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3 ***Running head: Climate and foraging performance in little penguin***

4 Environmental effects on foraging performance in Little penguins: a matter of phenology and
5 short-term variability.

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16 **Abstract**

17 Foraging provides an integrative view of the effects of environmental variability on marine
18 predators, from direct effects through increased energetic costs at sea to indirect effects
19 through modification of prey accessibility. Using a 19-year automated monitoring system of
20 ~400 individuals (>45,000 foraging trips), we investigated short-term and interannual
21 variability in foraging performance (trip duration and mass gain) of breeding little penguins
22 (*Eudyptula minor*), nearshore seabirds living in a climate change hotspot. We found marked
23 but variable seasonal patterns in foraging performance with clear optimum periods but no
24 decreases in trip duration nor mass gain throughout the breeding season. Although foraging
25 performance was less variable at the inter-annual scale, we highlighted three groups of low,
26 average, and good annual foraging performance. Low foraging performance during post-
27 guard was associated with significantly lower breeding success. To understand how the
28 environment might explain such variability, we simultaneously studied the effect of variables
29 that may affect penguin foraging directly by altering energy costs at sea (currents, waves, and
30 tides) and indirectly by modifying prey availability (primary production and vertical
31 stratification). Although foraging performance is often thought to mainly depend on prey
32 accessibility, lower foraging performances was mostly associated with increased waves and
33 currents and only secondarily with a decreased and shallower stratification. Finally,
34 synchrony between penguin phenology and primary production cycles explained inter-annual
35 foraging performance, highlighting the importance of seabird breeding phenology.

36

37 **Key words:** *Climate variation, breeding ecology, breeding success, little penguin,*
38 *match/mismatch, stratification, waves, currents*

39 **1. Introduction**

40 Marine predators such as seabirds integrate direct and indirect effects of the environment
41 through lower trophic levels of the ecosystem (Parrish et Zador 2003, Piatt et al. 2007). For
42 instance, seabird energetics can be directly affected by wind regime (Spear & Ainley 1997,
43 Mateos & Arroyo 2011) and indirectly by prey availability (Piatt & Anderson 1996, Romano
44 et al. 2006). An efficient way to study environment-driven changes in marine ecosystems is to
45 assess seabird foraging performance, because this should reflect both energetic costs at sea
46 (Mullers et al. 2009, Collins et al. 2020) and prey availability (Cairns 1988, Grémillet et al.
47 2004).

48 The environment is expected to affect seabird foraging (thus survival, breeding, and
49 ultimately population dynamics, Baird 1990) differently depending on the time scale
50 considered, especially during breeding when biological constraints due to parental care are
51 maximal. Prey availability, which constrains central place foragers (Hunt 1999, Burke &
52 Montevecchi 2009), could be modified by short-term (days to weeks) changes in spatial
53 (vertical and horizontal) prey distribution. Indeed, prey are neither randomly nor uniformly
54 distributed in time and space, but rather aggregate until a specific density in favorable areas
55 (Fauchald 2009). Prey aggregations are created by ocean vertical and horizontal mixing
56 including fronts, eddies, upwellings or water column stratification (Spear et al. 2001,
57 Charrassin & Bost 2001). At a medium temporal scale (several weeks to months), prey
58 availability changes according to seasonal cycles (especially in temperate and polar
59 environments). Seabird foraging performance should thus be optimal when foraging is
60 synchronised with maximum prey availability (Regular et al. 2014). However, this optimum
61 period may shift when a predator's range is limited, and prey abundance is concentrated
62 within a limited area, leading to local prey depletion, mismatches between predators and their
63 prey or interference competition during the breeding season (Ashmole 1963, Birt et al. 1987,

64 Lewis et al. 2001). At even larger time scales, inter-annual variability can affect prey
65 phenology and therefore shift the optimum period between successive years (Watanuki et al.
66 2009), prey recruitment causing a delayed effect on prey abundance during successive seasons
67 (Biela et al. 2019), and prey quality (*e.g.* energetic composition) associated with different
68 levels of ocean productivity (Wanless et al. 2005).

69 In such complex marine ecosystems, little penguin (*Eudyptula minor*) is an appropriate
70 species to study the integrated effects of climate on foraging performance. Due to their limited
71 diving capacities (around 65m, Ropert-Coudert et al. 2006) and restricted, central place
72 foraging range (average 20 km from the coast in most cases, Collins et al. 1999), little
73 penguins are strong central place foragers during breeding (*i.e.* when adults have to feed their
74 chicks regularly; Reilly & Cullen 1981, Chiaradia et al. 2007). Their small size also leads to
75 high metabolic rates and limited energy storage capacity (Schmidt-Nielsen 1984), making
76 them particularly sensitive to short-term environmental variability. Moreover, the little
77 penguin has a long and asynchronous breeding season (Reilly & Cullen 1981), meaning that
78 environmental conditions may differ among individuals throughout the season depending on
79 breeding phenology.

80 Little penguins have been suggested to be sensitive to any change in local prey abundance,
81 distribution and diversity (Chiaradia et al. 2003, 2016). As such, they should be affected by
82 any environmental parameters that affect these prey dynamics. For example, little penguin
83 rely on vertical stratification to target prey aggregated around the thermocline (Hansen et al.
84 2001) and thus improve foraging success (Ropert-Coudert et al. 2009, Pelletier et al. 2012).
85 Yet, direct effects of environmental variability on their energy expenditure at sea should not
86 be discounted, as shown with the effect of currents and tides in a closely related species, the
87 Magellanic penguin (*Spheniscus magellanicus*, Raya Rey et al. 2010). While stronger winds
88 are detrimental for little penguin foraging performance (Saraux et al. 2016), the underlying

89 mechanisms (*i.e.* increased energetic costs due to foraging in rough seas or decreased
90 efficiency due to more dispersed prey associated with a lower vertical stratification) remains
91 to be investigated. Large-scale decadal oscillations such as ENSO, which can be more
92 influential than local climate parameters and cause greater impacts on certain life-history
93 traits (Hallett et al. 2004, Stenseth & Mysterud 2005), may also affect little penguin foraging
94 performance (Berlincourt & Arnould 2015). Finally, the match between annual primary
95 production cycles (ultimately linked to prey availability) and phenology could also affect
96 penguin inter-annual foraging performances (Afán et al. 2015, Chiaradia et al. 2021).

97 This study examined how little penguin foraging performance at the world's largest colony for
98 this species at Phillip Island, Australia varied through time according to changes in their
99 environment . Using an automated penguin monitoring system deployed continuously over 19
100 years, we compiled a unique dataset of foraging performance (*i.e.* foraging trip duration and
101 associated mass gain) across a wide range of environmental conditions ($\geq 45,000$ trips). First,
102 we investigated little penguin foraging performance variability at different timescales (within-
103 and among breeding years). Specifically, within the year, we tested whether foraging
104 performance decreased throughout the year (as would be expected in case of substantial local
105 prey depletion) or instead reached an optimum during the breeding season (as would be
106 expected during a temporal match with maximal prey availability). Among years, we tested
107 differences in overall foraging performance and examined potential links with annual
108 breeding success.

109 Second, we investigated how foraging performance responded to the environment at three
110 different time scales: short-term (*i.e.* environmental conditions varying from one trip to
111 another), seasonal, and inter-annual scales. We simultaneously studied the effects of multiple
112 environmental parameters known (thermocline, wind, primary production), or suspected
113 stressors (waves, currents, tides, and two climatic oscillations: Antarctic Oscillations (AAO)

114 & El Nino Southern Oscillations (ENSO)) to affect little penguin foraging success. We
115 expected to partition the variance in foraging performance between different environment-
116 driven processes by doing so. In particular, we expected foraging performance to be affected
117 both directly through energetic costs at sea (*e.g.* currents, waves) and indirectly through prey
118 availability (*e.g.*, vertical stratification, primary production). Further, we predicted very
119 different effects and relative importance of these parameters depending on the time scale
120 considered. While short-term, unfavourable conditions should be driven by environmental
121 variables known to increase energetic costs and decrease prey accessibility, inter-annual
122 differences in foraging performance should depend on ecosystem productivity and synchrony
123 with prey availability (*i.e.* penguins phenology). A single variable could even have opposite
124 effects depending on the time scale considered. For example, wind and current speed are
125 expected to instantaneously increase swimming and foraging costs while decreasing vertical
126 stratification (Raya Rey et al. 2010, Saraux et al. 2016), whereas they should improve water
127 mixing and thus enhance primary production in the longer run, favouring energy transfer
128 throughout the entire food web (Marra 1980).

129 **2. Methods**

130 **1.1. Little penguin long-term monitoring**

131 *1.1.1 Study site and breeding monitoring*

132 The studied colony located in the Summerland Peninsula on Phillip Island (38°15' S, 143°30'
133 E), Victoria, Australia, consists of 28,000 to 32,000 little penguin breeding adults (*Figure 1*;
134 Sutherland & Dann 2012). The 399 birds monitored in this study were subcutaneously
135 implanted with numbered, 23-mm ISO HDX transponders (Allflex, Australia) between the
136 scapulae (shoulder blades; Chiaradia & Kerry 1999) either as chicks (70%) just before
137 fledging, or when first encountered as an adult and nested in a part of the colony containing
138 100 artificial burrows (wooden nest boxes). All nests were checked three times per week

139 using a custom-built portable transponder reader, allowing us to determine every nest and
140 individual's breeding stage and performance.

