



Parental body condition and high energy value of fish determine nestling success in Magellanic penguin (*Spheniscus magellanicus*)

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Abstract

Nestling growth and survival of marine birds are influenced by multiple factors. Oceanic conditions influence food availability and energy value of the diet and affect nestling condition. Climate variables, like heavy rains, could drown or cause hypothermia of nestlings. Besides oceanic conditions, parental conditions and hatching asynchrony can also affect nestling growth and survival. Magellanic penguins are long-lived seabirds with multiple breeding opportunities that lay a two-egg clutch, but they may raise only one of the two chicks depending on the breeding season. We studied nestling growth and survival for four breeding seasons (2010–2013) and related these to parents' body condition and hatching asynchrony. We also analysed the effect of nestling diet, rainfall, chlorophyll *a* concentrations (*c-a*), and sea surface temperature (SST) of known foraging sites to evaluate nestling performance. We found that parents' body condition, especially that of males, were positively related to nestling growth. Hatching asynchrony appears not to have an important role in nestling growth/survival. Nestling growth/survival, rain, diet, *c-a* and SST differed drastically among breeding seasons. During the breeding season with the highest mortality and lowest asymptotic mass of nestlings (2012), we registered heavy daily rains within the first stage of the raising period. We also found that high/low concentrations of *c-a* were related to high/low mortality of nestlings, respectively, and that SST was inversely related to asymptotic mass. Nonetheless, neither of these oceanic variables was related clearly to nestling growth/survival during breeding seasons with intermediate breeding success. On the contrary, the estimated proportion of low quality compared to high quality items in nestling diets coincided in every breeding season with the survival/growth of nestlings. We concluded that *c-a* and SST were not precise enough to determine nestling success or survival of nestlings during breeding seasons with intermediate nestling success, but that the proportion of high quality compared to low quality items in the diet were key for nestling survival and growth. Although the breeding seasons did not seem to be so "unfavourable" in terms of *c-a* and SST, when low quality items predominated in the diet, this had a strong impact on the condition of the chicks.

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Introduction

Variability of oceanographic conditions influences marine ecosystems throughout their trophic web (Croxall 1992). Top predators are affected by the abundance of fish or krill (Croxall et al. 1999; Cury et al. 2011), which are influenced by plankton abundance (Frederiksen et al. 2006), and plankton

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abundance is determined by abiotic factors (McGowan et al. 1998; Nicol et al. 2000; Mueter et al. 2002). In this sense, oceanographic anomalies produce strong effects on recruitment and reproductive performance of top predators, like marine birds (Inchausti et al. 2003; Weimerskirch et al. 2003). For example, fluctuations in oceanic temperatures can influence breeding success (Hipfner 2008) and fledgling mass (Weimerskirch et al. 2001). Nonetheless, other factors like parental quality or intrinsic traits related to the breeding biology of each species (like hatching order and hatching asynchrony) also affect nestling performance (Furness 1983; Lequette and Weimerskirch 1990; Reid and Boersma 1990).

Oceanic variables, like chlorophyll *a* (*c-a*) and sea surface temperature (SST), are often used as indicators of oceanic productivity (Lee et al. 2015; Roxy et al. 2016). They can also be good estimators of abundance several trophic levels higher up the food chain, like pelagic fish (Luch-Belda et al. 1991; Noto and Yasuda 1999), in relatively unperturbed ecosystems (Grémillet et al. 2008). Foraging sites during chick food provisioning in a piscivorous penguin coincide with high *c-a* concentrations (Boersma et al. 2009). SST affects *c-a* concentrations by their influence on the depth of the mixed water column, which affects the abundance of nutrients for primary productivity (Behrenfeld et al. 2006). Increased SST results in a more stable stratification of the water column, which leads to a depletion of macronutrients (O'Reilly et al. 2003).

The energy value of food is also important for breeding success (Hedd et al. 2002; Kadin et al. 2016). In years when diets have a high amount of low energy items, breeding success was lower than in years with more high energy items (Wanless et al. 2005). Stable isotopes have become an important tool to quantify the diet and foraging strategies of seabirds and other organisms (Meier et al. 2017; Kowalczyk et al. 2014; Edwards et al. 2015).

Heavy rains could be a negative determinant of nestling survival (Schreiber 2001) by wetting nestlings (Ropert-Coudert et al. 2015) and/or flooding nest-burrows (Frere et al. 1998; Boersma and Rebstock 2014). Because in most seabird species, the chicks' plumage is not waterproof, so their ability to thermoregulate can be compromised. Even rain and ambient temperatures during moult affected adult survival (Ganendran et al. 2016).

On the other hand, nestling growth and nutritional state are highly correlated with the physical condition of adults (Hamer et al. 2001; Ferrer et al. 2017). Parents in better condition can be more efficient at foraging and can provide more food to nestlings, and they may even be able to compensate during periods of low food abundance when they are in prime condition (Tveraa et al. 1998). Marine birds are long-lived animals with multiple breeding opportunities, so their strategy should be that of "prudent parents" (Navarro and González-Solís 2007). The "Prudent Parent Hypothesis" postulates

that animals should not breed when the value of immediate reproduction is low relative to the value of future breeding opportunities and survival (Drent and Daan 1980). According to their physical condition and food abundance, parents can skip reproduction (Cam et al. 1998) or invest less in reproduction (Ballard et al. 2010). Nevertheless, in several studies with breeding adults that were handicapped experimentally or under low quality/quantity food scenarios, seabirds compensate those disadvantages by increasing their reproductive effort without affecting their physical condition or survival (Navarro and González-Solís 2007; Bijleveld and Mullers 2009; Regular et al. 2014; Kadin et al. 2016).

