *et al.*, 2006). The isotopic signatures indicated that during the early Holocene
560 (9.5 – 8.5 kya) snow petrels were consuming pelagic (rather than neritic) prey, suggesting
561 that they were foraging further offshore, presumably forced by the expansive sea ice field
562 (Ainley *et al.*, 2006). From 8.5 kya onward, the isotopic record is consistent with
563 consumption of neritic prey and, therefore, a foraging range closer to the continent (Ainley *et*
564 *al.*, 2006).

565 It has been proposed that snow petrel persistence in Dronning Maud Land throughout the
566 LGM was made possible by polynyas proximate to the coast that provided feeding grounds
567 (Hiller *et al.*, 1988, Thatje *et al.*, 2008). There is sediment core evidence for polynyas in this
568 region during the LGM, the nearest of which is only 300 km from the LGM nesting sites in
569 Dronning Maud Land (Figure 3f) (Thatje *et al.*, 2008). There is no evidence of any LGM
570 polynyas proximate to the Bunger Hills that could have supported snow petrels. Snow petrel
571 settlement of the Bunger Hills may therefore have been limited by sea ice extent in the
572 region, with settlement occurring in the early Holocene once sea ice had retreated, placing
573 foraging grounds within reach of nesting sites. The Dronning Maud Land population also
574 expanded during the Holocene; this may have been driven by sea ice retreat that provided
575 more foraging habitat than polynyas alone, therefore supporting greater numbers of snow
576 petrels (Hiller *et al.*, 1995). In both the Bunger Hills and Dronning Maud Land, increasing
577 biological productivity from 10 kya (Denis *et al.*, 2009b) may have contributed to the rise in
578 snow petrel numbers. At present, the occupation history of snow petrels has been
579 reconstructed solely from mumiyo radiocarbon dates (Table 1); future genetic coalescent
580 studies could shed light on the timing and magnitude of the expansions of both the Bunger
581 Hills and Dronning Maud Land populations.

582 While the rate of snow accumulation at nesting sites is known to be a factor in the breeding
583 success of snow petrels today (Einoder *et al.*, 2014), we found no historical correlation
584 between accumulation rates and snow petrel occupation at either the Bunger Hills or
585 Dronning Maud Land, based on ice core records (Severi *et al.*, 2007, van Ommen *et al.*,
586 2004).

587 **Antarctic sea ice breeders**

588 Several Southern Ocean predators have life cycles that are closely tied to the seasonal
589 Antarctic sea ice field; these predators use the sea ice as a breeding platform upon which to
590 raise their offspring. These ice-dependent predators are likely to be especially vulnerable to
591 climate change (Jenouvrier *et al.*, 2014), as Antarctic sea ice is expected to undergo
592 substantial declines in the future. In the most extreme climate model scenario (RCP8.5), sea
593 ice would be completely absent from East Antarctica during February by 2081–2100 and
594 only retained in small areas of the Weddell and Ross Seas (Collins *et al.*, 2013a).

595 Emperor penguins (*Aptenodytes forsteri*) and Weddell seals (*Leptonychotes weddellii*) both
596 form breeding colonies on coastal fast ice (Figure 3g,h), whereas the leopard (*Hydrurga*
597 *leptonyx*), Ross (*Ommatophoca rossii*) and crabeater (*Lobodon carcinophagus*) seals breed
598 on icefloes within the pack ice zone (Budd, 1961, Siniff, 1991). Fast ice is the stable region
599 of sea ice that is attached to the continent, whereas pack ice drifts with the currents offshore.
600 Physical remnants of sea ice predators are scarce, as most physical remains are lost to the
601 ocean when the sea ice undergoes its annual melt. In these cases, genetic studies are
602 particularly useful.

603 **Emperor penguins**

604 Thatje *et al.* (2008) hypothesised that the emperor penguin, as the only penguin able to breed
605 on sea ice, may have flourished during the LGM when there was a lack of competition for
606 resources. However, a genetic coalescent study revealed that emperor penguins were far less
607 abundant during the LGM than they are today (Younger *et al.*, 2015). The East Antarctic
608 emperor penguin population expanded nine-fold during the Holocene from *ca.* 12 kya, while
609 the Ross Sea population expanded three-fold, commencing *ca.* 9.5 kya (Younger *et al.*,
610 2015). Given that emperor penguins breed on sea ice, it seems unlikely that breeding habitat
611 would have been a limiting factor during the LGM. However, the increased sea ice extent
612 during the LGM (Allen *et al.*, 2011, Collins *et al.*, 2012, Gersonde *et al.*, 2005) may have
613 restricted foraging habitat and, coupled with low biological productivity (Kohfeld *et al.*,
614 2005), could have resulted in a scarcity of prey resources.

