



# Environmental effects on foraging performance in little penguins: a matter of phenology and short-term variability

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**ABSTRACT:** Foraging provides an integrative view of the effects of environmental variability on marine predators, from direct effects through increased energetic costs at sea to indirect effects through modification of prey accessibility. Using a 19 yr automated monitoring system of ~400 individuals (>45 000 foraging trips), we investigated short-term and interannual variability in foraging performance (trip duration and mass gain) of breeding little penguins *Eudyptula minor*, nearshore seabirds living in a climate change hotspot. We found marked but variable seasonal patterns in foraging performance, with clear optimum periods but no decreases in trip duration or mass gain throughout the breeding season. Although foraging performance was less variable at the inter-annual scale, we highlighted 3 groups of low, average and good annual foraging performance. Low foraging performance during post-guard was associated with significantly lower breeding success. To understand how the environment might explain such variability, we simultaneously studied the effect of variables that may affect penguin foraging directly by altering energy costs at sea (currents, waves and tides) and indirectly by modifying prey availability (primary production and vertical stratification). Although foraging performance is often thought to mainly depend on prey accessibility, lower foraging performance was mostly associated with increased waves and currents and only secondarily with a decreased and shallower stratification. Finally, synchrony between penguin phenology and primary production cycles explained inter-annual foraging performance, highlighting the importance of seabird breeding phenology.

**KEY WORDS:** Climate variation · Breeding ecology · Breeding success · Little penguin · Match/mismatch · Stratification · Waves · Currents

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## 1. INTRODUCTION

Marine predators such as seabirds integrate direct and indirect environmental effects, the latter through lower trophic levels of the ecosystem (Parrish et Zador 2003, Piatt et al. 2007). For instance, seabird energetics can be affected directly by wind regimes (Spear & Ainley 1997, Mateos & Arroyo 2011) and indirectly by prey availability (Piatt & Anderson 1996, Romano et al. 2006). An efficient way to study the effects of environment-driven changes upon marine seabirds is to assess their foraging performance,

as this should reflect both energetic costs at sea (Mullers et al. 2009, Collins et al. 2020) and prey availability (Cairns 1988, Grémillet et al. 2004).

The environment is expected to affect seabird foraging (and thus survival, breeding and ultimately population dynamics; Baird 1990) differently depending on the time scale considered—especially during breeding, when biological constraints due to parental care are maximal. Prey availability, which constrains central place foragers (Hunt et al. 1999, Burke & Montevecchi 2009), could be modified by short-term (days to weeks) changes in spatial (verti-

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cal and horizontal) prey distribution. Indeed, prey are neither randomly nor uniformly distributed in time and space but rather aggregate until achieving a specific density in favorable areas (Fauchald 2009). Prey aggregations are created by ocean vertical and horizontal mixing, including fronts, eddies, upwellings or water column stratification (Charrassin & Bost 2001, Spear et al. 2001). At a medium temporal scale (several weeks to months), prey availability changes according to seasonal cycles (especially in temperate and polar environments). Seabird foraging performance should thus be optimal when foraging is synchronised with maximum prey availability (Regular et al. 2014). However, this optimum period may shift when a predator's range is limited and prey abundance is concentrated within a limited area, leading to local prey depletion, mismatches between predators and their prey or interference competition during the breeding season (Ashmole 1963, Birt et al. 1987, Lewis et al. 2001). At even larger time scales, inter-annual variability can affect (1) prey phenology and therefore shift the optimum period between successive years (Watanuki et al. 2009), (2) prey recruitment, causing a delayed effect on prey abundance during successive seasons (von Biela et al. 2019) and (3) prey quality (e.g. energetic composition) associated with different levels of ocean productivity (Wanless et al. 2005).

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

Little penguins have been suggested to be sensitive to changes in local prey abundance, distribution and diversity (Chiaradia et al. 2003, 2016). As such, they should be affected by any environmental parameters that affect these prey dynamics. For example, little penguins rely on vertical stratification

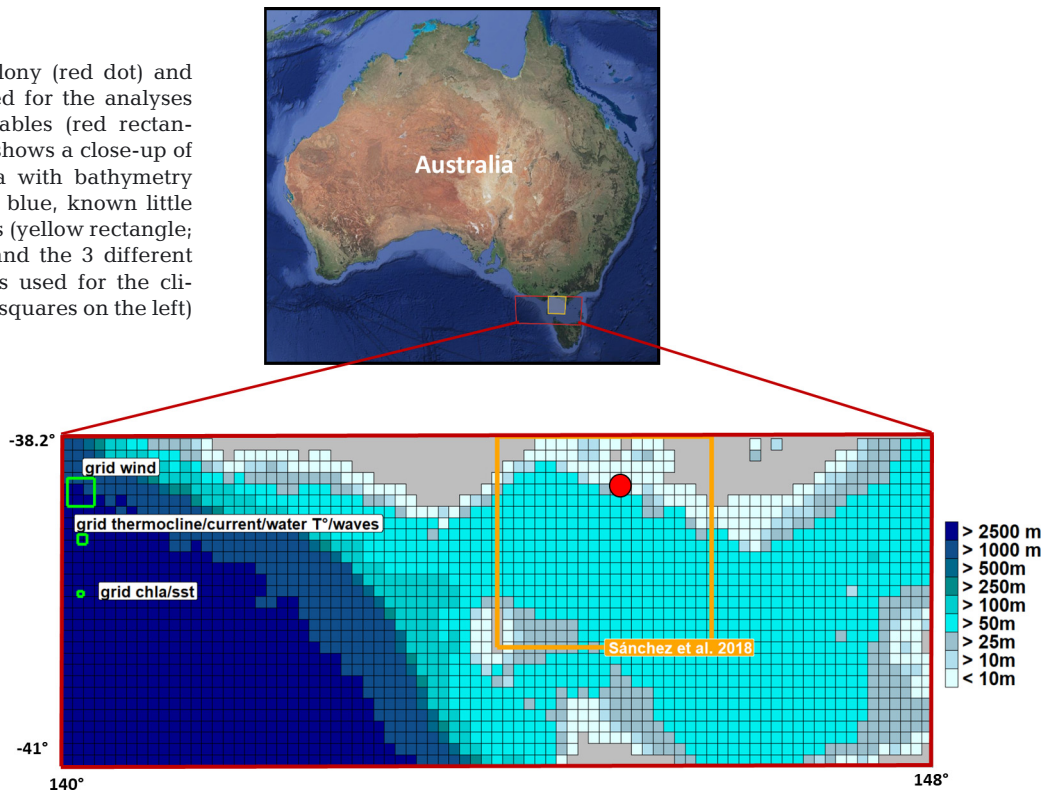
to target prey aggregated around the thermocline (Hansen et al. 2001) and thus improve foraging success (Ropert-Coudert et al. 2009, Pelletier et al. 2012). Yet, direct effects of environmental variability on their energy expenditure at sea should not be discounted, as shown by the effect of currents and tides in a closely related species, the Magellanic penguin *Spheniscus magellanicus* (Raya Rey et al. 2010). While strong winds are detrimental for little penguin foraging performance (Saraux et al. 2016), the underlying mechanisms (i.e. increased energetic costs due to foraging in rough seas or decreased efficiency due to more dispersed prey associated with weaker vertical stratification) remain to be investigated. Large-scale decadal oscillations such as El Niño–Southern Oscillation (ENSO), which can be more influential than local climate parameters and cause greater impacts on certain life-history traits (Hallett et al. 2004, Stenseth & Mysterud 2005), may also affect little penguin foraging performance (Berlincourt & Arnould 2015). Finally, the match between annual primary production cycles (ultimately linked to prey availability) and phenology could also affect penguin inter-annual foraging performances (Afán et al. 2015).

