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# Declining juvenile survival of Adélie penguins in Antarctica

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33 **Abstract:**

34 As summer sea ice around Antarctica reaches historical lows, quantifying the demographic  
35 response of polar species to such environmental changes becomes critical. To achieve this,  
36 synthesizing results from across species' ranges and elucidating the environmental factors  
37 driving population dynamics are key. Adélie penguins are considered reliable indicators of  
38 changes in Antarctica but the pathways through which sea ice and other environmental factors  
39 shape their population dynamics are still unclear, especially for the juvenile stage. Using a 17-  
40 year dataset of electronically tagged Adélie penguins from Adélie Land (Antarctica), we found  
41 that juvenile survival probability was most impacted by sea ice concentration near their natal  
42 colony right after fledging, with lower ice concentrations detrimental to survival. Importantly,  
43 we found that juvenile survival declined by 32% from 2007 to 2020, mirroring trends at other  
44 distant colonies. The emergence of similar patterns at opposite ends of the continent may be an  
45 early signal for shifts in population trends expected from climate change.

46

47 **Teaser:**

48 Similar declines in the survival of juvenile Adélie penguins have emerged at distant locations  
49 around Antarctica and receding sea ice could be at play.

50 **MAIN TEXT**

51

52 **Introduction:**

53 Antarctica is at the center of large and rapid environmental shifts, with both accelerating  
54 climate changes (1, 2) and increasing exploitation pressure by fisheries (3). Quantifying the  
55 response of animal populations to such environmental forcing is essential to determine their  
56 potential dynamics and persistence (4, 5). Yet, our understanding of how Antarctic species  
57 respond to such changes is still fragmented. Typically, the heterogeneous dynamics of climate  
58 (6) and environmental parameters such as sea ice (7) makes identifying drivers of any  
59 demographic rate challenging (8–10). This hampers our ability to project species response to  
60 environmental changes, especially over scales relevant to ecosystem management (11, 12).

61

62 The Adélie penguin (*Pygoscelis adeliae*), an iconic Antarctic species, exemplifies this  
63 challenge particularly well. Early observations of contrasting population trends between the  
64 Ross Sea and the Antarctic Peninsula in response to sea ice declines have fostered a population  
65 dynamics' model, where abundance is maximal at intermediate sea ice concentrations (13, 14).

66 This model has been instrumental in projecting the response of Adélie penguins to climate  
67 variability across large spatial and temporal scales (15–17). However, more localized and  
68 shorter-term predictions are still hindered by the inherent variability and noise in abundance  
69 time series which most studies are constrained to rely on (17–19). Since abundance results from  
70 the complex interplay of several demographic rates, each influenced by specific environmental  
71 drivers, and some of which are poorly understood (20), focusing on single vital rates could  
72 enhance the accuracy of projecting species responses to environmental change (21). The need  
73 for such an approach is twofold; it can provide short-term feedback for ecological management  
74 at the local scale and be integrated at larger spatial scales as more studies become available  
75 across the species range (22–25).

76  
77 In long-lived species such as the Adélie penguin, adult survival typically holds the greatest  
78 potential to influence population dynamics (26). Yet, juvenile survival appears to play a  
79 disproportionate role in driving Adélie penguin population fluctuations. For example, Adélie  
80 penguin's abundance (as measured by the number of breeding pairs) correlates with sea ice  
81 conditions with a 5-years lag (27); which is consistent with effects of sea ice on juvenile  
82 survival during their first months at sea (28). In the Antarctic Peninsula (29, 30) and East  
83 Antarctica (31), population size decreased when juvenile survival also did, further emphasizing  
84 its central role in shaping overall population trends. Despite such findings, we still lack clear  
85 evidence for a relationship between juvenile survival and environmental parameters known to  
86 affect population dynamics, such as sea ice concentration (11). Although adult survival has  
87 been convincingly linked to environmental variables (e.g., Southern Oscillation Index, winter  
88 sea ice concentration) in several populations around Antarctica (29, 32–35), the drivers of  
89 juvenile survival remain unclear (29, 31, 34). Given the importance of this demographic  
90 parameter, evaluating its trends across the species' range and elucidating its environmental  
91 drivers are required to adequately predict the species' response to future environmental changes  
92 facing Antarctica (36).

93  
94 Here, we quantify juvenile survival probabilities for the first time in the Western Pacific Ocean  
95 sector (90°E to 160°E, Fig. S1) using a 17-year-long dataset of known-age, electronically  
96 tagged Adélie penguins from Pointe Géologie archipelago, Adélie Land. By investigating  
97 trends in survival for this population located thousands of kilometers away from other studied  
98 colonies and synthesizing previously published studies on this vital rate, we provide a  
99 comprehensive picture of trends in Adélie penguin juvenile survival across Antarctica. To

100 uncover the mechanisms behind variations in juvenile survival, we also investigate the drivers  
101 of juvenile survival at Pointe Géologie by linking survival probabilities to intrinsic and  
102 environmental parameters such as body mass at fledging and sea ice concentrations.

103

## 104 **Results:**

105 We used a multi-state capture-recapture framework accounting for short-range dispersion  
106 within a 10-km radius to model the survival probability of juvenile Adélie penguins (0-2 years  
107 old). This model (see methods) enabled us to quantify juvenile survival probabilities between  
108 2007 and 2020. Over this period, juvenile survival estimates averaged  $0.42 \pm 0.18$  and showed  
109 high inter-annual variability (CV = 44%, Fig. 2A). Notably, juvenile survival probabilities  
110 exhibited a negative trend (Fig. 2A ; Table 1, model 30, analysis of deviance:  $p$ -ANODEV =  
111 0.016). The annual rate of change was of -2.5% ( $\pm$  95%CI: -3.2, -1.9), translating into a 32%  
112 loss between 2007 and 2020. An exhaustive literature search showed that juvenile survival had  
113 previously been quantified at 5 other locations around Antarctica ((29, 31, 33, 37, 38),  
114 summarized in Fig. 2). Temporal variation was investigated at only two of them, and juvenile  
115 survival probabilities were found to decline at both sites (Admiralty Bay, King George Island,  
116 Western Antarctic Peninsula, -1.3% per year for 1982-2000 (29) ; Béchervaise Island, Mac.  
117 Robertson Land, East Antarctica, -1.8% per year for 1992-2015 (31) ; Fig. 2).

118

119 To understand the drivers behind the decline observed at our study site, we used our previously  
120 developed model to test the effect of various intrinsic (mass at fledging, cohort size) and  
121 environmental covariates such as sea ice concentrations (SIC), large-scale climatic indices, and  
122 windchill temperatures on juvenile survival probabilities. Among the original set of covariates,  
123 we considered (Table S2), only autumn sea ice concentrations near the natal colony  
124 (SIC.autumn) accounted for more than 20% of the temporal variance (DEV) in juvenile  
125 survival rates (Table 1, model 22, %DEV = 28.2). After decomposing this variable into  
126 monthly data (SIC.march and SIC.april), only SIC.april reached the 20% DEV threshold (Table  
127 1, model 26, %DEV = 39.4). By decomposing SIC.april into the fraction of total ice area (15-  
128 100% SIC) covered by the marginal ice zone (15-80% SIC, MIZFRAC.april) and the fraction  
129 of total ice area covered by dense sea ice (80-100% SIC, DENSEFRAC.april), we then revealed  
130 that the amount of loose sea ice in the vicinity of the colony (MIZFRAC.april) was negatively  
131 related to juvenile survival rates (slope  $\pm$  95%CI = -0.97 (-0.99, -0.94), Fig. 3B) and accounted  
132 for 78.8% of the temporal variation (Table 1, model 27). Conversely, the amount of dense sea

133 ice (DENSEFRAC.april) was positively related to juvenile survival rates (slope  $\pm$  95%CI =  
134 0.85 (0.83 , 0.87), Fig. 3C) and accounted for 39.7% of the temporal variation (Table 1, model  
135 28). This amount of April dense sea ice near the colony declined by 13% during the time of  
136 our study (linear model:  $F = 7.65$ ,  $p = 0.016$ ,  $R^2 = 0.37$ , Fig. 3D).

137

138 Linear models showed that chick body mass at tagging, an important driver of post-fledging  
139 survival in birds, decreased slightly over the study period ( $F = 57.87$ ,  $p < 0.001$ ,  $R^2 = 0.02$ ,  
140 2007-2022 average =  $3.60 \pm 0.61$  kg), and varied more within (average of annual mass SD =  
141 0.54 kg) than across cohorts (SD of annual average mass = 0.33 kg, Fig. S8). Multi-state  
142 capture-recapture modeling showed that chick body mass was positively related to juvenile  
143 survival probability, both across cohorts (mean annual fledging mass, MFM, Table 1, model  
144 29, %DEV = 22.0, slope  $\pm$  95%CI = 0.04 (0.04, 0.04)), and also at the individual level, with a  
145 model-predicted 5.4 % increase in survival probability for every 500 grams of chick body mass  
146 (i.e. within cohorts, Fig. 4, LRT,  $\chi^2_1 = 48.014$ ,  $p < 0.001$ ). The slope of this relationship did not  
147 differ among years, as indicated by the additive model having a lower AIC than the interactive  
148 model (Table 1, models 33 and 34, respectively).

149

150 To ensure that our study colony was representative of the larger Pointe Géologie archipelago  
151 population (see methods), we compared the breeding productivity of the study colony to that  
152 of the entire population. Over the 2011-2024 period, breeding productivity for our study colony  
153 averaged  $0.63 \pm 0.44$  chicks per breeding pair (Fig. S5) and was highly correlated to that of the  
154 entire Pointe Géologie archipelago (2011-2017, Pearson correlation:  $r = 0.99$ ,  $p < 0.001$ , Fig.  
155 S6). The number of breeding pairs in the study colony averaged  $273 \pm 62$  between 2011 and  
156 2024 and remained comparable with two undisturbed control colonies located on the same  
157 island (Spearman rank correlations, both  $p < 0.022$ , Fig. S7).

158

## 159 **Discussion:**

160 Using 17 years of individual electronic monitoring, we observed a loss of 2.5% per year in  
161 Adélie penguin juvenile survival over 14 years (2007-2020) in an Adélie Land population, a  
162 rate likely stronger than the declines already observed in the only two other populations for  
163 which juvenile survival time series are available (in Mac. Robertson Land, East Antarctica, -  
164 1.8% per year (31), and in the Western Antarctic Peninsula, -1.3% per year (29)). By  
165 quantifying the survival of juvenile Adélie penguins for the first time in a region located

166 thousands of kilometers (3400 km and 6300 km, respectively) away from other monitored  
167 colonies, our results point to emerging negative trends across the continent. We also highlight  
168 potential mechanisms at play, since the decline in juvenile survival probability recorded in  
169 Adélie Land was associated with decreasing amounts of landfast (dense) sea ice in the vicinity  
170 of the natal colony within two months after fledging. As sea ice declines are predicted to shrink  
171 Adélie penguin populations in the latter part of the century (15, 16), steady declines in juvenile  
172 survival may already foreshadow such shifts.

173

174 • *Range-wide declines in juvenile survival*

175

176 Permanent dispersion of marked individuals away from study sites can bias the results of  
177 capture-recapture studies when incorrectly accounted for (39). Here, our deployment of a  
178 mobile RFID antenna network, radiating 10 kilometers around the main study colony (Fig. 1),  
179 has unveiled compelling evidence of high local philopatry, allowing a robust estimation of  
180 survival probability in spite of local dispersion. Long-distance permanent dispersion of  
181 juveniles, which could bias our survival estimates low, remains nonetheless largely unknown  
182 and should be addressed in the future.

183

184 Because of these difficulties and exceptional logistic constraints, temporal variations in the  
185 survival of juvenile Adélie penguins had only been investigated at two other locations in  
186 Antarctica before this study, and only at a single one (Béchervaise Island) without the negative  
187 impact of flipper bands on penguin vital rates (40, 41). Hinke et al. (29) were the first to report  
188 an annual decline in juvenile survival probability, with a decline of -1.3% per year (1982-2000)  
189 for Admiralty Bay (King George Island, Western Antarctic Peninsula). Survival probability at  
190 this site then seemed to stabilize up to 2011, although a change in marking methodology (from  
191 aluminum to stainless steel flipper bands) and high inter-annual variability in survival  
192 probabilities made it difficult to compare the two periods (29, 30). More recently, Emmerson  
193 and Southwell (31) extended the analysis of the capture-recapture dataset from Béchervaise  
194 Island (Mac. Robertson Land, East Antarctica) to reveal that juvenile survival had also declined  
195 (-1.8% per year, 1992-2015) in this population located halfway between the Antarctic  
196 Peninsula and Adélie Land (Fig. 2).

197

198 With an annual decrease of -2.5% between 2007 and 2020 in Adélie Land, our study adds to  
199 the picture of declining juvenile survival across the species range (Fig. 2). Juvenile survival

200 has now declined at all three locations where time trends have been investigated (Fig 2). The  
201 time series used here (14 years) is shorter than those for Admiralty Bay (18 years) and  
202 Béchervaise Island (24 years), but it is worth noting that the -2.5% annual decline at Pointe  
203 Géologie exceeds that of these two other colonies. In addition, such an annual decline in Pointe  
204 Géologie exceeds the average inter-annual variability in survival probabilities (2.50% vs.  
205 1.79%) as in Béchervaise Island (1.80% vs. 1.57%) but unlike Admiralty Bay (1.30% vs.  
206 2.90%).

207

208 • *Drivers of juvenile survival*

209

210 The existence of a relationship between Adélie penguin population dynamics and sea ice is  
211 well established (11, 16, 38, 42). However, in spite of the importance of juvenile survival in  
212 driving population trends (31, 43, 44), previous studies have found relatively limited evidence  
213 for a relationship between SIC and juvenile survival (29, 31, 34). Here, unlike for the two  
214 populations previously studied (29, 31), we found that local sea ice concentration within 200  
215 km of the natal colony in the timeframe of one to two months after fledging (April) accounted  
216 for up to 40% of the temporal variation in survival probability (Fig. 3). Specifically, higher SIC  
217 in April had a positive effect on juvenile survival. The timing of this relationship, together with  
218 the fact that we did not detect effects of environmental variables later in the year, is highly  
219 consistent with a survival bottleneck occurring in the weeks following fledging, as identified  
220 for *Pygoscelis* penguins in the Antarctic Peninsula (45). A mortality peak immediately  
221 following fledging is also consistent with previous studies in mammals (46, 47) and birds (48,  
222 49).

223

224 Our finding that SIC in April, but not in March, was correlated to juvenile survival may be  
225 particularly informative on the mechanisms linking sea ice to the survival of young Adélie  
226 penguins. Although the winter freeze-up of the Antarctic Ocean begins in March, sea ice  
227 usually consolidates markedly and expands equatorward in April (Fig. S10, (50, 51)). Newly  
228 fledged Adélie penguins therefore appear to be reliant on the rapid formation of sea ice at the  
229 onset of winter, and especially dense landfast ice (Fig. 3, Fig. S11). By decomposing April SIC  
230 into its loose (the marginal ice zone, between 15 and 80% SIC) and dense (80-100%) fractions,  
231 we were able to show that juveniles survived better in years when sea ice was made of large,  
232 fully frozen areas, rather than patchy ice (Fig. 3, Fig. S11).

233



234 To explain this relationship, we suggest that dense sea ice could provide more suitable resting  
235 grounds for fledglings, in a context where they are at high risk of energy reserves depletion  
236 (45). Furthermore, the formation of large areas of solid ice allows the emergence of polynyas  
237 and flaw leads (52), where prey may be more abundant (53) and/or more localized and thus  
238 easier to detect and capture, especially for inexperienced individuals likely to display lower  
239 foraging abilities compared to adults as shown in king penguins (*Aptenodytes patagonicus*)  
240 (54). Finally, patchier sea ice may favor predation, especially by leopard seals (*Hydrurga*  
241 *leptonyx*) (55), although predation pressure during fall and winter has never been investigated.  
242 Biologging studies have shown that during the winter, adult Adélie penguins tend to be  
243 associated with dense sea ice areas (56), with higher SIC promoting higher survival to the next  
244 breeding season (35). For juveniles, however, knowledge of post-fledging behavior is  
245 extremely limited. Only two studies so far have investigated their post-fledging movements  
246 (45, 57), while their diving behavior and association with specific sea ice types remain  
247 completely unexplored.

248

249 While SIC measured right after fledging accounted for most of the inter-annual variation in  
250 juvenile survival, conditions during the breeding season may also play a significant role, as  
251 juvenile survival was positively related to chick mass prior to fledgling (Fig. 4). The decline in  
252 juvenile survival we observed over the study period may therefore be partly accounted for by  
253 a concurrent but slight decrease in fledging mass (Fig. S8). Both the diet (58, 59) and the  
254 foraging efficiency of breeders (60, 61) have indeed been linked to sea ice conditions during  
255 chick rearing, and these parameters may directly affect chick fledging mass (62, 63). Land-  
256 based, food-independent, factors may also act, with higher precipitation and stronger winds  
257 late in the breeding season negatively affecting chick fledging mass (64), likely because of  
258 higher thermoregulatory costs for the chicks (63). Interestingly, the individual-level and  
259 positive effect of juvenile body mass at fledging on survival probabilities was similar across  
260 years, corroborating results from a previous study in the Ross Sea (62). These findings suggest  
261 that heavier chicks may maintain their survival advantage over lighter ones across a range of  
262 environmental conditions.

263

264 ● *Demographic consequences and perspectives*

265

266 In long-lived species, the survival of young age classes can have major impacts on population  
267 dynamics (65). For Adélie penguins, this is exemplified by declines in abundance of breeders

268 that followed declines in juvenile survival probabilities in two distinct populations from the  
269 Western Antarctic Peninsula (29, 30) and East Antarctica (31). As in the present study, it was  
270 not possible to identify the onset of the decline in juvenile survival in these two populations,  
271 since trends were observable right from the beginning of the monitoring (Fig. 2). Nonetheless,  
272 evidence from East Antarctica suggests that declining juvenile survival may not cascade into  
273 an abundance decline immediately, with a ~10 years lag between the onset of decline in  
274 juvenile survival and the breakup in the abundance time series ((31), Fig. 2). Furthermore,  
275 events of low adult survival and repeatedly low breeding productivity may have acted in  
276 conjunction to generate the decline in abundance at Admiralty Bay (30) and Béchervaise Island  
277 (31), respectively. This may help explain why abundance at Pointe Géologie has not yet shown  
278 signs of decline ((66), Fig. 2). However, given the occurrence of two near-total breeding  
279 failures in the past decade alone (67) and the stronger rate of decline in juvenile survival  
280 observed at Pointe Géologie compared to other studies and to local inter-annual variability in  
281 this vital rate, it is possible that the Pointe Géologie population will also decline in the coming  
282 years.