Other factors also affect nestling growth patterns or survival, which include hatching order within a clutch (Lack 1968; Kasprzykowski et al. 2014) and hatching asynchrony (Saino et al. 2001; Dey et al. 2014; Sicurella et al. 2014). Hatching asynchrony imposes a size asymmetry between the siblings of a clutch (Stokland and Amundsen 1988; Viñuela 1996). In this case, hatching order and hatching asynchrony influenced nestling competition for food (Whittingham et al. 2003), which reduced the growth rates and increased the death rate of the smaller/late hatched nestlings (Saino et al. 2001; Dey et al. 2014; Sicurella et al. 2014).

The objective of our work was to study the factors that affected breeding success and nestling growth in Magellanic penguins (*Spheniscus magellanicus*). We performed a global analysis that included variables related to: (1) intrinsic parameters of the breeding biology of penguins (i.e., parental conditions and hatching asynchrony); (2) oceanic and climatic variables (i.e., precipitation, SST, and *c-a*); and (3) the diet of nestlings. Data that we collected during four breeding seasons (2010–2013) allowed us to examine different scenarios. We predicted that: (1) (i) because Magellanic penguins have intensive bi-parental care and are long-lived animals with multiple breeding opportunities (Boersma et al. 1990), parental condition of both parents would affect nestling growth and survival positively, and (ii) because we have already seen that hatching asynchrony affected nestling growth but not mortality in experimental clutches with controlled hatching asynchrony (Barrionuevo and Frere 2017), hatching asynchrony would negatively influence second-hatched nestling growth but not survival; (2) (i) higher rainfall would be associated with higher nestling mortality, and (ii/iii) lower SST and higher *c-a* would be related to higher nestling survival and better growth; and (3) we predicted higher nestling survival and fledgling mass in breeding seasons with more high quality prey items in the diet of the nestlings.

Materials and methods

Study site

The study was carried out at Isla Quiroga, located in the Ría Deseado, Santa Cruz Province, Argentina (47°45'S, 65°53'W) (Fig. 1). This island is situated approximately 80 m off the coast and hosts a breeding population of 1500 pairs of Magellanic penguins (Frere, personal observation). Penguins nest mostly beneath bushes, and, usually having no terrestrial predators; the main predators of eggs and nestlings are kelp gulls (*Larus dominicanus*) (Gandini and Frere 1998a, b).

Study species

Magellanic penguins start breeding in early October, and they are very synchronous within colonies; within 2 weeks all first eggs are laid. They lay only one clutch of two eggs per breeding season, with the last egg being 2% larger than the first (Barrionuevo and Frere 2014; but see Boersma and

Rebstock 2010). Previous studies showed that egg volume affects nestling growth only in their earlier stages (Barrionuevo and Frere 2014). Both adults incubate the eggs by taking long spells of 15 days each and then short spells of 2–3 days until incubation is complete, which is about 40 days after the first egg is laid (Boersma et al. 1990). Eggs hatch with a 1.6-day asynchrony (ranging from 0 to 4 days) (Barrionuevo 2015). Both adults feed the nestlings for 70–90 days (Boersma et al. 1990; Frere et al. 1996a), and the main cause of death of nestlings in most colonies is starvation due to food scarcity (Boersma et al. 1990, 2015; Frere et al. 1998). The diet of Magellanic penguins in the study site and surroundings is composed mostly of Patagonian sprat (*Sprattus fuegensis*), Patagonian squid (*Loligo gahi*) and Silverside (*Odontesthes nigricans*) (Frere et al. 1996b; Ciancio et al. 2015).

Field methods

We studied the colony from October to January during four breeding seasons 2010, 2011, 2012 and 2013. Breeding seasons were named by the year in which the breeding