141 This study spans 19 consecutive breeding years from 2001 to 2019. As little penguin breeding
142 season occurs during the austral summer from May to February (Reilly & Cullen 1981), a
143 breeding year refers to the austral summer (*e.g.* 2001 corresponds to birds breeding in the
144 austral summer of 2001–2002). The stages of the breeding cycle after egg laying are separated
145 into 3 stages: the egg-incubation period (lasting about 35 days), the guard period (~2 weeks)
146 when one parent stays with young chicks while the other forages at sea, and the post-guard
147 period (5 to 8 weeks), when older chicks are left alone during the day and parents return at
148 night to feed them (Chiaradia & Kerry 1999). Breeding success was the number of chicks
149 fledged per breeding event. Because little penguins may sometimes produce a second clutch
150 during the same season (Reilly & Cullen 1981), only first clutches were considered here to
151 prevent pseudoreplication and bias due to the first clutch investment.

152 *1.1.2 Foraging performance*

153 Foraging performance was assessed based on trip duration and associated mass gain as
154 monitored by an Automated Penguin Monitoring System (APMS) located on the main
155 passage used by the penguins between the colony and the sea. This automatic monitoring
156 system consists of a transponder-reader, a weighing platform (calculating mass to the nearest
157 gram, Salton et al. 2015), and a datalogger recording ID and body mass of individual
158 penguins going in or out of the colony. The second entry point was monitored by a simpler
159 platform (transponder reading without weighing), so that some detections had no associated
160 body mass (26% of the detections during the breeding period).

161 Foraging trip duration was calculated as the number of days between sequential recordings of
162 a "departure" and an "arrival", considering little penguins leave the site before sunrise and

163 return after sunset (Chiaradia & Kerry 1999). As foraging duration was mostly one day long
164 during guard trips (96% 1-d trips and 4% 2-d trips), variability in trip duration was only
165 investigated during incubation and post-guard stages. Trips longer than 17 days (193 trips
166 either in incubation or post-guard) were considered as missing detections and discarded
167 (Saraux et al. 2016).

168 Body mass gain was defined as the amount of mass change per foraging trip and was
169 calculated as the difference between a penguin's body mass after and before a given foraging
170 trip. Only body mass ranging from 700 to 1700g and body mass change ranging from [-75 to
171 500 g] during incubation and [0 to 600 g] during chick-rearing were considered to avoid
172 incorrect scale estimates (2786 discarded trips for mass gain, based on Salton et al. 2015 and
173 Saraux & Chiaradia 2021).

174 For our two measures of performance (trip duration and mass gain) to be independent, mass
175 gain was corrected for each breeding stage separately using residual values from the linear
176 model [mass gain ~ trip duration] (see Supplementary Material Fig S8).

177 **2.2 Environmental data**

178 *2.2.1. Environmental parameters*

179 All data handling was performed using R 3.5.1 (*R Core Team, 2018*) and *ncdf4* 1.17 package
180 (Pierce 2019) for NetCDF files opening and shaping. Water column temperature, chlorophyll
181 concentration, wave height, current speed, wind speed, tides and decadal oscillations (AAO &
182 ENSO) were gathered from different online databases as detailed in *Table 1*. Water column
183 temperature was used to construct several thermocline variables (presence, depth, and
184 intensity) using an innovative method, because unequal depth segments (precision of one
185 value every 1-5m until 30m deep, 5-10m until 100m deep and 10-25m until 200m) and
186 coastal pixels (with very shallow depths) prevented the use of classically used ones (Fiedler

187 2010). Briefly, we estimated temperature gradients between each consecutive depth ($\frac{\Delta T}{\Delta Depth}$)
188 and then looked for changes in these gradients throughout depth using breakpoints (see
189 Supplementary material Fig. S2 for details). The segment with the highest gradient was
190 identified as the thermocline. The depth of the thermocline was defined as the top of this
191 segment. The intensity of the thermocline was the mean temperature gradient (in absolute
192 value) within this segment. The thermocline was assessed as present in a pixel when its
193 gradient was $>0.02^{\circ}\text{C}/\text{m}$ (based on slope breakpoints in the thermocline depth/gradient
194 relationship), and its depth shallower than 70m (*i.e.* reachable for little penguins).

195 Water level (tides) data were available as hourly values, from which we assessed the water
196 level (m) at both penguins departure at sea and arrival on land (*i.e.* the periods during which
197 tides are expected to affect energetic costs of swimming for penguins).

198 Finally, wind speed affects little penguins at sea (Saraux et al. 2016). Because penguins are
199 non-flying seabirds, we do not expect wind to affect penguin foraging directly. Rather, we
200 expect wind to affect other environmental variables (waves, currents, stratification) that in
201 return affect penguin foraging. Therefore, to understand the paths through which wind
202 affected foraging, wind speed was included in this study only to assess its correlation with
203 other variables for which we expected strong effects on foraging performance (see
204 Supplementary material Fig. S3 & Fig. S4) but not in models explaining foraging
205 performance.

206 2.2.2 Building time series of environmental variables

207 To build time series, data from more than one dataset (*e.g.* MODIS/SeaWifs) were merged as
208 specified in *Table 1*.

209 Daily time series were built for all parameters (apart from decadal oscillations for which data
210 was available as monthly values) by averaging gridded data, except for thermocline presence,

211 defined as the daily proportion of pixels where the thermocline was considered present in the
212 area. The area used to extract environmental parameters (140 to 148° E, 38.2 to 41° S, approx.
213 120,000 km², *Figure 1*) was much larger than the known little penguin foraging areas to
214 account for oceanographic processes occurring outside of the foraging area but which can still
215 be influential (*e.g.* phytoplankton bloom). However, some other parameters might be more
216 local, affecting little penguins foraging directly at the locations they travel or forage (*e.g.*
217 currents, waves, stratification). To assess the sensitivity of the time series to the chosen area,
218 we compared two different time series averaged over either the entire large area (red
219 rectangle) or a smaller one corresponding to foraging grounds only (yellow rectangle,
220 Sánchez et al. 2018). No significant differences were observed (see Supplementary material
221 Fig. S6), so that results were considered unbiased by the area and are only presented using the
222 larger area.

223 A seasonal time series was then built by extracting the seasonal signal from the above-
224 described daily time series (except for tides, which do not present strong seasonal patterns).
225 The seasonal signal was computed as the average value of each week among years to assess
226 medium-term environmental patterns. Anomalies from this seasonal signal were estimated as
227 the daily value minus the corresponding weekly seasonal signal and represented short-term
228 patterns. This method was compared with other methods using additive or multiplicative time
229 series decomposition; all yielded similar results (see Supplementary material Fig. S7).

230 Finally, a time series was created for inter-annual average comparisons and synchrony
231 between phenology and environment. It was composed of yearly environment variable
232 anomalies (averaged over the breeding season, from the first to the last breeding day of each
233 season), annual oscillation indices (ENSO & AAO, from April to March) and annual
234 phytoplankton bloom beginning and end dates (dates at which 10 and 90%, respectively, of
235 the yearly cumulated daily Chl_a were reached, Brody et al. 2013).

236 **2.3. Analyses and statistics**

237 All analyses were performed using R 3.5.1 (*R Core Team, 2018*) . Results are presented as
238 means \pm standard errors (SE). Whenever running a linear model (or linear mixed model,
239 LMM), the normality of the residuals was verified using density plots and q-q plots.

240 *2.3.1. Seasonal patterns in foraging performance*

241 Trip duration and associated mass gain were averaged per calendar week to assess seasonal
242 patterns in foraging performances throughout the year. Generalised Additive Models from
243 `mgcv 1.8-33` (Wood 2011, $GAM = Mass\ gain\ or\ Trip\ duration \sim smooth\{week\}$) were
244 then run for each breeding stage separately. However, in these models an early week could
245 result from two different processes: individual foraging early in the year and/or an overall
246 early year. To understand the interplay between these two processes and assess the variability
247 of seasonal patterns among years with different overall timing, we computed the average
248 foraging week of each breeding year and the relative week of each trip (Van de Pol & Wright
249 2009). The relative week is the week of the trip (the week of the trip being defined as the day
250 of departure) centered around the average week of the season (*i.e* the week value of each trip
251 minus the average week of the season, *Figure 2*) in a way that the relative week accounts for
252 the individual timing with no regards the overall season timing. Effects of the average week
253 (overall timing, rather early or delayed years compared to others), relative week (timing of
254 each week within the season) and their interaction were assessed using the following
255 Generalised Additive Mixed Models:

256 $GAMM = Mass\ gain\ or\ Trip\ duration \sim smooth\{relative\ week\} + smooth\{average$
257 $week\} + tensor\ product\{average\ week, relative\ week\}$

258 We added individual ID as random effect (intercept) for both foraging parameters and a
259 random effect (intercept) of chick age for trip duration and adult sex for mass gain (based on
260 preliminary variance analysis, see Supplementary material Tab. S1 & Text S2).