283

284 While Adélie penguin population declines for the Western Antarctic Peninsula are well  
285 documented (68–71) and consistent with the stronger rate of warming in the region (72),  
286 declines in other regions and notably in East Antarctica were not expected before the later part  
287 of the 21st century (16), with the Ross sea likely being the main refugia for the species (15).  
288 However, our findings in the Western Pacific Ocean sector of Antarctica, combined with recent  
289 evidence that an entire metapopulation elsewhere in East Antarctica has already declined by  
290 almost half in the past decade alone (31) suggest that changes could happen earlier than  
291 expected.

292

293 Such rapid changes are likely to challenge the adaptive abilities of the Adélie penguin. One of  
294 the main mechanisms through which Adélie penguins may respond to these changes is dispersal  
295 towards areas where environmental conditions remain or become favorable as ice melts (16,  
296 73). Although mid-range (< 120 km) dispersion is possible in adult Adélie penguins (74), we  
297 still lack estimations of long-distance dispersion over time scales relevant with the current rate  
298 of environmental change. Similarly, we have highlighted that no clear universal environmental  
299 drivers of juvenile survival stand out, although similar temporal trends have emerged across  
300 the species range.

301

302 In this context, the next steps would first be to harmonize demographic databases across study  
303 sites and analyze them collectively. Specifically, quantifying the temporal variation in juvenile  
304 survival for the two Ross sea populations (33, 74, 75) is key. Completing the transition from  
305 flipper bands to RFID-tags (40) could also facilitate comparisons of demographic rates among  
306 populations. Second, conducting biologging studies of juvenile movement and diving behavior,  
307 in conjunction with sea ice analyses (akin to (35)), would help identify range-wide  
308 environmental drivers of survival. Third, rigorous efforts should be made to assess the dispersal  
309 capabilities of juvenile Adélie penguins under climate change, such as deploying autonomous  
310 RFID-tag detection systems (Fig. S2) in populations adjacent to the main colonies where this  
311 method is used. With the forthcoming fifth International Polar Year (2032-2033) and the likely  
312 large-scale decline in the survival of juvenile Adélie penguins, a significant window of  
313 opportunity emerges for closely monitoring the demographic trends of vulnerable species and  
314 unraveling the underlying factors driving these trends.

315

## 316 **Methods:**

317

- 318 • *Study area and design*

319

320 Fieldwork was carried out at Pointe Géologie archipelago (Adélie Land, Antarctica; Fig. 1),  
321 close to the Dumont d'Urville research station (66°40'S, 140°01'E). This archipelago has hosted  
322 30,000-50,000 breeding pairs of Adélie penguins annually for the last two decades (66).

323

324 From the 2006-2007 breeding season onwards (breeding season will be referred to by the  
325 fledging year, e.g., 2007 in this case), Radio Frequency IDentification tags (RFID-tags) were  
326 implanted in chicks from a colony of about 270 breeding pairs located in a natural canyon  
327 (hereafter study colony). Unlike flipper bands (40, 41, 76), RFID-tags are not known to  
328 negatively affect penguin vital rates. All chicks still alive right before fledging were tagged ( $n$   
329 = 3,138). A few RFID-tagged chicks ( $n$  = 76) were found dead within the colony prior to  
330 fledging and were consequently excluded from subsequent analyses, bringing the final dataset  
331 to 3,062 individuals (range = 0-350/year, annual average = 192 from 2007 to 2022).

332

333 The study colony was fenced off in 2009 and instrumented with RFID gateways similar to  
334 those used in other penguin populations (Adélie penguins: (77-79); King penguins: (80, 81);

335 Southern rockhopper penguins: (82); Macaroni penguins: (83); Little penguins: (84)). This  
336 setting made it impossible to miss tagged individuals visiting the colony. To account for  
337 dispersal from the study colony to neighboring colonies within a 10-km radius (Fig. 1), a grid  
338 of mobile RFID detection units (2-8 units, Fig. S2) was deployed every year from November  
339 to March, starting in 2013. Mobile RFID units were positioned at natural bottlenecks frequently  
340 used by penguins traveling between colonies and the sea. Units were moved every one to two  
341 weeks to maximize the number of detections. Among the 1061 individuals reobserved at least  
342 once after their tagging year, only 19 (1.8%) were detected exclusively by mobile RFID  
343 antennas, i.e. away from their natal colony. The mobile RFID-units resighting effort was more  
344 intensive closer to the study colony (< 200 m) but was performed up to 10 km from it (Fig. 1).

345

346 • *Colony and individual-scale parameters*

347

348 Colony-scale breeding productivity was defined as the number of fledglings, divided by the  
349 annual maximum number of adults inside the colony divided by two (a proxy for the number  
350 of breeding pairs). Individuals present in the colony were photo-counted weekly during the  
351 whole breeding season, starting in 2011. Cohort size was taken as the total number of RFID-  
352 tagged chicks that fledged. We ensured that observations from the study colony were  
353 representative of the larger-scale Pointe Géologie archipelago by comparing our local estimate  
354 of breeding productivity with data available from the literature for Pointe Géologie (2011-2017,  
355 (85)). Similarly, to ensure that our monitoring setup did not impact breeding abundance at the  
356 colony, we compared the trend in number of breeding pairs in the study colony with that of two  
357 other undisturbed colonies located on the same island for the 2011-2024 period (Fig. S7).

358

359 All RFID-tagged chicks were weighed during tagging to the nearest 0.05 kg. The timing of  
360 tagging was adjusted to annual chick departure phenology (i.e. starting when the first molting  
361 chick was observed in the colony), ensuring mass was comparable across years. Each year,  
362 tagging occurred 10-15 days prior to fledging, making chick mass at tagging a reliable and  
363 consistent proxy for fledging mass (62). In Pointe Géologie archipelago, fledging occurs from  
364 late February to early March.

365

366 • *Capture Mark Recapture (CMR) modeling and statistical analyses*

367

368 To model apparent survival and recapture probabilities of juvenile Adélie penguins, we  
369 constructed capture histories for all individuals ( $n = 3,062$ ) fledged between 2007 and 2022,  
370 and subsequently observed between the 2009 and 2023 breeding seasons. Out of these 3,062  
371 fledglings, 1,061 were observed again in subsequent years.

372

373 Given the dispersal of some birds from the study colony to neighboring colonies, and the higher  
374 resighting effort on and near the study colony, we adopted a multi-state framework to model  
375 survival, recapture, and transition probabilities (86). We implemented this framework in the  
376 program MARK v.9.0 (87). Different resighting probabilities among colonies were accounted  
377 for using a two-state classification: a local state (1) for the study colony and adjacent colonies  
378 within 200 meters, and a distant state (2) for all colonies located more than 200 meters from  
379 the study colony. This allowed closing the system and enhancing the robustness of survival  
380 estimates despite short-range dispersal dynamics. As the detection probability of 1-year-old  
381 individuals was near 0 (only a single bird was detected at age 1, Fig. S3), it was not possible to  
382 compute survival probability between ages 0 and 1. The first recapture occasion following  
383 tagging was thus deleted for all individuals (supplementary text). Consequently, juvenile  
384 survival was estimated between 0 and 2 years old.

385

386 We used U-CARE software (88) to evaluate the goodness of fit (GOF) of the two-states time-  
387 dependent (JollyMoVe, JMV) model to our dataset (89). The JMV model did not fit the original  
388 dataset because of transients (i.e. individuals never reencountered after tagging, Table S1a).  
389 We thus tested the GOF of the JMV model to a dataset where the first capture was set to 0 for  
390 each individual (i.e. effectively making capture history of each individual start at first  
391 reencounter following tagging, see supplementary text), thereby allowing to test the fit of a  
392 model with extended age-dependence on survival and recapture probabilities. The fit of the  
393 JMV model to this dataset was satisfactory (Table S1), albeit with indications of further age  
394 structure (i.e.  $>$  two age classes) in survival probabilities (significant test 3G.SM, Table S1b)  
395 and capture probabilities (almost significant Test M.ITEC, Table S1b). This validated the use  
396 of an initial umbrella model incorporating  $\geq$  two age classes on recapture, survival, and  
397 transition probabilities (model 1, Table S3).

398

399 In Adélie penguins, presence at the breeding colony (and thus availability for detection) is  
400 conditional on age, with reproductively mature individuals more likely to visit colonies than  
401 pre-breeders. Survival is also age-dependent, with lower survival probability in juveniles

402 compared to adults (33). Earlier studies of known-age Adélie penguins have therefore  
403 accounted for age-structured recapture and survival probabilities, with either two (29), three  
404 (34), or five age classes (33). Here, we started from a model with five age classes on survival,  
405 recapture, and transition probabilities, and explored all the possibilities in each submodel down  
406 to only two age classes. Finally, our starting (umbrella) model was adjusted to account for the  
407 low number of individuals detected in distant colonies. This model was framed with age  
408 variation only (no time effects) for all transition probabilities, and recapture probabilities in the  
409 distant colonies (state 2). The survival probabilities in both states (i.e. local and distant) were  
410 also set to be equal in that model, which appears as a reasonable assumption considering that  
411 all colonies belong to the same population of Pointe Géologie archipelago (Fig. 1). We  
412 successively looked for the most appropriate age and time structure for recapture, transition,  
413 and survival probabilities, using the previously retained best structure for each submodel. The  
414 most parsimonious model was retained when two models were within two AIC points of each  
415 other. This selection process yielded an optimal model (model 13, Table S3) including two age  
416 classes (0-2 and 3+) and time effects within each age class for survival probabilities. Recapture  
417 probabilities were best modeled using three age classes in both states. The best structure  
418 included additional time effects in each of these three age classes for the local state only (Table  
419 S3). Transition probabilities were best modeled with state and age effects (five age classes in  
420 each state, Table S3). Because survival and recapture probabilities are not separable for the last  
421 year (2021) in time-dependent CMR models, this model allowed to estimate juvenile (0-2)  
422 survival from 2007 to 2020 only. Estimates of recapture probability in the local state were low  
423 and displayed high inter-annual variability for the first age class (mean  $\pm$  SD:  $0.33 \pm 0.24$ , Fig.  
424 S9), but were high and stable in the last age class (mean  $\pm$  SD:  $0.96 \pm 0.05$ , Fig. S9). Recapture  
425 probabilities in the distant state were estimated for the last age class only and were particularly  
426 low (0.02, SE = 0.009, Fig. S9). This model was then used as a basis for testing the effect of  
427 selected covariates on juvenile survival (see below).

428

429 • *Covariate selection and definition*

430

431 Candidate environmental variables were considered based on relevance to the Adélie penguin's  
432 ecology and previous studies of Antarctic seabirds (Table S2). We first considered two large-  
433 scale indices, indicators of broad climatic variations in Antarctica and the surrounding Southern  
434 Ocean: the Southern Oscillation Index (SOI) and the Southern Annular Mode (SAM).  
435 Together, they affect wind patterns, temperatures, and sea ice dynamics, with complex

436 regional-specific variability (6, 90). Such variability has been linked to opposite responses both  
437 among and within species. For instance, positive SOI values were previously linked to lower  
438 survival in adult Adélie penguins in Adélie Land (32) but no support for such an effect was  
439 found in Mac. Robertson Land (34), the Western Ross Sea (33), or the Antarctic Peninsula  
440 (29). High SAM values were also found to affect the survival of other Antarctic seabirds, either  
441 positively (adult Cape petrel, *Daption capense*, (91); juvenile Emperor penguins, *Aptenodytes*  
442 *forsteri*, (92) or negatively (juvenile Snow petrels, *Pagodroma nivea*, (93)). Monthly SOI data  
443 were downloaded from the NOAA National Centers for Environmental Information  
444 (<https://www.cpc.ncep.noaa.gov/data/indices/soi>) and daily SAM data from the NOAA  
445 Climate Prediction Center  
446 ([https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily\\_ao\\_index/aao/aao.shtml](https://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao.shtml)).

447  
448 Regional sea ice extent anomalies (SIEA) were also considered because of the quadratic  
449 relationship previously observed between SIEA and the survival of adult Adélie penguins in  
450 the Western Ross Sea (33). Monthly data for the Western Pacific sector (90°E to 150°E), which  
451 encompasses our study site, were downloaded from the National Snow and Ice Data Center  
452 (NSDIC, <https://nsidc.org/data/g02135/versions/3>). To capture the conditions experienced by  
453 juveniles after fledging and during their first winter at sea, each index (SOI, SAM, SIEA) was  
454 averaged from March to September (34), resulting in one value per year per index.

455  
456 At the local scale, we considered both linear and quadratic effects of the average windchill  
457 temperatures (WCT) between April and September, based on the quadratic relationship  
458 previously observed between WCT and the survival of juvenile Adélie penguins (31). Ten-day  
459 average data of minimum temperature and average relative humidity from the Dumont  
460 D'Urville weather station were downloaded from Meteo France (<https://meteo.data.gouv.fr/>)  
461 and used to calculate WCT following the Australian Bureau of Meteorology calculation (as in  
462 (31)).

463  
464 Finally, we considered sea ice concentrations (SIC, average sea ice concentration in a specific  
465 area) at three different spatio-temporal scales (Fig. S4). As tracking data for juveniles is  
466 currently not available in our focal region, we considered broadly similar migration routes as  
467 those of adults previously studied at Pointe Géologie and found to gradually move westward  
468 after reproduction following the Antarctic coastal current (94). This pattern is corroborated by  
469 the tracking of both juveniles and adults in another east Antarctica population (34, 57) and

470 therefore likely in our study area. To reflect post-fledging (autumn) conditions experienced by  
471 birds near their natal colony, we considered March-April SIC between 135°E and 145°E  
472 (SIC.autumn). We also considered winter (May-July, SIC.winter) and late winter (August-  
473 September, SIC.latewinter) conditions, both between 110°E and 135°E. Sea ice concentrations  
474 were computed by averaging daily concentration values from 25×25 km grids downloaded  
475 from the NSDIC ((95), <https://nsidc.org/data/g02202/versions/4>) over the spatio-temporal  
476 windows defined above. Following initial analyses, we further adjusted our sea ice metrics by  
477 first decomposing SIC.autumn into March and April SIC (SIC.march, SIC.april). Because  
478 different types of ice may affect seabirds differently (96), we then calculated the April fraction  
479 of the total ice area (15-100% SIC) covered by the marginal ice zone (loose sea ice between  
480 15-80% SIC, MIZFRAC.april) and the April fraction of the total ice area covered by dense  
481 pack ice (80-100% SIC, DENSEFRAC.april).

482

483 We also considered cohort size and average mass at tagging (as a proxy for fledging mass, (62))  
484 as likely intrinsic drivers of juvenile survival in Adélie penguins. Cohort size was shown to  
485 correlate positively with fledgling survival in a previous study (31), while fledging mass is a  
486 common predictor for juvenile survival in birds (e.g., (97)), including penguins (62, 98). The  
487 effect of fledging mass on inter-annual differences in survival probabilities was investigated  
488 by using mean fledging mass (MFM) for each cohort. Inter-individual, within-season effects  
489 of fledging mass were also investigated, using chick mass as an individual covariate.

490

491 To avoid including covariates that are correlated with each other (multicollinearity, see (23)),  
492 we checked for pair-wise correlations among our initial set of covariates (SOI, SAM, SIEA,  
493 SIC.autumn, SIC.winter, SIC.latewinter, WCT, MFM, cohort size). Only SIC.winter was  
494 correlated strongly enough ( $r > 0.7$ , (99)) with two other closely related sea ice metrics (SIEA  
495 and SIC.latewinter) so that we decided to drop this covariate from analyses. Remaining  
496 covariates were scaled to improve model convergence and facilitate parameters comparisons.  
497 Covariates were tested in isolation and considered influential when the 95% confidence interval  
498 (CI) of the effect size did not overlap 0 and when accounting for  $\geq 20\%$  of the temporal  
499 variation in survival rates (23). The support for a linear trend in juvenile survival was assessed  
500 using ANODEV (23). The effect of individual mass on survival was investigated using  
501 Likelihood Ratio Tests (LRT).

502



503 Homoscedasticity and normality assumptions were assessed where appropriate. Values are  
504 reported as means  $\pm$  SD unless mentioned otherwise. Statistical analyses other than the CMR  
505 modeling were conducted in R version 4.3.2 (100).