615 Evidence for three ancestral clades originating during the LGM suggests that emperor
616 penguins were isolated within three glacial refugia at the time, one of which was most likely
617 located in or adjacent to the Ross Sea, north of the Ross Sea ice sheet (Figure 3g) (Younger *et*
618 *al.*, 2015). The other two clades had no geographic bias and have now hybridized to form a
619 single breeding population in East Antarctica (Younger *et al.*, 2015); incomplete mixing of
620 ancestral lineages in this manner is a typical indication of survival of the Pleistocene ice-ages
621 within multiple refugia (Hewitt, 1996). Interestingly, the geographic pattern of the lineages
622 mirrors that found for Adélie penguins, with one lineage restricted to the Ross Sea, while the
623 other is distributed around the continent to the Weddell Sea (Younger *et al.*, 2015).

624 It is possible that emperor penguin glacial refugia were associated with polynyas (Younger *et*
625 *al.*, 2015). Several extant colonies are located near polynyas, which are used as feeding
626 grounds during the winter months when sea ice extent is at its greatest (Croxall *et al.*, 2002).

627 There is evidence for several LGM polynyas in the Weddell and Ross Seas (Figure 3g)
628 (Brambati *et al.*, 2002, Hiller *et al.*, 1988, Mackensen *et al.*, 1994, Smith *et al.*, 2010, Sprenk
629 *et al.*, 2014, Thatje *et al.*, 2008). Some of these polynyas may have sustained refugial
630 populations of emperor penguins throughout the LGM, with populations then expanding
631 coeval with local sea ice retreat and increasing biological productivity, which happened
632 asynchronously between the Ross Sea and East Antarctica (Anderson *et al.*, 2009, Barbara *et*
633 *al.*, 2010, Denis *et al.*, 2009a,b, Licht & Andrews, 2002, Sedwick *et al.*, 2001), accounting
634 for the different expansion times of the two populations. Another possible limiting factor for
635 emperor penguins was the extreme decrease in air temperatures during the LGM, which were
636 *ca.* 13°C colder than the present day (Jouzel *et al.*, 2007). LGM air temperatures during the
637 winter breeding months may have been near the penguins' lower limit of temperature
638 tolerance (Le Maho *et al.*, 1978), potentially impacting breeding success and adult survival.

639 A pairwise sequentially Markovian coalescent analysis of an emperor penguin genome from
640 East Antarctica indicated a gradual increase in emperor numbers from *ca.* 1 mya to 100 kya
641 (Li *et al.*, 2014). Throughout the period of expansion the Antarctic climate went through
642 many glacial cycles (Jouzel *et al.*, 2007, Li *et al.*, 2014), which had no noticeable effect on
643 emperor penguin numbers. However, the effective population size during this period was less
644 than the LGM effective population size (Li *et al.*, 2014), suggesting that emperor penguins
645 may not have reached carrying capacity yet, possibly explaining the continued gradual
646 growth of emperor penguin numbers even during glacial periods. Based on the pairwise
647 sequentially Markovian coalescent method, emperor penguin effective population size was
648 relatively stable during the LGM and Holocene (Li *et al.*, 2014); however this method is
649 known to have low resolution over shorter timescales (i.e. tens of thousands of years), due to
650 the infrequency of coalescent events in a single genome (Sheehan *et al.*, 2013).