This study examined how little penguin foraging performance at the world's largest colony for this species on Phillip Island, Australia, varied through time according to changes in their environment. Using an automated penguin monitoring system deployed continuously over 19 yr, we compiled a unique data set of foraging performance (i.e. foraging trip duration and associated mass gain) across a wide range of environmental conditions ( $\geq 45\,000$  trips).

First, we investigated little penguin foraging performance variability at different time scales (within and among breeding years). Specifically, within years, we tested whether foraging performance decreased throughout the year (as would be expected in cases of substantial local prey depletion) or instead reached an optimum during the breeding season (as would be expected during a temporal match with maximal prey availability). Among years, we tested differences in overall foraging performance and examined potential links with annual breeding success.

Second, we investigated how foraging performance responded to the environment at 3 different time scales: short-term (i.e. environmental conditions varying from one trip to another), seasonal and inter-annual scales. We simultaneously studied the effects of multiple environmental parameters that are known (thermocline, wind, primary production) or sus-

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



pected (waves, currents, tides and 2 climatic oscillations: Antarctic Oscillation [AAO] and ENSO) to affect little penguin foraging success. By doing so, we expected to partition the variance in foraging performance between different environment-driven processes. In particular, we expected foraging performance to be affected both directly through energetic costs at sea (e.g. currents, waves) and indirectly through prey availability (e.g. vertical stratification, primary production). Further, we predicted very different effects and relative importance of these parameters depending on the time scale considered. While short-term, unfavourable conditions should be driven by environmental variables known to increase energetic costs and decrease prey accessibility, inter-annual differences in foraging performance should depend on ecosystem productivity and synchrony with prey availability (i.e. penguin phenology). A single variable could then have opposite effects depending on the time scale considered. For example, wind and current speed are expected to instantaneously increase swimming and foraging costs while decreasing vertical stratification (Raya Rey et al. 2010, Saraux et al. 2016), whereas they should improve water mixing and thus enhance primary production in the longer term, favouring energy transfer throughout the entire food web (Marra 1980).

## 2. MATERIALS AND METHODS

### 2.1. Little penguin long-term monitoring

#### 2.1.1. Study site and breeding monitoring

The studied colony, located in the Summerland Peninsula on Phillip Island ( $38^{\circ} 15' S$ ,  $143^{\circ} 30' E$ ), Victoria, Australia, consists of 28 000–32 000 little penguin breeding adults (Fig. 1; Sutherland & Dann 2012). The 399 birds monitored in this study were subcutaneously implanted with numbered, 23 mm ISO HDX transponders (Allflex) between the scapulae (shoulder blades; Chiaradia & Kerry 1999), either as chicks (70%) just before fledging, or when first encountered as an adult nesting in a part of the colony containing 100 artificial burrows (wooden nest boxes). All nests were checked 3 times per week using a custom-built portable transponder reader, allowing us to determine every nest and individual's breeding stage and performance.

This study spanned 19 consecutive breeding years from 2001 to 2019. As little penguin breeding season occurs during the austral summer from May to February (Reilly & Cullen 1981), a breeding year refers to the austral summer (e.g. 2001 corresponds to birds breeding in the austral summer of 2001–2002). The

breeding cycle after egg-laying is separated into 3 stages: the egg-incubation period (lasting about 35 d), the guard period (~2 wk), when one parent stays with young chicks while the other forages at sea, and the post-guard period (5–8 wk), when older chicks are left alone during the day and parents return at night to feed them (Chiaradia & Kerry 1999). Breeding success was defined as the number of chicks fledged per breeding event. Because little penguins may sometimes produce a second clutch during the same season (Reilly & Cullen 1981), only first clutches were considered here to prevent pseudoreplication and bias due to the first-clutch investment.

### 2.1.2. Foraging performance

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

Foraging trip duration was calculated as the number of days between sequential recordings of a 'departure' and an 'arrival', considering little penguins leave the site before sunrise and return after sunset (Chiaradia & Kerry 1999). As foraging duration was mostly 1 d long during guard trips (96% 1 d trips and 4% 2 d trips), variability in trip duration was only investigated during incubation and post-guard stages. Trips longer than 17 d (193 trips either in incubation or post-guard) were considered to be missing detections and were discarded (Saraux et al. 2016).

Body mass gain was defined as the amount of mass change per foraging trip and was calculated as the difference between a penguin's body mass after and before a given foraging trip. Only body mass ranging from 700 to 1700 g and body mass change ranging from -75 to 500 g during incubation and from 0 to 600 g during chick-rearing were considered to avoid incorrect scale estimates (2786 discarded trips for mass gain, based on Salton et al. 2015 and Saraux & Chiaradia 2022).

For our 2 measures of performance (trip duration and mass gain) to be independent, mass gain was

corrected for each breeding stage separately using residual values from the linear model (LM) [LM = mass gain ~ trip duration] (see Fig. S8 in the Supplement at [www.int-res.com/articles/suppl/m692p151\\_supp.pdf](http://www.int-res.com/articles/suppl/m692p151_supp.pdf)). Yearly mass gain and trip duration were assessed as the average of all trips scaled per breeding stage.

## 2.2. Environmental data

### 2.2.1. Environmental parameters

All data handling was performed using R v.3.5.1 (R Core Team 2018) and the 'ncdf4' v.1.17 package (Pierce 2019) for opening and shaping NetCDF files. Water column temperature, chlorophyll *a* (chl *a*) concentration, wave height, current speed, wind speed, tides and decadal oscillations (AAO and ENSO) were gathered from different online databases as detailed in Table 1 (see also Fig. S5). Water column temperature was used to construct several thermocline variables (presence, depth and intensity) using an innovative method because unequal depth segments (precision of one value every 1–5 m until 30 m deep, 5–10 m until 100 m deep and 10–25 m until 200 m) and coastal pixels (with very shallow depths) prevented the use of classically used methods (Fiedler 2010). Briefly, we estimated temperature gradients between each consecutive depth ( $\frac{\Delta T}{\Delta \text{Depth}}$ ) and then looked for changes in these gradients throughout depth using breakpoints (see Fig. S2 for details). The segment with the highest gradient was identified as the thermocline. The depth of the thermocline was defined as the top of this segment. The intensity of the thermocline was the mean temperature gradient (in absolute value) within this segment. The thermocline was assessed as present in a pixel when its gradient was  $>0.02^\circ\text{C m}^{-1}$  (based on slope breakpoints in the thermocline depth/gradient relationship) and its depth shallower than 70 m (i.e. reachable for little penguins).

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

Finally, wind speed affects little penguins at sea (Saraux et al. 2016). Because penguins are non-flying seabirds, we did not expect wind to affect penguin foraging directly. Rather, we expected wind to affect other environmental variables (waves, currents, stratification) that in turn would affect penguin foraging.