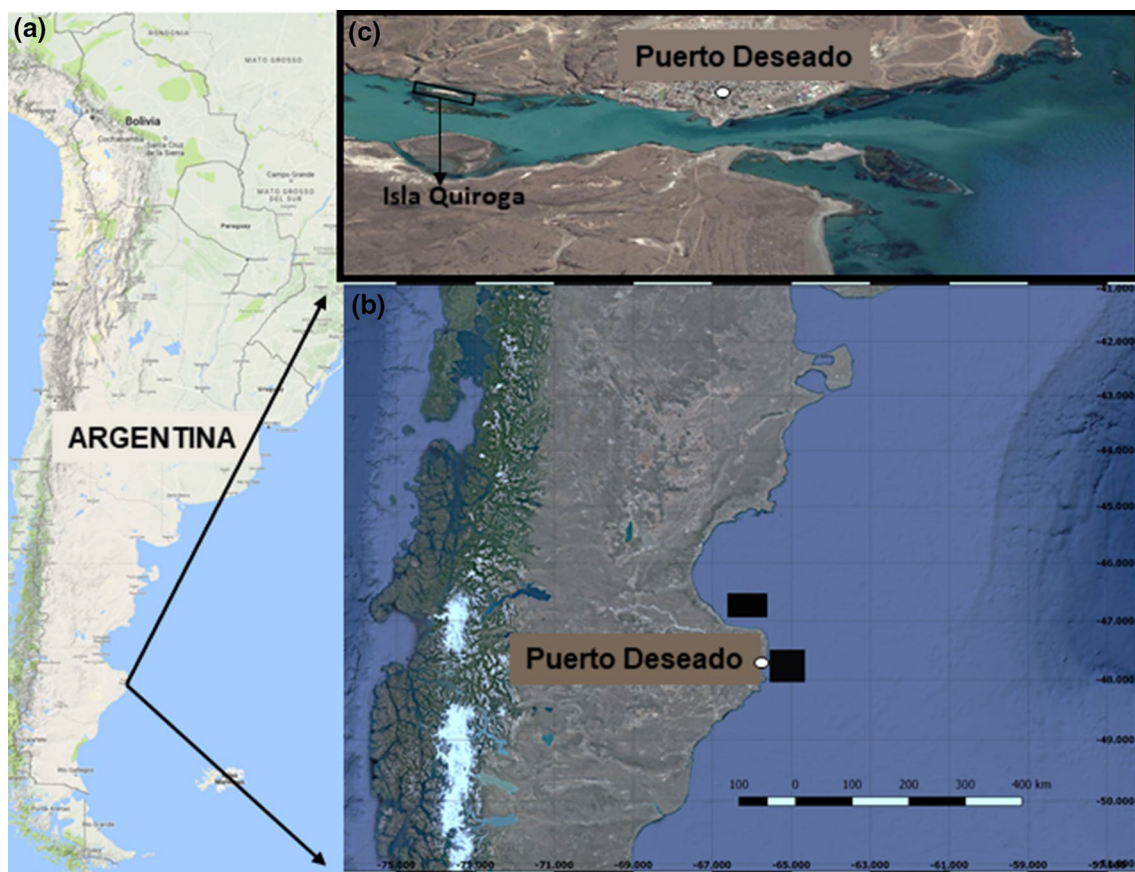


Fig. 1 **a** Map of Argentina; **b** location of Puerto Deseado in Santa Cruz Province and, in black squares, sites where Magellanic penguins foraged during December and that we used to estimate *c-a* and SST; **c** location of Isla Quiroga inside the Ría Deseado, 4 km away from Puerto Deseado

season began (e.g., breeding season 2011 lasted from August 2011 to January 2012). In early October, we chose active nests randomly that were occupied and defended by a breeding pair and marked these nests with flagging tape (Tapebrothers, Longwood, FL) with a unique nest number (approximately 50 per breeding season). Given that the same pair usually returned to the same nest every breeding season (Boersma et al. 1990), we chose different nests in each breeding season to avoid taking repeated measurements of the same pair of breeders. During laying, we checked nests daily and marked the freshly laid eggs with a waterproof pen with their laying order number. After the laying period finished, nest checks were conducted every 4 days to check for egg predation.

To estimate adult body condition, on the laying day of the second egg and when males returned to take their incubation spell (approximately 15 days after the laying period finished), we captured females and males, respectively. We measured bill length and depth (with callipers, ± 0.1 mm, Mitutoyo, Illinois, USA) and flipper and foot length (with a ruler, ± 1 mm). We then weighed each bird with a spring scale (± 25 g, Pesola AG, Baar, Suiza). Following Gandini et al. (1992), we determined the sex of adults by the dimorphism of the bill depth.

Thirty-five days after the first egg was laid, we started checking nests daily to record hatching date. Once they hatched, we weighed hatchlings with a spring scale (± 1 g) and measured bill depth and length and flipper and foot length with callipers. Then, starting the day the second nestling hatched, we weighed nestlings every 3 days and measured them every 6 days until they were 52 days old. Starting from approximately 24 ± 3 day-old, we took foot and flipper measurements with a ruler (± 1 mm). During 2013, we did not measure nestling body size, and we only weighed them. As nestlings grew, we changed precision spring scales: < 300 g: ± 2 g, $301 < 500$ g: ± 5 g, $501 < 1000$ g: ± 10 g, < 1001 g: ± 25 g.

Nestlings within a nest were identified individually. First-hatched nestlings were marked with permanent markers (Sharpies, Sanford, USA) in the inner part of the right flipper and the right foot, and second-hatched nestlings were marked on the left flipper and foot. As nestlings tend to move from the nest once they grow, we marked nestlings of contiguous nests with different colours, and we marked them with a wing ring made of scotch filament tape (3M, St. Paul, MN) on which we wrote the nest number and nestling ID. We assumed that the nestling fledged if at 52 day-old it was heavier than 1900 g and had started to moult (Reid and Boersma 1990; Boersma and Rebstock 2009).

Climatic and oceanic variables

Rainfall data were provided by the National Meteorological Service, Puerto Deseado Station, which is located 5 km away from Isla Quiroga. We were provided with total rainfall each 6 h for the breeding seasons 2011, 2012 and 2013 from October to January.