261

262 *2.3.2. Inter-annual differences in foraging performance and link with breeding success*

263 To categorise years based on their overall foraging performance (*e.g.* low, average, high), we
264 used a clustering analysis performed using k-means method and `kmeans` function from
265 `stats` 3.6-2. Years were clustered using two dimensions (mass gain and trip duration),
266 except for guard during which clustering is made only based on mass gain (to avoid the 4%
267 two days trips to drive the variability of an entire clustering dimension although accounting
268 for a very small part of the data). For each breeding stage and for the whole season, the
269 optimal number of clusters was assessed by running the `kmeans` function 1000 times for each
270 cluster number from 1 to 10. Both within- and among-clusters square sum of distances were
271 then computed for all cluster numbers, and the strongest break in slope for these two
272 parameters was used to define the optimum number of clusters.

273 Finally, we investigated whether years with contrasting foraging performance resulted in
274 different breeding success and whether this applied for each breeding stage and the whole
275 year. To do so, we tested for differences in annual breeding success among clusters of
276 foraging performance using Kruskal-Wallis followed by Holm adjusted (to account for
277 multiple comparison) Post-Hoc Dunn tests (`dunnTest` function from FSA 0.9.1, Ogle et al.
278 2021).

279

280 *2.3.3. Effects of short-term environmental variation on foraging performance*

281 We assessed the link between environmental parameters and trip duration and associated mass
282 gain on the short-term (*i.e.* at the trip scale) using linear mixed models for each breeding stage
283 separately because effects were expected to differ due to different constraints among breeding
284 stages. Daily parameter anomalies and seasonal signals were averaged per foraging trip,
285 except for tides (closest hourly water level measure) and used as explanatory variables in the

286 models. Effects on mass gain were tested using LMM with random effects of year, individual
287 and sex, while effects on trip duration were tested using GLMM with Poisson distribution
288 (Saraux et al. 2016) and random effects of year, individual, and chick age (based on
289 preliminary variance analysis, Supplementary material Tab. S1). Variance Inflation Factors
290 (VIF) were estimated on full models, including all variable anomalies and seasonal signals.
291 Variables with the greatest VIF were then sequentially removed until no variable had VIF >3
292 to avoid collinearity issues (Zuur et al. 2010).

293 *2.3.4. Effects of inter-annual climate variability and breeding timing on foraging* 294 *performance*

295 To test for the relation between the environment and foraging performance at the inter-annual
296 scale, we computed linear models explaining annual means of either mass gain or trip
297 duration by yearly means of environmental anomalies averaged over the breeding season
298 (except for tides that were expected to present no inter-annual differences) as well as annual
299 ENSO and AAO indices. Considering the small sample size (n=19 years) compared to the
300 number of explanatory variables tested, we decided to run separate linear models for each
301 explanatory variable (lm = mass gain or trip duration ~ environmental variable).

302 Finally, we studied the effect of synchrony between phenology and primary production by
303 testing the effect of match or mismatch between foraging period and optimal conditions (as
304 inferred by chlorophyll a). Because the primary production bloom occurs mainly during
305 winter in this zone (*i.e.* finishing in spring, Kämpf & Kavi 2017) while little penguins breed in
306 spring/summer, we assessed penguin foraging performance and primary production
307 synchrony as the yearly average week of foraging minus the bloom end week. The link
308 between this synchrony and foraging performances was assessed separately using GAMs on
309 annual mass gain and trip duration.

310 **3. Results**

311 **3.1. Variability in foraging performance**

312 Over all individuals (N = 399) and years (N=19), foraging trips (n = 45,363) lasted on average
313 3.21 ± 0.03 days during incubation (n = 7,075), 1.09 ± 0.00 days during guard (n = 11,767),
314 and 1.40 ± 0.01 days during post-guard (n = 26,521), ranging from one to 17 days (in
315 incubation and post-guard, 1-2 days in guard). Relative mass gain (*i.e.* mass gain corrected
316 according to trip duration) was estimated for 28,633 trips (63%) and varied from -394g to
317 +352g. Due to the significance of breeding stage on foraging performance (Supplementary
318 material Tab. S1), further analyses were run separately per breeding stage.

319 *3.1.1 Seasonal and optimal patterns in foraging performance*

320 Except for relative mass gain during incubation (GAM, $p = 0.32$, $n = 29$ weeks, *Figure 3 C*),
321 little penguin foraging performance presented non-linear changes within a season during all
322 breeding stages (*Figure 3*, detailed models summary in *Supplementary material Tab S2*). All
323 four GAMs showed a similar optimal period of foraging (*i.e.* shorter trips and higher mass
324 gains) in October (weeks 40–42), except regarding trip duration in incubation where optimum
325 was slightly delayed (weeks 47-49) . Foraging performance also increased for the latest trips
326 in the season with shorter trips in January during incubation (week 55, GAM, $p < 0.001$, $n =$
327 29 weeks) and shorter trips with higher mass gains in March during post-guard (week 63,
328 GAM, $p < 0.001$, $n = 34$ weeks).

329 *3.1.2 Interaction between phenology and foraging performance*

330 To assess how optimal patterns were affected by differences in overall years timing, further
331 analyses considered the effects of average year week (inter-annual variability, *i.e.* precocious
332 versus delayed breeding year) and week relative to average year week (within-year variability,
333 *i.e.* early versus late within the year, see *Figure 2* for more details). The time of the year

334 (average year week) and individual timing relative to others (relative weeks) had a significant
335 effect on penguin trip durations during incubation and post-guard, as did their interaction
336 (GAMMs, $n = 5,705$ and $21,604$, all $p < 0.001$). It indicated that intra-annual patterns in
337 foraging performance varied depending on the year overall timing (*i.e.* precocious or delayed
338 years). Penguins conducted shorter trips just before mid-year (relative weeks -5 to 0) during
339 incubation and post-guard and at the end of incubation (relative week 8 to 10). While this
340 remained true regardless of the year timing (average week in *Figure 4 A and B*), the effect
341 was much more pronounced during delayed years than in precocious years (see average week
342 40 to 45 against week 50 to 55 in *Figure 4 A & B*).

343 During incubation, the relative mass gain of penguins was related to both year timing and
344 individual timing, yet the interaction was not significant (GAMM, $n = 3,422$, $p < 0.001$ for
345 single effects and $p = 0.378$ for their interaction). Their mass gain was significantly lower
346 during delayed years (*Figure 4 C*) and was very similar early and late within the year, but
347 slightly higher in early mid-year (relative weeks from -10 to 0). During guard, the relative
348 mass gain was affected by individual timing (relative week) and its interaction with the year
349 (average week) timing (GAMM, $n = 6,367$, $p < 0.001$ for relative week and interaction, $p =$
350 0.171 for the average week). Mass gain of penguins followed a clear optimal pattern with a
351 peak during early mid-year weeks (relative week around -10 to 0, *Figure 4 D*). However, this
352 was very important in precocious and delayed years but less so in average years (see average
353 week 50 against week 40 or 55 in *Figure 4 D & E*). Finally, the year timing and its interaction
354 with the individual timing affected the post-guard mass gain (GAMM, $n = 13,874$, $p < 0.001$).
355 Overall, as during guard, the mass gain was lower when breeding year timing was average
356 than for precocious and delayed years (*Figure 4 E*). While individual mass gains were higher
357 in mid-year for early years (around relative week 0 when average week 45) it was the

358 opposite in delayed years, when mass gain was higher early or late in the year (around relative
359 week -5 or 10 when average week 55).

360 *3.1.3 Inter-annual differences in foraging performance*

361 Based on the combination of little penguin trip duration and mass gain (or just mass gain
362 during guard), three distinct clusters (low, average, and high foraging performance) were
363 defined for each breeding stage (and for the entire breeding season when all three breeding
364 stages were pooled), according to the optimum number of cluster assessment described in
365 methods (*Figure 5 A, C, E, G*). Apart from incubation, clusters reflected real differences in
366 quality, with both foraging parameters varying together (*e.g.* clusters of high foraging
367 performance were characterised by high mass gain and short trips, *Figure 5 C, E, G*). During
368 incubation, however, clusters also reflected different strategies. One cluster was characterised
369 by average mass gain, but very long trips; while another cluster displayed the exact opposite
370 (*i.e.* average trip duration, but low mass gain, *Figure 5 A*).

371 Some years were associated with the same foraging performance cluster for all three breeding
372 stages (*e.g.* 2001 and 2015 being defined as low and high foraging performance years,
373 respectively). However, most of the years consisted of breeding stages assigned to different
374 foraging performances (*e.g.* 2018 was a composite of high performance during incubation but
375 low performance during guard and post-guard).

376 *3.1.4 Breeding success*

377 Penguin breeding success increased with foraging performance for each breeding stage
378 (*Figure 5, B, D, F and H*). Yet, differences in breeding success among categories of foraging
379 performance were only significant during post-guard (Kruskal-Wallis, $p = 0.018$) or after
380 pooling all stages ($p = 0.026$). During these periods, breeding success in low foraging

381 performance was about half that in years of average and high foraging performance (Holm
382 adj. Post-hoc Dunn tests, *Figure 5 F*).