Table 1. Studied environmental parameters with their temporal and spatial resolutions, types and origins. Blank cells indicate that no specificities apply, or that no additional data-processing methods were used beyond those detailed in Section 2.3

	Obtained from	Specificity	Temporal resolution	Spatial resolution	Type	Data processing	
						in each pixel	in time series
Water column temperature (°C) (Thermocline)	Copernicus ( <a href="https://marine.copernicus.eu">https://marine.copernicus.eu</a> )	Two data sets (reanalysis up to 2019, then analysis)	Daily	0.083°, 27 depths (from 0.5–220 m)	Satellite observations + models		
Chl <i>a</i>	NASA ( <a href="https://earthdata.nasa.gov">https://earthdata.nasa.gov</a> )	SeaWiFS satellite before 2002 and MODIS satellite from 2002–2019	Daily	9 km (SeaWiFS) and 4 km (MODIS)	Satellite observations	To avoid inconsistent data, only values under 1.6 mg l <sup>-1</sup> were kept (i.e. the 99% quantile, coherent with Gibbs et al. 1986)	Biased daily means (too few pixels due to cloud cover) removed based on random subsampling (1341 out of 3304 d for SeaWiFS and 1348 out of 6250 d for MODIS; Fig. S1, Text S1)
Wave height	Copernicus ( <a href="https://marine.copernicus.eu">https://marine.copernicus.eu</a> )	Two data sets (reanalysis up to 2019, then analysis)	Daily	0.083° grid	Satellite observations + models		
Current speed	Copernicus ( <a href="https://marine.copernicus.eu">https://marine.copernicus.eu</a> )	Two data sets (reanalysis up to 2019, then analysis)	Daily	0.083°, 20 depths (from 0.5–65 m)	Satellite observations + models	Current speed was computed as the square root of the sum of the squared norms of <i>u</i> and <i>v</i> vectors	
Wind speed	Remote Sensing Systems Research Company ( <a href="http://www.remss.com">www.remss.com</a> )		Daily	0.25° grid	Satellite observations + models (CCMP)	Wind speed was computed as the square root of the sum of the squared norms of <i>u</i> and <i>v</i> vectors	
Shore water level (Tides)	Australian Bureau of Meteorology ( <a href="http://www.bom.gov.au">www.bom.gov.au</a> )		Hourly	13 km from the site (Stony Point station)	Direct measures		
AAO	NOAA ( <a href="https://psl.noaa.gov/data/climateindices">https://psl.noaa.gov/data/climateindices</a> )		Monthly		Measures		
ENSO	NOAA ( <a href="https://psl.noaa.gov/data/climateindices">https://psl.noaa.gov/data/climateindices</a> )		Monthly (15 <sup>th</sup> to 15 <sup>th</sup> )		Measures		

Therefore, to understand the manner in which wind affected foraging, wind speed was included in this study only to assess its correlation with other variables for which we expected strong effects on foraging performance (see Figs. S3 & S4) but not in models explaining foraging performance.

### 2.2.2. Building time series of environmental variables

To build the time series, data from more than one data set (e.g. MODIS/SeaWiFS) were merged as spec-

ified in Table 1. Daily time series were built for all parameters (apart from decadal oscillations, for which data were available as monthly values) by averaging gridded data (except for thermocline presence, defined as the daily proportion of pixels where the thermocline was considered present in the area). The area used to extract environmental parameters (38.2–41° S, 140–148° E, approx. 120 000 km<sup>2</sup>; Fig. 1) was much larger than the known little penguin foraging areas to account for oceanographic processes occurring outside of the foraging area but which can still be influential (e.g. phytoplankton blooms). However, some other parameters might be more local,



affecting little penguins directly at the locations where they forage or travel to (e.g. currents, waves, stratification). To assess the sensitivity of the time series to the chosen area, we compared 2 different time series averaged over either the entire large area (Fig. 1, red rectangle) or a smaller one corresponding to foraging grounds only (Fig. 1, yellow rectangle) (see Sánchez et al. 2018). No significant differences were observed (see Fig. S6); therefore, results were considered unbiased by area and are only presented using the larger area.

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

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

### 2.3. Analyses and statistics

All analyses were performed using R v.3.5.1 (R Core Team 2018). Results are presented as means  $\pm$  SE. Whenever running a LM (or linear mixed model [LMM]), the normality of the residuals was verified using density plots and Q–Q plots.

#### 2.3.1. Seasonal patterns in foraging performance

Trip duration and associated mass gain were averaged per calendar week to assess seasonal patterns in foraging performances throughout the year. Generalised additive models (GAMs) from the R package ‘mgcv’ v.1.8-33 (Wood 2011; [GAM = mass gain or

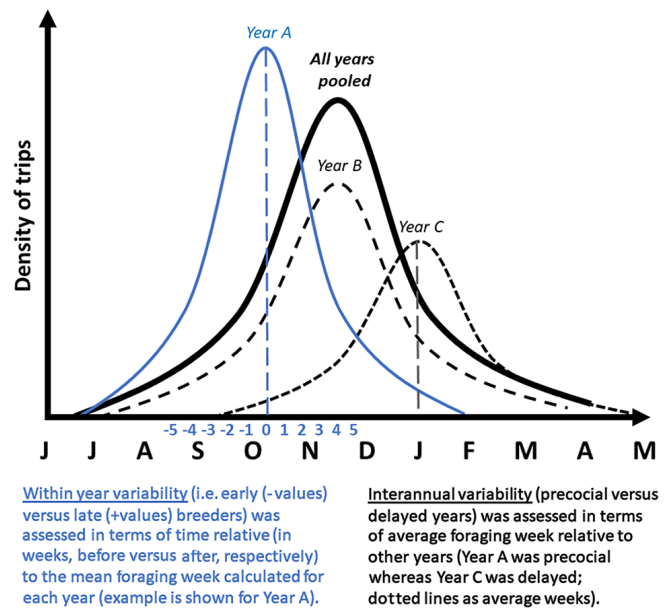


Fig. 2. Schematic view of little penguin within-year (early vs. late breeders) and interannual (precocious vs. delayed years) breeding timing variability assessment

trip duration  $\sim$  smooth{week}) were then run separately for each breeding stage. However, in these models, an early week could result from 2 different processes: individuals foraging early in the year and/or an overall early year. To understand the interplay between these 2 processes and assess the variability of seasonal patterns among years with different overall timing, we computed the average foraging week of each breeding year and the relative week of each trip (van de Pol & Wright 2009). The relative week is the week of the trip (the week of the trip being defined by the day of departure) centered around the average week of the season (i.e. the week value of each trip minus the average week of the season; Fig. 2) in a way that the relative week accounts for individual timing with no regard for overall season timing. Effects of the average week (overall timing, rather early or delayed years compared to others), relative week (timing of each week within the season) and their interaction were assessed using the following generalised additive mixed model (GAMM): [GAMM = mass gain or trip duration  $\sim$  smooth{relative week} + smooth{average week} + tensor product{average week, relative week}]. We added individual ID as a random effect (intercept) for both foraging parameters and a random effect (intercept) of chick age for trip duration and adult sex for mass gain (based on preliminary variance analysis; see Table S1 & Text S2).

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

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

Finally, we investigated whether years with contrasting foraging performance resulted in different breeding success, and whether this applied for each breeding stage. To do so, we tested for differences in annual breeding success among clusters of foraging performances using a Kruskal-Wallis test followed by Holm-adjusted (to account for multiple comparisons) post hoc Dunn tests ('dunnTest' function from 'FSA' v.0.9.1; Ogle et al. 2021).

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

We assessed the link between environmental parameters and trip duration and associated mass gain in the short-term (i.e. at the trip scale) using LMMs for each breeding stage separately because effects were expected to differ due to different constraints among breeding stages. Daily parameter anomalies and seasonal signals were averaged per foraging trip, except for tides (closest hourly water level measure), and were used as explanatory variables in the models. Effects on mass gain were tested using a LMM with random effects of year, individual and sex, while effects on trip duration were tested using a GLMM with a Poisson distribution (Saraux et al. 2016) and random effects of year, individual and chick age (based on preliminary variance analysis; Table S1). Variance inflation factors (VIFs) were estimated on full models, including all variable anomalies and seasonal signals. Variables with the greatest VIFs were then sequentially removed until no

variable had VIF > 3 to avoid collinearity issues (Zuur et al. 2010).