SST and *c-a* were estimated for breeding seasons 2010, 2011, 2012 and 2013 from August to January. August and September are not breeding months, but penguins begin to arrive at their breeding sites at that time (Frere, personal observation), therefore, we thought that these months were also important to their breeding performance (Sorensen et al. 2009; Crossin et al. 2010). Also, there might be a delay between the concentration of *c-a* and the arrival of the penguins' prey.

For estimating *c-a* concentrations, we used data from the Ocean Productivity web site <http://www.science.oregonstate.edu/ocean.productivity/index.php>. They base their estimation of *c-a* concentration on the vertically generalized production model (VGPM) (Behrenfeld and Falkowski 1997) as the standard algorithm. The spatial resolution is 1/6 of a degree in both latitude and longitude. We downloaded data from August to January within a period of 8 days.

For the SST, we downloaded the data from NOAA (National Oceanic and Atmospheric Administration) http://iridl.ldeo.columbia.edu/SOURCES/NOAA/NCEP/EMC/CMB/GLOBAL/Reyn_SmithOiv2/weekly/sst. The spatial resolution was 1° by 1° . We download weekly data from August to January.

Because Boersma et al. (2009) and Sala et al. (2012) published foraging sites for colonies of Puerto Deseado (Fig. 1), we downloaded the data on SST and *c-a* concentrations from these two foraging sites. Both studies were carried out during the nestling stage and covered two areas: the southern end of the Golfo San Jorge ($66.5W-65.5W$ and $46.5S-47.5S$) and the area east/southeast of the mouth of Ría Deseado ($65.0W-63.8W$ and $47.0W-48.0W$) (Fig. 1).

Collection and processing of stable isotope samples

During the late chick-rearing period of the breeding seasons 2011, 2012 and 2013, penguin chicks from Isla Quiroga were captured from the nests to take blood samples for stable isotope analyses. These nestlings were chosen randomly and were not necessarily those of study nests. Whole blood samples (cell + plasma) of 0.5 ml were obtained from the metatarsal veins of 31 chicks (11, 10, 10 in 2011, 2012, and 2013 seasons, respectively). Blood samples were preserved in 70% ethanol prior to ^{13}C and ^{15}N stable isotope analysis. Subsequently, samples were dried at $60^\circ C$ for 48 h and ground to a fine powder before stable isotope analysis was carried out at the Stable Isotopes Facility, University of California,

Davis. The ratios of stable isotopes were measured against the reference standards Vienna PeeDee Belemnite for ^{13}C and atmospheric air for ^{15}N , which were expressed as δ values ‰: $X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. For secondary isotopic reference materials, we used Nylon (SD were 0.056 and 0.05 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), Bovine Liver (SD 0.007 and 0.07 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), USGS-41 Glutamic Acid (SD 0.17 and 0.16 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), and Glutamic Acid (SD 0.06 and 0.26 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively).

Data analysis

Effects of breeding parameters on nestling survival

To assess the relationships between nestling survival and breeding season, condition of parents, hatching order, and hatching asynchrony, we ran a generalized linear mixed model (GLMM) with binomial distribution and logit link function ($n = 115$ nests, 230 nestlings). Survival was the response variable and the fixed effects were: breeding season (as a four level factor: 2010, 2011, 2012, and 2013), hatching order (as a two level factor: 1st and 2nd), hatching asynchrony (as a four level factor: 0, 1, 2, and 3), female body condition, male body condition, and the interactions between hatching order and hatching asynchrony, hatching order and breeding season, and hatching asynchrony and breeding season. To account for the lack of independence of the nestlings that belonged to the same clutch, we considered the nest as a random effect in our analyses.

We calculated the Marginal R^2 and Conditional R^2 for this binomial GLMM as explained by Nakagawa and Schielzeth (2013). The Marginal R^2 represents the variance explained by fixed factors and the Conditional R^2 also includes the variance explained by random factors.

Effects of breeding parameters on nestling growth

To assess the relationship between nestling growth and breeding season, condition of parents, hatching order, and hatching asynchrony, we ran Non-linear Mixed Models (NLMM) (Lindstrom and Bates 1990) that were adjusted to a Gompertz curve for nestling mass ($n = 146$ nestlings) and to a Sigmoidal curve for body size index ($n = 112$ nestlings). To estimate the body size index for nestlings, we ran a PCA on all the measurements for each age in which the measurements were taken (hatching day, 6 days old—and all the multiples of six). The first principal component of the PCA was used as an index of nestling body size. NLMM allowed us to check for differences in the parameters of the curves within the variability of the predictor variables that we analysed. In the fixed part of the equation, each parameter of the growth

curve had its own linear model in which we added the same predictor variables (Pinheiro et al. 2015). The parameters of the curves were a , the asymptotic value; c , the inflexion point; and b , the growth rate constant. We ran a model with nestling mass and a model with nestling body size as response variables. The predictor variables for all the models were female and male body condition, hatching order (1st and 2nd), hatching asynchrony (0, 1, 2, and 3), whether the sibling of the nestling fledged (yes, no), and breeding season (2010, 2011, 2012, and 2013) as predictor variables. We did not have data for body size in 2013, so data on that breeding season was excluded from the model with body size as the response variable. The nest and the nestling itself were the random factors to account for the lack of independence between siblings and within measurements of the nestlings. Random effects were included for the three parameters in the model, a , b , and c , which allowed for the parameter estimates to vary across individuals.

