

1 **Quantifying climate change impacts emphasises the importance**
2 **of managing regional threats in the endangered Yellow-eyed**
3 **penguin**

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14 **Abstract**

15 Climate change is a global issue with effects that are difficult to manage at a regional scale.
16 Yet more often than not climate factors are just some of multiple stressors affecting species
17 on a population level. Non-climatic factors – especially those of anthropogenic origins –
18 may play equally important roles with regard to impacts on species and are often more
19 feasible to address. Here we assess the influence of climate change on population trends of
20 the endangered Yellow-eyed penguin (*Megadyptes antipodes*) over the last 30 years, using a
21 Bayesian model. Sea surface temperature (SST) proved to be the dominating factor
22 influencing survival of both adult birds and fledglings. Increasing SST since the mid-1990s
23 was accompanied by a reduction in survival rates and population decline. The population
24 model showed that 33% of the variation in population numbers could be explained by SST
25 alone, significantly increasing pressure on the penguin population. Consequently, the
26 population becomes less resilient to non-climate related impacts, such as fisheries
27 interactions, habitat degradation and human disturbance. However, the extent of the
28 contribution of these factors to declining population trends is extremely difficult to assess
29 principally due to the absence of quantifiable data, creating a discussion bias towards
30 climate variables, and effectively distracting from non-climate factors that can be managed
31 on a regional scale to ensure the viability of the population.

32 **Keywords**

33 Climate change, anthropogenic threats, population modelling, penguins, species
34 management, demography, survival rates, New Zealand, conservation, endangered species

35 **Introduction**

36 Climate change significantly alters the phenology and distribution of the world's fauna and
37 flora (Parmesan 2006). Species with spatially limited distributions suffer particularly from
38 climate-related change in their habitats, which can drive range shifts (e.g. Sekercioglu et al.,
39 2008; Grémillet & Boulinier, 2009), range restrictions (Sexton et al., 2009) or, in the worst
40 case, extinction (Thomas et al., 2004). Current climate predictions suggest that the
41 pressure on ecosystems will continue to increase (Stocker, 2014), especially affecting
42 species that occupy fragmented habitats. The spatial segregation of suitable habitat might
43 preclude range shift adjustments and increase the risk of local extinctions (Opdam &
44 Wascher, 2004).

45 For species conservation, this creates a daunting scenario. With resources for conservation
46 often limited, the inevitability of climate change could be used as an argument against
47 taking action to conserve species at locations that may become sub-optimal due to
48 environmental change (Sitas, Baillie & Isaac, 2009). However, often cumulative
49 anthropogenic impacts (e.g. habitat destruction, pollution, resource competition, accidental
50 mortality) significantly add to – or even exceed – the impact of climate-related
51 environmental change (Parmesan & Yohe, 2003; Trathan et al., 2015). While climate
52 change is a global issue that is difficult to tackle at a regional scale, addressing local-scale
53 anthropogenic factors can enhance species' resilience to environmental change.
54 Quantifiable data on climate variables are usually readily available through international
55 and regional monitoring programmes (e.g. Kriticos et al., 2012), whereas this is generally
56 not the case with other non-climate related data. Lack of monitoring or commercial

57 interests often prevent the compilation of data (e.g. Chen, Chen & Stergiou, 2003; Mesnil et
58 al., 2009) which may be relevant to species survival. This creates the risk of an analytical
59 bias towards climate impacts, thereby distracting from and potentially understating non-
60 climate threats.

61 The population status of New Zealand's endemic Yellow-eyed penguin (YEP, *Megadyptes*
62 *antipodes*) illustrates the complexity of this issue. YEP is a species of significant cultural and
63 economic value for New Zealand (Seddon, Ellenberg & van Heezik, 2013). Particularly the
64 tourism industry of the Otago Peninsula benefits from the presence of the birds with an
65 annual contribution per breeding pair to the local economy estimated at about NZ\$250,000
66 (Tisdell, 2007). Ensuring the survival of the species is therefore not only a matter of ethical
67 considerations, but also of economic importance.

68 With an estimated 1,700 breeding pairs the YEP is one of the rarest penguin species world-
69 wide (Garcia Borboroglu & Boersma, 2013). Compared to other penguins, the YEP's
70 distributional range is fairly limited. About 60% of the species' population is thought to
71 inhabit the sub-Antarctic Auckland and Campbell Islands, while the remaining ~40% breed
72 along the south-eastern coastline of New Zealand's South Island (Seddon, Ellenberg & van
73 Heezik, 2013). Genetic analyses revealed that there is virtually no gene flow between the
74 sub-Antarctic and mainland YEP populations (Boessenkool et al., 2009a).

75 While little is known about the sub-Antarctic populations, mainland YEPs have received
76 considerable scientific attention. The first comprehensive studies of breeding biology and
77 population dynamics were carried out in the first half of the 20th century by Lance Richdale
78 (Richdale, 1949, 1951, 1957). Interest in the species waned after Richdale's retirement

79 from active research, but was rekindled in the late 1970s (Darby, 1985). Regular
80 monitoring of some breeding sites commenced in the early 1980s, and was expanded and
81 intensified following a catastrophic die-off affected breeding adult penguins on the Otago
82 Peninsula in the austral summer of 1989-90 (Efford, Spencer & Darby, 1994). Parts of the
83 population have been monitored without interruption since 1982 resulting in a data set
84 spanning more than three decades (Ellenberg & Mattern, 2012). A recent review of
85 available information revealed that a steady decline of the population might have been
86 masked by more intensive monitoring since the early 2000s (Ellenberg & Mattern, 2012).

87 Most New Zealand penguin species including YEPs are believed to have undergone
88 significant population declines in the past century, with climate change suspected to be
89 playing a major role (e.g. Cunningham & Moors, 1994; Peacock, Paulin & Darby, 2000). At
90 the same time, penguin populations are exposed to numerous anthropogenic threats
91 (Trathan et al., 2015). Climate variables and anthropogenic influences create a complex mix
92 of factors that make it challenging to decipher the causation of population developments.

93 Using population data recorded between 1982 and 2015 from one of the YEP's mainland
94 strongholds, we developed a population model that integrates observed population
95 changes with key climatic variables. While climate data are readily available as continuous
96 data sets, data on anthropogenic factors are often sparse or of low temporal and spatial
97 resolution which inhibits quantitative analysis. We assess to which extent population
98 trends can be attributed to climate change so as to highlight and discuss the likely
99 importance of other, not readily quantifiable but more manageable threats.

100 **Methods**

101 **Species information**

102 The IUCN Red list classifies Yellow-eyed penguins as “Endangered” (BirdLife International
103 2012), and they are listed as “Nationally Vulnerable” under the New Zealand Threat
104 Classification System (Robertson et al., 2013). The three main subpopulations are
105 estimated to range between 520-570 breeding pairs on the Auckland Islands, 350-540
106 pairs on Campbell Island, and 580-780 pairs along New Zealand’s south-eastern coastlines
107 and Stewart Island (Seddon, Ellenberg & van Heezik, 2013). On the mainland, the Otago
108 Peninsula represents the species’ stronghold where numbers of breeding pairs in the past
109 three decades have been as high as 385 in 1996, but have steadily declined over the last 20
110 years to only 108 pairs in 2011 (Ellenberg & Mattern, 2012).

111 Yellow-eyed penguins breed in the austral summer (September-February) so that their
112 annual breeding period spans the turn of the calendar year. Socialising and courtship in
113 July marks the onset of a new breeding season that ends in March/April with annual moult
114 and subsequent replenishing of resources in preparation for the next breeding season
115 (Seddon, Ellenberg & van Heezik, 2013). Hence, we used austral year (i.e. July to June) to
116 calculate means and for summarising annual statistics of demographic and environmental
117 parameters.

118 **Study sites**

119 The Otago Peninsula penguin population has received considerable scientific attention in
120 the past century, with Richdale conducting his seminal population research between 1936
121 and 1954 (Richdale, 1949, 1951, 1957), followed by a string of projects from the 1980s

122 onwards addressing many aspects of the Yellow-eyed penguin's biology including
123 phylogeny (e.g. Boessenkool et al., 2009b), breeding biology (e.g. Darby, Seddon & Davis,
124 1990), diet (e.g. van Heezik, 1990), foraging ecology (e.g. Mattern et al., 2007), and
125 conservation (e.g. (Ellenberg, Mattern & Seddon, 2013)). While Richdale conducted most of
126 his work at Kumo Kumo Whero Bay, most of the recent research was carried out at the
127 Boulder Beach complex (Fig 1) which, as a result, has the longest ongoing population
128 monitoring program and the most reliable data set available (Ellenberg & Mattern, 2012).