### 2.3.4. Effects of inter-annual climate variability and breeding timing on foraging performance

To test for the relationship between the environment and foraging performance at the inter-annual scale, we computed LMs explaining annual means of either mass gain or trip duration by yearly means of environmental anomalies averaged over the breeding season (except for tides, which were expected to present no inter-annual differences) as well as annual ENSO and AAO indices. Considering the small sample size ( $n = 19$  yr) compared to the number of explanatory variables tested, we decided to run separate LMs for each explanatory variable [LM = mass gain or trip duration ~ environmental variable].

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

## 3. RESULTS

### 3.1. Variability in foraging performance

Across all individuals ( $N = 399$ ) and years ( $N = 19$ ), foraging trips ( $n = 45\,363$ ) lasted on average  $3.21 \pm 0.03$  d during incubation ( $n = 7\,075$ ),  $1.09 \pm 0.00$  d during guard ( $n = 11\,767$ ) and  $1.40 \pm 0.01$  d during post-guard ( $n = 26\,521$ ), ranging from 1 to 17 d (in incubation and post-guard, 1–2 d in guard). Relative mass gain (i.e. mass gain corrected according to trip duration) was estimated for 28 633 trips (63%) and varied from  $-394$  to  $+352$  g. Due to the significance of breeding stage on foraging performance (Table S1), further analyses were run separately per breeding stage.

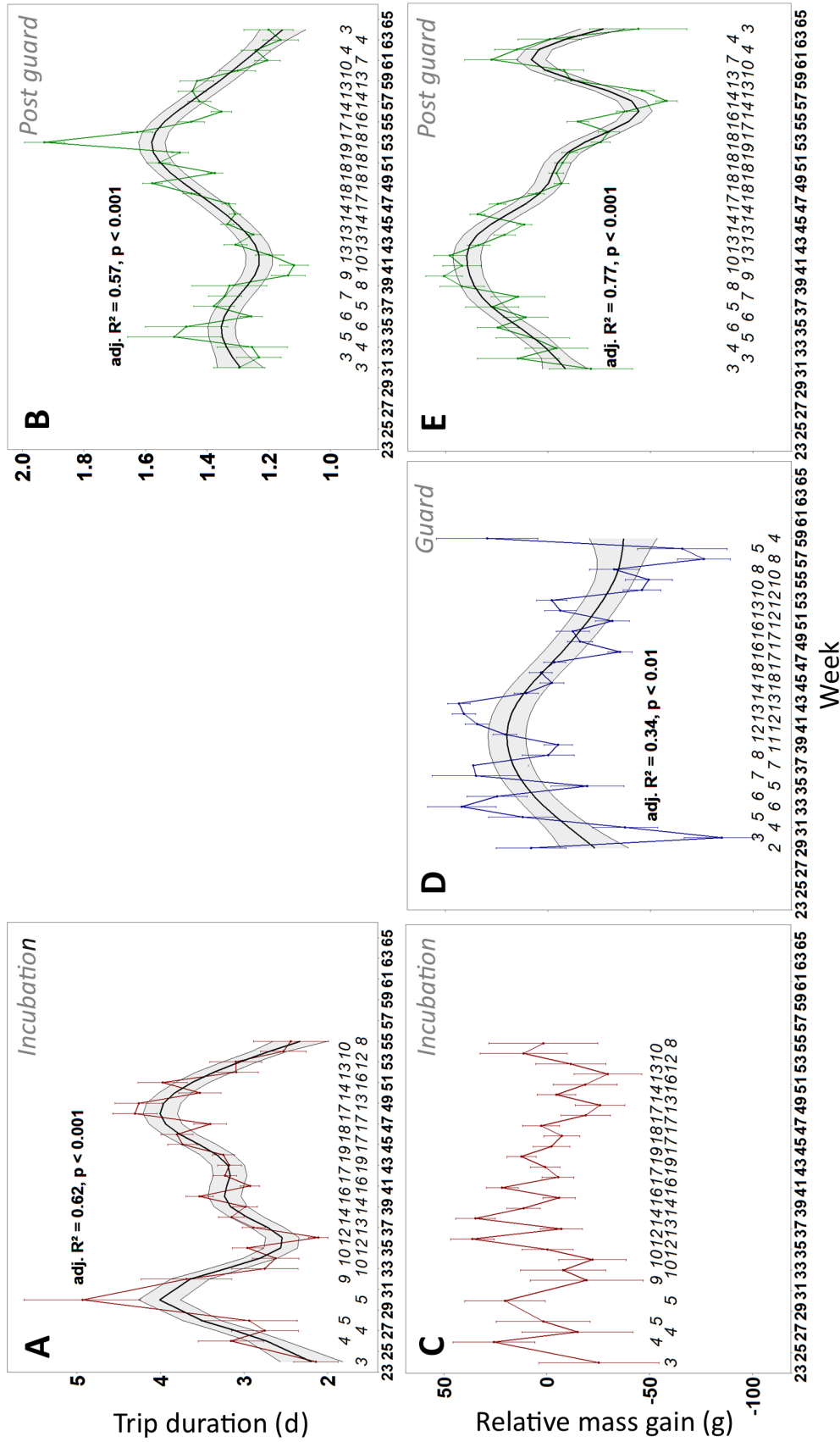


Fig. 3. Weekly mean  $\pm$  SE relative mass gain and trip duration in little penguin (A,C) incubation (red), (D) guard (blue), and (B,E) post-guard (green) periods. The prediction (black curve) and standard error (grey area) of the generalised additive models are superimposed when week was significant. Italic numbers at the bottom of each panel indicate the number of years in which a given breeding week occurred