In all previous analyses described above regarding hatching asynchrony, we grouped clutches with 4 days of hatching asynchrony with those with 3 days, because of low sample sizes. Also, those clutches with reversed asynchrony (−1 day, second laid egg hatched first, $n = 4$ nests) were grouped with those with 1 day asynchrony. All nests that did not have a clutch of two eggs, or where at least one egg was preyed on or did not hatch, were discarded from the analyses because the sample size was too low to perform any other statistical analysis ($n = 22$ nests for the four breeding seasons). To estimate adult body condition, we ran a principal component analysis (PCA) with all the body measurements. We then regressed adult mass against the first component of the PCA (Yorio et al. 2001).

Oceanic variables

To see how c - a concentrations and SST varied within and between breeding seasons, we ran linear models (LM), where the predictor variables were the breeding season, the month of the breeding season, and the interaction between both factors. The data entered in the model were the raw data downloaded from the internet pages previously mentioned. Therefore, for each month, we entered in the models the weekly data and the data of both foraging sites.

Effect of oceanic variables on asymptotic nestling mass

We evaluated if c - a and SST affected nestling asymptotic mass through two linear mixed models (LMM). We extracted the asymptotic mass for each nestling from a Gompertz curve. Then, we ran a model with asymptotic mass as the response variable. In one model, we added c - a as the predictor variable and, in the other model, we added SST. For c - a , we used the sum of all the available data for

each breeding season (summing the data for each foraging site and for each week of the month). For the predictor variable SST, we averaged all the row data available for each breeding season (including weekly and foraging site data). In these models, the random factor was the breeding season (2010, 2011, 2012, and 2013).

Stable isotopes

The Bayesian stable isotope mixing model SIAR v4.0 was used to evaluate the relative contribution of the different prey sources to chicks (Stable Isotope Analysis in R, Parnell et al. 2010) implemented in R v3.3.1 for Windows (R Development Core Team 2010). We fitted the models using prey isotope values from prey from the same season in the vicinity of the colony that were collected by Morgenthaler et al. (2016), one model for each season (2011–2013). We ran the models for 500,000 iterations, with 50,000 initial discards. The remaining iterations were thinned by a factor of 15 to estimate the proportional distribution of the prey. We checked the convergence of Markov chains by inspecting the trace plots visually. We used the species discrimination factors for whole blood for lipid extracted prey ($2.31 \pm 0.17\%$ for $\delta^{15}\text{N}$ and 0.41 ± 0.12 for $\delta^{13}\text{C}$; Ciancio et al. 2016). Selected prey for running the models were Patagonian sprat, Silverside, notothenids (*Patagonotothen cornucola*), and Patagonian squid.

Effect of estimated diet on nestling growth

Using the estimated proportions of Patagonian sprat and Patagonian squid, we calculated the proportion of low quality compared to high quality food (*Loligo/Sprattus*) found in the diet of nestlings in each breeding season. We evaluated if this estimated proportion affected nestling growth using NLMM. We ran one model with body size and another model with nestling mass as response variables, and with the estimated proportion of *Loligo/Sprattus* as the predictor variable. In these models, the random factors were nestling ID and breeding season (2011, 2012, and 2013).

General model selection

For all models, we used a backwards selection procedure (Crawley 2007) by removing the terms one by one, which followed a decreasing level of complexity (when interactions were present in the model) and a decreasing P value. Then, we compared the models with and without the eliminated variables with the function “anova” using the Chi-square test goodness of fit (χ^2 parameter) for GLMM and the likelihood ratio test (L -ratio) for NLMM and LMM. In GLMM there was no need to correct for over-dispersion (Zuur et al. 2009); when it was necessary to compare

between significant factors, we used Tukey’s HSD tests a posteriori. For some NLMMs, we report the statistics of the model output (t-stats). The selection method for NLMM was more complex, because we eliminated each variable for each parameter from the linear models one at a time (e.g., a variable could be eliminated from the linear model of parameter a , but not from the model of parameter b).

We ran the models using R software version 2.12.1 (R Development Core Team 2010). For the GLMM, we used the package “lme4” (Bates et al. 2015) and the function “lmer”, and for the NLMM and LMM we used the package “nlme” (Pinheiro et al. 2014) with the function “nlme” for NLMM and the function “lme” for LMM. For the Tukey’s HSD tests, we used the package “multcomp” (Hothorn et al. 2008) and the function “glht”. We report values as mean \pm SE and considered differences to be significant at $P < 0.05$. All graphs were plotted using Statistica v.7 (Statsoft Inc. 2004) or Sigma Plot (Systat Software Inc 2006).

Results

Effect of breeding parameters on nestling survival

Breeding success, which we defined as the number of fledglings/nest with at least two eggs laid, was 1.10 nestlings/nest for 2010, 1.13 nestlings/nest for 2011, 0.65 nestlings/nest for 2012, and 0.91 nestlings/nest for 2013. In 2012, few nests successfully fledged both nestlings of a brood (only 5 nests of 34), but in 2010 and 2011, most nests raised two fledglings (25 of 31 and 23 of 28, respectively) and in 2013 half of the nests did so (13 of 22). We found that nestling mortality was significantly related to the breeding seasons ($\chi^2_9 = 25.3$, $P < 0.001$), the interaction between breeding seasons and hatching order ($\chi^2_3 = 18.2$, $P < 0.001$) and between breeding seasons and hatching asynchrony ($\chi^2_{17} = 45.0$, $P < 0.001$).