506

## 507 **References:**

- 508 1. A. Constable, J. Melbourne-Thomas, S. Corney, K. Arrigo, D. Barnes, N. Bindoff, P. Boyd, A.  
509 Brandt, D. Costa, A. Davidson, H. Ducklow, L. Emmerson, M. Fukuchi, J. Gutt, M. Hindell, E.  
510 Hofmann, G. Hosie, T. Iida, P. Ziegler, Climate change and Southern Ocean ecosystems I: How  
511 changes in physical habitats directly affect marine biota. *Glob. Change Biol.* **20** (2014).
- 512 2. S. L. Chown, R. I. Leihy, T. R. Naish, C. M. Brooks, P. Convey, B. J. Henley, A. N. Mackintosh,  
513 L. M. Phillips, M. C. K. Ii, S. M. Grant, Antarctic Climate Change and the Environment.
- 514 3. C. M. Brooks, D. G. Ainley, P. A. Abrams, P. K. Dayton, R. J. Hofman, J. Jacquet, D. B. Siniff,  
515 Antarctic fisheries: factor climate change into their management. *Nature* **558**, 177–180 (2018).
- 516 4. M. C. Urban, G. Bocedi, A. P. Hendry, J.-B. Mihoub, G. Pe'er, A. Singer, J. R. Bridle, L. G.  
517 Crozier, L. De Meester, W. Godsoe, A. Gonzalez, J. J. Hellmann, R. D. Holt, A. Huth, K. Johst,  
518 C. B. Krug, P. W. Leadley, S. C. F. Palmer, J. H. Pantel, A. Schmitz, P. A. Zollner, J. M. J.  
519 Travis, Improving the forecast for biodiversity under climate change. *Science* **353**, aad8466  
520 (2016).
- 521 5. H. Lee, K. Calvin, D. Dasgupta, G. Krinner, A. Mukherji, P. W. Thorne, C. Trisos, J. Romero, P.  
522 Aldunce, K. Barrett, G. Blanco, W. W. L. Cheung, S. Connors, F. Denton, A. Diongue-Niang, D.  
523 Dodman, M. Garschagen, O. Geden, B. Hayward, C. Jones, F. Jotzo, T. Krug, R. Lasco, Y. -Y.  
524 Lee, V. Masson-Delmotte, M. Meinshausen, K. Mintenbeck, A. Mokssit, F. E. L. Otto, M.  
525 Pathak, A. Pirani, E. Poloczanska, H. -O. Pörtner, A. Revi, D. C. Roberts, J. Roy, A. C. Ruane, J.  
526 Skea, P. R. Shukla, R. Slade, A. Slangen, Y. Sokona, A. A. Sörensson, M. Tignor, D. Van  
527 Vuuren, Y. -M. Wei, H. Winkler, P. Zhai, Z. Zommers, J. -C. Hourcade, F. X. Johnson, S.  
528 Pachauri, N. P. Simpson, C. Singh, A. Thomas, E. Totin, P. Arias, M. Bustamante, I. Elgizouli,  
529 G. Flato, M. Howden, C. Méndez-Vallejo, J. J. Pereira, R. Pichs-Madruga, S. K. Rose, Y. Saheb,  
530 R. Sánchez Rodríguez, D. Üрге-Vorsatz, C. Xiao, N. Yassaa, A. Alegría, K. Armour, B. Bednar-  
531 Friedl, K. Blok, G. Cissé, F. Dentener, S. Eriksen, E. Fischer, G. Garner, C. Guivarch, M.  
532 Haasnoot, G. Hansen, M. Hauser, E. Hawkins, T. Hermans, R. Kopp, N. Leprince-Ringuet, J.  
533 Lewis, D. Ley, C. Ludden, L. Niamir, Z. Nicholls, S. Some, S. Szopa, B. Trewin, K. -I. Van Der  
534 Wijnst, G. Winter, M. Witting, A. Birt, M. Ha, J. Romero, J. Kim, E. F. Haites, Y. Jung, R.  
535 Stavins, A. Birt, M. Ha, D. J. A. Orendain, L. Ignon, S. Park, Y. Park, A. Reisinger, D.

- 536 Cammaramo, A. Fischlin, J. S. Fuglestedt, G. Hansen, C. Ludden, V. Masson-Delmotte, J. B. R.  
537 Matthews, K. Mintenbeck, A. Pirani, E. Poloczanska, N. Leprince-Ringuet, C. Péan, “IPCC,  
538 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to  
539 the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing  
540 Team, H. Lee and J. Romero (eds.)]. IPCC, Geneva, Switzerland.” (Intergovernmental Panel on  
541 Climate Change (IPCC), 2023); <https://doi.org/10.59327/IPCC/AR6-9789291691647>.
- 542 6. R. L. Fogt, G. J. Marshall, The Southern Annular Mode: Variability, trends, and climate impacts  
543 across the Southern Hemisphere. *WIREs Clim. Change* **11**, e652 (2020).
- 544 7. C. L. Parkinson, D. J. Cavalieri, Antarctic sea ice variability and trends, 1979&ndash;2010. *The*  
545 *Cryosphere* **6**, 871–880 (2012).
- 546 8. F. Olivier, J. A. van Franeker, J. C. S. Creuwels, E. J. Woehler, Variations of snow petrel  
547 breeding success in relation to sea-ice extent: detecting local response to large-scale processes?  
548 *Polar Biol.* **28**, 687–699 (2005).
- 549 9. S. Descamps, A. Tarroux, S.-H. Lorentsen, O. P. Love, Ø. Varpe, N. G. Yoccoz, Large-scale  
550 oceanographic fluctuations drive Antarctic petrel survival and reproduction. *Ecography* **39**, 496–  
551 505 (2016).
- 552 10. S. Labrousse, A. D. Fraser, M. Sumner, F. Le Manach, C. Sauser, I. Horstmann, E. Devane, K.  
553 Delord, S. Jenouvrier, C. Barbraud, Landfast ice: a major driver of reproductive success in a polar  
554 seabird. *Biol. Lett.* **17**, 20210097 (2021).
- 555 11. D. T. Iles, H. Lynch, R. Ji, C. Barbraud, K. Delord, S. Jenouvrier, Sea ice predicts long-term  
556 trends in Adélie penguin population growth, but not annual fluctuations: Results from a range-  
557 wide multiscale analysis. *Glob. Change Biol.* **26**, 3788–3798 (2020).
- 558 12. B. Şen, C. Che-Castaldo, K. M. Krumhardt, L. Landrum, M. M. Holland, M. A. LaRue, M. C.  
559 Long, S. Jenouvrier, H. J. Lynch, Spatio-temporal transferability of environmentally-dependent  
560 population models: Insights from the intrinsic predictabilities of Adélie penguin abundance time  
561 series. *Ecol. Indic.* **150**, 110239 (2023).
- 562 13. W. R. Fraser, W. Z. Trivelpiece, *Factors Controlling the Distribution of Seabirds: Winter-*  
563 *Summer Heterogeneity in the Distribution of Adélie Penguin Populations* (American Geophysical  
564 Union, Washington, D. C., 1996; <http://doi.wiley.com/10.1029/AR070>) vol. 70 of *Antarctic*  
565 *Research Series*.
- 566 14. R. C. Smith, D. Ainley, K. Baker, E. Domack, S. Emslie, B. Fraser, J. Kennett, A. Leventer, E.

- 567 Mosley-Thompson, S. Stammerjohn, M. Vernet, Marine Ecosystem Sensitivity to Climate  
568 Change: Historical observations and paleoecological records reveal ecological transitions in the  
569 Antarctic Peninsula region. *BioScience* **49**, 393–404 (1999).
- 570 15. D. Ainley, J. Russell, S. Jenouvrier, E. Woehler, P. O. Lyver, W. R. Fraser, G. L. Kooyman,  
571 Antarctic penguin response to habitat change as Earth’s troposphere reaches 2°C above  
572 preindustrial levels. *Ecol. Monogr.* **80**, 49–66 (2010).
- 573 16. M. A. Cimino, H. J. Lynch, V. S. Saba, M. J. Oliver, Projected asymmetric response of Adélie  
574 penguins to Antarctic climate change. *Sci. Rep.* **6**, 28785 (2016).
- 575 17. C. Che-Castaldo, S. Jenouvrier, C. Youngflesh, K. T. Shoemaker, G. Humphries, P. McDowall,  
576 L. Landrum, M. M. Holland, Y. Li, R. Ji, H. J. Lynch, Pan-Antarctic analysis aggregating spatial  
577 estimates of Adélie penguin abundance reveals robust dynamics despite stochastic noise. *Nat.*  
578 *Commun.* **8**, 832 (2017).
- 579 18. H. J. Lynch, M. A. LaRue, First global census of the Adélie Penguin. *The Auk* **131**, 457–466  
580 (2014).
- 581 19. G. R. W. Humphries, C. Che-Castaldo, P. J. Bull, G. Lipstein, A. Ravia, B. Carrión, T. Bolton, A.  
582 Ganguly, H. J. Lynch, Predicting the future is hard and other lessons from a population time  
583 series data science competition. *Ecol. Inform.* **48**, 1–11 (2018).
- 584 20. E. J. Talis, C. Che-Castaldo, B. Şen, K. Krumhardt, H. J. Lynch, Variability, skipped breeding  
585 and heavy-tailed dynamics in an Antarctic seabird. *J. Anim. Ecol.* **91**, 2437–2450 (2022).
- 586 21. D. Iles, S. Jenouvrier, “Projected population consequences of climate change” in *Effects of*  
587 *Climate Change on Birds* (Oxford University Press, 2019);  
588 [https://oxford.universitypressscholarship.com/view/10.1093/oso/9780198824268.001.0001/oso-](https://oxford.universitypressscholarship.com/view/10.1093/oso/9780198824268.001.0001/oso-9780198824268-chapter-12)  
589 [9780198824268-chapter-12](https://oxford.universitypressscholarship.com/view/10.1093/oso/9780198824268.001.0001/oso-9780198824268-chapter-12)), pp. 147–164.
- 590 22. M. Frederiksen, M. P. Harris, S. Wanless, Inter-population variation in demographic parameters:  
591 a neglected subject? *Oikos* **111**, 209–214 (2005).
- 592 23. V. Grosbois, O. Gimenez, J.-M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Møller, H.  
593 Weimerskirch, Assessing the impact of climate variation on survival in vertebrate populations.  
594 *Biol. Rev.* **83**, 357–399 (2008).
- 595 24. D. Irons, A. Petersen, T. Anker-Nilssen, Y. Artukhin, R. Barrett, D. Boertmann, M. Gavrilov, H.  
596 Gilchrist, E. Hansen, M. Hario, K. Kuletz, M. Mallory, F. Merkel, A. Mosbech, A. Labansen, B.

- 597 Olsen, H. Österblom, J. Reid, G. Robertson, H. Strøm, *Circumpolar Seabird Monitoring Plan*  
598 (2015).
- 599 25. A. Nicol-Harper, C. P. Doncaster, G. M. Hilton, K. A. Wood, T. H. G. Ezard, Conservation  
600 implications of a mismatch between data availability and demographic impact. *Ecol. Evol.* **13**,  
601 e10269 (2023).
- 602 26. B.-E. Sæther, Ø. Bakke, Avian Life History Variation and Contribution of Demographic Traits to  
603 the Population Growth Rate. *Ecology* **81**, 642–653 (2000).
- 604 27. C. Southwell, L. Emmerson, J. McKinlay, K. Newbery, A. Takahashi, A. Kato, C. Barbraud, K.  
605 DeLord, H. Weimerskirch, Spatially Extensive Standardized Surveys Reveal Widespread, Multi-  
606 Decadal Increase in East Antarctic Adélie Penguin Populations. *PLOS ONE* **10**, e0139877 (2015).
- 607 28. P. J. Kappes, K. M. Dugger, A. Lescroël, D. G. Ainley, G. Ballard, K. J. Barton, P. O. Lyver, P.  
608 R. Wilson, Age-related reproductive performance of the Adélie penguin, a long-lived seabird  
609 exhibiting similar outcomes regardless of individual life-history strategy. *J. Anim. Ecol.* **90**, 931–  
610 942 (2021).
- 611 29. J. T. Hinke, S. G. Trivelpiece, W. Z. Trivelpiece, Adélie penguin (*Pygoscelis adeliae*) survival  
612 rates and their relationship to environmental indices in the South Shetland Islands, Antarctica.  
613 *Polar Biol.* **37**, 1797–1809 (2014).
- 614 30. J. T. Hinke, S. G. Trivelpiece, W. Z. Trivelpiece, Variable vital rates and the risk of population  
615 declines in Adélie penguins from the Antarctic Peninsula region. *Ecosphere* **8**, e01666 (2017).
- 616 31. L. Emmerson, C. Southwell, Environment-triggered demographic changes cascade and compound  
617 to propel a dramatic decline of an Antarctic seabird metapopulation. *Glob. Change Biol.* **28**  
618 (2022).
- 619 32. S. Jenouvrier, C. Barbraud, H. Weimerskirch, Sea ice affects the population dynamics of Adélie  
620 penguins in Terre Adélie. *Polar Biol.* **29**, 413–423 (2006).
- 621 33. T. Ballerini, G. Tavecchia, S. Olmastroni, F. Pezzo, S. Focardi, Nonlinear effects of winter sea ice  
622 on the survival probabilities of Adélie penguins. *Oecologia* **161**, 253–265 (2009).
- 623 34. L. Emmerson, C. Southwell, Adélie penguin survival: age structure, temporal variability and  
624 environmental influences. *15* (2011).
- 625 35. A. E. Schmidt, A. Lescroël, S. Lisovski, M. Elrod, D. Jongsomjit, K. M. Dugger, G. Ballard, Sea  
626 ice concentration decline in an important Adélie penguin molt area. *Proc. Natl. Acad. Sci.* **120**,

- 627 e2306840120 (2023).
- 628 36. S. R. Rintoul, S. L. Chown, R. M. DeConto, M. H. England, H. A. Fricker, V. Masson-Delmotte,  
629 T. R. Naish, M. J. Siegert, J. C. Xavier, Choosing the future of Antarctica. *Nature* **558**, 233–241  
630 (2018).
- 631 37. B. Reid, An interpretation of the age structure and breeding status of an Adélie penguin  
632 population. *Notornis Q. J. Ornithol. Soc. N. Z.*, 193 (1968).
- 633 38. D. G. Ainley, *The Adélie Penguin: Bellwether of Climate Change* (Columbia University Press,  
634 New York, 2002).
- 635 39. J. A. Badia-Boher, J. Real, J. L. Riera, F. Bartumeus, F. Parés, J. M. Bas, A. Hernández-Matías,  
636 Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in  
637 mark-recapture analyses. *Sci. Rep.* **13**, 6970 (2023).
- 638 40. K. M. Dugger, G. Ballard, D. G. Ainley, K. J. Barton, Effects of Flipper Bands on Foraging  
639 Behavior and Survival of Adélie Penguins (*Pygoscelis Adeliae*). *The Auk* **123**, 858–869 (2006).
- 640 41. C. Saraux, C. Le Bohec, J. M. Durant, V. A. Viblanc, M. Gauthier-Clerc, D. Beaune, Y.-H. Park,  
641 N. G. Yoccoz, N. C. Stenseth, Y. Le Maho, Reliability of flipper-banded penguins as indicators  
642 of climate change. *Nature* **469**, 203–206 (2011).
- 643 42. W. R. Fraser, Wayne Z. Trivelpiece, D. G. Ainley, Susan G. Trivelpiece, Increases in Antarctic  
644 penguin populations: reduced competition with whales or a loss of sea ice due to environmental  
645 warming? *Polar Biol.* **11**, 525–531 (1992).
- 646 43. P. Wilson, D. Ainley, N. Nur, S. Jacobs, K. Barton, G. Ballard, J. Comiso, Adélie penguin  
647 population change in the pacific sector of Antarctica: relation to sea-ice extent and the Antarctic  
648 Circumpolar Current. *Mar. Ecol. Prog. Ser.* **213**, 301–309 (2001).
- 649 44. J. T. Hinke, K. Salwicka, S. G. Trivelpiece, G. M. Watters, W. Z. Trivelpiece, Divergent  
650 responses of *Pygoscelis* penguins reveal a common environmental driver. *Oecologia* **153**, 845–  
651 855 (2007).
- 652 45. J. T. Hinke, G. M. Watters, C. S. Reiss, J. A. Santora, M. M. Santos, Acute bottlenecks to the  
653 survival of juvenile *Pygoscelis* penguins occur immediately after fledging. *Biol. Lett.* **16**,  
654 20200645 (2020).
- 655 46. S. L. Cox, M. Authier, F. Orgeret, H. Weimerskirch, C. Guinet, High mortality rates in a juvenile  
656 free-ranging marine predator and links to dive and forage ability. *Ecol. Evol.* **10**, 410–430 (2020).

- 657 47. J.-M. Gaillard, C. Toïgo, Temporal variation in fitness component and population dynamics of  
658 large herbivores. **31**, 367–393 (2000).
- 659 48. B. Naef-Daenzer, M. U. Grüebler, Post-fledging survival of altricial birds: ecological  
660 determinants and adaptation. *J. Field Ornithol.* **87**, 227–250 (2016).
- 661 49. C. L. McIntyre, M. W. Collopy, M. S. Lindberg, Survival Probability and Mortality of Migratory  
662 Juvenile Golden Eagles from Interior Alaska. *J. Wildl. Manag.* **70**, 717–722 (2006).
- 663 50. R. Massom, P. Reid, S. Stammerjohn, B. Raymond, A. Fraser, S. Ushio, Change and Variability  
664 in East Antarctic Sea Ice Seasonality, 1979/80–2009/10. *PLoS ONE* **8**, e64756 (2013).
- 665 51. C. Eayrs, D. Holland, D. Francis, T. Wagner, R. Kumar, X. Li, Understanding the Seasonal Cycle  
666 of Antarctic Sea Ice Extent in the Context of Longer-Term Variability. *Rev. Geophys.* **57**, 1037–  
667 1064 (2019).
- 668 52. M. A. Morales Maqueda, A. J. Willmott, N. R. T. Biggs, Polynya Dynamics: a Review of  
669 Observations and Modeling. *Rev. Geophys.* **42** (2004).
- 670 53. K. R. Arrigo, G. L. van Dijken, A. L. Strong, Environmental controls of marine productivity hot  
671 spots around Antarctica. *J. Geophys. Res. Oceans* **120**, 5545–5565 (2015).
- 672 54. M. R. Enstipp, C.-A. Bost, C. Le Bohec, N. Chatelain, H. Weimerskirch, Y. Handrich, The early  
673 life of king penguins: ontogeny of dive capacity and foraging behaviour in an expert diver. *J. Exp.*  
674 *Biol.* **224**, jeb242512 (2021).
- 675 55. D. G. Ainley, G. Ballard, B. J. Karl, K. M. Dugger, Leopard seal predation rates at penguin  
676 colonies of different size. *Antarct. Sci.* **17**, 335–340 (2005).
- 677 56. A. Takahashi, M. Ito, K. Nagai, J. Thiebot, H. Mitamura, T. Noda, P. Trathan, T. Tamura, Y.  
678 Watanabe, Migratory movements and winter diving activity of Adélie penguins in East  
679 Antarctica. *Mar. Ecol. Prog. Ser.* **589**, 227–239 (2018).
- 680 57. J. Clarke, K. Kerry, C. Fowler, R. Lawless, S. Eberhard, R. Murphy, Post-fledging and winter  
681 migration of Adélie penguins *Pygoscelis adeliae* in the Mawson region of East Antarctica. *Mar.*  
682 *Ecol. Prog. Ser.* **248**, 267–278 (2003).
- 683 58. D. G. Ainley, G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, P. R. Wilson, Spatial  
684 and Temporal Variation of Diet Within a Presumed Metapopulation Of Adélie Penguins. *The*  
685 *Condor* **105**, 95–106 (2003).