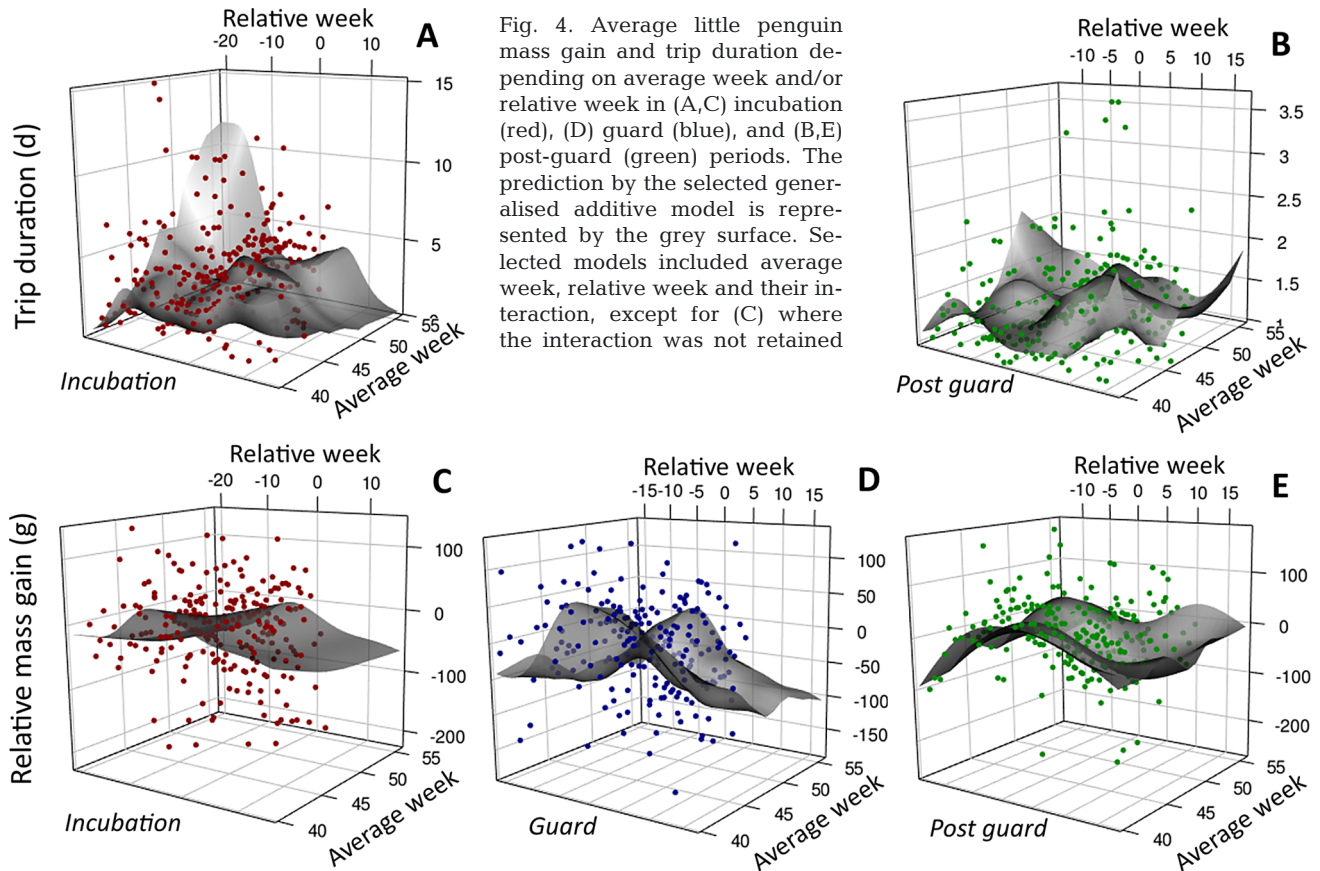


Fig. 4. Average little penguin mass gain and trip duration depending on average week and/or relative week in (A,C) incubation (red), (D) guard (blue), and (B,E) post-guard (green) periods. The prediction by the selected generalised additive model is represented by the grey surface. Selected models included average week, relative week and their interaction, except for (C) where the interaction was not retained

### 3.1.1. Seasonal and optimal patterns in foraging performance

Except for relative mass gain during incubation (GAM,  $p = 0.32$ ,  $n = 29$  wk; Fig. 3C), little penguin foraging performance presented non-linear changes within a season during all breeding stages (Fig. 3, detailed model summaries in Table S2). All 4 GAMs showed a similar optimal period of foraging (i.e. shorter trips and higher mass gains) in October (weeks 40–42), except regarding trip duration in incubation where the optimum was slightly delayed (weeks 47–49). Foraging performance also increased for the latest trips in the season, with shorter trips in January during incubation (week 55; GAM,  $p < 0.001$ ,  $n = 29$  wk) and shorter trips with higher mass gains in March during post-guard (week 63; GAM,  $p < 0.001$ ,  $n = 34$  wk).

### 3.1.2. Interaction between phenology and foraging performance

To assess how optimal patterns were affected by differences in overall years timing, further analyses

considered the effects of average year week (inter-annual variability, i.e. precocious vs. delayed breeding year) and week relative to average year week (within-year variability, i.e. early versus late within the year; see Fig. 2 for more details). The time of the year (average year week) and individual timing relative to others (relative week) had a significant effect on penguin trip durations during incubation and post-guard, as did their interaction (GAMMs;  $n = 5705$  and  $21604$ , all  $p < 0.001$ ). This indicates that intra-annual patterns in foraging performance varied depending on the year overall timing (i.e. precocious or delayed years). Penguins conducted shorter trips just before mid-year (relative week  $-5$  to  $0$ ) during incubation and post-guard and at the end of incubation (relative week  $8-10$ ). While this remained true regardless of the year timing (average week in Fig. 4A,B), the effect was much more pronounced during delayed years than in precocious years (see average week 40–45 compared to week 50–55 in Fig. 4A,B).

During incubation, the relative mass gain of penguins was related to both year timing and individual timing, yet the interaction was not significant (GAMM,  $n = 3422$ ,  $p < 0.001$  for single effects and  $p = 0.378$  for their interaction). Their mass gain was sig-

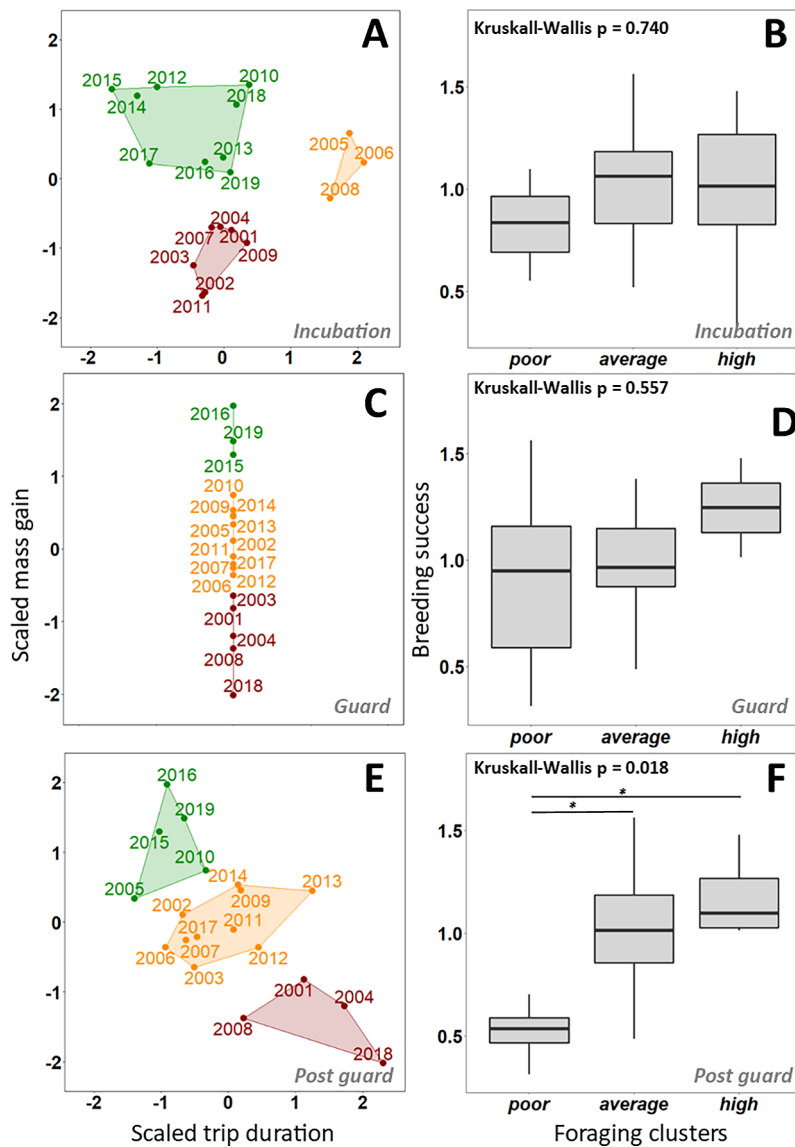


Fig. 5. (A,C,E) Annual little penguin foraging performances grouped by *k*-means clustering (*n*start = 1000) based on both scaled trip duration and mass gain (only based on mass gain for guard). For each breeding stage, years were clustered into 3 groups of poor (red), average (orange), and high (green) foraging performances. (B,D,F) Breeding success (no. of chicks fledged per breeding event) compared between clusters. Bar: median; box: interquartile range; whiskers: max./min. Asterisks: significant differences between groups according to Dunn's (Holm-adj.) post hoc test