383 **3.2 Environment variability and foraging performance**

384 *3.2.1 Short term effects of the environment on foraging performance*

385 Although environmental anomalies and seasonal signals were modelled together to explain
386 short-term effects of the environment on foraging performance (*Figure 6*), only the effect of
387 the anomalies are described here. Indeed, because seasonal signals were correlated, several
388 variables had to be removed to avoid collinearity that might confound interpretation. A
389 detailed description of seasonal signals and model outputs can be found in the Supplementary
390 material Tab. S2 to Tab. S6 & Text S3.

391 All environmental variables included in our analysis affected foraging performance at some
392 point, although some variables were always present, while others specifically affected only
393 certain breeding stages or foraging parameters (either only mass gain or trip duration). Waves
394 had the most consistent effect on foraging; higher waves resulted in penguins simultaneously
395 gaining less mass and making longer trips (LMM, $p < 0.001$ in all cases, not tested in
396 incubation because of high VIF caused by correlation with current speed). The current speed
397 also affected foraging performance, but with less consistency. Indeed, increased current speed
398 had a negative effect on individual mass gain during incubation (LMM, $p = 0.002$), but
399 penguins conducted shorter trips during that same stage ($p = 0.002$) and displayed higher
400 mass gain during guard ($p < 0.001$).

401 Vertical stratification had a more contrasted influence on penguin foraging performance. We
402 observed no effects on mass gain, but for a positive effect of thermocline depth during post-
403 guard ($p = 0.004$). However, deeper and more extensive thermoclines resulted in significantly
404 shorter trips during incubation ($p = 0.004$ and $p < 0.001$, *Figure 6 A*). Additionally, penguins

405 made significantly shorter post-guard trips when thermoclines were stronger but less
406 extensive (LMM, $p < 0.001$ in all cases, *Figure 6 B*).

407 Finally, tide effects were only detected during post-guard (*Figure 6 B & E*) and had opposite
408 effects on mass gain and trip duration. Penguins going to sea at high tides had lower mass
409 gain and tended to perform shorter trips (LMM, $p = 0.019$ and 0.071), whereas the opposite
410 occurred when they returned on land during high tide ($p = 0.017$ and 0.002).

411 *3.2.2 Annual effects of the environment on foraging performance*

412 Trips were significantly shorter in duration when Chlorophyll concentration anomalies were
413 greater during the breeding season (LM: 0.24 ± 0.10 days shorter per $0.1 \mu\text{g/l}$ more Chla, $p =$
414 0.034). No other effects of the environment were found otherwise, neither on trip duration nor
415 on mass gain ($p > 0.1$).

416 Furthermore, penguin yearly foraging performance was associated with the synchrony
417 between timing of breeding (*i.e.* average foraging week) and the timing of the spring decrease
418 in primary production (hereafter, winter bloom end; *Figure 7 A & B*, GAMM, $p < 0.001$ for
419 mass gain and $p = 0.027$ for the trip duration). More precisely, years were optimal in terms of
420 foraging performance when the average foraging week happened around one month before
421 the winter bloom end, and minimal foraging performance occurred when the average week
422 happened one month after winter bloom end (*Figure 7*). Extremely delayed seasons (average
423 timing of breeding week 5 to 7 weeks after winter bloom end) had an intermediate effect on
424 foraging performance, potentially due to higher synchrony with the start of the next winter
425 bloom at the end of summer (*Figure 7 A, B & D*). Years with low foraging performance were
426 mainly characterised by delayed breeding (*Figure 7 C*), while years with high foraging were
427 characterised by precocious breeding (*Figure 7 E*). Using only post-guard foraging instead of
428 yearly foraging led to very similar results (Supplementary material Fig. S9).

429

430 **4. Discussion**

431 We showed that foraging performance during breeding varied within and among years based
432 on trip duration and mass gain of 399 little penguins over 19 breeding seasons and 45,363
433 trips. Some periods within the year were consistently more successful in terms of foraging
434 performance than others, *i.e.* birds conducted shorter trips and gained more mass. We further
435 identified groups of low, average, and good foraging performance years. These trends
436 coincided with annual breeding success. Finally, we evaluated different climatic and
437 oceanographic variables and highlighted the importance of waves and currents on the short-
438 term, thought to affect foraging directly through increased costs while swimming or diving.
439 We identified the additional role of vertical stratification that affected foraging indirectly
440 through a modification of prey distribution affecting travelled distances or capture efficiency.
441 However, these environmental variables explained a very small part of the total foraging
442 variability (Supplementary material Tab S3 to S7), highlighting the importance of many other
443 factors We showed that breeding phenology and its match with primary production cycles
444 affected foraging performance variability at the interannual scale.

445 **4.1 Variability at the trip scale**

446 Sudden and short environmental variations can affect seabird foraging behaviour and
447 efficiency (Raya Rey et al. 2010, Dehnhard et al. 2013, Osborne et al. 2020). In little
448 penguins, changes in foraging were associated with vertical stratification (Pelletier et al.
449 2012) and wind speed (Saraux et al. 2016). However, although wind can impart an energetic
450 cost during foraging among flying seabirds (Amélineau et al. 2014, Elliott et al. 2014,
451 Tarroux et al. 2016), the question remains on the mechanism by which wind could affect non-
452 flying little penguins. Wind can affect vertical stratification and water mixing (Klein & Coste
453 1984, Warrach 1998), potentially modifying prey distribution (Sanvicente-Añorve et al. 2007)

454 and can also increase wave height and surface currents (Mao & Heron 2008, Young et al.
455 2011), making swimming conditions at sea more difficult. We found strong correlations
456 between daily wind speed, current speed, and wave height, but weak correlations with vertical
457 stratification (thermocline intensity and proportion, see Supplementary material *Fig. S3*).
458 Furthermore, wave height and current speed had the strongest and most consistent adverse
459 effects on foraging trip duration. We argue that wind speed effects previously highlighted for
460 penguins (Dehnhard et al. 2013, Saraux et al. 2016) might be primarily mediated through
461 waves and currents (energy spent) rather than by increased water mixing (prey accessibility).
462 We suggest this pattern shows penguins face adverse foraging conditions while commuting
463 during strong wind days.

464 Based on previous studies of Magellanic penguins, we also expected little penguins to be
465 affected by tidal cycles when commuting from land to sea (Wilson et al. 2001, Raya Rey et al.
466 2010). However, effects of tides were only significant during post-guard, when higher water
467 levels upon return to land resulted in longer trips but greater mass gain (mass gain was
468 conversely less when the water level increased when departing to sea). These unexpected
469 results might suggest that tidal effects reflect prey accessibility rather than unfavourable
470 commuting conditions (Adélie penguin, Oliver et al. 2013). According to tidal cycles, small
471 pelagic fish migrate either vertically or horizontally (Gibson 2003), modifying little penguin
472 prey distribution. These effects of tides cycles are highlighted on several piscivorous seabirds
473 foraging behaviour, especially modifying their diving depth (Holm & Burger 2002).
474 However, tidal effects on little penguins foraging would need further investigation to better
475 understand their underlying processes.

476 Consistent with previous studies, vertical stratification also affected little penguin foraging
477 performance (Ropert-Coudert et al. 2009, Pelletier et al. 2012, Meyer et al. 2020). Overall,
478 stronger thermocline was associated with shorter trips in post-guard. More stratified waters

479 could enhance small fish (*i.e* little penguins prey) aggregation around thermocline (Hansen et
480 al. 2001), which should be beneficial to foraging seabirds (Kokubun et al. 2010, Pelletier et al.
481 2012). Thermocline ubiquity was also related to shorter trips during incubation but was
482 detrimental (conducted to longer trips) during post-guard. One explanation may be that during
483 incubation (*i.e* early in the season) the thermocline is not well established (average of 42%
484 thermocline in the area during incubation trips), so a regionally more extensive thermocline
485 should lead to greater areas of prey aggregation and profitable foraging grounds. Conversely,
486 during post-guard, once thermocline is well established (average of 76% thermocline in the
487 area per trip), a further increase in the regional area with thermocline presence (*e.g.*
488 stratification) might reflect a more uniform physical barrier with the absence of horizontal
489 gradients and effective prey aggregation areas (*e.g.* fronts, Spear et al. 2001). A deeper
490 thermocline generally had positive effects on little penguins foraging performances (no
491 adverse effects expected in such shallow waters) which might result from higher prey
492 aggregation at deeper stratification (Spear et al. 2001) or from a decrease in energy costs in
493 deep dives compared to shallow ones (Wilson et al. 1992).