Mortality in 2012 was higher than in other breeding seasons: 2010 ($z = 3.36$, $P = 0.001$), 2011 ($z = 3.83$, $P < 0.001$), and 2013 ($z = 2.14$, $P = 0.03$), and in 2013 mortality was higher than in 2010 ($z = 2.03$, $P = 0.04$) (Tukey HSD). Second hatchlings in 2012 died more often than first and second hatchlings of all other breeding seasons (2010, 2011, and 2013), and they died more often than first hatchlings in the same breeding season (2012) (Tukey HSD: $0.02 < P < 0.0001$; Fig. 2). Furthermore, nestlings that hatched in 2012 with asynchronies of 1, 2, or 3 days died at a higher rate than nestlings that hatched in 2011 with an asynchrony of 1 day (Tukey HSD (breeding season-hatching asynchrony): 2012-1 vs. 2011-1: $z = 3.71$, $P = 0.02$; 2012-2 vs. 2011-1: $z = 3.40$, $P = 0.05$; 2012-3 vs. 2011-1: $z = 3.51$, $P = 0.03$).

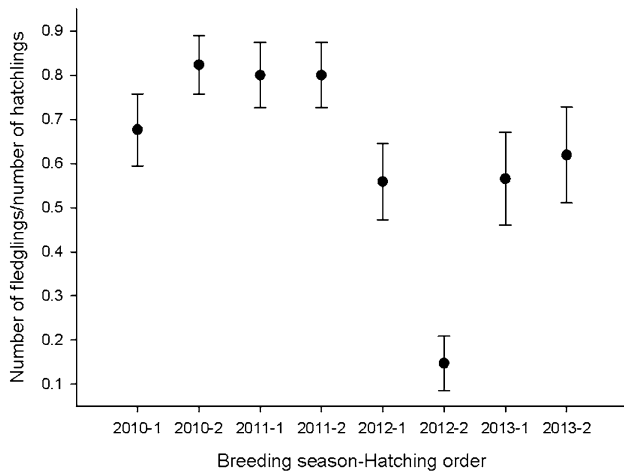


Fig. 2 Proportion of Magellanic penguin fledglings relative to hatchlings by breeding seasons (2010, 2011, 2012, or 2013) and hatching order (1=1st hatchlings, 2=2nd hatchlings). Proportions are calculated within each category (breeding season–hatching order). Means \pm SE are shown

All the other variables analysed in the GLMM did not affect nestling survival: female body condition ($\chi^2_{24} = 0.37$, $P = 0.54$), male body condition ($\chi^2_{25} = 0.01$, $P = 0.99$), laying date of the first egg ($\chi^2_{23} = 0.07$, $P = 0.79$), hatching order ($\chi^2_{18} = 1.28$, $P = 0.26$), hatching asynchrony ($\chi^2_{12} = 0.91$, $P = 0.82$), and the interaction between hatching order and hatching asynchrony ($\chi^2_{28} = 0.27$, $P = 0.97$). In this model (GLMM), the percentage of the variance explained by the fixed factors was 43% (Marginal R^2) and the percentage explained also by the random factor was 62% (Conditional R^2).

Effect of breeding parameters on nestling growth

The breeding season was a significant variable that affected asymptotic mass, and it affected the inflexion point and growth rate constant of the mass curve (NLMM: a : L -ratio = 32.5, $P < 0.0001$; b : L -ratio = 71.2, $P < 0.0001$; c : L -ratio = 100.6, $P < 0.0001$; Fig. 3a). Also, the breeding season affected the growth rate constant and the inflexion point of the body size curve (NLMM: b : L -ratio = 58.3, $P < 0.0001$; c : L -ratio = 62.8, $P < 0.0001$; Fig. 3b) (Table 1).

Nestlings with a fledged sibling had a lower asymptotic mass than nestlings that fledged alone in the nest (NLMM: $t = 5.64$, $P < 0.0001$), but the inflexion point was lower in nests with two fledglings than in the nests with one (NLMM: $t = -3.44$, $P = 0.001$). Also, fledglings with a sibling had higher body size growth rate constants than nestlings that fledged alone (NLMM: $t = 5.18$, $P < 0.0001$).

The body condition of parents positively affected the asymptotic mass of nestlings (NLMM: female: $t = 2.91$, $P = 0.004$; male: $t = 2.29$, $P = 0.02$). A onefold increase in

the condition of males and females resulted in an increase in asymptotic mass of nestlings of 209 ± 91 and 439 ± 151 g, respectively. Also, the better the male condition was, the lower was the growth rate constant and the inflexion point of the body size (NLMM: b : $t = -2.31$, $P = 0.02$; c : $t = -2.43$, $P = 0.02$) and the higher the asymptotic body size of the nestlings (NLMM: $t = 2.12$, $P = 0.03$), no significant relation was found between female condition and body size (Online Appendix 1). Adult condition did not vary among breeding seasons (male: $F_{112,3} = 0.33$, $P = 0.81$; female: $F_{112,3} = 0.33$, $P = 0.80$). No other variables (hatching asynchrony and hatching order) affected nestling growth (Online Appendix 1).