nificantly lower during delayed years (Fig. 4C) and was very similar early and late within the year but slightly higher in early mid-year (relative weeks –10 to 0). During guard, the relative mass gain was affected by individual timing (relative week) and its interaction with the year (average week) timing (GAMM,  $n = 6367$ ,  $p < 0.001$  for relative week and interaction,  $p = 0.171$  for the average week). Mass

gain of penguins followed a clear optimal pattern, with a peak during early mid-year weeks (relative week around –10 to 0; Fig. 4D). However, this was very important in precocious and delayed years but less so in average years (see average week 50 compared to week 40 or 55 in Fig. 4D,E). Finally, the year timing and its interaction with individual timing affected the post-guard mass gain (GAMM,  $n = 13874$ ,  $p < 0.001$ ). Overall, as during guard, mass gain was lower when breeding year timing was average than for precocious and delayed years (Fig. 4E). While individual mass gains were higher in mid-year for early years (around relative week 0 when average week was 45), it was the opposite in delayed years, when mass gain was higher early or late in the year (around relative week –5 or 10 when average week was 55).

### 3.1.3. Inter-annual differences in foraging performance

Based on the combination of little penguin trip duration and mass gain (or just mass gain during guard), 3 distinct clusters (low, average and high foraging performance) were defined for each breeding stage according to the optimum number of cluster assessments described in Section 2.3.2 (Fig. 5A,C,E). Apart from incubation, clusters reflected real differences in quality, with both foraging parameters varying together (e.g. clusters of high foraging performance were characterised by high mass gain and short trips; Fig. 5C,E). During incubation, however, clusters also reflected different strategies. One cluster was characterised by average mass gain but very long trips, while another cluster displayed the exact opposite (i.e. average trip duration but low mass gain; Fig. 5A).

Some years were associated with the same foraging performance cluster for all 3 breeding stages (e.g. 2001 and 2015 being defined as low and high foraging performance years, respectively). However, most of the years consisted of breeding stages assigned to different foraging performances (e.g. 2018 was a composite of high performance during incubation but low performance during guard and post-guard).

### 3.1.4. Breeding success

Penguin breeding success increased with foraging performance for each breeding stage (Fig. 5B,D,F). Yet, differences in breeding success among categories of foraging performance were only significant during post-guard (Kruskal-Wallis,  $p = 0.018$ ). During this period, breeding success in low foraging performance was about half that in years of average and high foraging performance (Holm-adj. post hoc Dunn tests; Fig. 5F).

## 3.2. Environment variability and foraging performance

### 3.2.1. Short-term effects of the environment on foraging performance

Although environmental anomalies and seasonal signals were modelled together to explain short-term effects of the environment on foraging performance (Fig. 6), only the effect of the anomalies are described here. Indeed, because seasonal signals were correlated, several variables had to be removed to avoid collinearity that might confound interpretation. A detailed description of seasonal signals and model outputs can be found in Tables S2–S6, Text S3.

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

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

guard trips when thermoclines were stronger but less extensive (LMM,  $p < 0.001$  in all cases; Fig. 6B).

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

### 3.2.2. Annual effects of the environment on foraging performance

Trips were significantly shorter in duration when chl *a* concentration anomalies were greater during the breeding season (LM,  $0.24 \pm 0.10$  d shorter per  $0.1 \mu\text{g l}^{-1}$  more chl *a*,  $p = 0.034$ ). No other effects of the environment were found otherwise, either on trip duration or on mass gain ( $p > 0.1$ ).

Furthermore, penguin yearly foraging performance was associated with the synchrony between timing of breeding (i.e. average foraging week) and the timing of the spring decrease in primary production (hereafter, winter bloom end) (Fig. 7A,B; GAMM,  $p < 0.001$  for mass gain and  $p = 0.027$  for trip duration). More precisely, years were optimal in terms of foraging performance when the average foraging week happened around 1 mo before the winter bloom end, and minimal foraging performance occurred when the average week happened 1 mo after winter bloom end (Fig. 7). Extremely delayed seasons (average timing of breeding week occurring 5–7 wk after winter bloom end) had an intermediate effect on foraging performance, potentially due to higher synchrony with the start of the next winter bloom at the end of summer (Fig. 7A,B,D). Years with low foraging performance were mainly characterised by delayed breeding (Fig. 7C), while years with high foraging were characterised by precocious breeding (Fig. 7E). Using only post-guard foraging instead of yearly foraging led to similar results (Fig. S9).

## 4. DISCUSSION

We showed that foraging performance during breeding varied within and among years based on trip duration and mass gain of 399 little penguins over 19 breeding seasons and 45363 trips. Some periods within the year were consistently more successful in terms of foraging performance than others, i.e. birds conducted shorter trips and gained more