- 686 59. M. Beaulieu, A. Dervaux, A.-M. Thierry, D. Lazin, Y. Le Maho, Y. Ropert-Coudert, M. Spée, T.  
687 Raclot, A. Ancel, When sea-ice clock is ahead of Adélie penguins' clock. *Funct. Ecol.* **24**, 93–  
688 102 (2010).
- 689 60. Y. Y. Watanabe, K. Ito, N. Kokubun, A. Takahashi, Foraging behavior links sea ice to breeding  
690 success in Antarctic penguins. *Sci. Adv.* **6**, eaba4828 (2020).
- 691 61. C. L. Guen, A. Kato, B. Raymond, C. Barbraud, M. Beaulieu, C.-A. Bost, K. Delord, A. J. J.  
692 MacIntosh, X. Meyer, T. Raclot, M. Sumner, A. Takahashi, J.-B. Thiebot, Y. Ropert-Coudert,  
693 Reproductive performance and diving behaviour share a common sea-ice concentration optimum  
694 in Adélie penguins (*Pygoscelis adeliae*). *Glob. Change Biol.* **24**, 5304–5317 (2018).
- 695 62. D. G. Ainley, K. M. Dugger, M. L. Mesa, G. Ballard, K. J. Barton, S. Jennings, B. J. Karl, A.  
696 Lescroël, P. O. Lyver, A. Schmidt, P. Wilson, Post-fledging survival of Adélie penguins at  
697 multiple colonies: chicks raised on fish do well. *Mar. Ecol. Prog. Ser.* **601**, 239–251 (2018).
- 698 63. E. Chapman, E. Hofmann, D. Patterson, C. Ribic, W. Fraser, Marine and terrestrial factors  
699 affecting Adélie-penguin *Pygoscelis adeliae* chick growth and recruitment off the western  
700 Antarctic Peninsula. *Mar. Ecol. Prog. Ser.* **436**, 273–289 (2011).
- 701 64. M. A. Cimino, J. A. Conroy, E. Connors, J. Bowman, A. Corso, H. Ducklow, W. Fraser, A.  
702 Friedlaender, H. H. Kim, G. D. Larsen, C. Moffat, R. Nichols, L. Pallin, D. Patterson-Fraser, D.  
703 Roberts, M. Roberts, D. K. Steinberg, P. Thibodeau, R. Trinh, O. Schofield, S. Stammerjohn,  
704 Long-term patterns in ecosystem phenology near Palmer Station, Antarctica, from the perspective  
705 of the Adélie penguin. *Ecosphere* **14**, e4417 (2023).
- 706 65. B.-E. Sæther, T. Coulson, V. Grøtan, S. Engen, R. Altwegg, K. B. Armitage, C. Barbraud, P. H.  
707 Becker, D. T. Blumstein, F. S. Dobson, M. Festa-Bianchet, J.-M. Gaillard, A. Jenkins, C. Jones,  
708 M. A. C. Nicoll, K. Norris, M. K. Oli, A. Ozgul, H. Weimerskirch, How Life History Influences  
709 Population Dynamics in Fluctuating Environments. *Am. Nat.* **182**, 743–759 (2013).
- 710 66. C. Barbraud, K. Delord, C. A. Bost, A. Chaigne, C. Marteau, H. Weimerskirch, Population trends  
711 of penguins in the French Southern Territories. *Polar Biol.* **43**, 835–850 (2020).
- 712 67. Y. Ropert-Coudert, A. Kato, K. Shiomi, C. Barbraud, F. Angelier, K. Delord, T. Poupart, P.  
713 Koubbi, T. Raclot, Two Recent Massive Breeding Failures in an Adélie Penguin Colony Call for  
714 the Creation of a Marine Protected Area in D'Urville Sea/Mertz. *Front. Mar. Sci.* **5** (2018).
- 715 68. J. Forcada, P. N. Trathan, K. Reid, E. J. Murphy, J. P. Croxall, Contrasting population changes in  
716 sympatric penguin species in association with climate warming. *Glob. Change Biol.* **12**, 411–423

- 717 (2006).
- 718 69. W. Z. Trivelpiece, J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, G. M. Watters,  
719 Variability in krill biomass links harvesting and climate warming to penguin population changes  
720 in Antarctica. *Proc. Natl. Acad. Sci.* **108**, 7625–7628 (2011).
- 721 70. H. J. Lynch, R. Naveen, P. N. Trathan, W. F. Fagan, Spatially integrated assessment reveals  
722 widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* **93**, 1367–1377  
723 (2012).
- 724 71. M. Wethington, C. Flynn, A. Borowicz, H. J. Lynch, Adélie penguins north and east of the  
725 ‘Adélie gap’ continue to thrive in the face of dramatic declines elsewhere in the Antarctic  
726 Peninsula region. *Sci. Rep.* **13**, 2525 (2023).
- 727 72. J. Turner, G. J. Marshall, K. Clem, S. Colwell, T. Phillips, H. Lu, Antarctic temperature  
728 variability and change from station data. *Int. J. Climatol.* **40**, 2986–3007 (2020).
- 729 73. N. Lecomte, The great melt will shape unprotected ecosystems. *Nature* **620**, 499–500 (2023).
- 730 74. K. M. Dugger, D. G. Ainley, P. O. Lyver, K. Barton, G. Ballard, Survival differences and the  
731 effect of environmental instability on breeding dispersal in an Adélie penguin meta-population.  
732 *Proc. Natl. Acad. Sci.* **107**, 12375–12380 (2010).
- 733 75. V. Morandini, K. M. Dugger, A. E. Schmidt, A. Varsani, A. Lescroël, G. Ballard, P. O. Lyver, K.  
734 Barton, D. G. Ainley, Sex-specific recruitment rates contribute to male-biased sex ratio in Adélie  
735 penguins. *Ecol. Evol.* **14**, e10859 (2024).
- 736 76. M. Gauthier-Clerc, J. P. Gendner, C. A. Ribic, W. R. Fraser, E. J. Woehler, S. Descamps, C.  
737 Gilly, C. Le Bohec, Y. Le Maho, Long-term effects of flipper bands on penguins. *Proc. R. Soc. B*  
738 *Biol. Sci.* **271**, S423–S426 (2004).
- 739 77. K. Kerry, J. Clarke, G. Else, The use of an automated weighing and recording system for the  
740 study of the biology of Adélie penguins. *Proc NIPR Symp Polar Biol* **6**, 62–75 (1993).
- 741 78. S. Olmastroni, S. Corsolini, F. Pezzo, S. Focardi, K. Kerry, The first five years of the Italian-  
742 Australian joint programme on the Adélie Penguin: An overview. *Ital. J. Zool.* **67**, 141–145  
743 (2000).
- 744 79. A. Lescroël, G. Ballard, D. Grémillet, M. Authier, D. G. Ainley, Antarctic Climate Change:  
745 Extreme Events Disrupt Plastic Phenotypic Response in Adélie Penguins. *PLOS ONE* **9**, e85291  
746 (2014).



- 747 80. J.-P. Gendner, M. Gauthier-Clerc, C. Le Bohec, S. Descamps, Y. Le Maho, A new application for  
748 transponders in studying penguins. *J. Field Ornithol.* **76**, 138–142 (2005).
- 749 81. G. Bardon, R. Cristofari, A. Winterl, T. Barracho, M. Benoiste, C. Ceresa, N. Chatelain, J.  
750 Courtecuisse, F. A. N. Fernandes, M. Gauthier-Clerc, J.-P. Gendner, Y. Handrich, A. Houstin, A.  
751 Krellenstein, N. Lecomte, C.-E. Salmon, E. Trucchi, B. Vallas, E. M. Wong, D. P. Zitterbart, C.  
752 Le Bohec, RFIDeep: Unfolding the potential of deep learning for radio-frequency identification.  
753 *Methods Ecol. Evol.* **14**, 2814–2826 (2023).
- 754 82. N. Dehnhard, K. Ludynia, M. Poisbleau, L. Demongin, P. Quillfeldt, Good Days, Bad Days:  
755 Wind as a Driver of Foraging Success in a Flightless Seabird, the Southern Rockhopper Penguin.  
756 *PLOS ONE* **8**, e79487 (2013).
- 757 83. V. Afanasyev, S. V. Buldyrev, M. J. Dunn, J. Robst, M. Preston, S. F. Bremner, D. R. Briggs, R.  
758 Brown, S. Adlard, H. J. Peat, Increasing Accuracy: A New Design and Algorithm for  
759 Automatically Measuring Weights, Travel Direction and Radio Frequency Identification (RFID)  
760 of Penguins. *PLOS ONE* **10**, e0126292 (2015).
- 761 84. S. Robinson, A. Chiaradia, M. A. Hindell, The effect of body condition on the timing and success  
762 of breeding in Little Penguins *Eudyptula minor*. *Ibis* **147**, 483–489 (2005).
- 763 85. E. Barreau, Y. Ropert-Coudert, K. Delord, C. Barbraud, A. Kato-Ropert, Scale matters: sea ice  
764 and breeding success of Adélie penguins. *Polar Biol.* **42**, 1405–1410 (2019).
- 765 86. J. Lebreton, J. D. Nichols, R. J. Barker, R. Pradel, J. A. Spendelow, “Chapter 3 Modeling  
766 Individual Animal Histories with Multistate Capture–Recapture Models” in *Advances in*  
767 *Ecological Research* (Elsevier, 2009);  
768 <https://linkinghub.elsevier.com/retrieve/pii/S0065250409004036> vol. 41, pp. 87–173.
- 769 87. G. C. White, K. P. Burnham, Program MARK: survival estimation from populations of marked  
770 animals. *Bird Study* **46**, S120–S139 (1999).
- 771 88. R. Choquet, J.-D. Lebreton, O. Gimenez, A.-M. Reboulet, R. Pradel, U-CARE: Utilities for  
772 performing goodness of fit tests and manipulating CAPTURE–REcapture data. *Ecography* **32**,  
773 1071–1074 (2009).
- 774 89. R. Pradel, C. M. A. Wintrebert, O. Gimenez, A Proposal for a Goodness-of-Fit Test to the  
775 Arnason-Schwarz Multisite Capture-Recapture Model. *Biometrics* **59**, 43–53 (2003).
- 776 90. R. Kwok, J. C. Comiso, Southern Ocean Climate and Sea Ice Anomalies Associated with the

- 777 Southern Oscillation. *J. Clim.* **15**, 487–501 (2002).
- 778 91. C. Sauser, K. Delord, C. Barbraud, Demography of cape petrels in response to environmental  
779 changes. *Popul. Ecol.* **65**, 25–37 (2021).
- 780 92. F. Abadi, C. Barbraud, O. Gimenez, Integrated population modeling reveals the impact of climate  
781 on the survival of juvenile emperor penguins. *Glob. Change Biol.* **23**, 1353–1359 (2017).
- 782 93. C. Sauser, K. Delord, C. Barbraud, Increased sea ice concentration worsens fledging condition  
783 and juvenile survival in a pagophilic seabird, the snow petrel. *Biol. Lett.* **14**, 20180140 (2018).
- 784 94. J.-B. Thiebot, Y. Ropert-Coudert, T. Raclot, T. Poupart, A. Kato, A. Takahashi, Adélie penguins’  
785 extensive seasonal migration supports dynamic Marine Protected Area planning in Antarctica.  
786 *Mar. Policy* **109**, 103692 (2019).
- 787 95. W. Meier, F. Fetterer, A. Windnagel, S. Stewart, NOAA/NSIDC Climate Data Record of Passive  
788 Microwave Sea Ice Concentration, Version 4, NSIDC (2021); [https://doi.org/10.7265/EFMZ-](https://doi.org/10.7265/EFMZ-2T65)  
789 2T65.
- 790 96. C. Sauser, P. Blévin, O. Chastel, G. W. Gabrielsen, S. A. Hanssen, E. Lorentzen, B. Moe, S.  
791 Moreau, K. Sagerup, S. Descamps, Ice type matters: impacts of landfast and drift ice on body  
792 condition in a high Arctic seabird community. *Front. Mar. Sci.* **11**, 1326658 (2024).
- 793 97. T. J. Maness, D. J. Anderson, Predictors of Juvenile Survival in Birds - Predictores de la  
794 Supervivencia de Aves Juveniles. *Ornithol. Monogr.* **78**, 1–55 (2013).
- 795 98. C. Horswill, J. Matthiopoulos, J. A. Green, M. P. Meredith, J. Forcada, H. Peat, M. Preston, P. N.  
796 Trathan, N. Ratcliffe, Survival in macaroni penguins and the relative importance of different  
797 drivers: individual traits, predation pressure and environmental variability. *J. Anim. Ecol.* **83**,  
798 1057–1067 (2014).
- 799 99. C. F. Dormann, J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber,  
800 B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B.  
801 Schröder, A. K. Skidmore, D. Zurell, S. Lautenbach, Collinearity: a review of methods to deal  
802 with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46 (2013).
- 803 100. R Core Team (2023). *\_R: A Language and Environment for Statistical Computing\_*. R  
804 Foundation for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.
- 805 101. K. Matsuoka, A. Skoglund, G. Roth, J. de Pomereu, H. Griffiths, R. Headland, B. Herried, K.  
806 Katsumata, A. Le Brocq, K. Licht, F. Morgan, P. D. Neff, C. Ritz, M. Scheinert, T. Tamura, A.

807 Van de Putte, M. van den Broeke, A. von Deschanden, C. Deschamps-Berger, B. Van  
808 Liefferinge, S. Tronstad, Y. Melvær, Quantarctica, an integrated mapping environment for  
809 Antarctica, the Southern Ocean, and sub-Antarctic islands. *Environ. Model. Softw.* **140**, 105015  
810 (2021).

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828

## 829 **Author contribution:**

830 Author contributions follow the CRediT guidelines. In each section, authors are listed by order  
831 of appearance in the author list.

832

833 Conceptualization: TB, NL, CLB

834 Methodology: TB, RCH, AH, MBE, RCR, TR, NC, JC, MBU, NL, CLB

835 Software: TB, GB, RCH

836 Validation: TB, NL, CLB

837 Formal analysis: TB, GB, RCH, NL

838 Investigation: All authors

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840 Data Curation: TB, GB, CCC, CLB

841 Writing – original draft preparation: TB, NL, CLB

842 Writing – review and editing: All authors

843 Visualization: TB

844 Supervision: NL, CLB

845 Project administration: CLB

846 Funding acquisition: DPZ, NL, CLB

847

848 **Competing interests:**

849 We declare no competing interests.

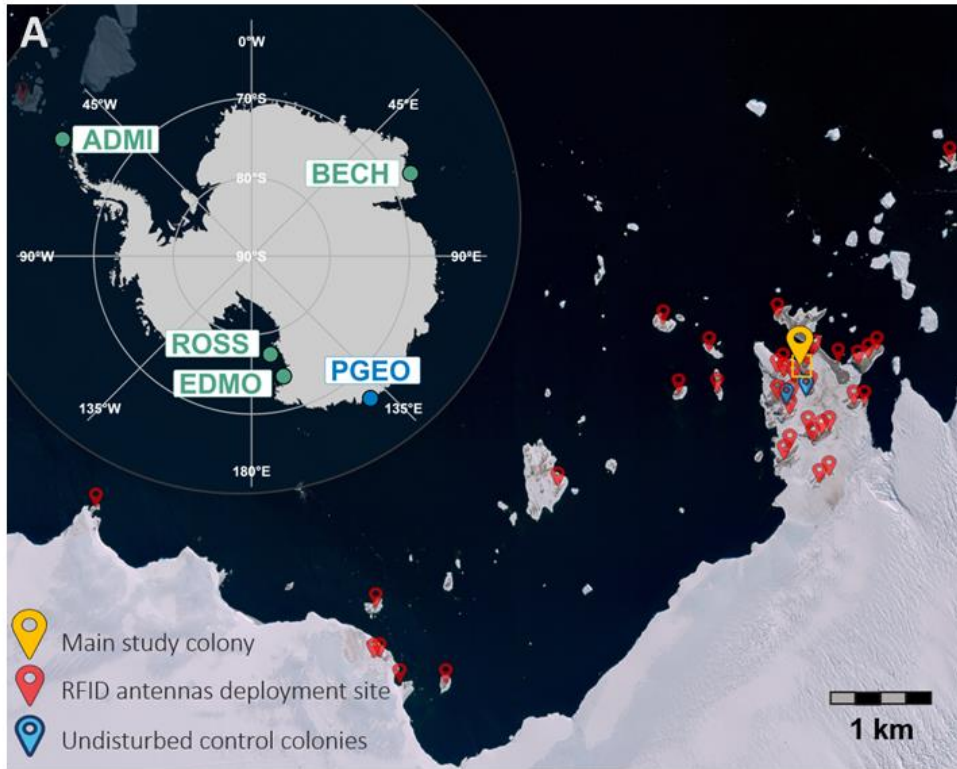
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851 **Data and material availability:**

852 Data and codes will be made available upon acceptance of the manuscript.

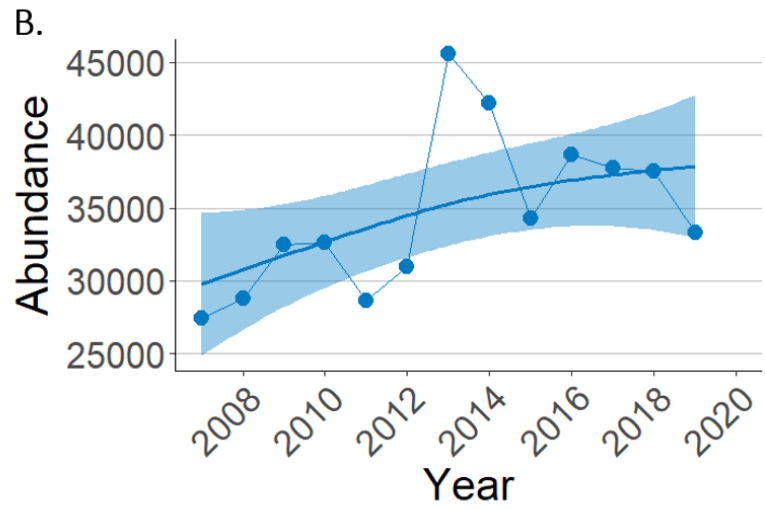
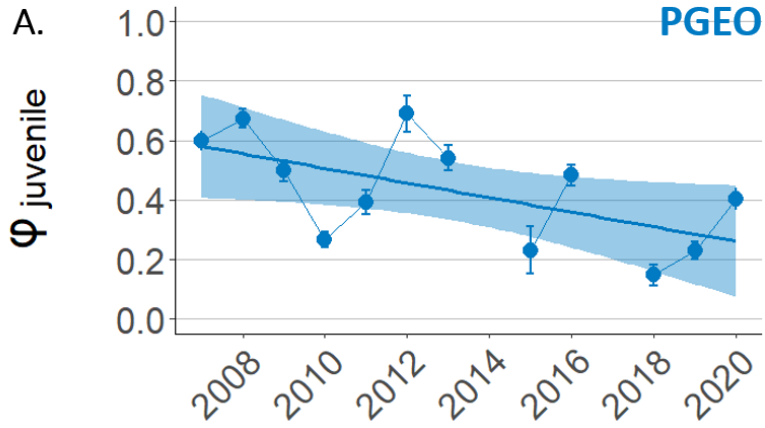
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854 **Figures and Tables:**