494 4.2 Seasonal patterns of variability in foraging performance

495 Variations in seabird foraging performance throughout a breeding season are mainly driven
496 by local prey depletion (Ashmole 1963, Birt et al. 1987, Lewis et al. 2001) or by a temporal
497 match with the period of maximum prey availability (Durant et al. 2007, Regular et al. 2014).
498 In the case of prey depletion, foraging performance is expected to decrease linearly during the
499 breeding season, while in the case of a match/mismatch with prey foraging performances are
500 is expected reach optimum pattern during the breeding season. However, in deep divers like
501 little penguins, prey depletion may not be linear (Chiaradia et al 2016), we might then expect
502 a response that indicates optimum foraging performance when foraging birds encounter
503 maximum prey availability at any stage of breeding. Indeed, we found optimum foraging

504 performance at around 1/3rd of the season, when mass gain was maximal and foraging trips
505 were the shortest. Conversely, we found no decrease in foraging performance throughout the
506 season, consistent with previous suggestions that prey depletion did not explain the overall
507 reduction of foraging performance of little penguins. Our results indicate little penguin
508 foraging performance at the season scale is more dependent on the match with their prey than
509 on potential prey depletion in their limited foraging area.

510 As optimum foraging performance had shorter trips and higher mass gain simultaneously
511 even for birds at different breeding stages. Our results also indicate that foraging variability is
512 driven by external (environmental) conditions rather than by intrinsic (behavioural) plasticity,
513 where one parameter could be traded-off with the other (*e.g.* increase trip duration to gain
514 more mass, Paiva et al. 2010, Saraux et al. 2011).

515 4.3 Variability at the inter-annual scale

516 Given the evidence for the seasonal optimums in foraging performance highlighted above, the
517 annual breeding phenology should play an important role in foraging variability (see,
518 Chambers 2004, Chiaradia & Nisbet 2006, Cullen et al. 2009, Ramírez et al. 2015).
519 Maximising foraging performance should thus depend on the population's overall timing (four
520 months difference between the earliest and latest years in breeding onset) and the individual
521 breeding onset within the season (Ramírez et al. 2021). We demonstrated the duality between
522 intra- and inter-annual breeding timing by assessing the interaction between these two
523 timescales. We showed that the best window of time to forage (*i.e.* optimum prey availability)
524 differed from the start to just past the middle of the breeding season, depending on how early
525 the overall season was.

526 Despite this critical role of phenology, no link between overall breeding season foraging
527 performance and oceanographic variables (stratification, wave and current regime) could be

528 established. This disconnection likely occurs because inter-annual environmental variability
529 of marine ecosystems is multifactorial (Grémillet & Boulinier 2009, Sydeman et al. 2012,
530 Quillfeldt & Masello 2013) composed of fluctuating parameters that are not easily integrated
531 at larger time scales. However, we showed that years when phenology better-matched winter
532 high primary production (maximum occurring during fall and winter in the region, Kämpf et
533 al. 2004) resulted in better foraging performance. Years with better foraging performance had
534 consistently early breeding start during which most trips occurred before the spring decrease
535 in primary production. Years of low foraging performance were delayed by around a month.
536 If temporal match with prey availability indeed drives seabird foraging and breeding success
537 (Hipfner 2008, Regular et al. 2014), few studies have directly established a relation with
538 primary production. One reason might be that seasonal variations in marine productivity in
539 most temperate areas are driven by temperature and photoperiod (Nicklisch et al. 2008),
540 which are the primary triggers for birds to initiate breeding (Mickelson et al. 1991, Dawson
541 2008). Therefore, it is unlikely that temporal mismatches would be expected between seasonal
542 marine productivity and breeding phenology in temperate regions. However, this is not the
543 case in the study region, the Bass Strait, where primary production is driven by winter high
544 nutrient levels (Gibbs et al. 1986) and penguins seem to respond to the peak of Chlorophyll-a
545 – a proxy to marine productivity (Afan et al 2015). Primary production, however, may not
546 affect prey dynamics at the year scale, although it may be vital at multiannual scale (Capuzzo
547 et al. 2018), but may be affecting prey quality (*sensu*, the junk-food hypothesis, Wanless et al.
548 2005, Österblom et al. 2008), presence and accessibility (Bost et al. 2009). Therefore, we
549 suggest the central hypothesis explaining the role of mismatch with primary production on
550 little penguin foraging performance may be an effect of the overall prey quality (size and
551 body condition) combined with the spatial distribution. The most delayed breeding seasons (5
552 to 9 weeks after the spring decrease in primary production) had higher foraging performance

553 than seasons delayed by only 2 to 4 weeks. We suggest that this supports the hypothesis of
554 prey quality/accessibility importance; specifically, late years were delayed enough to
555 potentially benefit from an increased prey quality/accessibility via the return of high primary
556 production in the fall.

557 The primary role of a prey-predator match could be the critical element to understand the link
558 between annual foraging performance and breeding success (Shultz et al. 2009, Regular et al.
559 2014). Phenological mismatches with primary production can set an upper limit on penguins
560 breeding success (Adélie penguins, Youngflesh et al. 2017). Here, we established a significant
561 relationship between breeding success and annual foraging performance, agreeing with
562 previous findings in this species (Chiaradia & Nisbet 2006). This link mainly relies on the
563 foraging conditions experienced by provisioning adult penguins during post-guard, a long and
564 spatially-constrained breeding stage (Reilly & Cullen 1981). Differences in breeding success
565 were only significant between years with low foraging performance and years of average or
566 good foraging performance, indicating that the relationship between breeding success and
567 foraging may not be linear. Instead, it may only occur below a threshold under which foraging
568 is too inefficient to allow successful breeding (Cury et al. 2011, Guillemette et al. 2018).

569 Conclusion

570 Little penguin foraging performance varied at different time scales with contrasting
571 environmental conditions. We showed that interannual variability in little penguin foraging
572 was associated with differences in breeding success, and phenology was the main driver of
573 interannual differences in foraging. Thus, breeding success might be strongly related to
574 phenology (Youngflesh et al. 2017) through foraging. This pattern may become even more
575 critical with climate change. While many seabirds phenology has not changed with warming
576 waters (Keogan et al. 2018), some other seabirds have responded dramatically to climate
577 changes in other parts of the world (Sydeman & Bograd 2009, Wanless et al. 2009). We also

578 highlighted significant concurrent effects of waves and currents (possibly driven by wind)
579 and, to a lesser extent, vertical stratification on seabirds foraging at shorter time scales. The
580 impact of these variables on breeding success may have increasing importance in the future as
581 waves and currents are expected to increase in intensity globally due to climate change
582 (Young et al. 2011, Capotondi et al. 2012).

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1 **Tables:**

	Obtained from	Specificity	Temporal resolution	Spatial resolution	Type	Data processing in each pixel	in time series
Water column T° (Thermocline)	Copernicus (https://marine.copernicus.eu)	Two datasets (reanalysis up to 2019, then analysis)	daily	0.083°, 27 depths (from 0.5 to 220 m)	Satellite observations + models		
[Chla]	NASA (https://earthdata.nasa.gov/)	SeaWiFS satellite before 2002 and MODIS satellite from 2002 to 2019	daily	9km (SeaWiFS) and 4km (MODIS)	Satellite observations	To avoid inconsistent data, only values under 1.6µg/l were kept (<i>i.e. the 99% quantile, coherent with Gibbs et al. 1986</i>)	Biased daily means (too few pixels due to cloud cover) removed based on random subsampling (1341 out of 3304 days for SeaWiFS and 1348 out of 6250 days for MODIS, Sup. mat. Fig. S1 & Text S1).
Wave height	Copernicus (https://marine.copernicus.eu)	Two datasets (reanalysis up to 2019, then analysis)	daily	0.083° grid	Satellite observations + models		
Current speed	Copernicus (https://marine.copernicus.eu)	Two datasets (reanalysis up to 2019, then analysis)	daily	0.083°, 20 depths (from 0.5 to 65 m)	Satellite observations + models	Current speed was computed as the square root of the sum of the squared norms of u and v vectors.	
Wind speed	Remote Sensing Systems Research Company (http://www.remss.com/)		daily	0.25° grid	Satellite observations + models (CCMP)	Wind speed was computed as the square root of the sum of the squared norms of u and v vectors.	