651 **Weddell, crabeater and Ross seals**

652 A genetic study of ice-breeding seals from the Ross Sea determined that both Weddell and
653 crabeater seals in the region underwent historical population expansions based on a mismatch
654 distribution test using the mitochondrial control region, whereas Ross seals showed no
655 evidence of a population expansion based on the same genetic marker (Curtis *et al.*, 2009,
656 2011). Curtis *et al.* (2009) stated that population expansion occurred 731 kya for Weddell
657 seals and 1.6 mya for crabeater seals. However, these estimates are somewhat implausible,
658 being much older than expansions generally detected using the mitochondrial control region,
659 which is a rapidly evolving region of the genome typically used to detect events that occurred
660 at timescales of tens of thousands of years ago, for example, in elephant seals (de Bruyn *et*
661 *al.*, 2009). In their follow-up paper (Curtis *et al.*, 2011), the authors corrected the estimate of
662 Weddell seal expansion time to 81 kya, and stated that Curtis *et al.* (2009) had incorrectly
663 reported the expansion time in generations rather than years. However, if the expansion time
664 was 731,000 generations ago, correcting this to years would date the population expansion
665 time at 6.58 mya, based on the generation time of nine years given in Curtis *et al.* (2009),
666 which predates the speciation of Weddell seals (which split from the leopard seal between
667 1.25 and 3.63 mya (Fulton & Strobeck, 2010)), suggesting that there may also be an error in
668 the original estimate of 731,000 generations (Curtis *et al.*, 2009). Due to the uncertainty in
669 the estimates of Curtis *et al.* (2009) and (2011), the timing of the population expansions of
670 Weddell seals and crabeater seals in the Ross Sea are unclear, and it is therefore difficult to
671 postulate any underlying environmental driver.

672 A coalescent study of East Antarctic Weddell seals indicated that the effective population
673 size in this region has been stable since 80 kya (Younger, 2015). Over this period there were
674 several major changes in climatic regime, including the LGM (Figure 1) (Jouzel *et al.*, 2007).

675 The lack of response of Weddell seal abundance to these changes suggests that suitable
676 breeding and foraging habitat were available throughout this entire period. This is plausible,
677 as the Weddell seal's breeding habitat (sea ice) has been available throughout the last 80 kyr.
678 As the sea ice field expanded during glacial periods, Weddell seals may have shifted their
679 breeding distribution northwards to stay within reach of water access for foraging.

680 **Key long-term drivers of Southern Ocean predator populations**

681 While the timing and magnitude of population changes varied by species and location (Table
682 1), our synthesis revealed two key factors underlying long-term Southern Ocean predator
683 population changes; 1) the availability of ice-free ground for breeding, and 2) access to
684 productive foraging grounds.

685 For those species that require ice-free ground for breeding, the processes of glaciation and sea
686 ice fluctuation were key drivers of population change. The distributions and abundances of
687 elephant seals, snow petrels, gentoo, chinstrap and Adélie penguins all responded strongly to
688 the emergence of new breeding habitat as deglaciation and reductions in sea ice opened up
689 new ice-free areas. The rate and extent of range-shifts in response to new breeding habitat
690 appear to be constrained both by the relative environmental tolerance of the species as well as
691 its mobility. For example, Adélie penguins are more tolerant to sea ice than chinstrap or
692 gentoo penguins and were therefore able to expand earlier in the warming period. The wide-
693 ranging elephant seal took swift advantage of emergent habitat 2,500 km from its main
694 breeding grounds, while the less mobile king penguin did not. This finding highlights the
695 need to take a species' environmental tolerance, dispersal ability and current foraging range
696 into account when considering future range-shifts.

697 Access to productive foraging grounds was another limiting factor for Southern Ocean
698 predator populations. King penguins, snow petrels and emperor penguins all had breeding
699 habitat available to them during the LGM, yet their numbers were much smaller than today.
700 Lower biological productivity of the Southern Ocean during the LGM is likely to have
701 reduced overall prey abundance. Additionally, the proximity of feeding grounds to breeding
702 sites may have been reduced. The preferred foraging grounds of the king penguins are the
703 polar fronts, which were shifted latitudinally northwards during the LGM. Snow petrels breed
704 on the Antarctic continent and fly to the ocean for foraging; during the LGM, the increased
705 sea ice extent placed open water access further away. In the case of the snow petrel, it
706 appears that colonies only persisted in regions that were proximate to polynyas, which could
707 have facilitated foraging. These findings highlight the importance of productive foraging
708 grounds proximate to breeding locations for Southern Ocean predators. With the physical and
709 biological changes that are currently occurring in the Southern Ocean, management bodies
710 need to recognise the importance of foraging grounds in reach of breeding sites and act to
711 minimise potential impacts in these areas from human activities such as fisheries or pollution.