129 **Population monitoring & Yellow-eyed penguin database (YEPDB)**

130 Flipper banding of Yellow-eyed penguins commenced at Boulder Beach in the 1970s and by
131 the mid-1980s the majority of the local population was marked. Annual nest searches were
132 conducted to determine number of breeders and repeated nest checks provided
133 information on bird identity and reproductive success (Darby, 1985). After a catastrophic
134 adult die-off during the 1989 breeding season (Gill & Darby, 1993), monitoring was
135 intensified to include 60% of the known South Island breeding sites (Seddon, Ellenberg &
136 van Heezik, 2013). The Yellow-eyed penguin database (YEPDB) was created in the early
137 1990s (Efford, Spencer & Darby, 1994) and is maintained by the New Zealand Department
138 of Conservation (DOC) which also maintains the YEP monitoring and banding program.
139 While the use of subcutaneous transponders has been introduced in the monitoring
140 population, DOC still maintains flipper bands as primary marking method for a transitional
141 period to ensure data consistency can be maintained before phasing out banding.
142 At the time of writing, the database contained banding records for 13,788 penguins (date
143 range: 1973-2013), and 9,006 nest records (range: 1979-2014). It also holds information

144 on incidental penguin recoveries or sightings outside the breeding season; however, these
145 recovery data are patchy and were deemed too unreliable for analysis.

146 **Data**

147 *Demographic data*

148 Nearly one third of all banding records (n=3,733) and nest records (n=2,342) originate
149 from Boulder Beach (Fig 1) providing consistent, uninterrupted monitoring data for our
150 analyses. While monitoring commenced in the late 1970s, first complete data sets are
151 available from 1982 onwards, although for the first season there are only records of six
152 nests.

153 Data were extracted from YEPDB as a series of SQL queries. Population numbers were
154 retrieved from the table holding nest records. Number of breeding adults was calculated by
155 multiplying the number of nests by two; number of fledglings is the sum of chicks fledged
156 from all nests, and number of new breeders represents the sum of all adults that were
157 recorded for the first time as breeders. Where possible we determined age of breeding
158 birds per year by querying their banding details; age is unknown for birds banded as adults
159 (ca. 15% of all banded birds).

160 To estimate demographic parameters, we first extracted ID numbers for individuals
161 banded at the Boulder Beach complex since 1982. Secondly, we identified the years in
162 which each bird was recorded as a breeding adult in the nest record table. Finally, we
163 compiled the information from both database queries into a table where each column
164 represented a nest year and rows comprised encounter histories for each individual. Birds
165 had to miss at least two consecutive breeding seasons before being defined as dead or

166 senescent. In a small number of cases a bird was not recorded as a breeder for three or
167 more consecutive years before reemerging as a nest occupant, but this applied to less than
168 1% of all birds.

169 ***Environmental data***

170 We obtained monthly averages for selected climatic variables deemed likely to have an
171 influence on demographic parameters (Table 1). The National Climate Database (CliFlo,
172 <http://cliflo.niwa.co.nz>) has kept records from weather stations in Dunedin and the Otago
173 Peninsula continuously since the early 20th century. Austral annual means were calculated
174 for each parameter (i.e. July – June) as well as for the months March to May, which covers
175 the penguins' annual moult and post-moult periods. During this time birds are particularly
176 susceptible to environmental perturbations due the increased energy requirements for
177 feather replacement (Croxall, 1982). Data on local sea surface temperatures (SST) were
178 obtained from the Portobello Marine Laboratory (University of Otago) which holds a near
179 continuous time series of daily measurements dating back to January 1953. We calculated
180 the monthly SST anomaly by subtracting monthly means from the average value calculated
181 from all monthly means ranging from January 1953 to December 2014; annual SST
182 anomaly is the mean of monthly SST anomalies for the corresponding year. To examine for
183 potential lag effects of SST anomaly on prey availability (Beentjes & Renwick, 2001), we
184 also examined SST anomalies shifted backwards in time by one and two years.

185 **Population model**

186 We estimated adult survival and fledgling survival by developing a Bayesian mark-
187 recapture (MR) model that incorporated effects of climate parameters. Chicks are only

188 banded shortly before fledging, so that the MR model could not consider hatchlings that
189 died before they were marked (i.e. chick survival). Hence, fledgling survival was adjusted
190 by incorporating the proportion of chicks fledged to chicks hatched. We modelled survival
191 in any year as a random process ranging around a mean of zero within the bounds of a total
192 temporal variance. This allowed us to determine the relative importance of each climate
193 covariate in terms of percentage of total variance explained (Grosbois et al., 2008). For
194 models with covariates explaining at least 20% of the total variance, we estimated
195 posterior model probabilities using Gibbs Variable Selection (GVS, Tavecchia et al., 2016)
196 Subsequently, we modelled YEP population dynamics via a female-only model assuming a
197 birth-pulse population (Tang & Chen, 2002). The effect of environmental factors on the
198 population growth rate was examined by using fixed survival rates (means) within the
199 population model, allowing it to approximate the deterministic population growth rate
200 between 1982 and 2014. Similarly, we estimated the population growth rate by changing
201 mean survival rates corresponding to low SSTs that were measured from 1982 to 1996,
202 and high SSTs characteristic for the time period from 1997 to 2015. Finally, we projected
203 future populations by running a series of stochastic projections that used a range of
204 survival rate estimates (i.e. omitting years with increasing uncertainty in estimate validity)
205 and predicted trends in influential environmental factors.

206 Detailed descriptions of all modelling procedures are provided as Electronic
207 Supplementary Material (ESM1).

208 **Comparison with historic population trends**

209 Richdale (1957) provides comprehensive data on penguin demography allowing it to draw
210 comparisons between historic and contemporary penguin numbers. We inferred
211 population parameters from three tables. Table 67 (p147) provides direct information
212 about the number of eggs laid and chicks fledged. Using number of eggs, we inferred the
213 number of nests for the reported years by assuming only two-egg clutches were present. In
214 table 72 (p154), Richdale reports the percentage of surviving breeders of both sexes for
215 each year, adjusted to the fractional format by dividing the reported values by 100. Finally,
216 table 62 (p138) provides clues about annual recruitment, which was calculated as
217 proportion of new breeders each year. We omitted Richdale's data for the 1936 season and
218 for the seasons following 1949, as he noted less frequent monitoring and incomplete data
219 sets for the initial and the latter years of his study (Richdale 1957).

220 **Results**

221 **Observed penguin numbers**

222 Numbers of adult breeders at Boulder Beach fluctuated considerably between 1982 and
223 2015 (Fig 2). Immigration of birds that had been banded outside Boulder Beach was a rare
224 occurrence throughout the study period (mean proportion of immigrants per year 1982-
225 2015: $2.7 \pm 2.2\%$). If birds banded as breeders are considered to have come from other
226 breeding sites, the median immigration is similar (2.0%) although three years (1991, 2010
227 and 2012) would stand out where unbanded adults made up 11, 10 and 8% of the breeding
228 population, respectively. An apparent rise in penguin numbers at the beginning of the
229 monitoring period (i.e. 1982-1985) reflects increasing monitoring effort. Reduced

230 monitoring effort may explain the drop in numbers after 1985-86; two areas were not
231 monitored in several years (A1: 1986-1989; Highcliff: 1989). Both areas account for $46 \pm 4\%$
232 of penguin counts (1990-2015), so that true penguin numbers in 1989 were likely
233 considerably higher than the database would suggest. Breeder numbers in the two areas
234 monitored in 1989 (Midsection; Double Bay) dropped by 62% in the following season
235 (1989: 74 birds, 1990: 28 birds) when the population was affected by a catastrophic adult
236 die-off. The population recovered between 1990 and 1996 to reach levels comparable to
237 those observed in 1985. The 1996 season had the highest numbers of breeders recorded at
238 Boulder Beach ($n=242$) and represents a turning point for the population. Subsequently
239 penguin numbers reached a low of 104 breeders in 2002, with losses compounded by
240 another adult die-off event occurring in the 2001 season. Between 2002 and 2012 the
241 population fluctuated between 100 and 150 breeders without any apparent trend before
242 another drastic decline in numbers began in the years following a third adult die-off event
243 at the end of the 2012 season. The steepest drop in numbers (41%) recorded since 1989
244 occurred between 2013 (128 breeders) and 2014 (76 breeders). In 2015, only 58 breeding
245 penguins were recorded, which translates to a 76% decline in numbers since 1996.