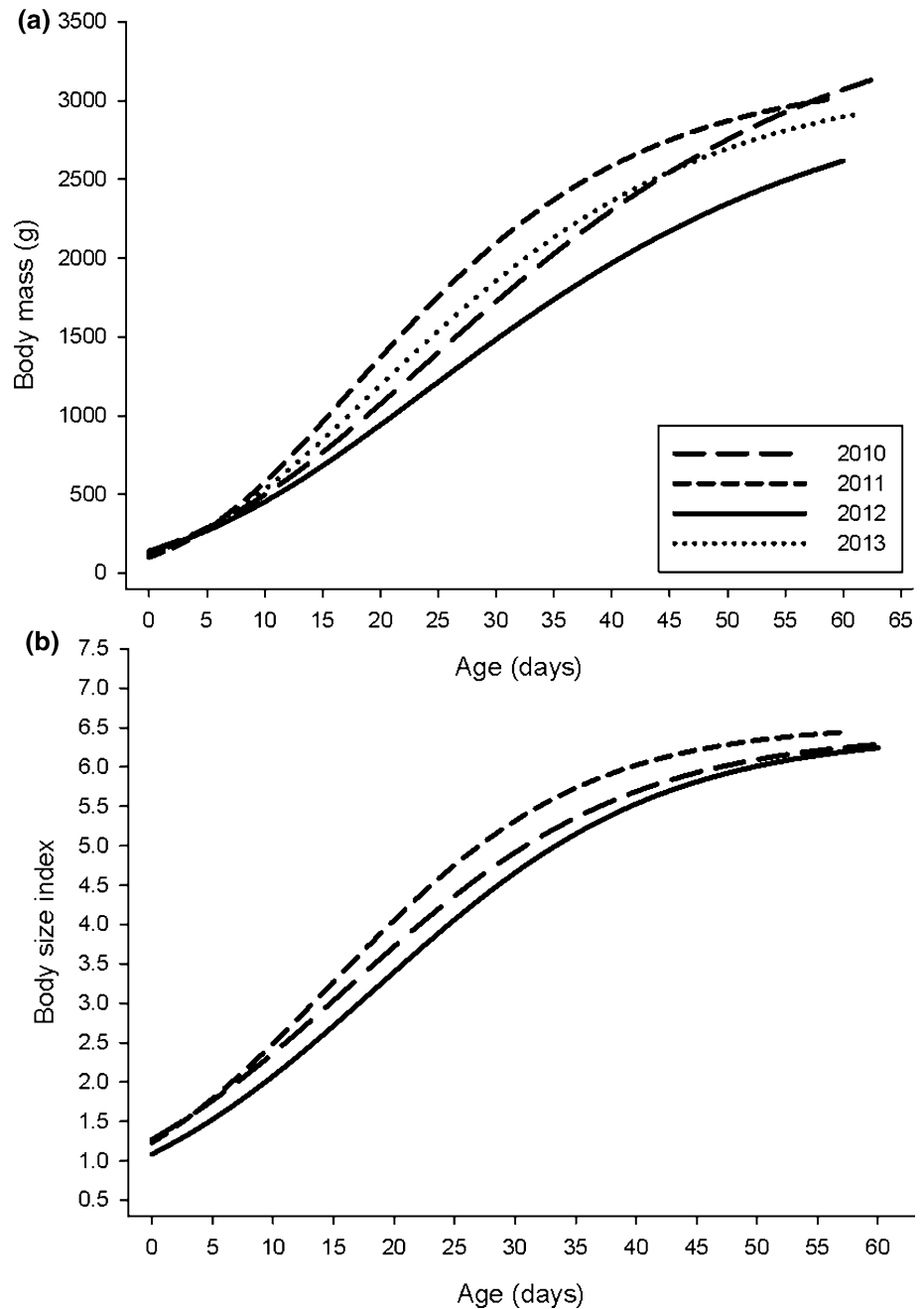
Climatic and oceanic variables

From October to January during the breeding season of 2011, the daily rainfall was not higher than 4 mm, although there was 1 day with 14 mm in the middle of October, which occurred during the incubation stage. In 2013, maximum rainfall per day during the nestling period was 5 mm at the end of January. December 2012 was the rainiest month of any season during the study (51.9 mm), when there were 2 days with 10 mm, 3 days with 5 mm, and all other days with lower amounts. Severe rains occurred on December 3–4 and during December 16–19 when it rained 13 and 21 mm, respectively. After these two periods of consecutive days of rain, we found that in each, 11% of the total number of nestlings died due to wet conditions.

Concentrations of c - a differed among breeding seasons (LM: $F_{180,3} = 7.82$, $P < 0.0001$), among months (LM: $F_{1800,5} = 49.6$, $P < 0.0001$) and between the interaction of breeding season and month (LM: $F_{180,15} = 18.2$, $P < 0.0001$). The concentration of c - a was larger in 2011 than in 2012 (141 mgC/m²/day larger, $t = 2.15$, $P = 0.03$; Fig. 4). November, December, and January had a lower concentration of c - a than in previous months (Tukey Contrasts all $P < 0.0001$), but concentrations did not differ among those 3 m (Tukey Contrasts all $P = 0.99$). August and September had no significant differences (Tukey Contrasts, $P = 0.99$), but concentrations were higher than in October (Tukey Contrasts all $P < 0.0001$). August and September 2011 had larger concentrations than August and September 2012 and 2013 (Tukey HSD all $P < 0.01$). Finally, October 2013 had larger concentrations than October 2012 (Tukey HSD $P < 0.01$).