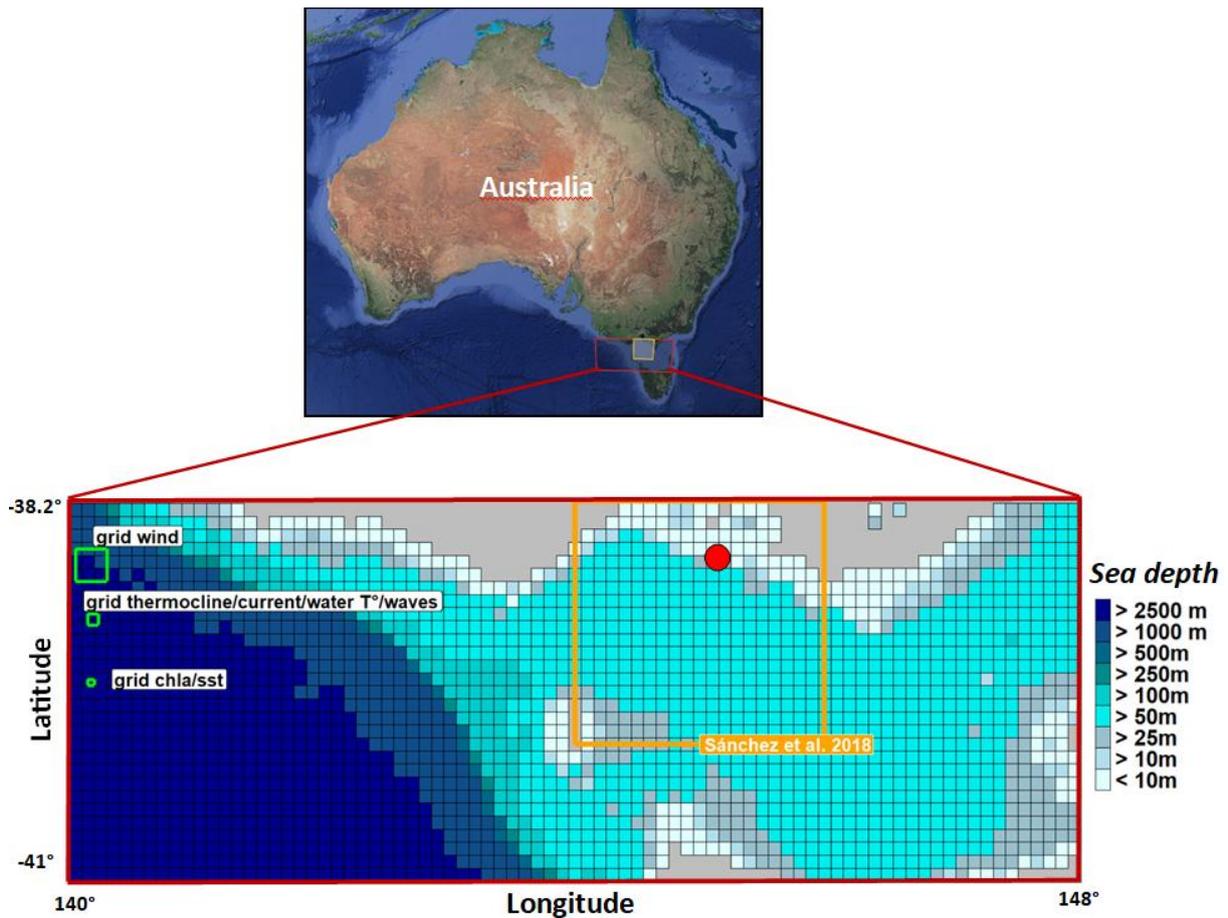
Shore water level (Tides)	Australian Bureau of Meteorology (http://www.bom.gov.au/)	hourly	13 km from the site (Stony point station)	Direct measures
AAO	NOAA (https://psl.noaa.gov/data/climateindices)	monthly		measures
ENSO	NOAA (https://psl.noaa.gov/data/climateindices)	monthly (15th to 15th)		measures

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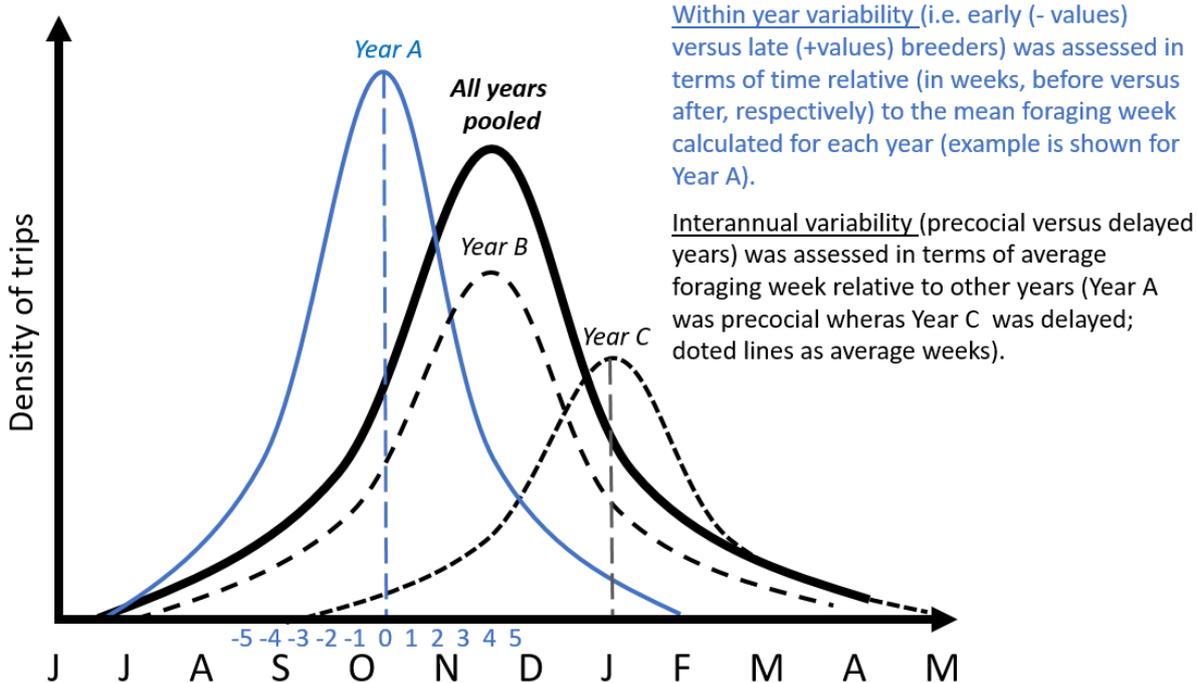
Table 1: Summary table of the studied environmental parameters with their temporal and spatial resolutions, their types and origins.

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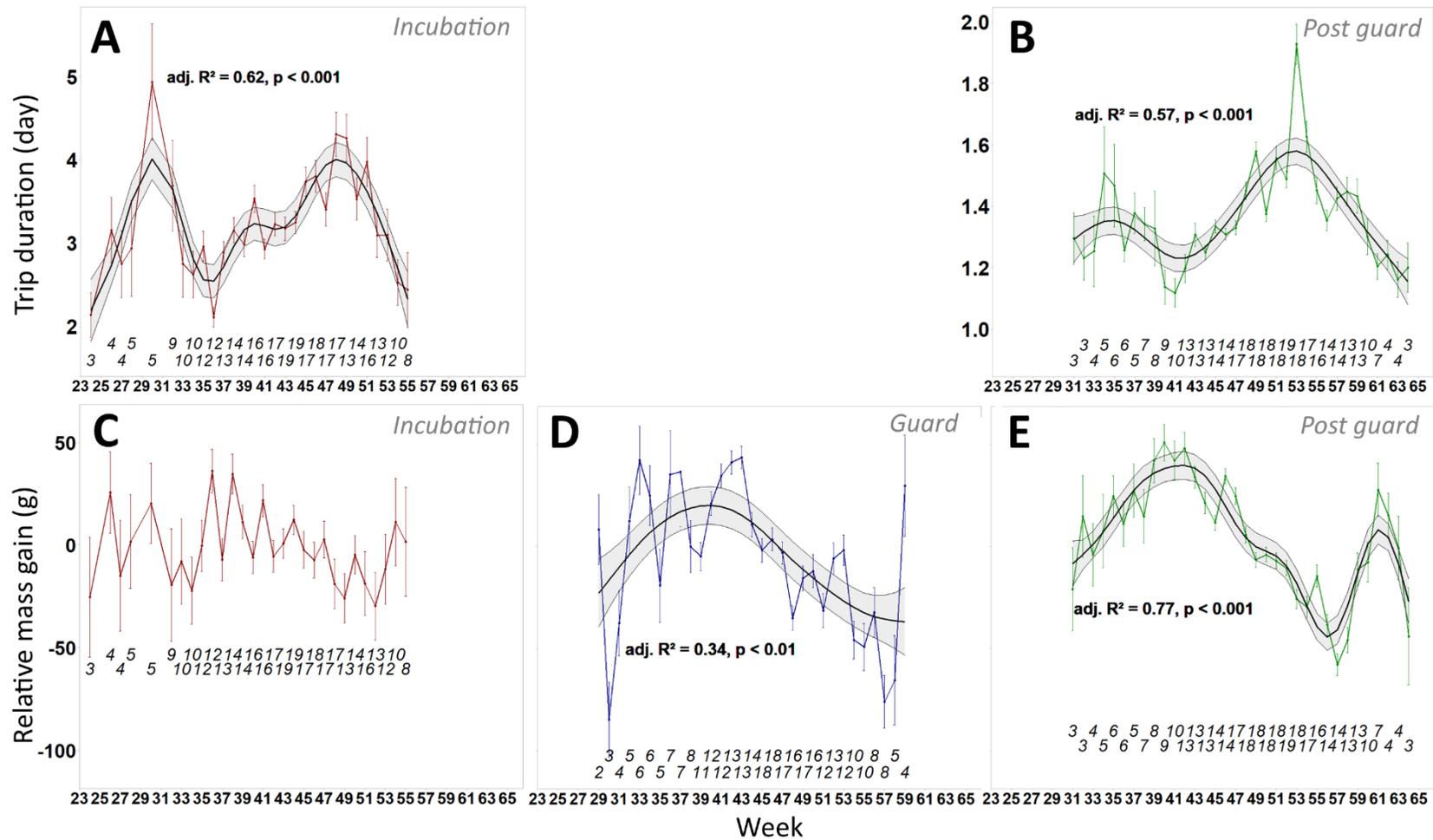
1
 2 Figure 1: Study area: colony (red dot) and marine area considered for the analyses of
 3 environmental variables (red rectangle). The lower panel shows a close-up of the marine
 4 study area with bathymetry indicated in shades of blue, known LP foraging areas (yellow
 5 rectangle, Sanchez et al. 2018) and the three different spatial grid resolutions used for the
 6 climatic variables (green squares on the left).