246 Number of chicks that fledged each year generally followed the trends observed for adults
247 (Fig. 2). However, significant variation between 2003 and 2010 reflects a series of years
248 with poor breeding success followed by better reproductive output in the following year.
249 Numbers of new breeders showed a similar albeit weakened pattern delayed by 5 years:
250 starting in 2004, numbers of new breeders seem to mimic those of fledglings beginning in
251 1999.

252 Age of breeding birds ranged between 8.4 years (1984) and 14.9 years (1990, mean:
253 12 ± 1.4 years, Fig. 3). Between 1990 and 2015 the average age of returning breeders
254 showed a slightly decreasing trend from around 14 to 11 years (Pearson correlation $\rho = -$
255 0.307 , $t_{24} = -1.5781$, $p = 0.13$). At the same time, average age of new breeders dropped
256 significantly from more than 10 years in the 1990s to only 4 years in 2015 ($\rho = -0.796$, $t_{24} = -$
257 1.5781 , $p < 0.001$). The average age of new breeders increased steeply after both the 1989
258 and 2001 adult die-offs (Fig 3) indicating a substantial pool of older non-breeders ready to
259 recruit following the disappearance of established breeders. No such spike is apparent after
260 the 2012 die-off suggesting that the pool of older recruits has dried up over the last decade.

261 **Demographic estimates from the mark-recapture model**

262 The MR model without covariate revealed a fledgling survival rate of 0.12 (95%, Credible
263 Interval: 0.08, 0.19) in chicks (Table 2). The survival of adults was 0.87 (95%, CrI: 0.83,
264 0.90). Throughout the study period (1982-2014), fledgling survival varied 2.56 times more
265 than adult survival (95%, CrI: 1.03, 6.45) (Table 2).

266 Years with increased wind activity had a positive effect on fledgling survival, whereas the
267 effect of higher than normal SST was negative; both covariates explained 33.2% of the
268 variance (Table 3a, ID 1 & 2). Similarly, SST anomaly during the first three months after
269 fledging as well as in the previous year both had a negative effect on survival, explaining
270 24.8% and 17.4% of the variance (IDs 3 & 4), while increased wind activity in the months
271 after fledging had a positive effect on fledgling survival (16.5% of variance explained, ID 5).
272 Furthermore, years with above average air temperatures had a negative effect on fledgling
273 survival, explaining 12.4% and 15.4% of the variance (IDs 6 & 7).

274 In adults, SST had the greatest effect on the survival rate, explaining 36.8% of the variance
275 (Table 3b, ID 1). The relationship of adult survival and SST becomes apparent when the
276 deviation of annual adult survival from the median survival rate is plotted against SST
277 anomaly (Fig 4). In periods with cooler than usual SST, adult survival was high (e.g.1990-
278 1996), whereas warm periods were characterized by lower adult survival. The same was
279 true for air temperature. Warmer years were associated with reduced adult survival; air
280 temperature-related covariates explained 34.4% of the variation in adult survival (Table
281 3b, IDs 2 & 3).

282 Refitting the MR model with the two most influential explanatory covariates each for
283 fledging and adult survival, and subsequent assessment of posterior model probability,
284 ranked highest the model where both chick and adult survival were fitted to the single
285 covariate SST anomaly (Table 4).

286 **Predictions for the adult female population**

287 Using year-specific survival rates from the MR model generates predictions of numbers of
288 adults that were similar to those determined during monitoring. For most years, the
289 observation-based number of adult female YEPs and the 95% credible intervals for the
290 predicted number of adult female YEPs overlapped (Fig 5).

291 Based on a deterministic model (i.e. without temporal variance in survival rates) the
292 population growth rate was 1.02 (95% CrI 0.98, 1.06) per year throughout the entire study
293 period. For the time period when SST was below average (1982 to 1996, Fig. 4) the
294 population showed an increasing trend with a growth rate of 1.038 (95% CrI 0.99, 1.080,
295 Fig 6). However, from 1996 onwards an ongoing period of mainly warmer than normal SST

296 went along with a growth rate of 0.94 (95% CrI 0.90, 0.98) indicating a population decline
297 (Fig 6).

298 **Future projections**

299 Based on projections of increasing SST at a rate of 0.02°C per year in the next decades
300 (Oliver et al. 2014), the penguin population at Boulder Beach will continue to decline.
301 Stochastic simulations using the most reliable estimates for adult survival (1982-2012)
302 suggest that the number of adult female penguins will drop below 10 individuals by 2048
303 (Fig 5a). If the recent poor breeding years 2013-2015 are included this negative trend gets
304 progressively worse (Fig 5b-d). Including adult survival rates estimated for 2015, the mean
305 projection predicts YEPs to be locally extinct by 2043.

306 **Discussion**

307 Numbers of Yellow-eyed penguins at Boulder Beach have declined since 1996 (Figs 5&6).
308 The local population seemed to experience a reprieve from this decline in the first decade
309 of the new millennium, despite unfavourable climatic conditions at that time. This might
310 have been driven by a temporary reduction in other, non-climate negative impacts, the
311 nature of which remain unclear due to a lack of data.

312 The ages of breeding penguins provide some explanation about the underlying mechanics
313 of the population decline. In the years following the 1989 and 2001 adult die-offs, the
314 average age of new breeders recruited into the population was substantially higher than in
315 the years prior to the events. All of these birds were locally banded individuals, which
316 suggests that there was a pool of older, previously unpaired birds which replaced
317 experienced breeders that had died during the event. After the 2012 die-off, the mean age

318 of new breeders reached an historic low (4.1 years, Fig 3). Hence, old breeders that had lost
319 their partner now paired up with younger penguins indicating that the pool of older non-
320 breeders available to replace lost birds had disappeared. This is supported by the number
321 of recruits reflecting the marked variation in fledgling numbers with a 5-year-lag (Fig 2). It
322 appears that since the turn of the century, penguins recruit into the breeding population at
323 the earliest possible opportunity. This likely has negative effects on breeding performance
324 since in seabirds age is an important determinant for foraging success (e.g. Daunt et al.,
325 2007; Zimmer et al., 2011) and subsequently reproductive success (e.g. Limmer & Becker,
326 2009; Nisbet & Dann, 2009). The decline in the mean age of new breeders in recent years
327 indicates that more inexperienced birds are recruiting as breeders, and possibly explains
328 the overall deteriorating reproductive success.

329 When the 2012 die-off of adult breeding birds occurred, penguin numbers were less than
330 60% of what they had been in the mid-1990s (Fig 2). While the penguin population showed
331 a remarkable recovery after the 1989 event this did not happen following 2012; instead
332 numbers have continued to decline. The most apparent differences following the two die-
333 offs are the trends in ocean temperatures with a cooler-than-normal period in the first half
334 of the 1990s whereas SST has been almost continuously higher than the 1953-2014
335 average since the late 1990s (Fig 4).

336 **Sea surface temperature effects**

337 Sea surface temperature explained 33% of the variation in observed population trends.
338 Hence, SST has an important influence on YEP population trends. Years with warmer than
339 usual SST result in reduced adult survival, whereas the reverse is true when SST is cooler.

340 Variation in SST likely influences the abundance and quality of YEP prey. In Little penguins
341 (*Eudyptula minor*) breeding on the Otago Peninsula, climatic fluctuations – and connected
342 to this, ocean temperatures – were found to affect prey composition (Perriman et al., 2000).
343 Little penguins are generalist foragers that take a variety of pelagic prey (Dann, 2013),
344 most likely a beneficial trait in relation to climate related change in resource abundance
345 (Thuiller, Lavorel & Araújo, 2005). YEPs on the other hand, are principally benthic foragers
346 (Mattern et al., 2007) that feed predominantly on demersal species (e.g. van Heezik, 1990;
347 Moore & Wakelin, 1997; Browne et al., 2011). Although this specialisation reduces
348 competition for pelagic prey with the abundant marine avifauna in New Zealand (Mattern
349 et al., 2007), it comes at the cost of reduced behavioural flexibility to respond to changes in
350 prey distribution or abundance (e.g. Browne et al., 2011; Mattern et al., 2013).