712 Our synthesis suggests that polynyas may have played an important role as seabird refugia in
713 the past. The range of snow petrels was reduced during the LGM, with a colony persisting in
714 Dronning Maud Land adjacent to a polynya in the region. The locations of Adélie and
715 emperor penguin refugia were most likely in the vicinity of known LGM polynyas adjacent to
716 the Ross Sea. The role of polynyas as past refugia could be further investigated in the future
717 via genetic analyses of other seabird species, in combination with more complete sediment
718 core records to indicate the locations and sizes of polynyas during the LGM. Given existing
719 evidence of the importance of polynyas in the past, and their high biological productivity in
720 general, it is possible that polynyas could act as future Southern Ocean predator refugia and
721 should therefore be considered in any future management for conservation in the Antarctic.

722 Interestingly, some Southern Ocean predators showed no response to climate cycling.
723 Indications that the Weddell seal has maintained a constant population size in East Antarctica
724 over the past 80 kyr are remarkable, and suggest a robustness of the species to climate
725 changes in the past. However, it should be noted that at all times during the past 80 kyr
726 suitable breeding habitat, in the form of extensive sea ice, was available. Future projections
727 of sea ice decline may mean that the Weddell seal, which has been so robust to climate
728 cycling in the past, is now under threat.

729 Future palaeoecological studies could fill several key gaps in our understanding of the
730 climate change responses of Southern Ocean predators. Pack ice seals, including the Ross,
731 crabeater and leopard seals, breed on pack ice and are therefore vulnerable to declines in sea
732 ice extent, but their responses to past climate regime shifts are largely unknown. It is possible
733 that they may be robust to climate changes, as their fast ice breeding cousins the Weddell
734 seals were, however, their pack ice breeding habitat is different to fast ice. Genetic coalescent
735 and phylogenetic studies across these species' ranges could provide crucial information
736 regarding key environmental drivers of their abundances and distributions, their sensitivities
737 to climate change, and identify past refugia that could be used as potential refugia in the
738 future.

739 **Conclusions and implications**

740 Contemporary ecological studies suggest that the availability of suitable breeding habitat and
741 access to productive foraging grounds are crucial to the success of Southern Ocean predator
742 populations in the short-term (i.e. over decadal timescales). Our synthesis of the
743 palaeoecological data highlights the importance of these same variables over millennial
744 timescales, and suggests that the availability of suitable breeding habitat proximate to

745 productive foraging grounds was the major driver of change in Southern Ocean predator
746 populations historically. Current climate models project substantial changes in both the
747 breeding and foraging habitats of Southern Ocean predators (Collins *et al.*, 2013a, Constable
748 *et al.*, 2014), and the palaeoecological data suggest that these are likely to drive long-term
749 changes in the distributions and abundances of most Southern Ocean predators.

750 The effects of current and projected environmental changes on Southern Ocean predators
751 have been thoroughly reviewed elsewhere (e.g. Ainley *et al.*, 2010, Constable *et al.*, 2014,
752 Forcada & Trathan, 2009, Siniff *et al.*, 2008), as have the compounding effects of other
753 anthropogenic forcings, such as competition for prey with commercial fisheries (Forcada *et*
754 *al.*, 2012, Trathan *et al.*, 2015). Therefore, we will give only a brief overview of potential
755 future long-term population trends based on the key drivers identified in our synthesis.

756 Many of the Southern Ocean predators reviewed here are likely to experience population
757 declines and range contractions in the future. King penguin numbers may decrease as a result
758 of a southerly displacement of the oceanographic fronts that they rely on as foraging grounds,
759 for example, the travelling distance for brooding individuals from the Crozet Archipelago to
760 frontal features will have doubled by 2100 (Péron *et al.*, 2012). Emperor penguins and
761 Weddell seals will experience a loss of breeding habitat as sea ice declines in the future, and
762 numbers of both species are likely to decrease in the long-term (Ainley *et al.*, 2010,
763 Jenouvrier *et al.*, 2014, Siniff *et al.*, 2008). The Weddell seal has shown a remarkable
764 robustness to climate cycling over the past 80,000 years, but whether this resilience will hold
765 in the face of widespread breeding habitat loss is unclear. Emperor penguins and Weddell
766 seals are also likely to alter their distributions as colonies relocate to stay on sea ice that is
767 sufficiently stable for breeding (Ancel *et al.*, 2014, Barbraud *et al.*, 2011, LaRue *et al.*, 2015).