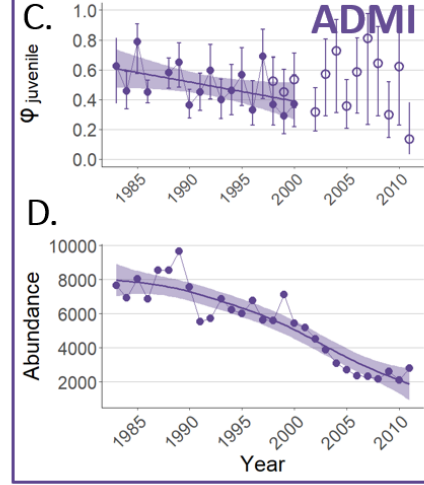


**Fig. 1. Overview of the Adélie penguin individual monitoring system operating in Pointe Géologie archipelago (Adélie Land) and location of similar monitoring sites across Antarctica still active as of 2024.** (A) Main panel: Satellite imagery of Pointe Géologie archipelago (Pléiades Neo, Airbus DS 2021, 12/10/2021) with locations of the mobile RFID-antennas deployment sites (red), undisturbed control colonies (blue) and the main study colony (yellow). Top-left inset: location of study sites across Antarctica where longitudinal monitoring of marked Adélie penguins is still carried out (ADMI: Admiralty Bay, BECH: Béchervaise Island, EDMO: Edmonson Point, PGEO: Pointe Géologie, ROSS: Ross Island (4 monitored colonies including one on neighboring Beaufort Island)). (B) Study colony in Pointe Géologie where all fledged chicks have been implanted with RFID-tags since 2007. (C) Penguins can only access or exit through two RFID-equipped passageways (only one shown here

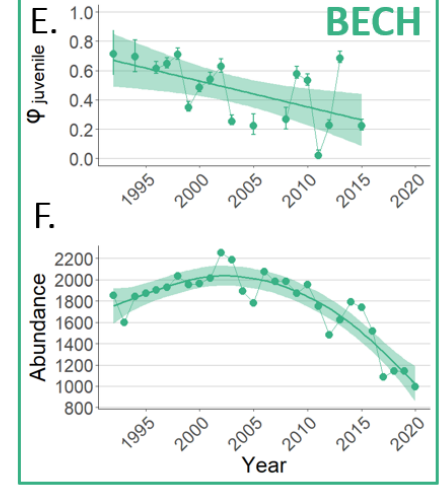
This study (survival) ; Barbraud et al. 2020 (abundance)



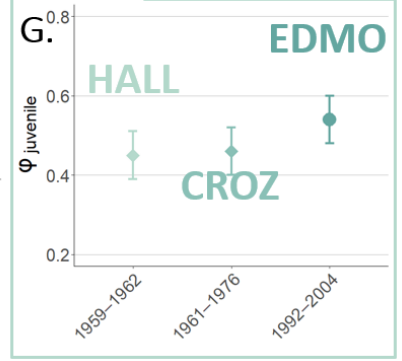
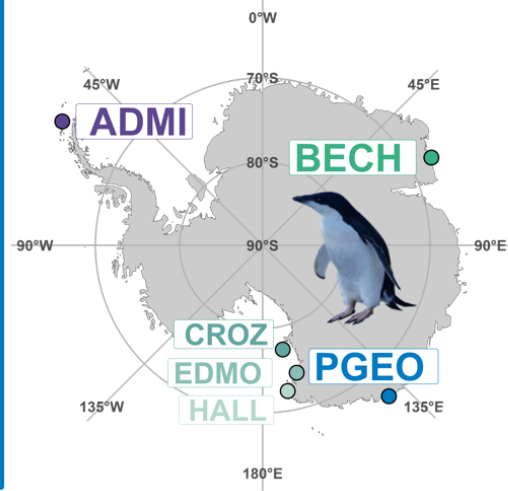
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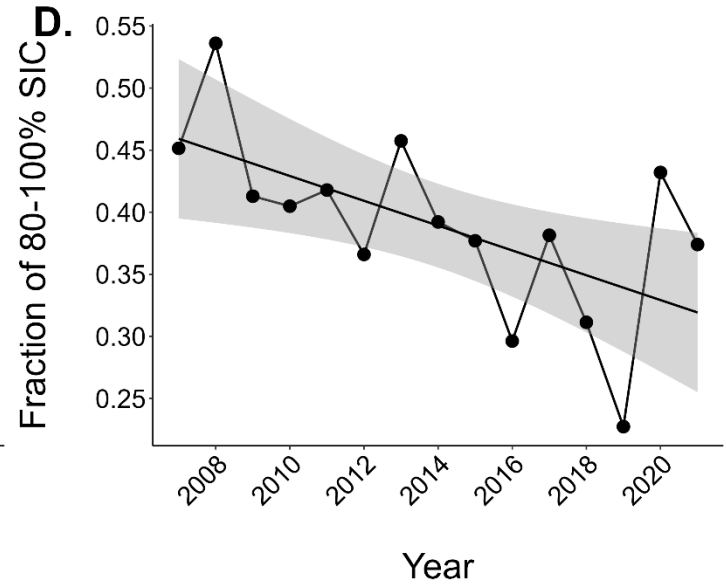
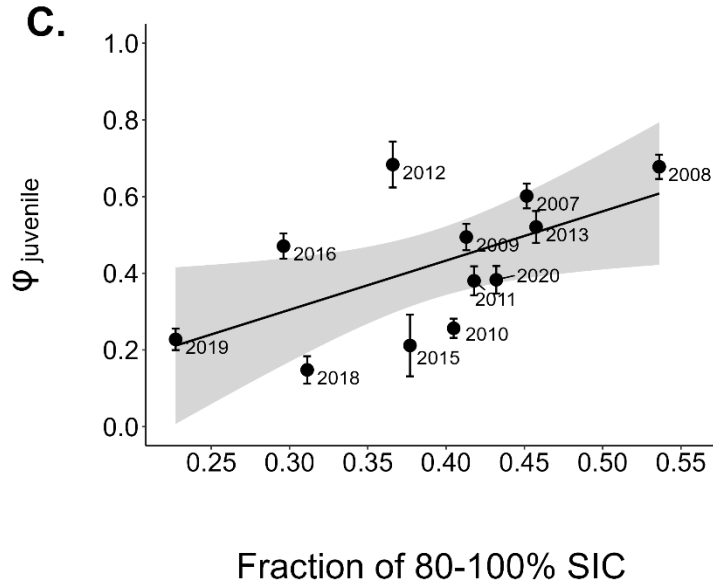
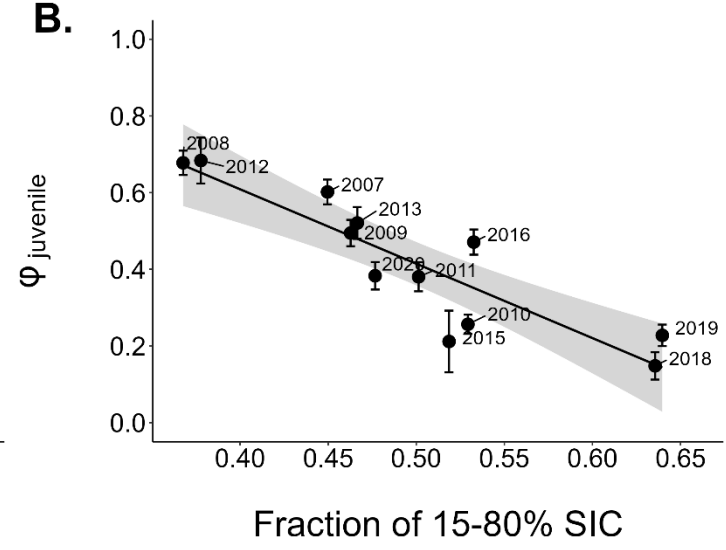
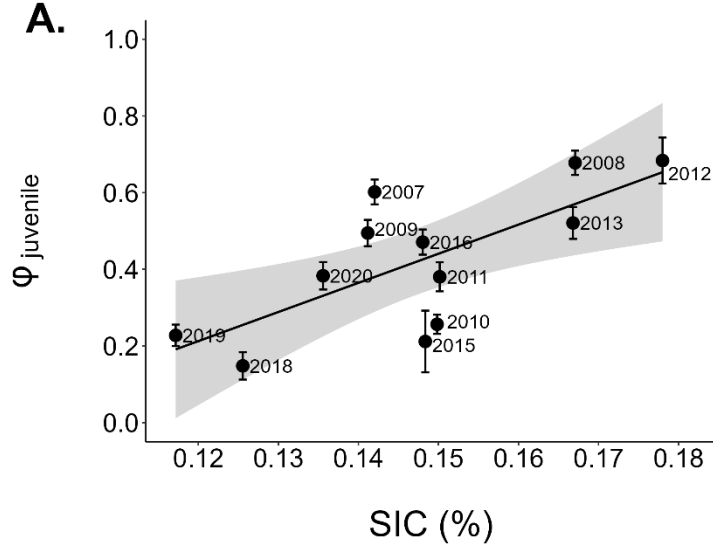


Reid 1968, Ainley 2002, Ballerini et al. 2009

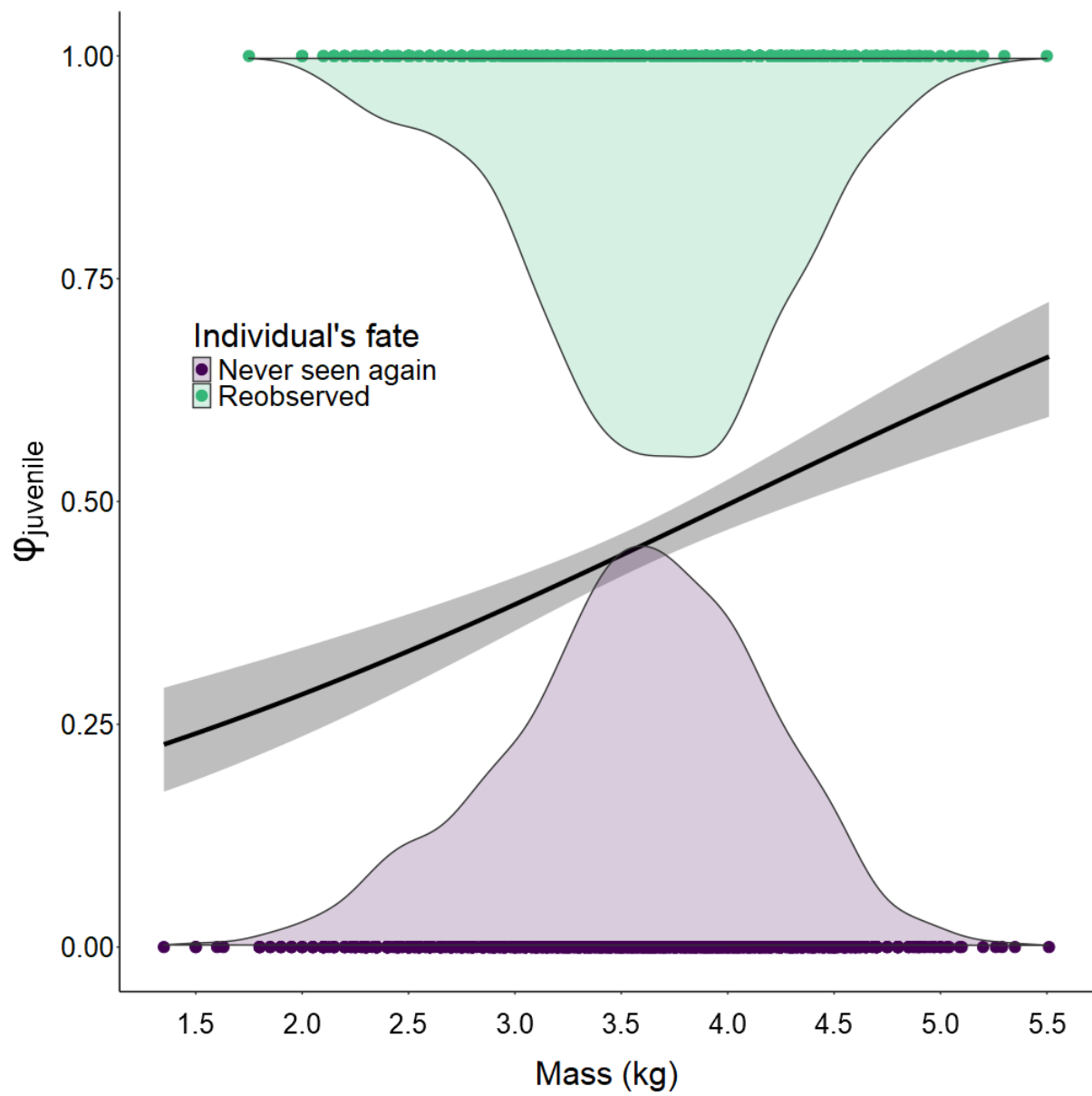


**Fig. 2. Summary of the six locations around Antarctica where Adélie penguin juvenile survival ( $\phi$ , 0-2 years old) has been quantified.** Among them, only three have investigated temporal variations. **A)** Survival of juvenile Adélie penguins from Pointe Géologie archipelago, Adélie Land (PGEO, electronic tagging, 2007-2020). The dots and intervals represent annual survival probabilities  $\pm$  SE. The regression line and associated SE are from a linear regression ( $p = 0.036$ ,  $R^2 = 0.37$ ); **B)** Adélie penguin abundance (number of breeding pairs) at Pointe Géologie Archipelago (2007-2019, data reproduced from (66)); **C-D)** Juvenile survival (1982-2000 aluminum bands, 1998-2011 stainless steel bands) and abundance (1982-2011) at Admiralty Bay, King George Island, Western Antarctic Peninsula (ADMI, data reproduced from (29, 30)); **E-F)** Juvenile survival (electronic tagging, 1992-2015) and abundance (1992-2020) at Béchervaise Island, Mac. Robertson Land (BECH, data reproduced from (31)); **G)** Only mean estimates were available for three populations in the Ross Sea: Cape Hallett, Victoria Land (HALL, metal bands, 1959-1962, data extracted from (37)), Cape Crozier, Ross Island (CROZ, aluminum bands, 1961-1976, data extracted from (38)), Edmondson Point, Victoria Land (EDMO, electronic tagging, 1994-2002, data extracted from (33)). Survival estimates from HALL and to a lesser extent CROZ should be compared to other estimates with caution because they were not computed using modern capture-recapture techniques accounting for imperfect detection as in the other studies. Juvenile survival time series were fitted with linear regressions when authors reported a linear trend (**A,C,E**). Abundance time series were fitted with Generalized Additive Models (GAM)





**Fig. 3. Relationships between the survival ( $\phi$ ) of juvenile Adélie penguins from Pointe Géologie archipelago (Adélie Land, East Antarctica) and several sea ice metrics within 200 kilometers of the natal colony for the month of April. A) Average sea ice concentration (SIC), B) Fraction of the total ice area (15-100% SIC) covered by the marginal ice zone (15-80% SIC), C) Fraction of total ice area (15-100% SIC) covered by dense ice (80-100% SIC). D) Time series (2007-2021) of the fraction of total ice area (15-100% SIC) covered by dense ice (80-100% SIC). Black thick lines and associated SE (gray shadow) on each panel are from linear regressions (respectively:  $p = 0.009$ ,  $R^2 = 0.51$  ;  $p < 0.001$ ,  $R^2 = 0.79$  ;  $p = 0.049$ ,  $R^2 = 0.33$  ;  $p = 0.016$ ,  $R^2 = 0.37$ ).**



**Fig. 4. Model-predicted relationship between Adélie penguin juvenile survival ( $\phi$ ) and body mass at tagging.** Modeling was carried out using the program MARK (87). The predicted relationship is drawn from model 34 (Table 1). Green and violet dots represent individuals, and shaded areas represent probability density for each fate.

**Table 1. Comparison of the effect of covariates on Adélie penguin juvenile survival probability.** Abbreviations: AICc, Akaike Information Criterion corrected for small sample sizes ;  $\Delta$ AICc, AICc difference between current model and time-dependant model ; K, number of parameters ; Dev, Model deviance ; p ANODEV, p-value of the analysis of deviance ; %DEV, percentage of the time-dependent model's deviance explained by the inclusion of covariate (23) ; LRT, Likelihood Ratio Test. Covariates abbreviations: see footnote and Table S2.

Footnote Table 1: MIZFRAC.april (April fraction of total ice area between 135°E-145°E covered by the marginal ice zone (15-80% SIC)) ; DENSEFRAC.april (April fraction of total ice area between 135°E-145°E covered by dense ice (80-100% SIC)) ; SIC.april (April average SIC in area between 135°E-145°E) ; SIC.autumn (Mar-Apr average SIC in area between 135°E-145°E) ; WCT (Windchill temperatures for Dumont D'Urville in Apr-Sept) ; SAM (Southern Annular Mode, Mar-Sept) ; SIC.march (March average SIC in area between 135°E-145°E) ; SIC.latewinter (Aug-Sept average SIC in area between 110°E-135°E) ; SOI (Southern Oscillation Index, Mar-Sept) ; SIEA (Sea Ice Extent Anomalies, Mar-Sept), SIC.winter (May-Jul average SIC in area between 110°E-135°E).