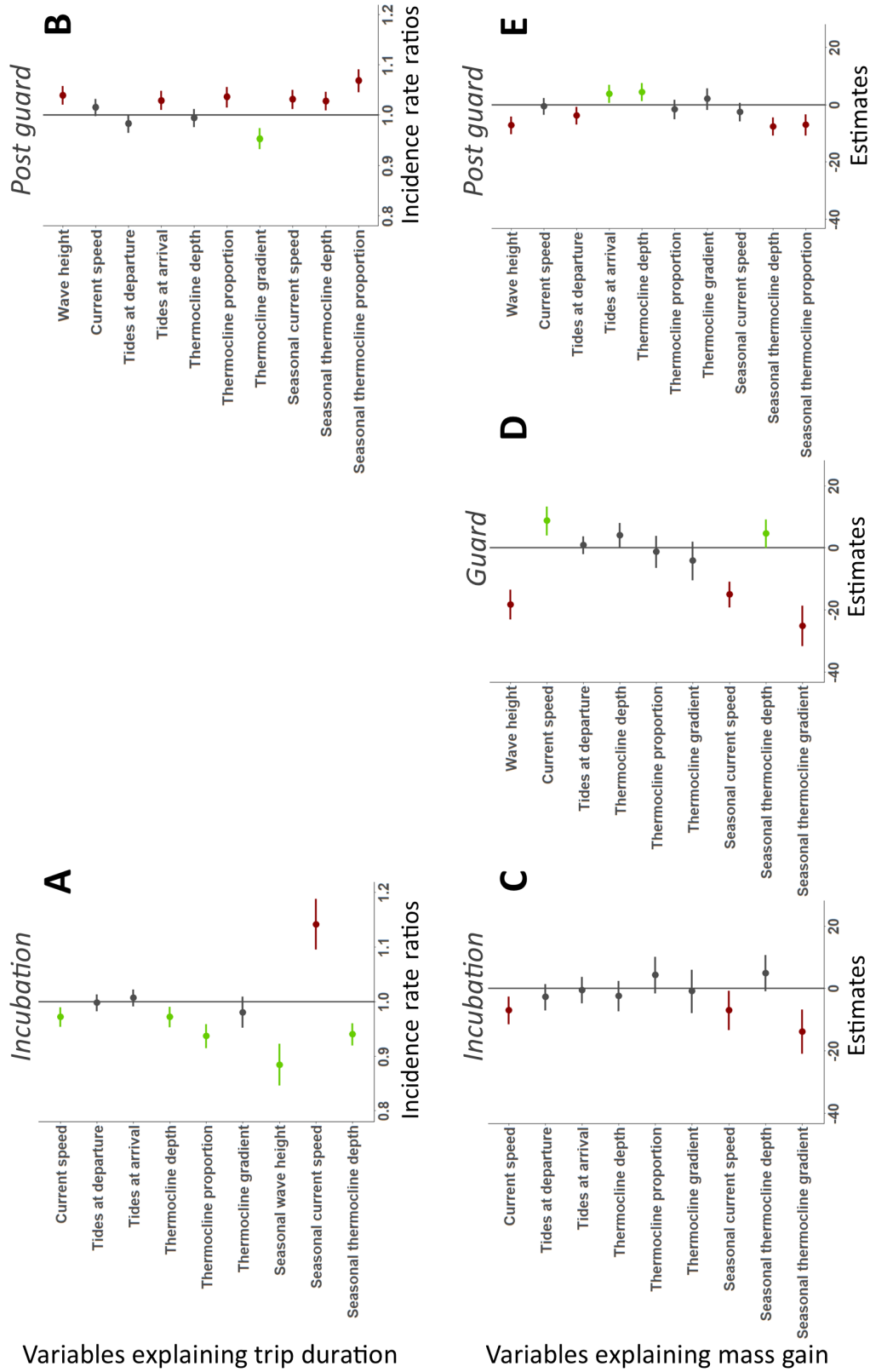


Fig. 6. Environmental effects on little penguin (A,B) foraging trip duration and (C,D,E) relative mass gain for each breeding stage. Estimates and 95 % confidence intervals from linear mixed models explaining mass gain and incidence rate ratios and 95 % confidence intervals from generalised linear mixed model (Poisson distribution) are presented. Significant effects are presented in color: red: significant detrimental effect (i.e. lower mass gain or longer trips); green: significant positive effect; grey: non-significant effects. Some variables were removed from the full models due to important variance inflation factors (i.e. >3)

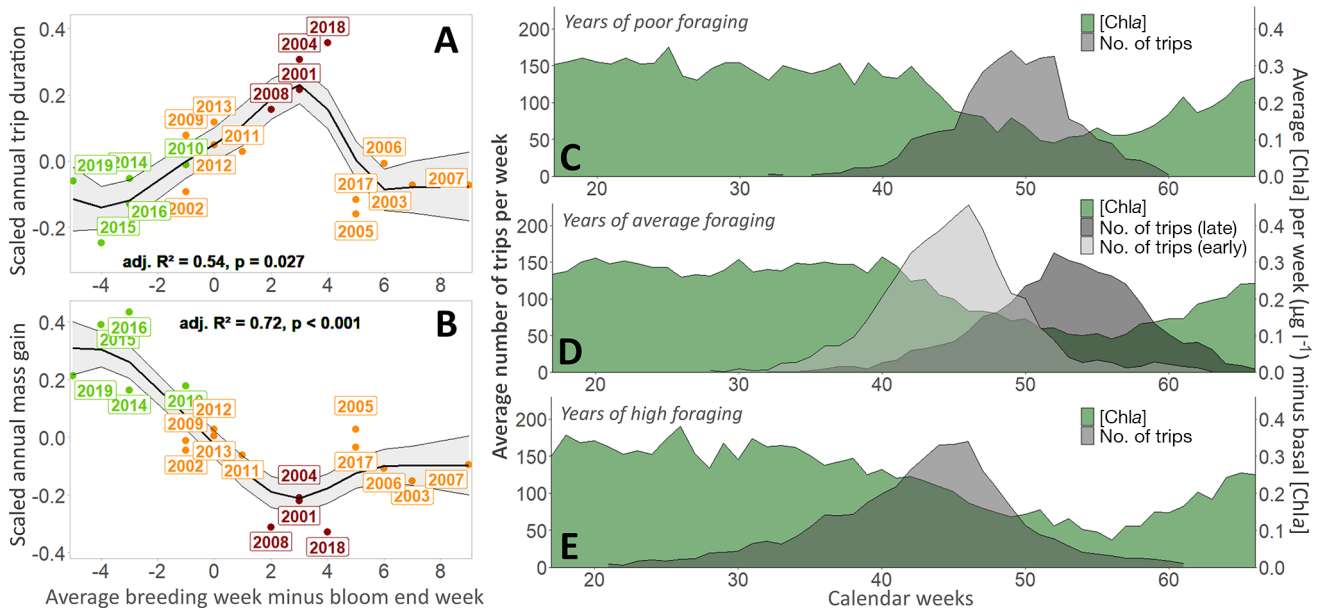


Fig. 7. Effect of synchrony between little penguin foraging and primary production on annual (A) trip duration and (B) mass gain, with generalised additive model (black curve)  $\pm$  SE (grey area). Points are coloured according to established high (green), average (orange) and poor (red) foraging clusters. (C,D,E) Weekly average chl a concentration (dark green) and trip density (grey) during the year for each of the 3 clusters. Trip density in the average foraging cluster (D) is split into 2 different categories based on breeding timing: early breeding (2002, 2009, 2011, 2012 and 2013 in light grey) and very late breeding (2003, 2005, 2006, 2007 and 2014 in grey) based on (A) and (B)

mass. We further identified groups of low, average and good foraging performance years. These trends coincided with annual breeding success. Finally, we evaluated different climatic and oceanographic variables and highlighted the importance of waves and currents in the short-term, thought to affect foraging directly through increased costs while swimming or diving. We identified the additional role of vertical stratification that affected foraging indirectly through a modification of prey distribution impacting travelled distances or capture efficiency. However, these environmental variables explained a very small part of the total foraging variability (Tables S3–S7), highlighting the importance of many other factors. Finally, we showed that breeding phenology and its match with primary production cycles affected foraging performance variability at the interannual scale.

#### 4.1. Variability at the trip scale

Sudden and short environmental variations can affect seabird foraging behaviour and efficiency (Raya Rey et al. 2010, Dehnhard et al. 2013, Osborne et al. 2020). In little penguins, changes in foraging were found to be associated with vertical stratification (Pelletier et al. 2012) and wind speed (Saraux et al. 2016). However, although wind can impart an energetic cost

during foraging among flying seabirds (Amélineau et al. 2014, Elliott et al. 2014, Tarrow et al. 2016), the question remains regarding the mechanism by which wind could affect non-flying little penguins. Wind can affect vertical stratification and water mixing (Klein & Coste 1984, Warrach 1998), potentially modifying prey distribution (Sanvicente-Añorve et al. 2007) but can also increase wave height and surface currents (Mao & Heron 2008, Young et al. 2011), making swimming conditions at sea more difficult. We found strong correlations between daily wind speed, current speed and wave height, but weak correlations with vertical stratification (thermocline intensity and proportion; see Fig. S3). Furthermore, wave height and current speed had the strongest and most consistent adverse effects on foraging. We argue that wind speed effects previously highlighted for penguins (Dehnhard et al. 2013, Saraux et al. 2016) might be primarily mediated through waves and currents (energy spent) rather than by increased water mixing (prey accessibility). We suggest this pattern shows penguins face adverse foraging conditions while commuting during strong-wind days.