351 Temperature affects the annual biomass of many fish species in New Zealand (Beentjes &
352 Renwick, 2001). Warmer than normal conditions negatively affect spawning in fish,
353 reducing subsequent recruitment (e.g. Takasuka, Oozeki & Kubota, 2008). Abundance of
354 the demersal Red cod (*Pseudophycis bacchus*), historically an important prey species for
355 YEP from Boulder Beach (van Heezik, 1990; Moore & Wakelin, 1997), shows a strong
356 correlation to SST fluctuations, albeit with a lag of 14 months (Beentjes & Renwick, 2001).
357 At Boulder Beach, a reduction in body mass of breeding YEPs in 1985 when compared to
358 1984 was associated with lower quantities of red cod taken (van Heezik & Davis, 1990).
359 1983 featured cooler than normal SST (mean monthly SST anomaly: -0.73), while 1984
360 temperatures were above average (SST anomaly: 0.17). As such the lagged correlation
361 between SST and red cod abundance reported by Beentjes & Renwick (2001) also seems to
362 be manifested in penguin body condition. This explains the relative importance of the

363 corresponding covariate (i.e. sst_anomaly_minus1year) for survival rates (Table 3a&b) and
364 corresponds to findings of a previous analysis of climate variables on YEP numbers
365 (Peacock, Paulin & Darby, 2000).

366 However, model selection showed an even stronger direct SST effect (Table 4). Ocean
367 temperatures play an important role in the spatial distribution of fish populations
368 (Beentjes et al., 2002). Warmer than usual SST is often an indication of increased
369 stratification of the water column where a layer of warmer water sits on top of cooler
370 water. This disrupts the benthic-pelagic coupling, i.e. mixing processes that regulate
371 nutrient flow between benthos and surface waters (Jones et al., 2014). Land run-off has
372 been identified as a major source of nutrients for the South Otago continental shelf, which
373 results in higher near-surface nutrient concentrations (Hawke, 1989), so that vertical
374 mixing is likely of crucial importance for benthic productivity and subsequent prey
375 abundance in the penguins' home ranges. Penguin foraging conditions are likely
376 compromised under stratified, warm-water conditions.

377 The three major die-offs of adult penguins (seasons 1989-90, 2001-02, and 2012-13) all
378 occurred in years with higher than normal SST suggesting that stratification might have
379 more severe impacts than can be explained by the disruption of nutrient fluxes alone.

380 **SST and relevance of die-off events**

381 Die-off events do not seem to be related to prey availability; body condition of adult
382 penguins examined during the 1989 event did not indicate malnutrition (Gill & Darby,
383 1993). The cause of mortality could not be identified although necropsies after the 2012
384 die-off indicated it to be toxin related (Gartrell et al., 2016). Harmful algal blooms (HAB)

385 that are known to have negative impacts on other penguin species (Shumway, Allen &
386 Boersma, 2003) were suspected to be involved in the die-offs as well (Gill & Darby, 1993).
387 Yet water samples taken along a transect through the penguin's known foraging ranges
388 found no evidence for the presence of harmful algae (Mattern et al, unpublished data).
389 Tests for the presence of marine biotoxins in freshly dead birds were negative (Gartrell et
390 al., 2016). Moreover, it seems unlikely that a HAB would selectively affect only one seabird
391 species (Shumway, Allen & Boersma, 2003); no other unexplained seabird deaths occurred
392 during any of the die-offs. Only bottom foraging YEPs were affected suggesting that the
393 distribution of a toxin was probably limited to the near-seafloor region. Stratification and
394 the disruption of vertical mixing potentially would contribute to a concentration of toxic
395 components at the sea floor. While the origin or exact nature of the toxin remains unclear,
396 it could be related to technical malfunctions that occurred at the time at Dunedin's sewage
397 treatment plant, which discharges at the seafloor about 1.5 km from the shore and ca. 5 km
398 upstream from Boulder Beach (Dunedin City Council, unpublished data).

399 Although the cause of die-off events remains a matter of speculation, their relevance for
400 population trends is closely tied to prevalent environmental conditions following these
401 events. The 1989 die-off, which removed about 50% of penguins from the breeding
402 population (Efford, Spencer & Darby, 1996) was followed by a six year period of population
403 recovery, likely aided by cooler than normal SST (Fig. 4). The next die-off event occurred at
404 Boulder Beach in 2001 (Alvin Setiawan, pers. comm.) and reduced the local population by
405 nearly 40%. Following this event, the population showed no sign of recovery during a
406 prolonged period of warmer-than-normal SST that began in 1998 and prevails until today.
407 The associated reduced adult survival explains the lack of recovery in the penguin

408 population. Consequently, the 2012 die-off had a cumulative effect, further reducing the
409 population to its lowest level on record.

410 With projected SST increases over the next decades it seems doubtful that optimal marine
411 conditions supporting the recovery of YEPs will occur in the future. Hence, future die-off
412 events will be increasingly critical for penguin numbers. However, sea surface
413 temperatures only explained about one third of the variation in survival rates. This means
414 that other factors also play important roles for YEP population dynamics.

415 **Other climate factors**

416 Daily minimum air temperature is a proxy for prevailing temperature regimes, where a
417 higher average minimum temperature indicates warmer years. Air temperature could
418 simply be a covariate of SST and affect penguin survival through the mechanisms suggested
419 above. In addition, air temperatures recorded during the moult (March-May) negatively
420 affected adult survival probably as a result of hyperthermia. Little penguins in Australia
421 suffer increased adult mortality when exposed to higher temperatures when moulting
422 (Ganendran et al., 2015). However, there is no evidence for comparable temperature-
423 related mortality events in YEP

424 Frequency of days with strong winds had a positive influence on fledgling survival. Wind
425 aids oceanic mixing processes and thereby can become a driver for foraging success in
426 penguins (Dehnhard et al., 2013). Wind generally acts as an antagonist to SST-related
427 stratification effects, creating enhanced foraging conditions for penguins thereby
428 increasing the survival chances of inexperienced fledglings.

429 **Non-climate factors**

430 In this study we were able to use comprehensive data to test the influence of a wide range
431 of climate related factors on the population developments of Yellow-eyed penguins from
432 Boulder Beach. Yet only about a third of the variation in penguin numbers can be explained
433 by climate factors. Hence, it is clear that other, non-climate factors significantly affect
434 penguin survival rates. While several of these factors are well known, it is impossible to
435 examine their impact on the penguin population in a modelling context due to a lack of any
436 quantifiable data. At the same time, unlike the effects of climate change, at least some of
437 these non-climatic factors could be managed on a regional scale to enhance the species'
438 chance for survival. Therefore it is imperative to discuss some of these non-climate factors
439 to avoid an undue focus on only the quantifiable factors (i.e. those driven by climate
440 change) and direct conservation management towards measures that can ensure
441 persistence of the Yellow-eyed penguin on the New Zealand mainland.

442 ***Fisheries interactions***

443 Potential impacts of incidental bycatch in gill net fisheries (Darby & Dawson, 2000) and
444 alteration of the penguins' benthic foraging habitat by bottom fishing activities (Ellenberg
445 & Mattern, 2012; Mattern et al., 2013) could not be quantified because data on gill net
446 fisheries supplied by the Ministry of Primary Industries (NZ Ministry Of Primary Industries,
447 Official Information Act Request OIA12-397) proved to be spatially coarse and temporally
448 limited, with approximate locations of gill net fishing events specified only from 2006
449 onwards. Provided data on bottom fishing effort only covered the years 2000-2012 and
450 originated from vessels operating outside the penguins' ranges (OIA12-460).

451 The impact of single fisheries interactions might have a much greater effect on penguin
452 numbers than annual fishing statistics would suggest. There are reports of multiple YEP
453 killed in a single gill net haul (Ellenberg & Mattern, 2012) and reported bycatch incidents in
454 gill net fisheries have been as high as 12 cases per year, many of which affected YEPs from
455 the Otago Peninsula (Darby & Dawson, 2000). Currently, less than 2% of gill net effort in
456 New Zealand is being independently observed (Richard & Abraham, 2015); this lack of
457 observer coverage prevents reliable quantification of bycatch mortality. Yet it stands to
458 reason that incidental fisheries mortality is an important factor affecting penguin survival
459 rates and, hence, population trends.