Index	Candidate model ( $\Phi$ 0-2)	AICc	$\Delta$ AICc	AICc Weights	K	Dev	Annual cov. models			Individual cov. models	
							p ANODEV	Slope [95%CI]	%DEV	$\chi^2$ LRT	p LRT
Annual covariate models											
13	time	12044.7	0	1	75	2303.7	-	-	-	-	-
<b>27</b>	<b>MIZFRAC.april</b>	<b>12068.2</b>	<b>23.4</b>	<b>0</b>	<b>62</b>	<b>2353.7</b>	<b>&lt;0.001</b>	<b>-0.97 [-0.99, -0.94]</b>	<b>78.8</b>	-	-
<b>28</b>	<b>DENSEFRAC.april</b>	<b>12160.1</b>	<b>115.3</b>	<b>0</b>	<b>62</b>	<b>2445.6</b>	<b>0.005</b>	<b>0.84 [0.82, 0.86]</b>	<b>39.7</b>	-	-
26	SIC.april	12160.8	116.1	0	62	2446.3	0.005	0.96 [0.93, 0.99]	39.4	-	-
30	linear	12180.5	135.7	0	62	2466.0	0.016	-0.02 [-0.03, -0.02]	31.1	-	-
22	SIC.autumn	12187.1	142.4	0	62	2472.6	0.023	0.92 [0.89, 0.95]	28.2	-	-
29	MFM	12201.8	157.1	0	62	2487.3	0.050	0.03 [0.03, 0.03]	22.0	-	-
20	WCT	12215.8	171.0	0	62	2501.3	0.099	0 [-0.03, 0.03]	16.1	-	-
21	WCT <sup>2</sup>	12217.0	172.2	0	63	2500.4	0.095	-	16.4	-	-
25	SIC.march	12220.3	175.5	0	62	2505.8	0.124	0.75 [0.74, 0.76]	14.2	-	-
17	SOI	12232.0	187.3	0	62	2525.7	0.340	0.03 [0, 0.07]	5.7	-	-
19	SIEA	12241.5	196.8	0	62	2527.0	0.365	0.02 [0.02, 0.03]	5.1	-	-
31	cohort size	12243.2	198.4	0	62	2528.6	0.400	0 [-0.01, 0.01]	4.4	-	-
23	SIC.winter	12244.6	199.9	0	62	2530.1	0.437	0.32 [0.31, 0.33]	3.8	-	-
18	SAM	12245.2	200.5	0	62	2530.7	0.453	-0.02 [-0.07, 0.04]	3.6	-	-
24	SIC.latewinter	12245.7	201.0	0	62	2531.2	0.467	-0.04 [-0.05, -0.02]	3.4	-	-
15	constant	12265.8	221.1	0	68	2539.1	-	-	0.0	-	-
Individual covariate models											
35	mass + time	12031.6	0.0	0.998	76	11878.0	-	-	-	15.227	<0.001
32	time	12044.7	13.2	0.001	75	11893.2	-	-	-	-	-
35	mass x time	12048.4	16.9	0.000	89	11868.3	-	-	-	24.935	0.0352
34	mass	12219.8	188.3	0.000	69	12080.6	-	-	-	48.014	<0.001
33	constant	12265.8	234.3	0.000	68	12128.6	-	-	-	-	-

## SUPPLEMENTARY MATERIAL:

### Supplementary Text

#### Manipulating capture histories to account for near-zero recapture probability at age 1 and for Goodness-Of-Fit (GOF) testing.

##### 1. Accounting for near-zero recapture probability at age 1

In capture-recapture modeling, the capture history (CH) of an individual is coded as a suite of numbers for each capture occasion. For example, if 0 = not seen ; 1 = seen in state 1 ; and 2 = seen in state 2, the individual A presented in the table below was tagged in state 1 in year 2, not seen in year 3, seen in state 1 in year 4 and seen in state 2 in year 5.

Year/Capture occasion	1	2	3	4	5
Capture history of individual A	0	1	0	1	2

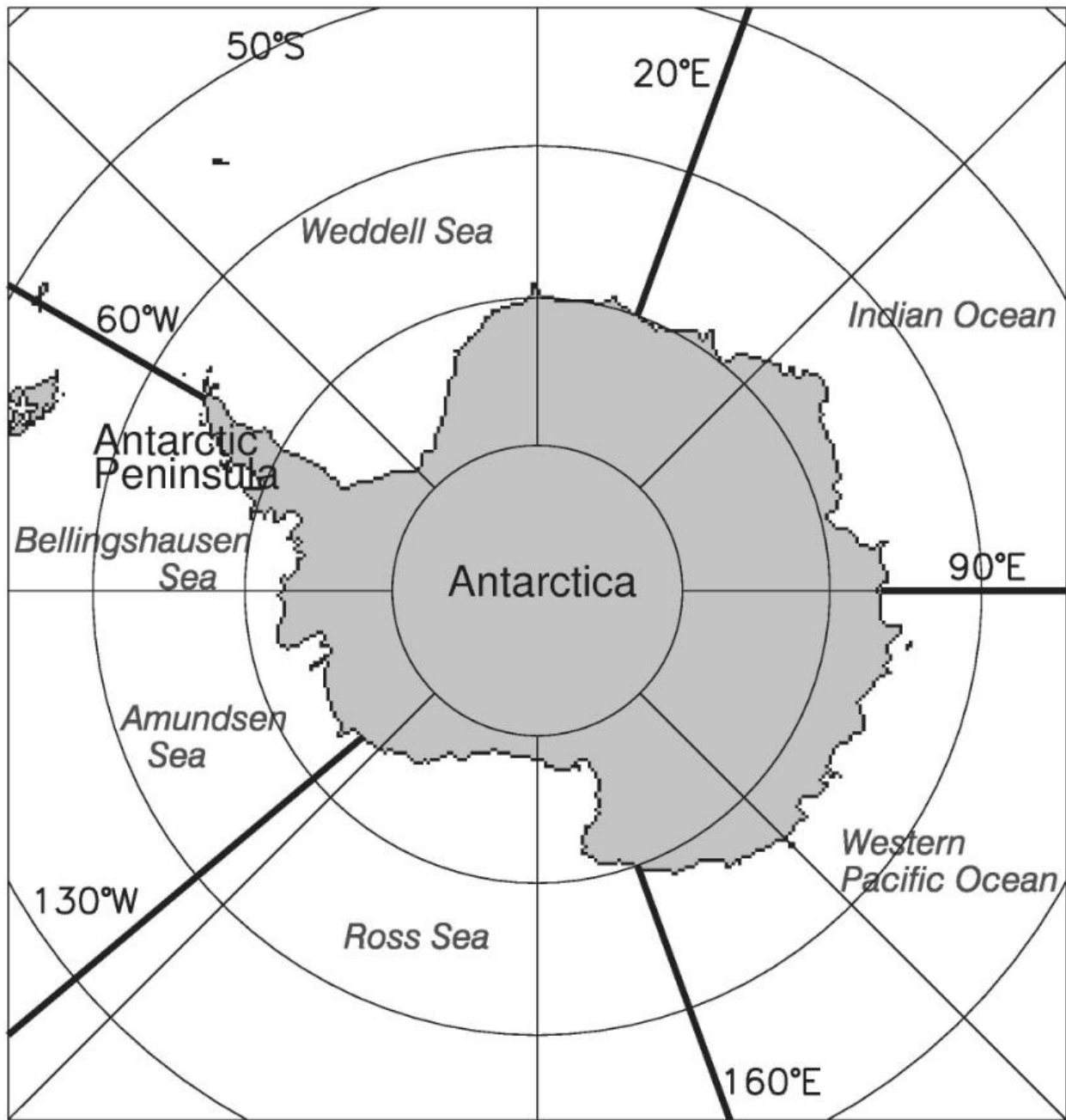
The CH of individual A can be written as: “01012”. Because recapture probabilities in the year following tagging (year 3 in the case of individual A) were near 0 in our study (only one individual was detected at one year old over our entire study period, Fig. S3), we rewrote CH of all individuals by removing the year after tagging. For example, the CH of individual A was transformed from “01012” into “0112”.

This allows accounting for the fact that with so few individuals seen again one year after fledging, it is not possible to estimate survival probability ( $\phi$ ) from age 0 to age 1 ( $\phi_{0 \rightarrow 1}$ ). Instead, we estimated survival from age 0 to age 2 ( $\phi_{0 \rightarrow 2}$ ). This is the typical “juvenile survival” in capture-recapture studies where individuals are not available for detection before two years after fledging. Under the specific (but untestable in this case) hypothesis that  $\phi_{0 \rightarrow 1} = \phi_{1 \rightarrow 2}$ , survival from age 0 to age 1 ( $\phi_{0 \rightarrow 1}$ ) can nonetheless be estimated as  $\sqrt{\phi_{0 \rightarrow 2}}$ .

##### 2. GOF testing

There is no direct GOF test for age-dependent, multistate capture-recapture models (88). However, the presence of transients (individuals never seen again after tagging) is a common source of age-dependence in recapture probabilities. To quantify how much of the lack of fit of a time-dependent (JollyMoVe, JMV) model can be attributed to transients, a common strategy is to test the GOF of the JMV model to a dataset where transients are removed by replacing the first capture of each individual by 0 in their capture histories. For example, in the dataset where transients are removed, the CH of individual A would be “00012”.

When the GOF of the dataset without transients is satisfactory, the original dataset (i.e. including transients) can be used but recapture probabilities must be specified as age-dependent in the starting model, therefore accounting for transience.



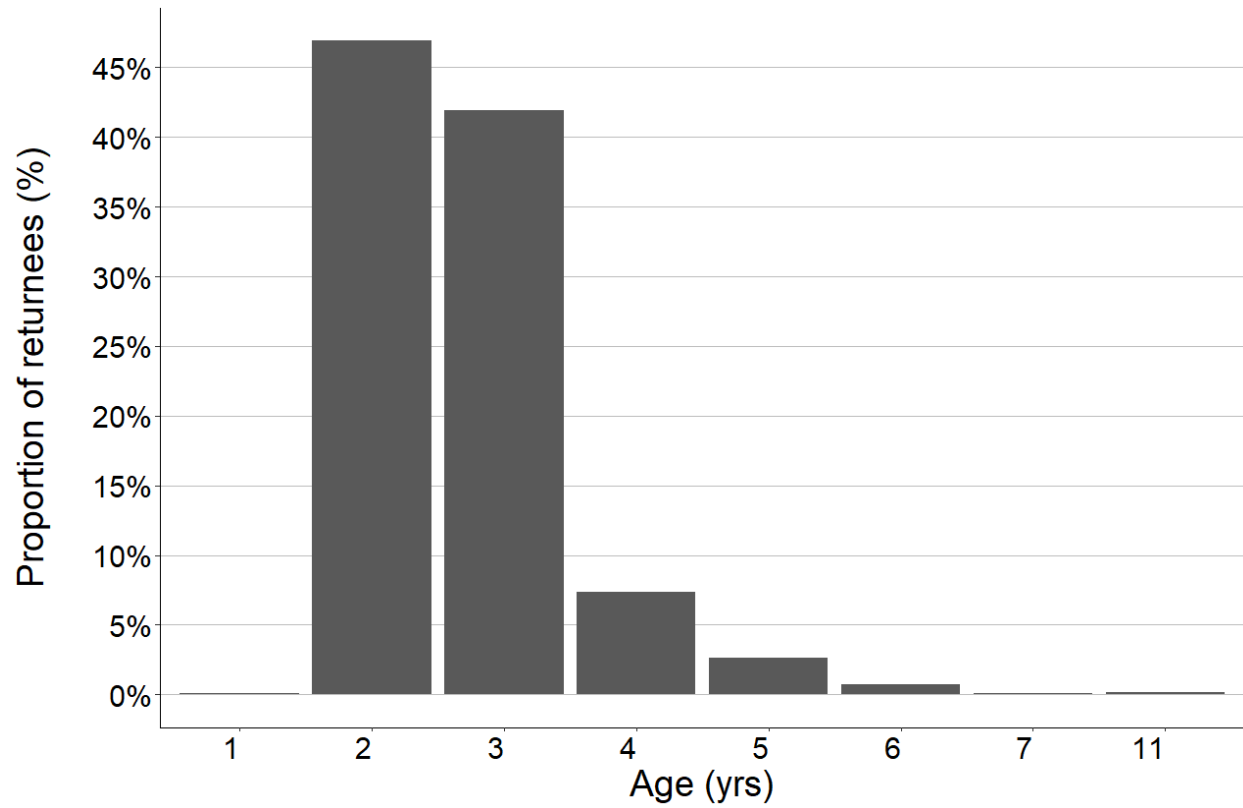
**Fig. S1.**  
Sectors of Antarctica used for large-scale sea ice analyses. Figure extracted from [\(7\)](#).



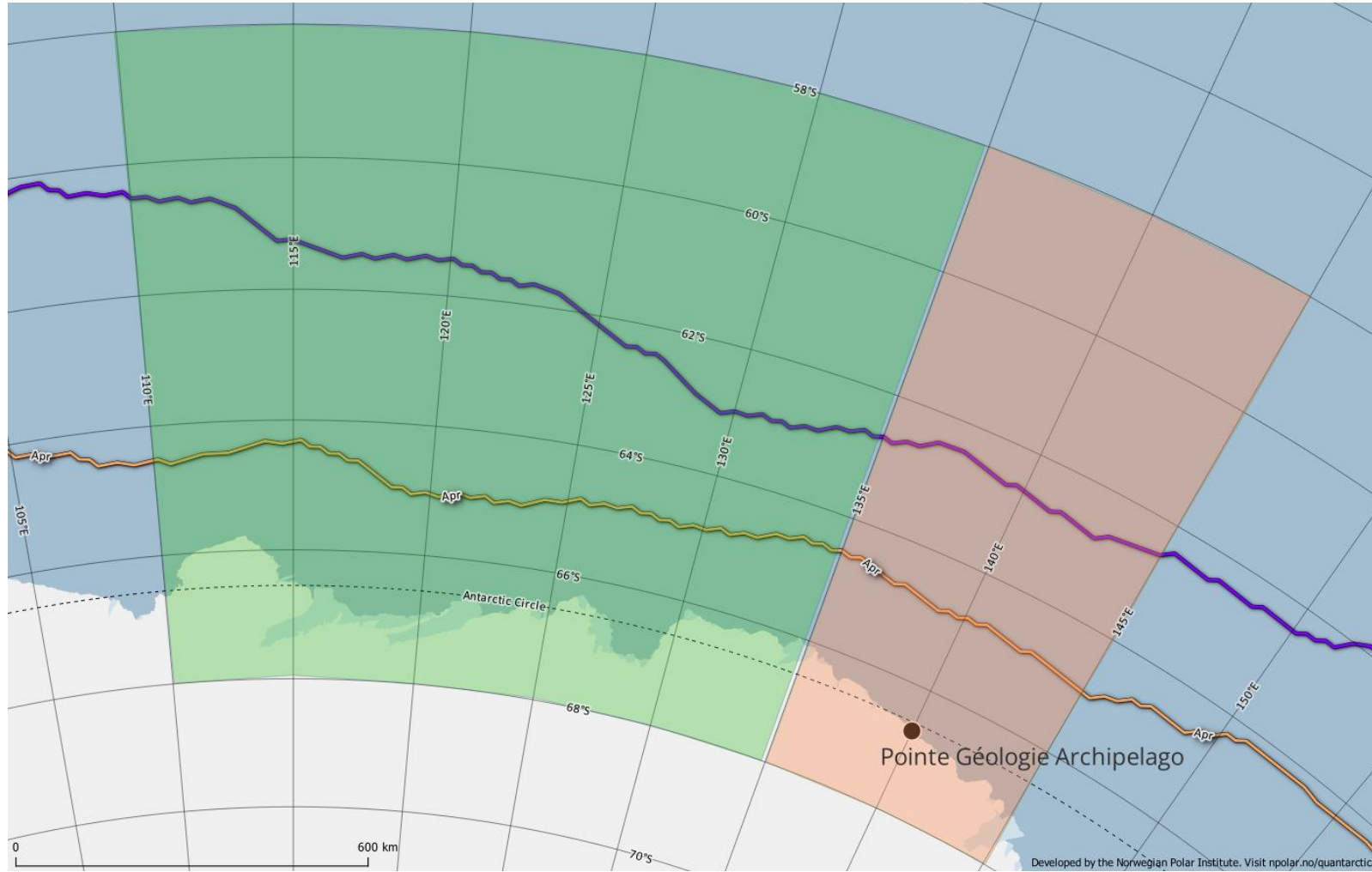


**Fig. S2.**

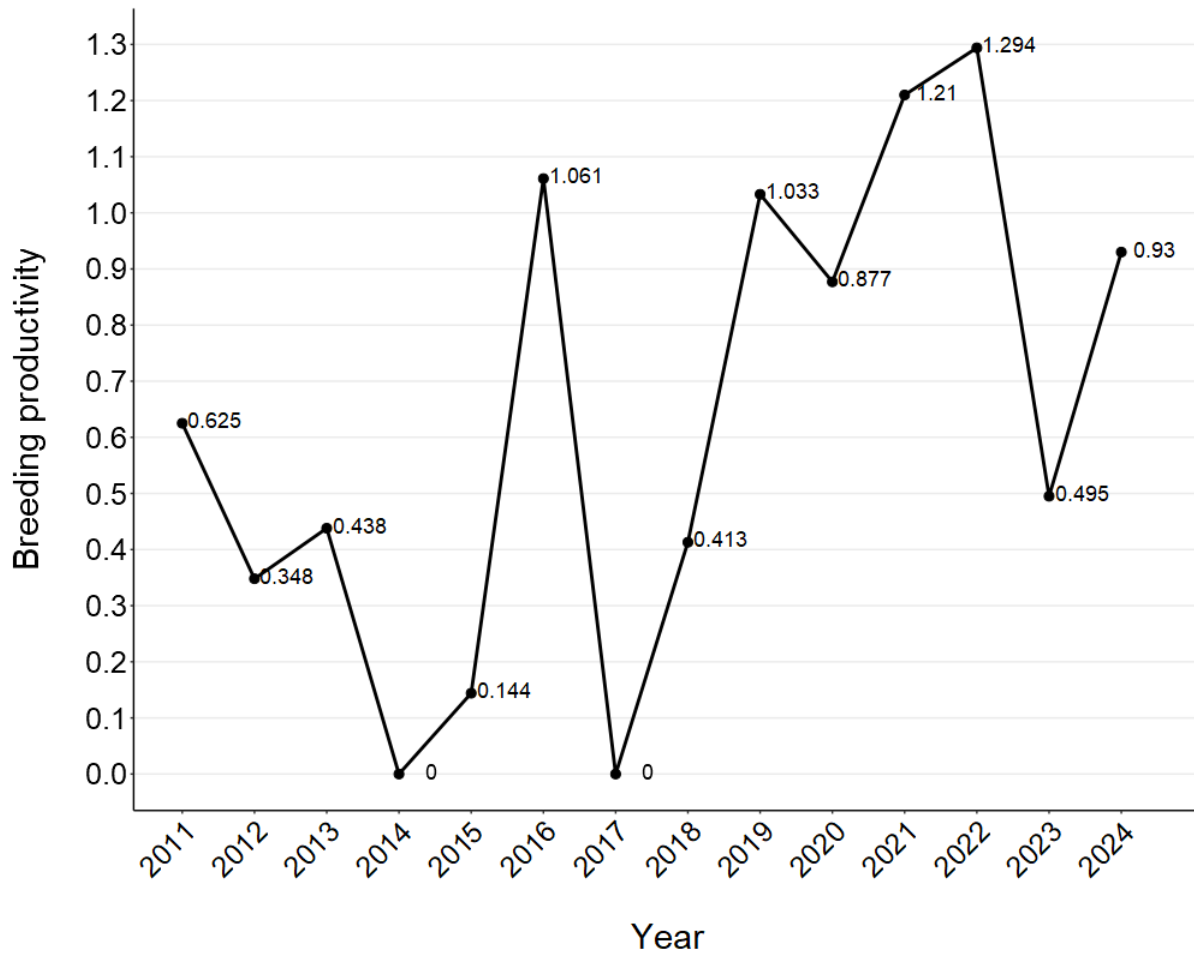
**A mobile RFID detection unit being deployed on an Adélie penguin (*Pygoscelis adeliae*) passageway near a breeding colony in Adélie Land.** This system allows the passive detection of RFID-tagged individuals away from the main study site where tagging is conducted. Detection data and batteries are stored in the acquisition box (1), to which an antenna is affixed and buried in the snow on penguin passageways (2, burying in process in this picture). To increase running time up to several weeks during the summer season, the system can be fitted with solar panels (3). © Gregory Tran (main panel), Téó Barracho (inset), Institut Polaire Français - French Polar Institute. Image rights: the person depicted in the picture is the first author.