768 The emperor penguin has demonstrated the ability to contract its range into refugia to endure
769 adverse environmental periods in the past, and may do so again in the future.

770 Other Southern Ocean predators may increase in either range or abundance under future
771 climate change scenarios. Southern elephant seals may benefit from reduced sea ice
772 conditions as they did earlier in the Holocene, with indications that the species is already
773 expanding its range at the Antarctic Peninsula in response to local reductions in sea ice
774 (Siniff *et al.*, 2008). The Macquarie Island elephant seal population has demonstrated
775 population growth in years with a reduced sea ice field south of the island, thought to be a
776 result of favourable foraging conditions (van den Hoff *et al.*, 2014). Adélie penguin
777 populations in some locales will likely expand their breeding range inline with deglaciation,
778 as already observed at the Beaufort Island colony in the Ross Sea in recent decades (LaRue *et*
779 *al.*, 2013). However, Adélie populations in areas with large reductions in sea ice are expected
780 to decline (Ainley *et al.*, 2010), as has been observed at the Antarctic Peninsula and Scotia
781 Arc in recent years (Lynch & LaRue, 2014, Lynch *et al.*, 2012, Trivelpiece *et al.*, 2011).
782 Adélie penguins demonstrated the ability to adapt their diet to different prey types according
783 to availability throughout the Holocene, and this flexibility may aid in their long-term
784 prospects as the Antarctic food web changes in the future. Gentoo penguins, which do not
785 have the same tolerance for sea ice as the sympatric Adélie penguins, rapidly colonised new
786 breeding habitat during the Holocene as ice sheets and sea ice retreated, and a similar range
787 expansion and abundance increase is now underway at the Antarctic Peninsula and expected
788 to continue into the future (Casanovas *et al.*, 2015, Lynch *et al.*, 2012). Chinstrap penguins,
789 which we may have expected to respond favourably to ice sheet and sea ice retreat based on
790 the available palaeoecological data, are currently in decline across their distribution (Lynch *et*
791 *al.*, 2012, Trivelpiece *et al.*, 2011). The cause of the current decline is thought to be a
792 reduction in abundance of krill, the chinstrap's main prey source, as a result of fisheries and

793 the recovery of baleen whale populations (Trivelpiece *et al.*, 2011). Whether the chinstrap is
794 capable of dietary flexibility is currently unknown and stable isotope studies to elucidate
795 palaeoecological dietary trends could shed light on this.

796 Overall, our findings suggest that while the underlying drivers of population change are
797 similar across most Southern Ocean predators, the responses of species to environmental
798 change vary because of species specific factors such as dispersal ability, environmental
799 sensitivity and dietary flexibility. These interspecific differences should be considered in
800 future management and conservation plans for the Southern Ocean. As the Earth shifts into
801 the Anthropocene and faces unprecedented extinction rates and environmental change,
802 understanding the long-term drivers of species' abundances and distributions will be crucial
803 to developing effective management strategies. Comparative palaeoecological studies can
804 provide valuable insight into the key environmental drivers underlying changes in species'
805 abundance and distribution and, in combination with contemporary ecological studies, will be
806 invaluable to future conservation strategies.

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7 **Table 1. Summary of Southern Ocean predator population changes reviewed**, including species, study location, palaeoecological data used with citations, key population trend, the
 8 proposed underlying environmental driver for population trend, and the corresponding ecological limitation.