460 Impacts of bottom fishing activities on YEP survival are even more difficult to quantify.
461 Bottom trawling and dredge fisheries can substantially alter the benthic environment,
462 reducing biodiversity, and prey abundance and quality for YEPs (Ellenberg & Mattern,
463 2012). Low quality prey were brought ashore by YEPs on Stewart Island, which had home
464 ranges that apparently avoided the vast areas of potential habitat subject to intensive
465 oyster dredging (Browne et al., 2011; Ellenberg & Mattern, 2012). On the Otago Peninsula,
466 some penguins forage along straight-line paths following bottom trawl scrape marks,
467 searching for scavenging prey that appears to be inadequate food for young chicks
468 (Mattern et al., 2013).

469 ***Disease outbreaks***

470 In the past decade several breeding seasons saw the occurrence of diphtheritic stomatitis,
471 a secondary infection negatively affecting chick survival (Houston & Hocken, 2005). We
472 could not test the effects of such disease outbreaks on population trends, because the YEP

473 database does not facilitate quantitative storage of disease-related data. Diphtheritic
474 stomatitis only affects chicks which generally survive when older than 2 weeks (Alley et al.,
475 2016). So the disease is unlikely to have a lasting effect on population trends as it does not
476 affect adults which are critical for the maintenance of a stable population (Benton & Grant,
477 1999). Although YEPs are subject to exposure to avian malaria parasites (Graczyk et al.,
478 1995), observed infections are low, hence, avian malaria currently does not present a
479 significant problem for the species (Sturrock & Tompkins, 2007). Avian pox which is
480 caused significant mortality events in Magellanic (*Spheniscus magellanicus*) and possibly
481 Gentoo penguins (*Pygoscelis papua*) has not been observed in Yellow-eyed penguin,
482 although diphtheritic stomatitis may be the result of a secondary bacterial infection caused
483 by a poxvirus (Alley et al., 2016).

484 ***Predators***

485 Introduced terrestrial predators are one of the biggest challenges for native wildlife in New
486 Zealand (Wilson, 2004). Mustelids (*Mustela sp.*), dogs (*Canis lupus familiaris*), and to a
487 lesser extent cats (*Felis catus*) and rats (*Rattus sp.*) can impact on YEP (e.g. Alterio, Moller &
488 Ratz, 1998; Ratz & Murphy, 1999), but it is very difficult to quantify these effects because
489 direct evidence of predation is sparse. A five year study investigating the impact of feral
490 cats on penguins on Stewart Island did not find any indication for predation events and
491 concluded that starvation and disease were the main factor of mortality (King, 2008). On
492 the mainland, predation by dogs or stoats appear to be very localised occurrences (Hocken,
493 2005). However, climate change may render this an increasing problem in the future
494 (Tompkins, Byrom & Pech, 2013)

495 Predation by the native NZ sea lion (*Phocarctos hookeri*) has to date been limited to two
496 female sea lions that were active between 1997 and 2005 (Lalas et al., 2007) that have
497 since died (Jim Fyfe, pers. com.). More recently, a number of YEPs have been reported with
498 injuries that were speculated to have been inflicted by Barracouta (*Thyrssites atun*).
499 Considering that barracouta are smaller than adult YEPs (mean body lengths – barracouta:
500 55 cm, Fishbase.org 2016; YEPs: 65 cm, Seddon, Ellenberg & van Heezik, 2013) such
501 injuries are at best an accidental consequence of penguins and fish targeting the same prey
502 patch. Some external injuries might be the result of interactions with humans; in Australia,
503 Little penguins (*Eudyptula minor*) have been injured and killed by water craft such as jet
504 skis (Cannell et al., 2016), a recreational activity that has also been observed in the penguin
505 landing zone at Boulder Beach (pers. obs).

506 ***Human impacts***

507 The significance of human impacts in the form of deforestation of breeding habitat, capture
508 by collectors, eggging, and shooting of adults on the YEP population was highlighted early by
509 Richdale (1952). While these impacts are no longer an issue, unregulated tourism has
510 become an important threat at some Yellow-eyed penguin colonies and is reflected in
511 reduced breeding performance and a steady decline of local penguin numbers (e.g.
512 McClung et al., 2004; Ellenberg et al., 2007; Ellenberg, Mattern & Seddon, 2009).

513 **Maladapted colonizer?**

514 Comprehensive analysis of ancient penguin DNA in recent years have revealed that YEP is
515 relatively recent colonizer originating from sub-Antarctic. The species is believed to have
516 replaced a sister taxon *Megadyptes waitaha* after it was hunted to extinction by humans as

517 recently as 500 years ago (Boessenkool et al., 2009b; Rawlence et al., 2015). In this light,
518 the question was raised whether the species' vulnerability to increasing ocean
519 temperatures may in fact reflect a maladaptation for a warmer climate (Waters & Grosser,
520 2016). While evidence for a physiological relationship between ocean warming and
521 survival rates in YEP is lacking, the specialized benthic foraging strategy renders the
522 species particularly sensitive to environmental change (Mattern et al., 2007; Gallagher et
523 al., 2015). With the various non-climatic factors discussed above all contributing to
524 significant shifts across the entire benthic ecosystem, reducing the penguins' struggle to a
525 species-specific maladaptation for a warming climate clearly oversimplifies the matter.

526 **Conservation implications**

527 Stochastic simulations of future population trends for Yellow-eyed penguins at Boulder
528 Beach, show that the population will continue to decline if current threats continue
529 unabated. Global ocean temperatures are rising (Stocker, 2014); projections for the
530 Tasman region until 2060 predict an increase in SST of up to 2°C (Oliver et al., 2014), hence
531 future climatic conditions will not be favorable for a recovery of the YEP population.

532 On the bright side, climate change-related pressure on YEP can likely be offset through
533 control of the other more manageable factors negatively affecting population trends. This
534 has already been demonstrated: positive YEP population growth during the 1940s, at a
535 time when SST was strongly increasing in the Pacific to levels comparable to those
536 recorded in the 1990s (Guan & Nigam, 2008), was attributed to a reduction in human
537 impacts such as conversion of breeding habitat to farm land, establishment of road
538 networks, road traffic and random acts of violence (Richdale, 1957). During World War II,

539 when resources were directed towards the war effort, ‘man’s destructive agencies were
540 practically negligible’ (Richdale, 1957, p157).

541 While climate change is a global phenomenon that is both inevitable and quantifiable, it is
542 important to bear in mind its impact on species population trends is relative to other more
543 regional factors, such as, in the case of penguins, fisheries, pollution, habitat destruction,
544 introduced terrestrial predators, and human disturbance (Trathan et al., 2015). Managing
545 local and regional factors can increase the resilience of species towards increasing pressure
546 from climate change.

547 The virtual absence of quantifiable data to examine the effects of non-climate factors makes
548 it difficult to provide fact-based management recommendations and puts a potentially
549 overbearing emphasis on climate change. However, these principally anthropogenic factors
550 likely also explain significant portions of the variation in survival rates, so that the focus
551 should be on improving our understanding and management of these impacts to enhance
552 this species’ resilience to climate change.