**Fig. S3.**  
**Age of first return at the colony after fledging for RFID-tagged Adélie penguins in Pointe Géologie archipelago, Adélie land, Antarctica (2007-2020)**

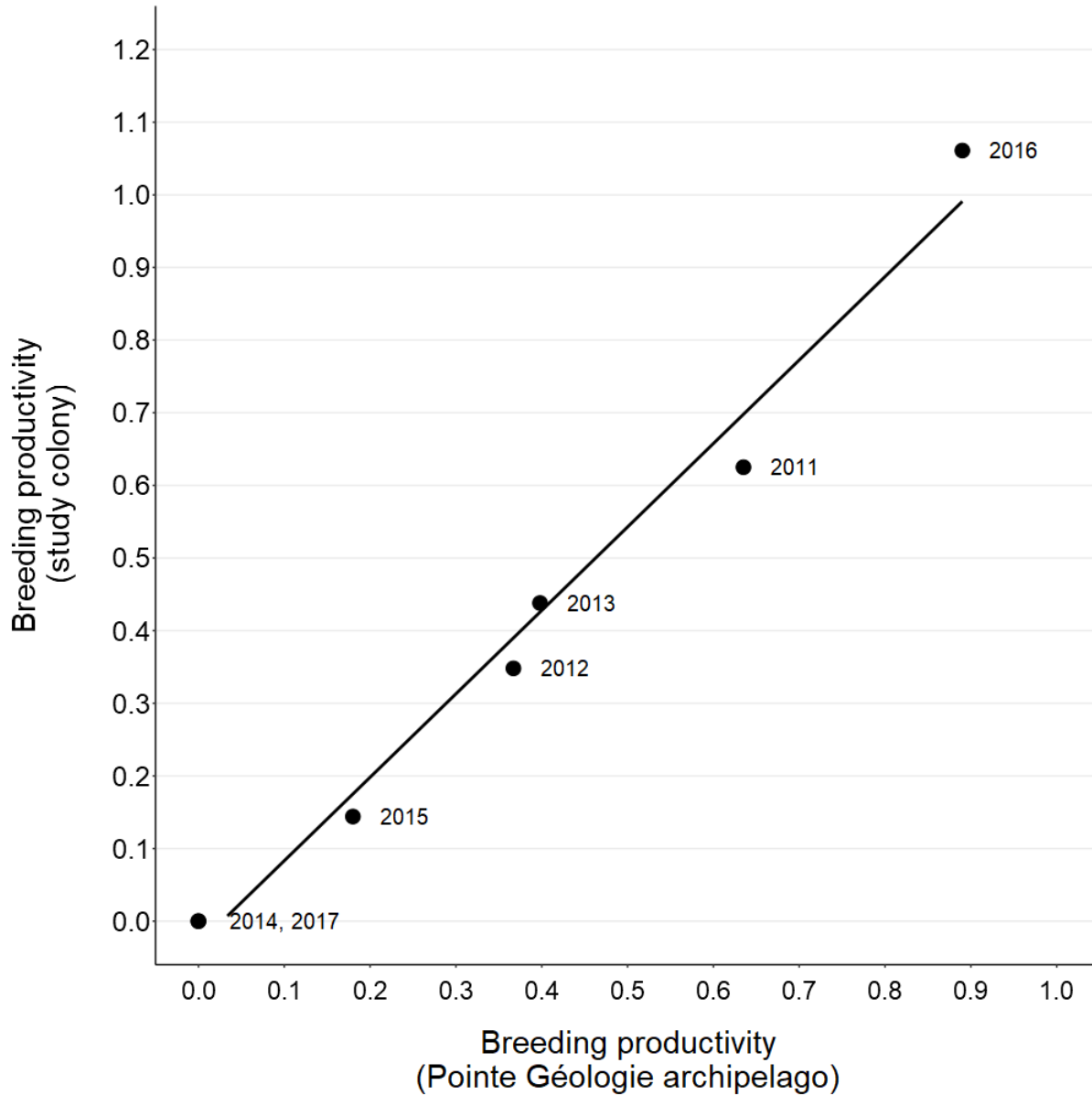


**Fig. S4.** Spatial windows considered for estimating the sea ice concentrations covariates for autumn (orange), and winter/late winter (green). The yellow line depicts the average April sea ice extent and the blue line the average maximal sea ice extent (both over the 1981-2010 period). Map produced using Quantarctica (<https://www.npolar.no/quantarctica/> ; (101))



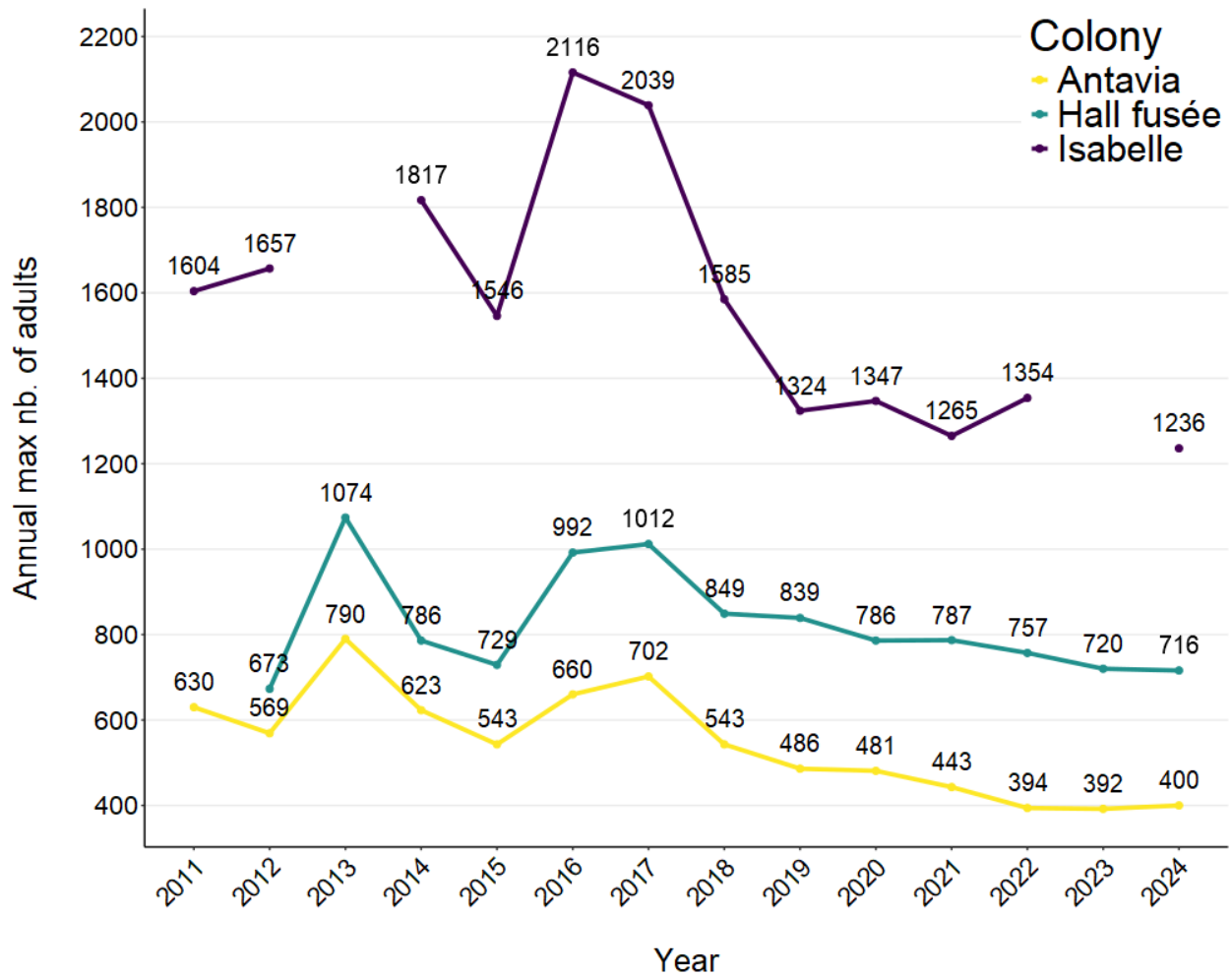
**Fig. S5.**

**Time series of breeding productivity for the study colony (2011-2024).** Breeding productivity was calculated as the number of chicks fledged divided by the annual maximum number of adults inside the colony divided by two). This proxy for breeding productivity is a slight overestimation of the actual breeding productivity, since all individuals present at the colony may not be breeders. However, it still reflects population-scale breeding productivity accurately (Fig. S5). Breeding productivity may be superior to 1 in some years because Adélie penguins can raise two chicks [\(38\)](#)

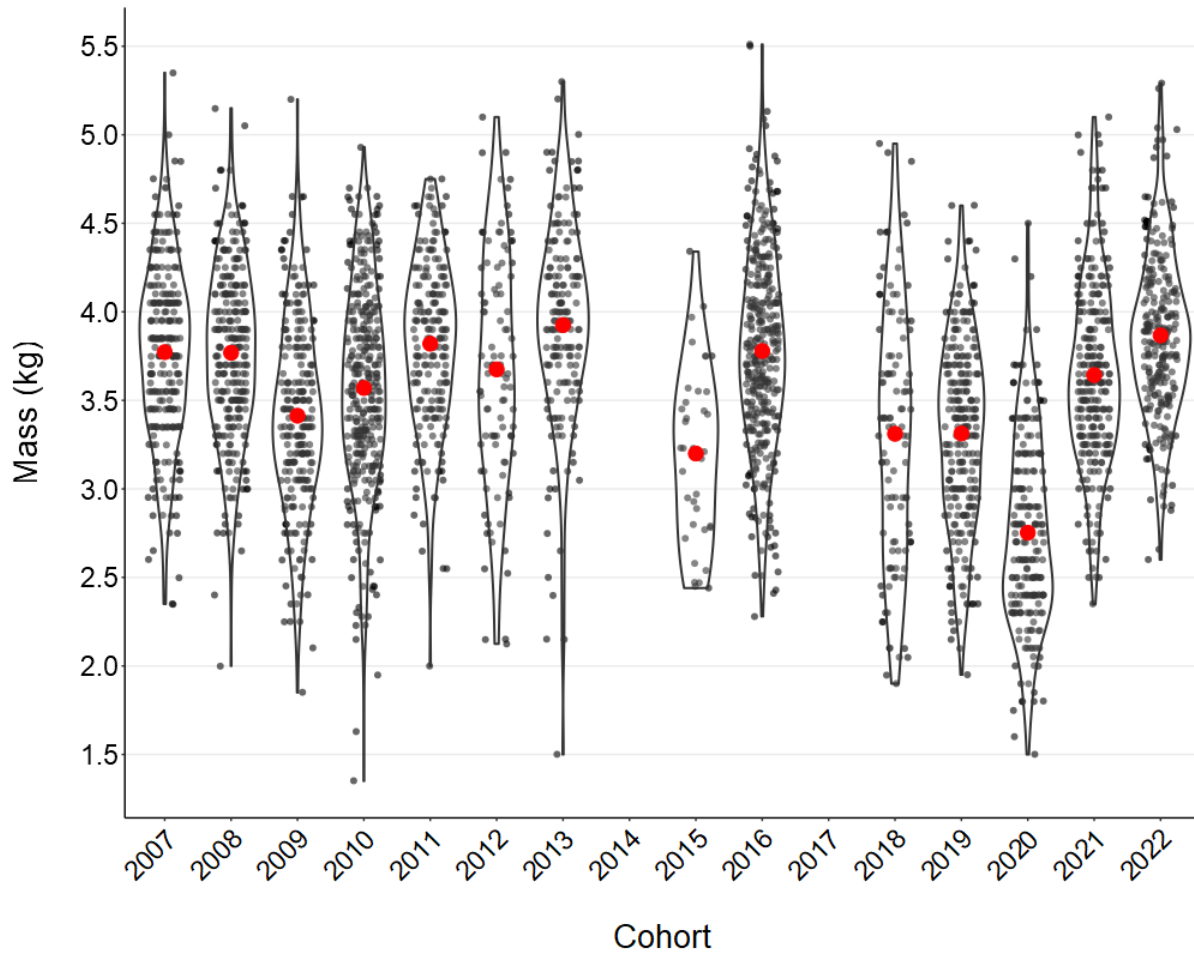


**Fig. S6.**

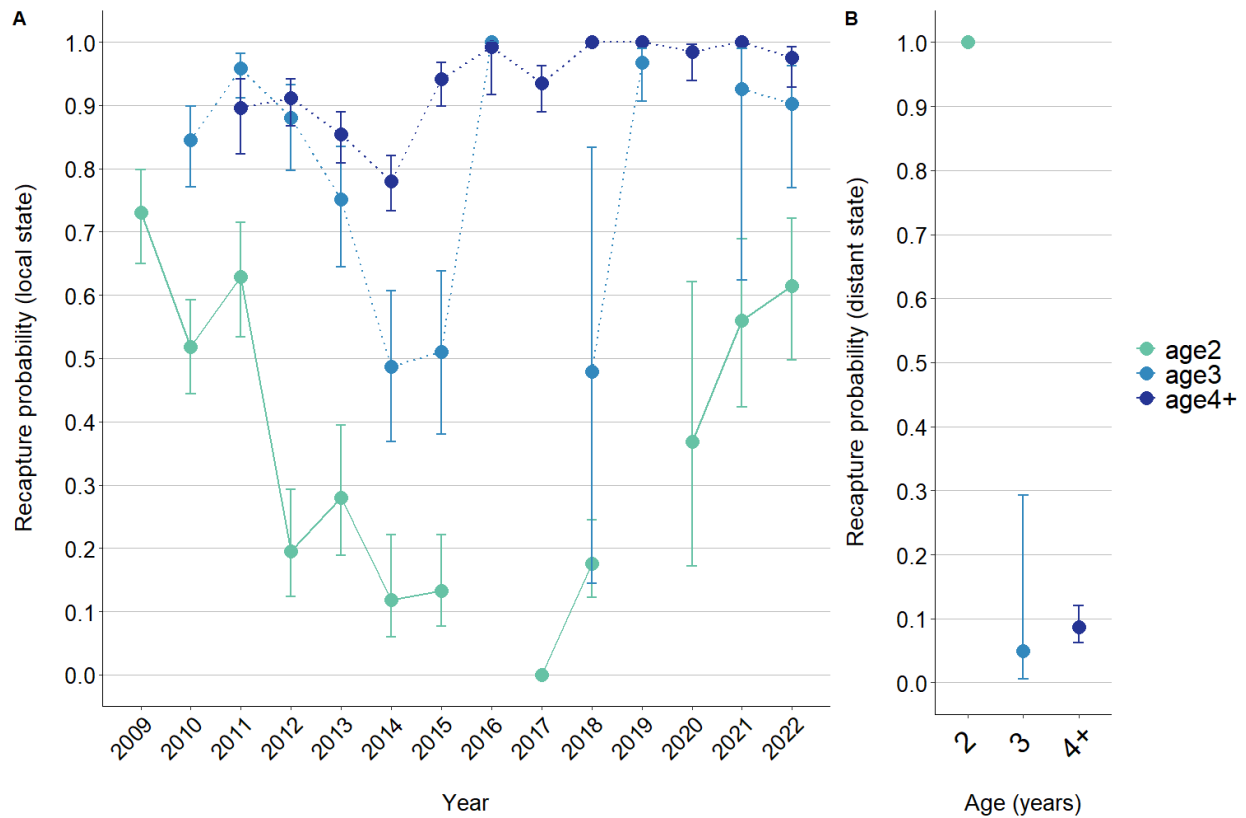
The annual breeding productivity (chicks per pair) of the study colony correlates with that of the whole population of Pointe Géologie archipelago, Adélie Land, Antarctica (2011-2017,  $r = 0.99$ ). Data for Pointe Géologie was extracted from [\(85\)](#). Breeding productivity may be superior to 1 in some years because Adélie penguins can raise two chicks [\(38\)](#).



**Fig. S7.** Annual maximal number of adults (a proxy for the number of breeding pairs, weekly surveys) in three neighboring Adélie penguin colonies in Pointe Géologie archipelago, Adélie Land, Antarctica. These three colonies include the study colony (Antavia) and two control colonies (Hall Fusée and Isabelle) where no monitoring activities are conducted except for weekly photo counts.