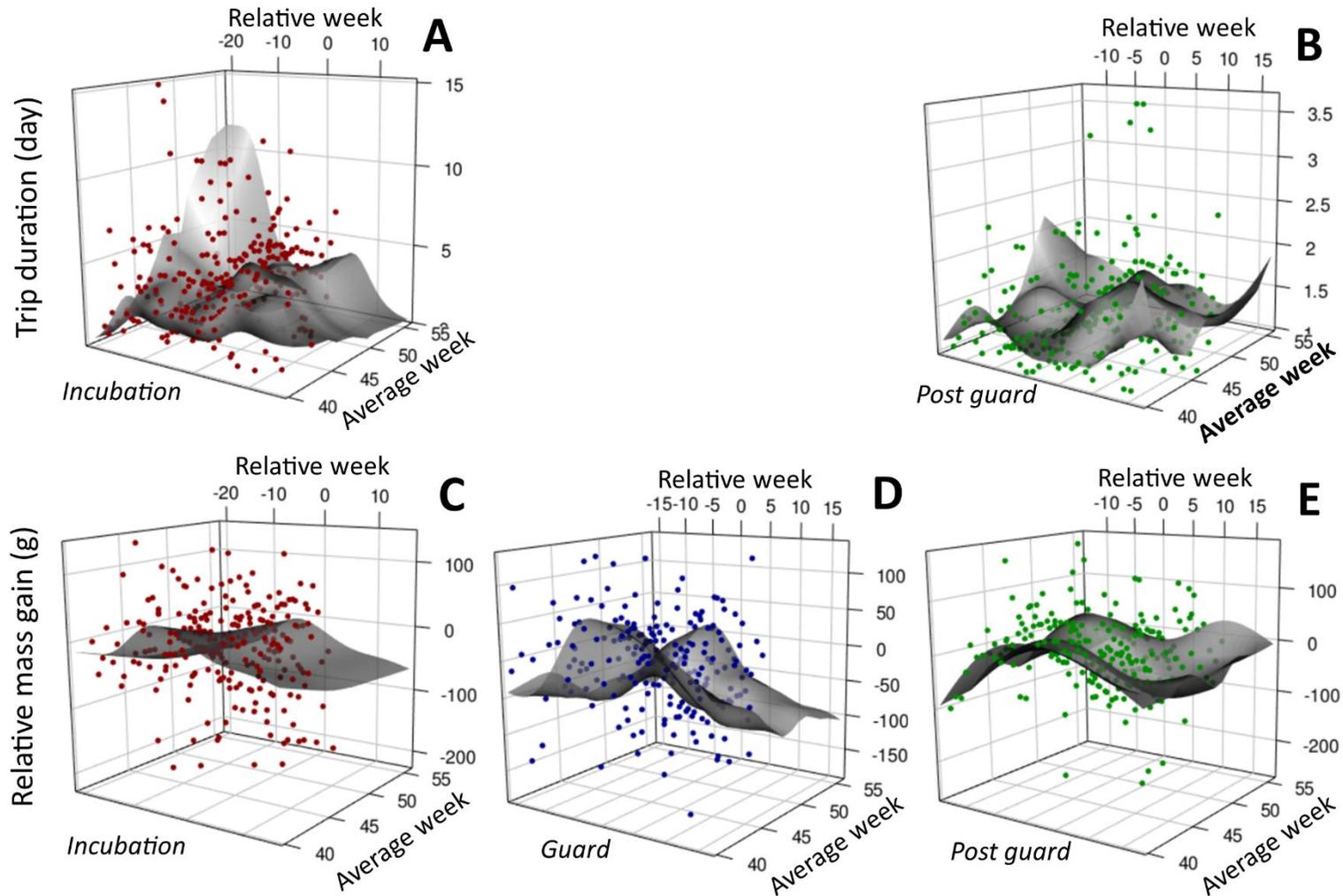
Within year variability (i.e. early (- values) versus late (+values) breeders) was assessed in terms of time relative (in weeks, before versus after, respectively) to the mean foraging week calculated for each year (example is shown for Year A).

Interannual variability (precocial versus delayed years) was assessed in terms of average foraging week relative to other years (Year A was precocial whereas Year C was delayed; dotted lines as average weeks).

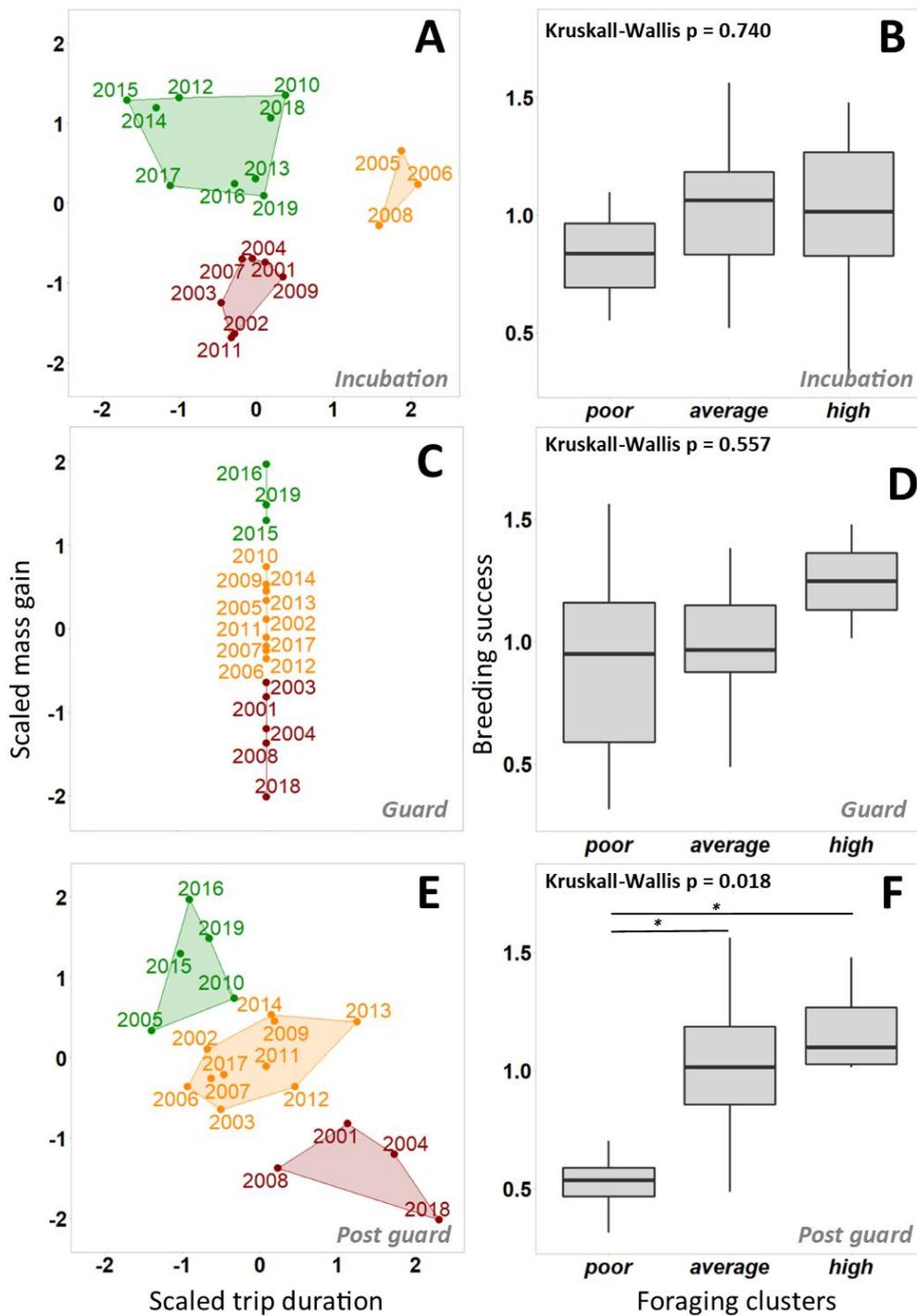
1
 2 Figure 2: Schematic view of within year (early vs late breeders) and interannual (precocious
 3 vs delayed years) breeding timing variability assessment.