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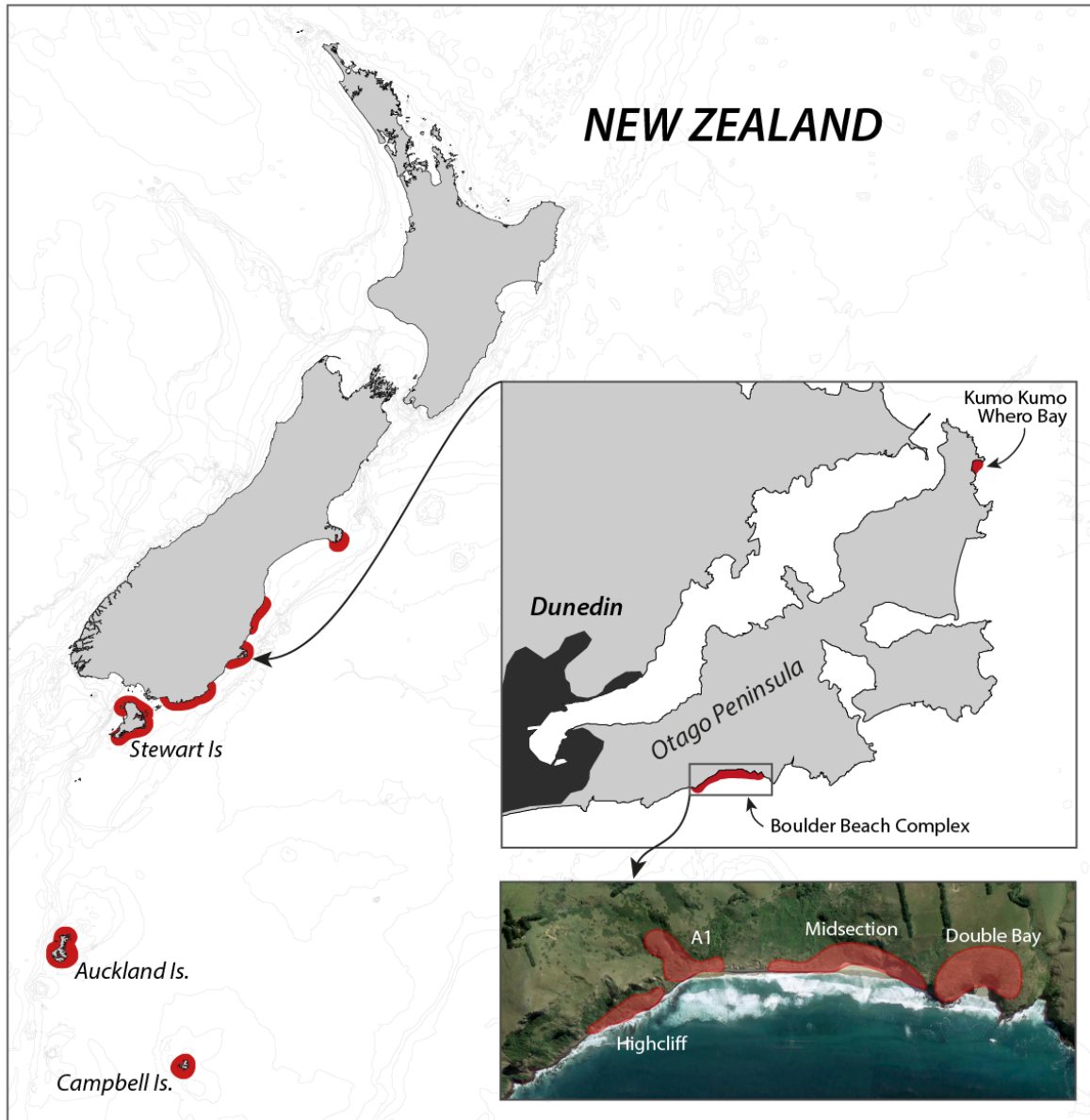
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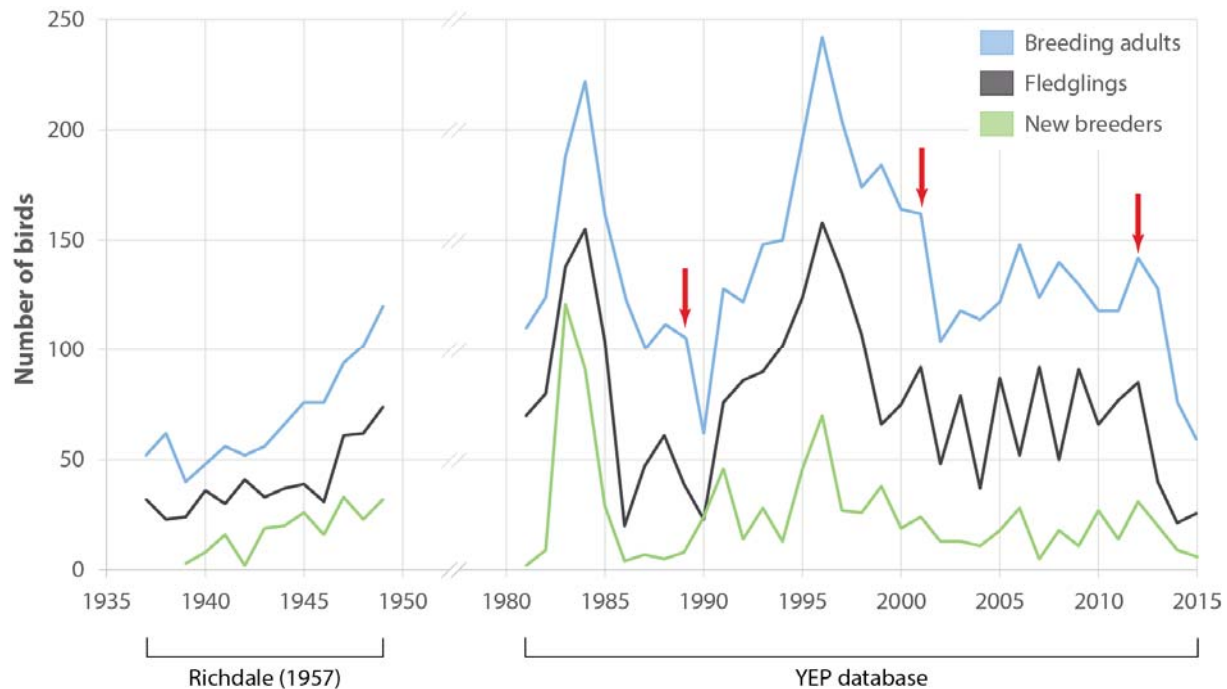
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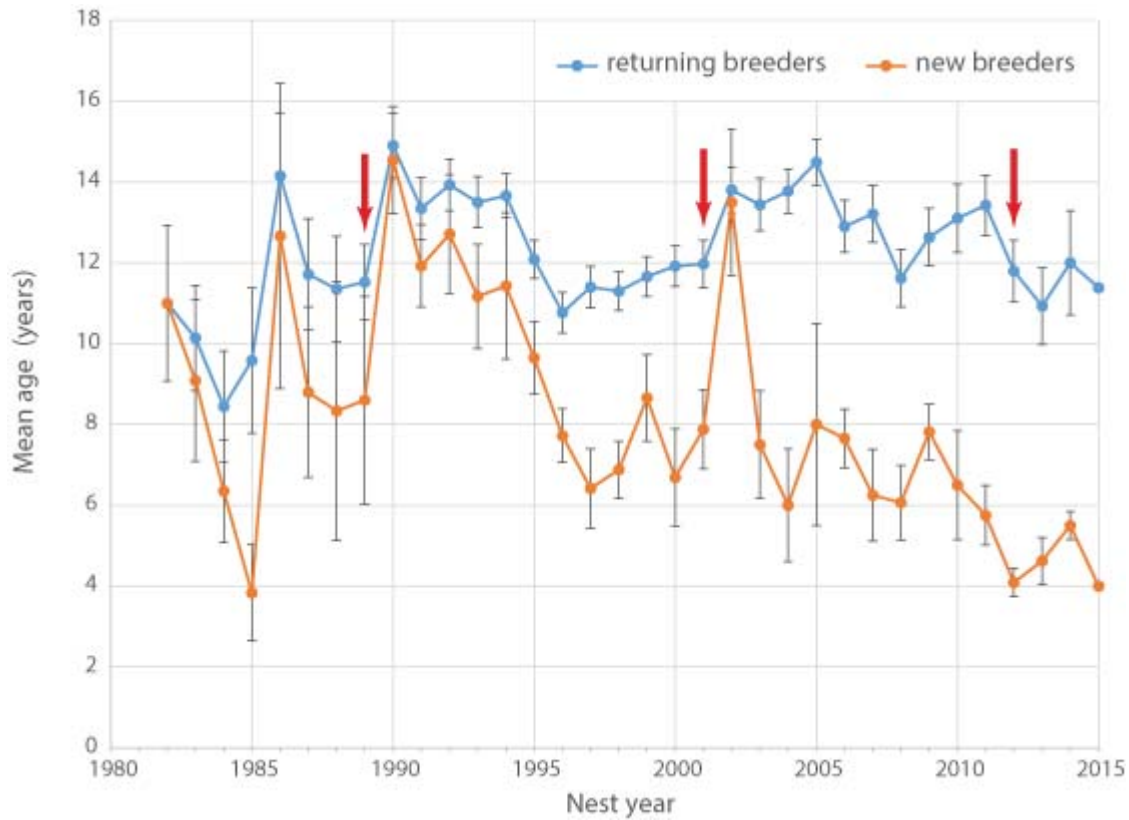
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771 **Figure 1.** Overview of the breeding range of Yellow-eyed penguins, detail of the Otago
772 Peninsula with an aerial view of the Boulder Beach Complex (henceforth Boulder Beach)
773 with outlines indicating the locations of the four main monitoring plots. The inset map also
774 indicates Kumo Kumo Whero Bay, the location of the historic population study conducted
775 from the 1930s to 1950s.