Based on previous studies of Magellanic penguins, we also expected little penguins to be affected by tidal cycles when commuting from land to sea (Wilson et al. 2001, Raya Rey et al. 2010). However, effects of tides were only significant during post-guard, when



higher water levels upon return to land resulted in longer trips but greater mass gain (mass gain was conversely less when the water level increased when departing to sea). These unexpected results might suggest that tidal effects reflect prey accessibility rather than unfavourable commuting conditions (Adélie penguin; Oliver et al. 2013). According to tidal cycles, small pelagic fish migrate either vertically or horizontally (Gibson 2003), modifying little penguin prey distribution. These effects of tidal cycles are evident in the foraging behaviour of several piscivorous seabirds, especially modifying their diving depth (Holm & Burger 2002). However, tidal effects on little penguin foraging would need further investigation to better understand their underlying processes.

Consistent with previous studies, vertical stratification also affected little penguin foraging performance (Ropert-Coudert et al. 2009, Pelletier et al. 2012, Meyer et al. 2020). Overall, a stronger thermocline was associated with shorter trips in post-guard. More stratified waters could enhance small fish (i.e. little penguin prey) aggregation around the thermocline (Hansen et al. 2001), which should be beneficial to foraging seabirds (Kokubun et al. 2010, Pelletier et al. 2012). Thermocline ubiquity was also related to shorter trips during incubation but was detrimental (conducted longer trips) during post-guard. One explanation may be that during incubation (i.e. early in the season), the thermocline is not well established (average of 42% thermocline in the area during incubation trips), so a regionally more extensive thermocline should lead to greater areas of prey aggregation and profitable foraging grounds. Conversely, during post-guard, once the thermocline is well established (average of 76% thermocline in the area per trip), a further increase in the regional area with thermocline presence (e.g. stratification) might reflect a more uniform physical barrier with the absence of horizontal gradients and effective prey aggregation areas (e.g. fronts; Spear et al. 2001). A deeper thermocline generally had positive effects on little penguin foraging performances (no adverse effects were expected in such shallow waters), which might result from higher prey aggregations at deeper stratification (Spear et al. 2001) or from a decrease in energy costs in deep dives compared to shallow ones (Wilson et al. 1992).

#### 4.2. Seasonal patterns of variability in foraging performance

Variations in seabird foraging performance throughout a breeding season are mainly driven by local

prey depletion (Ashmole 1963, Birt et al. 1987, Lewis et al. 2001) or by a temporal match with the period of maximum prey availability (Durant et al. 2007, Regular et al. 2014). In the case of prey depletion, foraging performance is expected to decrease linearly during the breeding season, while in the case of a match/mismatch with prey, foraging performances are expected to reach an optimum pattern during the breeding season. However, in deep divers like little penguins, prey depletion may not be linear (Chiaradia et al. 2016), and we might then expect a response that indicates optimum foraging performance when foraging birds encounter maximum prey availability at any stage of breeding. Indeed, we found optimum foraging performance at around 1/3<sup>rd</sup> of the way through the season, when mass gain was maximal and foraging trips were shortest. Conversely, we found no decrease in foraging performance throughout the season, consistent with previous suggestions that prey depletion did not explain the overall reduction of foraging performance of little penguins. Our results indicate little penguin foraging performance at the season scale is more dependent on the match with their prey than on potential prey depletion in their limited foraging area.

Optimum foraging performance was characterized by shorter trips and higher mass gain simultaneously. Thus, our results also indicate that foraging variability is driven by external (environmental) conditions rather than by intrinsic (behavioural) plasticity, where one parameter could be traded-off with the other (e.g. increase trip duration to gain more mass; Paiva et al. 2010, Saraux et al. 2011).

#### 4.3. Variability at the inter-annual scale

Given the evidence for the seasonal optimums in foraging performance highlighted above, the annual breeding phenology should play an important role in foraging variability (see Chambers 2004, Chiaradia & Nisbet 2006, Cullen et al. 2009, Ramírez et al. 2015). Maximising foraging performance should thus depend on the population's overall timing (4 mo difference between the earliest and latest years in breeding onset) and individual breeding onset within the season (Ramírez et al. 2021). We demonstrated the duality between intra- and inter-annual breeding timing by assessing the interaction between these 2 time scales. We showed that the best window of time to forage (i.e. optimum prey availability) differed from the start to just past the middle of the breeding

season, depending on how early the overall season was.

Despite this critical role of phenology, no link between overall breeding season foraging performance and oceanographic variables (stratification, wave and current regime) could be established. This disconnection likely occurs because inter-annual environmental variability of marine ecosystems is multifactorial (Grémillet & Boulinier 2009, Sydeman et al. 2012, Quillfeldt & Masello 2013), composed of fluctuating parameters that are not easily integrated at larger time scales. However, we showed that years when phenology better matched winter high primary production (maximum occurring during fall and winter in the region; Kämpf et al. 2004) resulted in better foraging performance. Years with better foraging performance had consistently early breeding start times, during which most trips occurred before the spring decrease in primary production. Years of low foraging performance were delayed by around 1 mo. If temporal match with prey availability indeed drives seabird foraging and breeding success (Hipfner 2008, Regular et al. 2014), few studies have directly established a relationship with primary production. One reason might be that seasonal variations in marine productivity in most temperate areas are driven by temperature and photoperiod (Nicklisch et al. 2008), which are the primary triggers for birds to initiate breeding (Mickelson et al. 1991, Dawson 2008). Therefore, it is unlikely that temporal mismatches would be expected between seasonal marine productivity and breeding phenology in temperate regions. However, this is not the case in the study region, the Bass Strait, where primary production is driven by winter high nutrient levels (Gibbs et al. 1986), and penguins seem to respond to the peak of chl *a*—a proxy for marine productivity (Afán et al. 2015). Primary production, however, may not affect prey dynamics at the year scale, although it may be vital at a multiannual scale (Capuzzo et al. 2018), but may be affecting prey quality (sensu the junk-food hypothesis; Wanless et al. 2005, Österblom et al. 2008), presence and accessibility (Bost et al. 2009). Therefore, we suggest the central hypothesis explaining the role of mismatch with primary production on little penguin foraging performance may be an effect of overall prey quality (size and body condition) combined with spatial distribution. The most delayed breeding seasons (5–9 wk after the spring decrease in primary production) had higher foraging performance than seasons delayed by only 2–4 wk, further supporting the hypothesis of prey

quality/accessibility importance. Specifically, late years were delayed enough to potentially benefit from an increased prey quality/accessibility via the return of high primary production in the fall.

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

## 5. CONCLUSIONS

Little penguin foraging performance varied at different time scales with contrasting environmental conditions. We showed that interannual variability in little penguin foraging was associated with differences in breeding success, and phenology was the main driver of interannual differences in foraging. Thus, breeding success might be strongly related to phenology (Youngflesh et al. 2017) through foraging. This pattern may become even more critical with climate change. While phenology in many seabirds has not changed with warming waters (Keogan et al. 2018), some other seabirds have responded dramatically to climate changes in other parts of the world (Sydeman & Bograd 2009, Wanless et al. 2009). We also highlighted significant concurrent effects of waves and currents (possibly driven by wind) and, to a lesser extent, vertical stratification on seabirds foraging at shorter time scales. The impact of these variables on breeding success may have increasing importance in the future, as waves and currents are expected to increase in intensity globally due to climate change (Young et al. 2011, Capotondi et al. 2012).

**Data accessibility.** Data are available at <https://doi.org/10.17632/st43c45j5w.1>

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