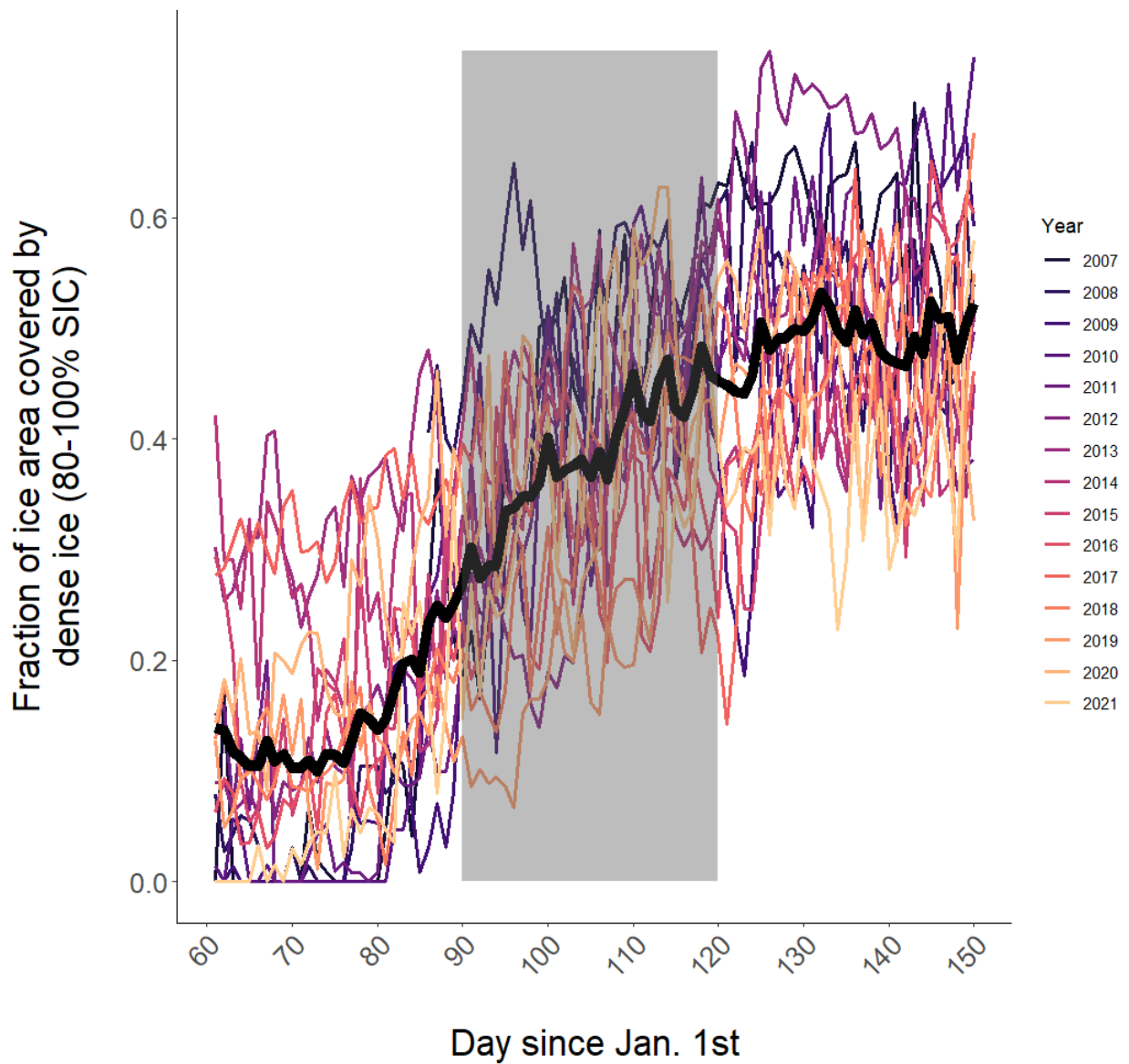


**Fig. S8.** Chick body mass at the time of RFID-tagging across cohorts (2007-2021) for Adélie penguins born in the study colony (Pointe Géologie archipelago, Adélie Land). Red dots represent annual means. Tagging consistently occurred 10-15 days prior to fledging, thus making mass at tagging a reliable proxy for fledging mass ([62](#)).

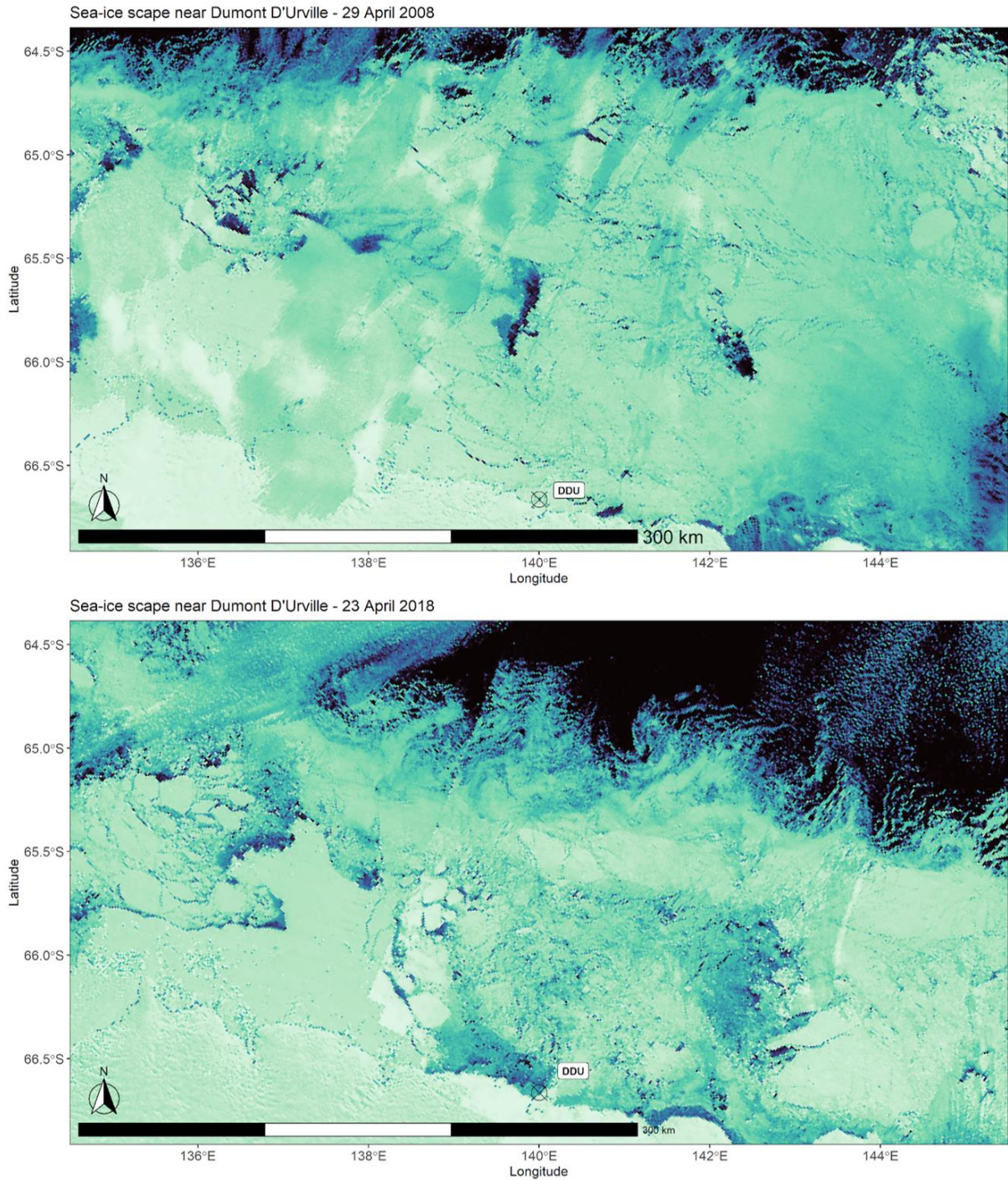


**Fig. S9.** **Estimated recapture probabilities of known-age RFID-tagged Adélie penguins in the local (A) and distant (B) states.** States refer to spatial locations of colonies where individuals are detected. The local state includes the study colony and adjacent colonies (< 200 m), while the distant state includes colonies elsewhere in Pointe Géologie archipelago (see Fig. 1 in the main text). Error bars indicate  $\pm$  SE.





**Fig. S10.** Annual increase in the proportion of dense sea ice (80-100% sea ice concentration) in the vicinity of Pointe Géologie archipelago (~200 km) between March and May of each year (2007-2021). The gray shaded area represents the month of April, where the increase in dense ice fraction is strongest. Daily sea ice concentration data over 25×25 km grids was downloaded from the NSDIC ((95), <https://nsidc.org/data/g02202/versions/4>).



**Fig. S11.**

**Sea ice-scape at the end of April near Pointe Géologie archipelago in two years of contrasting survival probabilities for juvenile Adélie penguins (2008, high survival probability; 2018, low survival probability). MODIS satellite images were downloaded from the NASA Worldview application (<https://worldview.earthdata.nasa.gov>), part of the NASA Earth Observing System Data and Information System (EOSDIS).**

**Table S1:**  
**Results of Goodness-of-fit tests for the multistate capture-recapture dataset used to estimate Adélie penguin juvenile survival probability at Pointe-Géologie archipelago, Adélie Land, Antarctica).** df, Degrees of freedom;  $\hat{c}$ , Deviance inflation factor.

Test	$\chi^2$	<i>pval</i>	df	$\hat{c} = \chi^2/Df$
A) Original dataset				
WBWA	2.469	0.7	4	0.617
3G.SR	1827.802	<0.001	12	152.317
3G.Sm	1393.189	<0.001	35	39.805
M.ITEC	18.37	0.005	6	3.062
M.LTEC	6.831	0.2	5	1.366
JMV model	3248.661	<0.001	62	52.398
B) Dataset where 1st capt. set to 0 (no transients)				
WBWA	3.428	0.5	4	0.857
3G.SR	14.744	0.324	13	1.134
3G.Sm	47.702	0.0	31	1.539
M.ITEC	12.541	0.051	6	0.805
M.LTEC	6.015	0.3	5	0.919
JMV model	84.429	0.017	59	1.431

**Table S2.**

**Annual covariates considered in the present study for explaining temporal variation in Adélie penguin juvenile survival.**

Variable type	Variable	Spatial scale	Temporal scale	Hypothesized mechanisms and previous results	Expected effects on Adélie penguin juvenile survival
Global climatic index	<b>Southern Oscillation Index (SOI)</b>	global	March-September	Low SOI values linked to higher winter temperatures were negatively related to adult survival in Adélie penguins in Adélie Land (32)	Negative
	<b>Southern Annular Mode (SAM)</b>	global	March-September	Positive SAM values were related to higher juvenile survival in Emperor penguins in Adélie Land, possibly through increased food availability (92). Also in Adélie Land, this relationship was negative for snow petrels, possibly because positive SAM	Positive

				increases fast ice extent and reduces food availability for this surface-feeding species (93).	
<b>Sea ice metrics</b>	<b>Sea ice extent anomalies (SIEA)</b>	regional (90°E - 150°E)	March-September	SIEA were quadratically related to Adélie penguin adult survival in the Ross sea (33) and positively related to juvenile survival in the WAP, possibly because increased ice extent provides more resting habitat (29).	Positive
	<b>SIC.autumn</b> (average SIC in area)	local (135°E - 145°E)	March-April	Increased autumn/winter sea ice concentrations were positively related to population growth rate across Antarctica, consistent with effects on juvenile survival (11). Furthermore, tracking data from the Western Antarctic Peninsula (WAP) suggest a survival bottleneck occurs right	Positive

				after fledging (45).	
	<b>SIC.march</b> (average SIC in area)	local (135°E - 145°E)	March	Increased autumn/winter sea ice concentrations were positively related to population growth rate across Antarctica, consistent with effects on juvenile survival (11). Furthermore, tracking data from the Western Antarctic Peninsula (WAP) suggest a survival bottleneck occurs right after fledging (45).	Positive
	<b>SIC.april</b> (average SIC in area)	local (135°E - 145°E)	April	Increased autumn/winter sea ice concentrations were positively related to population growth rate across Antarctica, consistent with effects on juvenile survival (11). Furthermore, tracking data from the Western Antarctic Peninsula (WAP) suggest a survival	Positive

				bottleneck occurs right after fledging (45).	
	<b>SIC.winter</b> (average SIC in area)	local/regional (110°E - 135°E)	May-July	Increased autumn/winter sea ice concentrations were positively related to population growth rate across Antarctica, consistent with effects on juvenile survival (11). Higher winter sea ice concentrations in the Weddell sea were positively related to juvenile survival in the WAP (29).	Positive
	<b>SIC.latewinter</b> (average SIC in area)	local/regional (110°E - 135°E)	August-September	Sea ice concentrations in Aug-Sept were weakly but negatively related to Adélie penguin juvenile survival in another east Antarctica population, possibly because too much ice pushes individuals away from foraging areas and/or affects predation pressure (34).	Negative

	<b>MIZFRAC.april</b> (% of ice area (15-100% SIC) covered by the marginal ice zone (15-80% SIC))	local (135°E - 145°E)	April	As different types of sea ice may affect seabird vital rates differently (96), we decomposed the April sea ice concentration into its loose fraction (MIZFRAC.april) and its solid fraction (DENSEFRAC.april).	Unknown
	<b>DENSEFRAC.april</b> (% of ice area (15-100% SIC) covered by dense ice (80-100% SIC))	local (135°E - 145°E)	April	As different types of sea ice may affect seabird vital rates differently (96), we decomposed the April sea ice concentration into its loose fraction (MIZFRAC.april) and its solid fraction (DENSEFRAC.april).-	Unknown
<b>Local climatic and intrinsic variables</b>	<b>Windchill temperature (WCT)</b>	local/regional	April-September	WCT were quadratically or positively related to Adélie penguin juvenile survival in another east Antarctica population possibly because higher temperatures decreased thermoregulatory costs	Positive



				(31).	
	<b>Cohort size</b>	local	Annual	Density-dependent effects (positive relationship between cohort size and juvenile survival) were reported in another east Antarctica Adélie penguin population (31), possibly acting through diluted predation (55) pressure or increased social foraging.	Positive
	<b>Average chick mass at tagging</b>	local	Annual	Higher mass at fledging buffers inexperienced fledglings against depletion of energy reserve and is a general predictor of juvenile survival in birds (97).	Positive

**Table S3:**

**Model selection for recapture, transition, and survival probabilities.** Abbreviations: AICc, Akaike Information Criterion corrected for small sample sizes ;  $\Delta AICc$ , AICc difference between current model and time-dependent model ; K, number of parameters ; Dev, Model deviance.

Submodel set	Index	Model	AICc	$\Delta AICc$ (for each submodel set)	AICc Weights	K	Dev
<i>Recapture (p)</i>							
	3	$\Phi$ (5 age classes $\times$ time) <b>p(state1: 3 age classes <math>\times</math> time; state2: 3 age classes)</b> $\Psi$ (5 age classes $\times$ state)	12076.5	0.0	0.902	10	2276.1
	2	$\Phi$ (5 age classes $\times$ time) <b>p(state1: 4 age classes <math>\times</math> time; state2: 4 age classes)</b> $\Psi$ (5 age classes $\times$ state)	12081.8	5.3	0.063	11	2260.8
	1	$\Phi$ (5 age classes $\times$ time) <b>p(state1: 5 age classes <math>\times</math> time; state2: 5 age classes)</b> $\Psi$ (5 age classes $\times$ state)	12083.0	6.5	0.035	12	2243.4
	5	$\Phi$ (5 age classes $\times$ time) <b>p(state1: 5 age classes + time; state2: 5 age classes)</b> $\Psi$ (5 age classes $\times$ state)	12095.7	19.2	0.000	74	2356.7
	6	$\Phi$ (5 age classes $\times$ time) <b>p(state1: 4 age classes + time; state2: 4 age classes)</b> $\Psi$ (5 age classes $\times$ state)	12098.2	21.7	0.000	73	2361.3
	4	$\Phi$ (5 age classes $\times$ time) <b>p(state1: 2 age classes + time; state2: 2 age classes)</b> $\Psi$ (5 age classes $\times$ state)	12135.6	59.1	0.000	93	2357.8
<i>State transition (<math>\Psi</math>)</i>							
	3	$\Phi$ (5 age classes $\times$ time) p(state1: 3 age classes $\times$ time; state2: 3 age classes) <b><math>\Psi</math>(5 age classes <math>\times</math> state)</b>	12076.5	0.0	0.991	10	2276.1
	8	$\Phi$ (5 age classes $\times$ time) p(state1: 3 age classes $\times$ time; state2: 3 age classes) <b><math>\Psi</math>(3 age classes <math>\times</math> state)</b>	12086.9	10.3	0.006	10	2294.7
	7	$\Phi$ (5 age classes $\times$ time) p(state1: 3 age classes $\times$ time; state2: 3 age classes) <b><math>\Psi</math>(4 age classes <math>\times</math> state)</b>	12087.7	11.2	0.004	10	2291.4
	9	$\Phi$ (5 age classes $\times$ time) p(state1: 3 age classes $\times$ time; state2: 3 age classes) <b><math>\Psi</math>(2 age classes <math>\times</math> state)</b>	12096.4	19.9	0.000	98	2308.3
	10	$\Phi$ (5 age classes $\times$ time) p(state1: 3 age classes $\times$ time; state2: 3 age classes) <b><math>\Psi</math>(state)</b>	12098.0	21.4	0.000	97	2311.9
<i>Survival (<math>\Phi</math>)</i>							

	13	<b><math>\Phi</math> (2 age classes <math>\times</math> time)</b> p(state1: 3 age classes $\times$ time; state2: 3 age classes) $\Psi$ (5 age classes $\times$ state)	12044. 7	0.0	0.997	75	2303. 7
	12	<b><math>\Phi</math> (3 age classes <math>\times</math> time)</b> p(state1: 3 age classes $\times$ time; state2: 3 age classes) $\Psi$ (5 age classes $\times$ state)	12056. 1	11.4	0.003	85	2294. 7
	11	<b><math>\Phi</math> (4 age classes <math>\times</math> time)</b> p(state1: 3 age classes $\times$ time; state2: 3 age classes) $\Psi$ (5 age classes $\times$ state)	12064. 6	19.9	0.000	95	2282. 7
	3	<b><math>\Phi</math> (5 age classes <math>\times</math> time)</b> p(state1: 3 age classes $\times$ time; state2: 3 age classes) $\Psi$ (5 age classes $\times$ state)	12076. 5	31.8	0.000	4	10 2276. 1
	16	<b><math>\Phi</math> (2 age classes + time)</b> p(state1: 3 age classes $\times$ time; state2: 3 age classes) $\Psi$ (5 age classes $\times$ state)	12127. 1	82.3	0.000	65	2406. 4
	15	<b><math>\Phi</math> (2 age classes: cst/time)</b> p(state1: 3 age classes $\times$ time; state2: 3 age classes) $\Psi$ (5 age classes $\times$ state)	12264. 6	219.8	0.000	68	2537. 9
	14	<b><math>\Phi</math> (5 age classes)</b> p(state1: 3 age classes $\times$ time; state2: 3 age classes) $\Psi$ (5 age classes $\times$ state)	12280. 2	235.5	0.000	55	2580. 0