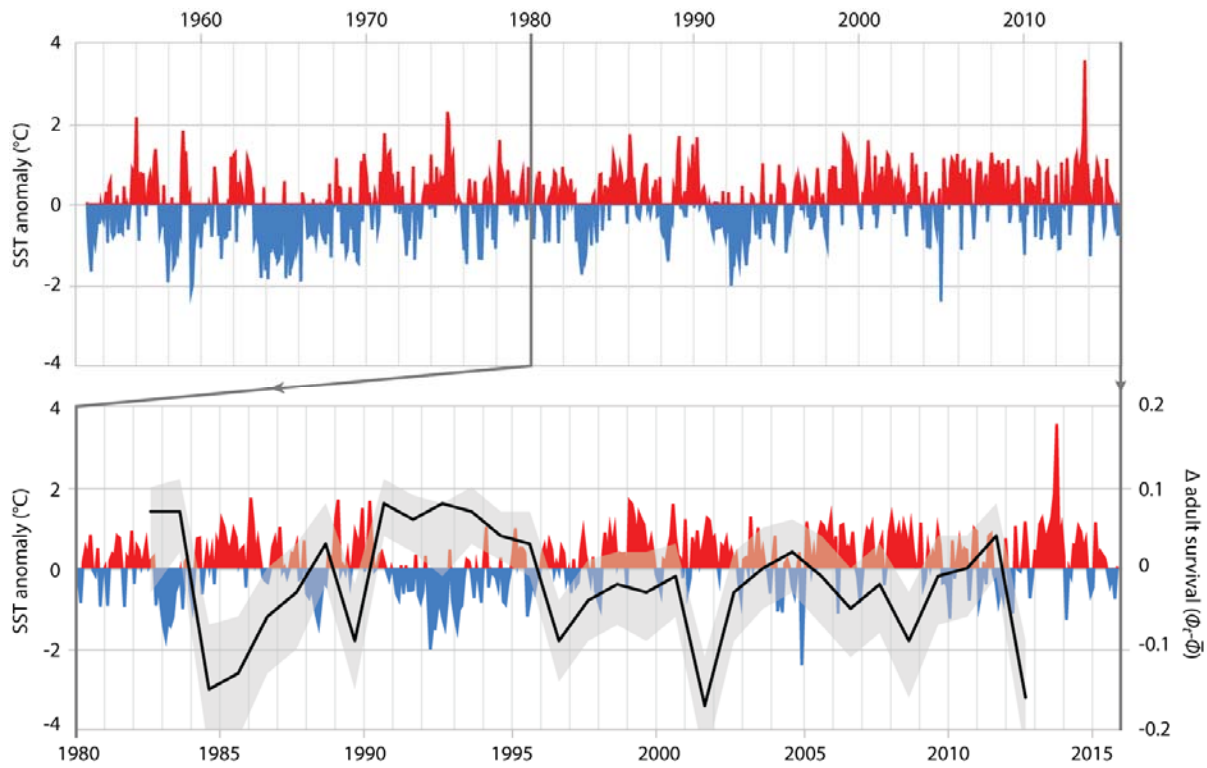
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777 **Figure 2.** Observed penguin numbers at Kumo Kumo Whero 1937-1948 (from data
778 published in Richdale 1957, see Methods for details) and at the Boulder Beach complex
779 1982-2015 as extracted from the Yellow-eyed penguin database. 'New breeders' represents
780 the portion of all 'breeding adults' that were recorded as breeders for the first time. Red
781 arrows indicate years with observed die-off events affecting adult breeders. Note that as
782 some sections of the Boulder Beach complex were not monitored in all years, data for the
783 years 1986-1989 were adjusted by adding the mean proportion these areas contributed to
784 the total count in all other years.



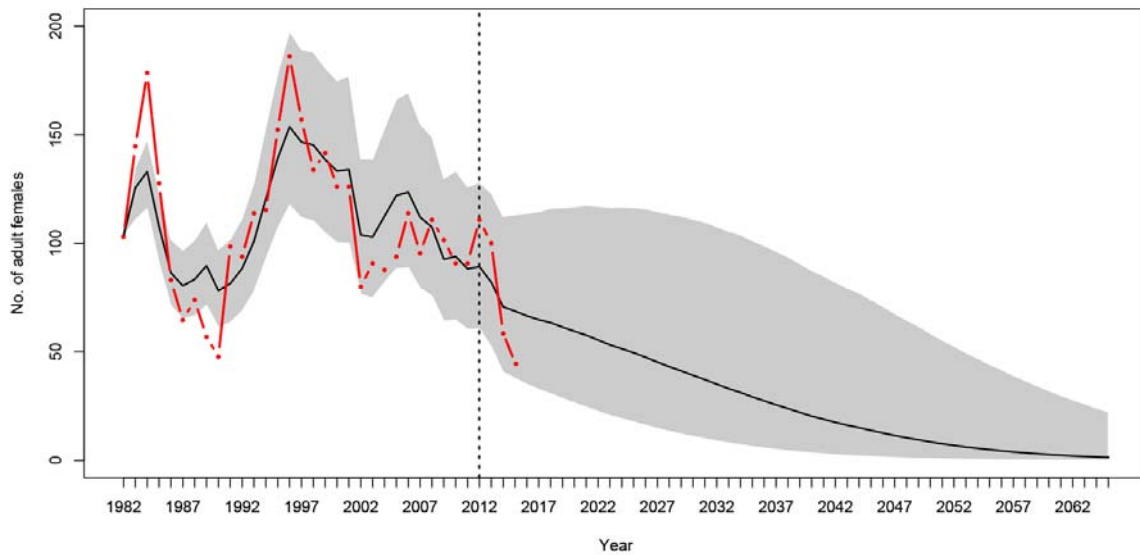
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786 **Figure 3.** Average age of breeding Yellow-eyed penguins active at Boulder Beach between
787 1982 and 2015. Red arrows indicate years with observed die-off events affecting adult
788 breeders.



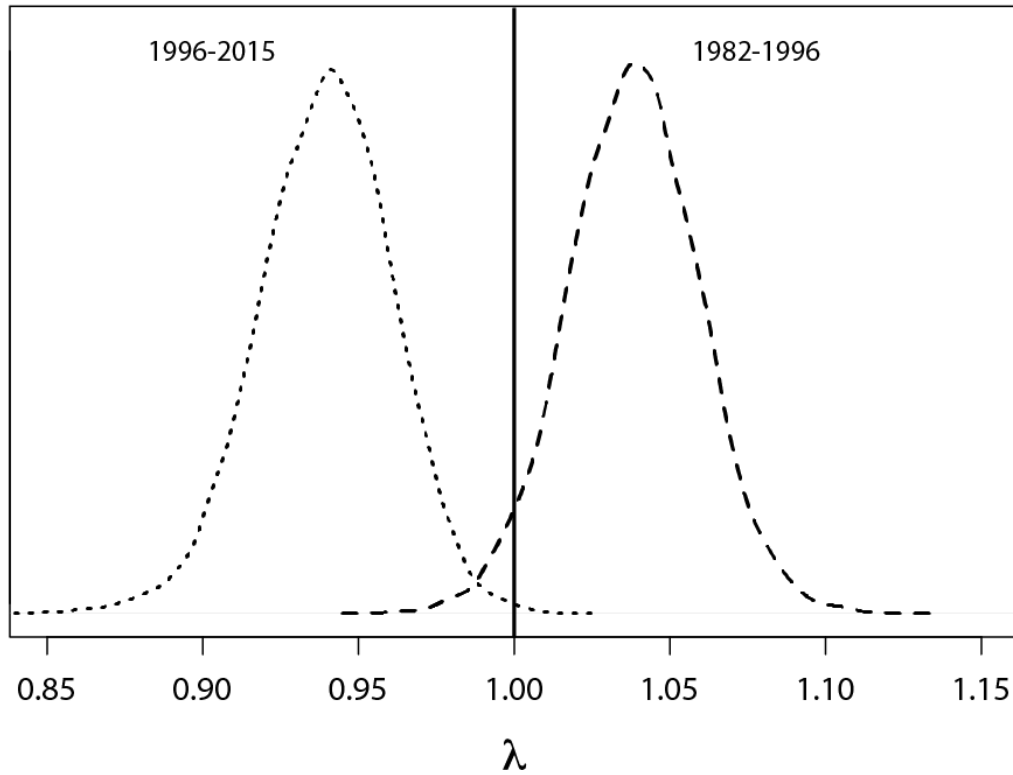
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790 **Figure 4.** Top graph: Local Sea Surface Temperature anomalies recorded at Portobello
791 Marine Lab, Otago Peninsula, between 1953 and 2016. Bottom graph: detail of SST
792 anomalies 1980-2016 and associated deviance (black line: mean; grey area: 95% credible
793 interval) in survival of adult Yellow-eyed penguins as determined from a MR recapture
794 model.