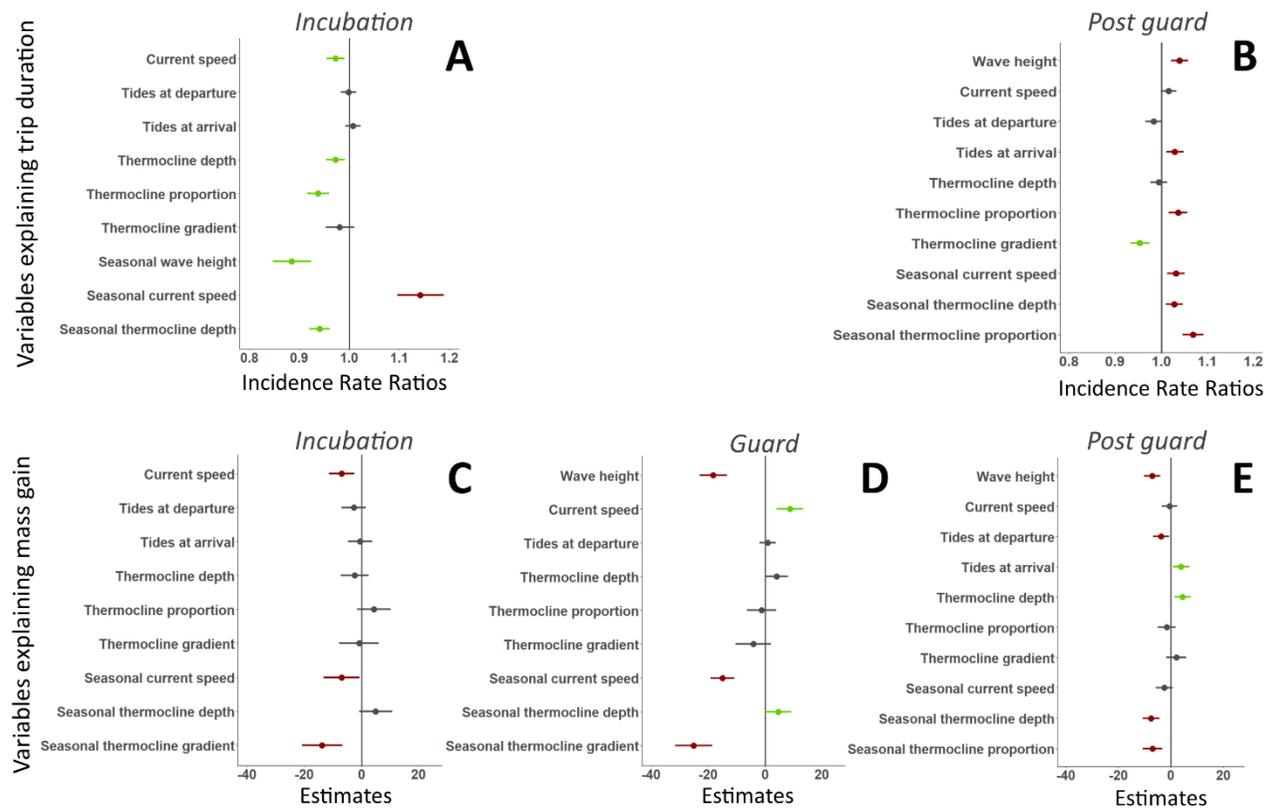
4 Figure 3: Weekly mean \pm SE relative mass gain and trip duration in incubation (red, A and C), guard (blue, D) and post-guard (green, B and E).
 5 The prediction (black curve) and standard error (grey area) of the GAM are superimposed when week was significant. Italic numbers at the
 6 bottom of each panel indicate the number of years per breeding week.



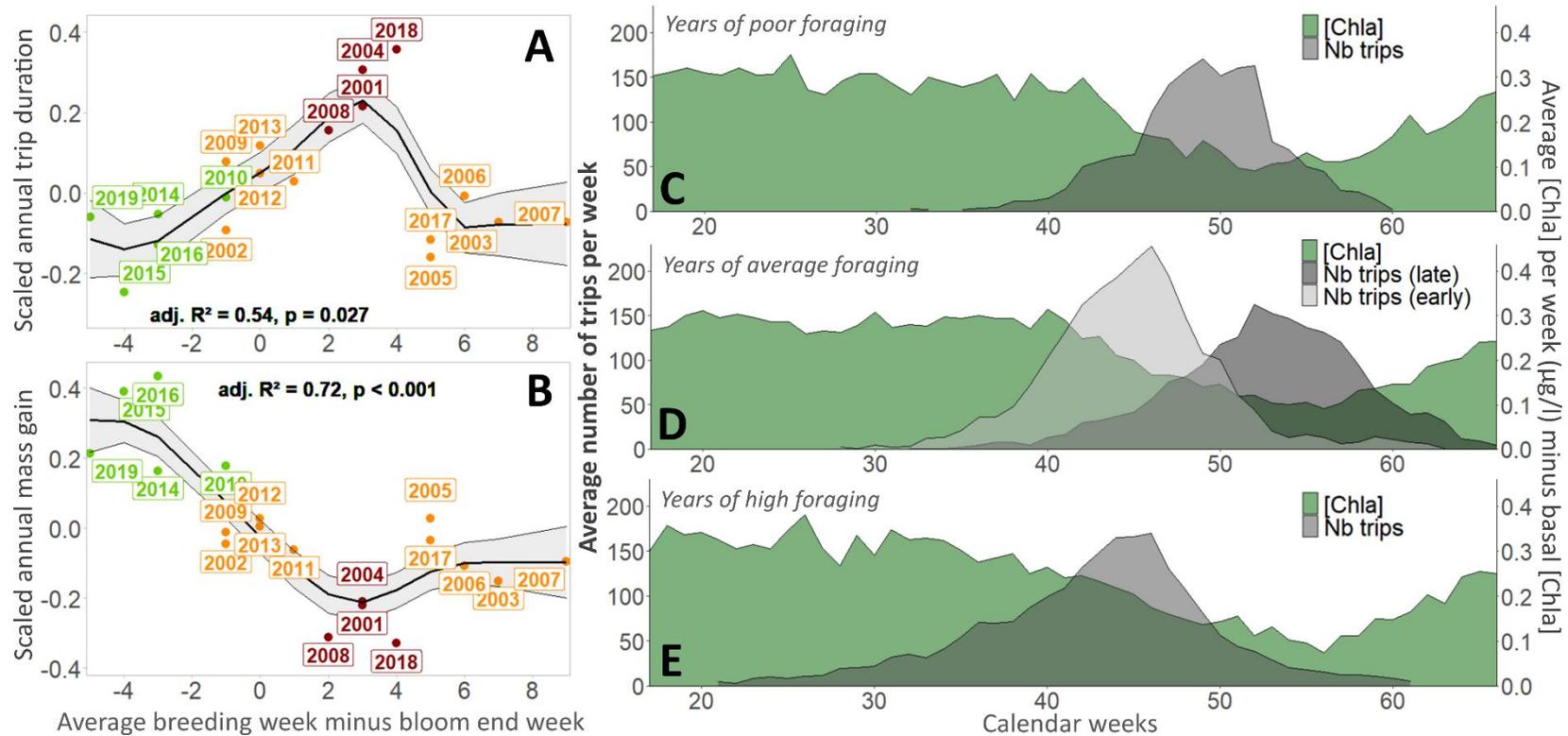
7 Figure 4: Average mass gain and trip duration depending on average week and/or relative week in incubation (red), guard (blue) and post-guard
 8 (green). The prediction by the GAM with average week, relative week and their interaction (but for panel C where the interaction was not
 9 significant) is represented by the grey surface.



10 Figure 5: Annual foraging performances grouped by kmeans clustering (A,C,E,G, nstart =
 11 1000) based on both scaled trip duration and mass gain (only based on mass gain for guard).
 12 For each breeding stage, as well as for all stages pooled, years were clustered in three groups
 13 of poor (in red), average (in orange) and high (green) foraging performances. Breeding
 14 success (nb. of chicks fledged per breeding event) is compared between clusters (B,D,F,H).
 15 Stars represent significant differences according to Dunn (holm adj.) post-hoc test.



16 Figure 6: Environmental effects on foraging trip duration (top panels A & B) and relative mass gain (bottom panels C, D & E) for each breeding
 17 stage. Estimates and 95% confidence intervals from LMMs explaining mass gain and incidence rate ratios and 95% confidence intervals from
 18 GLMM (Poisson distribution) are presented. Significant effects are presented in color (red for significant detrimental effect, i.e. lower mass gain
 19 or longer trips) and green for significant positive effect), while non-significant effects are presented in grey. Some variables were removed from
 20 the full models due to important VIF.



21 Figure 7: Effect of synchrony between foraging and primary production on annual mass gain and trip duration (A & B), with generalised additive
 22 model (black curve) \pm SE (grey area). Points are colored according to established high (green), average (orange) and poor (red) foraging clusters.
 23 Weekly average Chla concentration (dark green) and trip density (grey) during the year are presented for each of the 3 clusters (C, D & E). Trip
 24 density in the average foraging cluster (D) is split in two different categories based on breeding timing: early breeding (2002, 2009, 2011, 2012
 25 and 2013 in light grey) and very late breeding (2003, 2005, 2006, 2007 and 2014 in grey) based on A & B.