Species	Location	Coalescent Phylogeny	Ancient DNA	Sub-fossils	Diet	Mumiyo	Other	Population trend	Environmental driver	Ecological limitation
King penguin	Crozet Archipelago	1						Population expansion (~85x) following end of LGM	Increase in biological productivity, shift of oceanographic fronts	Prey availability
Southern elephant seal	Macquarie Island, Ross Sea	2	2,3,4	3				Range expansion to the Ross Sea 7 kya; retreat to Macquarie Island 1 kya	Retreat and advance of glacial and sea ice in the Ross Sea	Ice-free breeding habitat
Chinstrap penguin	Scotia Arc	5						Population expansion (~50x) commencing 10 kya	Deglaciation of the Scotia Arc and Antarctic Peninsula	Ice-free breeding habitat
Gentoo penguin	Scotia Arc	5,6	5	7				LGM refuge at Falkland Is, southerly range expansion and abundance increase (~70x) commencing 9 kya	Deglaciation of the Scotia Arc and Antarctic Peninsula	Ice-free breeding habitat
Adélie penguin	Scotia Arc, Ross Sea, East Antarctica, Antarctic Peninsula	5,8	9	9,10	11-16	15,17-21	22	Two glacial refugia, one in the Ross Sea; population expansion (~10x) in the Scotia Arc from 16 kya; optimum 3-5 kya	Glaciation, sea ice and sea level changes	Ice-free breeding habitat, sea ice foraging habitat
Snow petrel	Dronning Maud Land, Bunger Hills				23		23-29	Dronning Maud Land refuge during LGM, colonised Bunger Hills 10 kya	Polynyas, sea ice retreat, increasing biological productivity	Productive foraging habitat proximate to breeding locations
Emperor penguin	Ross Sea, Weddell Sea, East Antarctica	8,30	30					Three refugia during the LGM, one in the Ross Sea; population expansion (~7x) from 12 kya	Polynyas, sea ice retreat, increasing biological productivity	Productive foraging habitat proximate to breeding locations
Weddell seal	East Antarctica	31						Stable population size over the past 80 kyr	N/A	N/A

9 **Citations referred to in Table 1:** ¹Trucchi *et al.*, 2014, ²de Bruyn *et al.*, 2009, ³Hall *et al.*, 2006, ⁴de Bruyn *et al.*, 2014, ⁵Clucas *et al.*, 2014, ⁶Peña *et al.*, 2014, ⁷Del Valle *et al.*, 2002, ⁸Li *et al.*, 2014, ⁹Ritchie *et al.*,
 0 2004, ¹⁰Lambert *et al.*, 2002, ¹¹Baroni & Orombelli, 1994b, ¹²Emslie *et al.*, 1998, ¹³Emslie *et al.*, 2003, ¹⁴Emslie *et al.*, 2007, ¹⁵Emslie & Woehler, 2005, ¹⁶Huang *et al.*, 2009, ¹⁷Emslie & McDaniel, 2002, ¹⁸Emslie &
 1 Patterson, 2007, ¹⁹Huang *et al.*, 2013, ²⁰Lorenzini *et al.*, 2009, ²¹Lorenzini *et al.*, 2010, ²²Sun *et al.*, 2013, ²³Ainley *et al.*, 2006, ²⁴Hiller *et al.*, 1988, ²⁵Hiller *et al.*, 1995, ²⁶Steele & Hiller, 1997, ²⁷Thatje *et al.*, 2008,
 2 ²⁸Thor & Low, 2011, ²⁹Verkulich & Hiller, 1994, ³⁰Younger *et al.*, 2015, ³¹Younger, 2015

Figure Captions

Figure 1. The Antarctic temperature anomaly (the difference from the average of the last 1000 years) over the past 80,000 years. Temperatures are as estimated from the EPICA Dome C ice core (Jouzel *et al.*, 2007), with the last glacial maximum (LGM) indicated by blue shading and the Holocene by green shading.

Figure 2. Map of the Antarctic and sub-Antarctic with key physical features. The approximate positions of both modern and last glacial period sea ice extents and oceanographic fronts are indicated, after (Collins *et al.*, 2012, Gersonde *et al.*, 2005). The summer sea ice extents (SSI) are indicated by red lines, the winter sea ice extents (WSI) by blue lines, the polar front (PF) by green lines, and the sub-Antarctic front (SAF) by yellow lines. Solid lines indicate modern features, dashed lines are the inferred locations of last glacial period features. The approximate position of the LGM ice sheet extent (LGM-IS) is indicated by a dashed orange line (Bentley *et al.*, 2014). The locations of LGM polynyas are indicated by orange stars (Smith *et al.*, 2010, Spreng *et al.*, 2014).

Figure 3. Contemporary breeding distributions of Southern Ocean predators showing relevant environmental features.