795

796 **Figure 5.** Population projections for Yellow-eyed penguins at Boulder Beach, Otago
797 Peninsula. The graphs show the observed (red line) and estimated (black line) number
798 of female penguins, and associated 95% credible interval (grey area), as derived from
799 the population model. The dashed vertical line indicates the last year used to
800 parameterise the MR model and the starting year of the simulation. Population
801 projections were modelled using survival rate estimates until 2012; beyond this year
802 estimates get increasingly unreliable because these are based on data about individual
803 absence from breeding rather than from reported mortalities (see 'Methods').



804

805 **Figure 6.** Probability density functions for deterministic annual population growth rates
806 derived from survival rates that were rescaled for periods of cooler (1982-1996) and
807 warmer (1996-2014) than average sea surface temperatures.

808 **Table 1.** Description of basic environmental parameters used for the development of a
 809 YEP population model.

Parameter	shorthand	Station
Total Rainfall (mm)	total_rainfall	Southern Reservoir (National Climate database, CliFlo ID 5400)
Wet Days - Number Of Days With 1mm Or More Of Rain (days)	wet_days	Southern Reservoir (5400)
Maximum 1-Day Rainfall - 9am To 9am Local Time	max_1day_rain	Dunedin, Musselburgh (5402)
Mean Air Temperature	mean_air_temp	Dunedin, Musselburgh (5402)
Mean Daily Minimum Air Temperature	daily_min_temp	Dunedin, Musselburgh (5402)
Days Of Wind Gusts >=33 Knots	days_wind_gusts_33	Dunedin, Musselburgh (5402)
Sea Surface Temperature anomaly	sst_anomaly	Portobello Marine Lab, University of Otago

810 **Table 2.** Parameter estimates from the Bayesian mark-recapture model. $\bar{\Phi}$ indicates
811 estimated annual survival rates, σ^2 stands for the temporal variance of the stage-specific
812 annual survival. Refer to ESM1 for details.

Parameters	Median	Credible interval	
		2.5%	97.5%
$\bar{\Phi}_{chicks}$	0.124	0.077	0.189
σ^2_{chicks}	1.877	1.001	3.847
σ^2_{chicks} (on probability scale)	0.021	0.009	0.065
$\bar{\Phi}_{adults}$	0.872	0.832	0.904
σ^2_{adults}	0.732	0.414	1.398
σ^2_{adults} (on probability scale)	0.009	0.005	0.021

813 **Table 3a.** Estimated effect size for fledgling survival ($\beta_{\text{fledlings}}$); PVE: percentage of
 814 variance in fledgling survival explained by each covariate. Note, that negative values
 815 resulted from models that estimated slightly higher (or less precise) variance in
 816 fledgling survival, as it would result for the model without covariate. Except for
 817 covariate 2, 3, 4 and 15 all variables were standardized before fitted to the MR model.

ID	Covariate	Median	Credible interval		PVE
			2.5%	97.5%	
1	days_wind_gusts_33_annual	0.850	0.377	1.329	33.2
2	sst_anomaly_austral	-1.967	-3.148	-0.964	33.2
3	sst_anomaly_minus_1yr	-1.516	-2.649	-0.392	24.8
4	sst_anomaly_mar_june	-0.970	-1.845	-0.111	17.4
5	days_wind_gusts_33_mar_may	0.696	0.198	1.241	16.5
6	daily_min_temp_annual	-0.644	-1.190	-0.143	15.4
7	mean_air_temp_annual	-0.590	-1.167	-0.102	12.4
8	daily_min_temp_mar_may	-0.303	-0.829	0.204	0.7
9	mean_air_temp_mar_may	-0.304	-0.850	0.190	0.2
10	total_rainfall_may_may	-0.254	-0.823	0.296	-2.3
11	max_1day_rain_mar_may	-0.250	-0.835	0.318	-3.3
12	total_rainfall_annual	-0.260	-0.841	0.316	-3.5
13	max_1day_rain_annual	-0.167	-0.738	0.394	-5.2
14	wet_days_mar_may	-0.141	-0.702	0.431	-5.6
15	sst_anomaly_minus_2yr	-0.217	-1.451	1.045	-5.6
16	wet_days_annual	0.073	-0.461	0.623	-6.7

818 **Table 3b.** Estimated effect size for adult survival (β_{adults}); PVE: percentage of variance in
 819 adult survival explained by each covariate. Note, that negative values resulted from
 820 models that estimated slightly higher (or less precise) variance in adult survival, as it
 821 would result for the model without covariate. Except for covariate 1, 4, 5 and 14 all
 822 variables were standardized before fitted to the MR model.

ID	Covariate	Median	Credible interval		PVE
			2.5%	97.5%	
1	sst_anomaly_austral	-1.267	-1.925	-0.631	36.8
2	mean_air_temp_annual	-0.529	-0.817	-0.251	34.4
3	daily_min_temp_annual	-0.516	-0.796	-0.227	34.4
4	sst_anomaly_mar_june	-0.808	-1.329	-0.310	26.2
5	sst_anomaly_minus_1yr	-1.056	-1.719	-0.406	25.7
6	days_wind_gusts_33_annual	0.377	0.075	0.690	16.5
7	days_wind_gusts_33_mar_may	0.350	0.052	0.666	12.8
8	daily_min_temp_mar_may	-0.214	-0.537	0.088	2.0
9	total_rainfall_may_may	-0.146	-0.461	0.193	1.0
10	mean_air_temp_mar_may	-0.181	-0.513	0.140	-0.3
11	wet_days_mar_may	-0.113	-0.434	0.207	-1.0
12	max_1day_rain_mar_may	-0.098	-0.416	0.234	-2.0
13	max_1day_rain_annual	0.112	-0.206	0.435	-2.2
14	sst_anomaly_minus_2yr	-0.055	-0.867	0.720	-3.1
15	wet_days_annual	0.064	-0.275	0.393	-3.8
16	total_rainfall_annual	0.057	-0.268	0.391	-4.0

823 **Table 4.** Results of the Gibbs Variable Selection. 0 and 1 indicate whether each covariate
 824 is not included or included in the model, respectively. The MR considers covariates
 825 ‘sst_anomaly_austral’ for fledgling (A) and adult survival (C),
 826 ‘days_wind_gusts_33_annual’ (B) and ‘mean_air_temp_annual’ (D). For a detailed
 827 description of the GVS refer to ESM4.

	Model configuration				p(M_i y)
	Fledgling survival		Adult survival		
M_i	A	B	C	D	
1	1	0	1	0	0.42
2	0	1	1	0	0.13
3	1	1	1	0	0.12
4	1	0	0	1	0.09
5	0	1	0	1	0.06
6	0	0	0	0	0.04
7	1	0	0	0	0.03
8	0	1	0	0	0.03
9	1	1	0	0	0.02
10	0	0	1	0	0.01
11	0	0	0	1	0.01
12	1	1	0	1	0.01
13	0	0	1	1	0
14	1	0	1	1	0
15	0	1	1	1	0
16	1	1	1	1	0

828