SST also differed among breeding seasons (LM: $F_{465,2} = 16.9$, $P < 0.0001$), among months (LM: $F_{465,5} = 971.4$, $P < 0.0001$), and between the interaction of breeding seasons and months (LM: $F_{615,15} = 6.41$, $P < 0.0001$). In 2011, the SST was higher than in the other breeding seasons, although it was only significantly higher than in 2013 (0.64 °C higher, $t = -2.09$, $P = 0.04$; Fig. 4). SST was higher in January 2011 than in January 2012

Fig. 3 a Gains in mass of Magellanic penguin nestlings gain adjusted to a Gompertz curve and **b** growth of nestlings body size adjusted to a Sigmoidal curve, during 2010 (long dashed lines; mass = $3651 \times \exp(-\exp(-\text{age} - 24.1/20.5))$); body size = $6.43 \times (1 + \exp(-(x - 16.3)/11.7))$), 2011 (short dashed lines; mass = $3177 \times \exp(-\exp(-\text{age} - 17.6)/14.2))$; body size = $6.55 \times (1 + \exp(-(x - 15)/10.25))$), 2012 (solid lines; mass = $3132 \times \exp(-\exp(-\text{age} - 23.9)/21.1))$; body size = $6.42 \times (1 + \exp(-(x - 18.7)/11.7))$), 2013 (dotted lines; mass = $3159 \times \exp(-\exp(-\text{age} - 19.6)/16.6))$)



and 2013 (Tukey HSD all $P < 0.01$), and SST was higher in December 2011 than in December 2013 (Tukey HSD $P < 0.01$). As expected, SST increased as the breeding season progressed, and SST was significantly different among all months (all $P < 0.0001$), except between August and September ($t = -0.20$, $P = 0.984$).

Effect of oceanic variables on asymptotic mass of nestlings

The asymptotic mass was not related to the sum of *c-a* within a breeding season (from August to January and for

both foraging sites) (LMM: $t = 0.46$, $P = 0.65$), but it was affected by the average SST (from August to January and for both foraging sites) ($t = -2.44$, $P = 0.02$) (Fig. 4). The lower SST was, the higher the asymptotic mass (Fig. 4).

Stable isotope analysis of prey

In 2012, the estimated proportion of *Loligo* in the penguins' diet was higher than in other years. In 2013, the estimated proportion of *Loligo* was also high, but it was similar to the estimated proportion of *Sprattus*. In 2011, the estimated proportion of *Sprattus* was significantly higher than in the

Table 1 The Non-Linear Mixed Model revealed a significant effect of breeding season in growth parameters of Magellanic penguin nestlings

Variables	Parameters	Breeding seasons	P
Mass	Asymptotic mass	2010 > 2011	0.0008
		2010 > 2012	< 0.0001
		2010 > 2013	0.005
		2011 > 2012	0.0002
		2013 > 2012	0.0008
		2010 > 2011	< 0.0001
	Inflection point	2010 > 2012	0.02
		2010 > 2013	< 0.0001
		2012 > 2011	< 0.0001
		2012 > 2013	0.001
	Growth rate constant	2010 > 2011	< 0.0001
		2010 > 2013	0.0004
		2012 > 2011	< 0.0001
2013 > 2011		0.001	
2012 > 2013		0.013	
Body size	Inflection point	2012 > 2011	< 0.0001
		2012 > 2010	< 0.0001
		2010 > 2011	< 0.0001
	Growth rate constant	2010 > 2011	< 0.0001
		2012 > 2010	0.02
		2012 > 2011	< 0.0001

Significant differences analysed through Tukey HSD between breeding seasons are shown. Four breeding seasons were analysed (2010, 2011, 2012, and 2013) and the symbol “>” indicates which breeding season had the higher asymptotic mass or growth rate

other seasons, and the estimated proportion of *Loligo* was low (Fig. 5). The estimated proportion of *Loligo/Sprattus* was 0.445 in 2011, 5.228 for 2012 and 1.075 for 2013.

Effect of estimated diet on nestling growth

The growth rate constants and inflection points for nestlings were significantly and positively related to the estimated proportion of *Loligo/Sprattus* (NLMM: Inflection point~*b*: mass: *L*-ratio = 60.2, $P < 0.001$; body size: *L*-ratio = 23.7, $P < 0.001$. Growth rate constant~*c*: mass: *L*-ratio = 58.9, $P < 0.001$). On the contrary, asymptotic mass and body size of nestlings were not related to the proportion of *Loligo/Sprattus* in the diet (NLMM: mass: *L*-ratio = 0.35, $P = 0.55$; body size: *L*-ratio = 0.024, $P = 0.88$).

Discussion

By analysing data of nestling growth and survival and relating them to breeding parameters (like hatching asynchrony and parental body condition), rainfall, oceanic conditions,

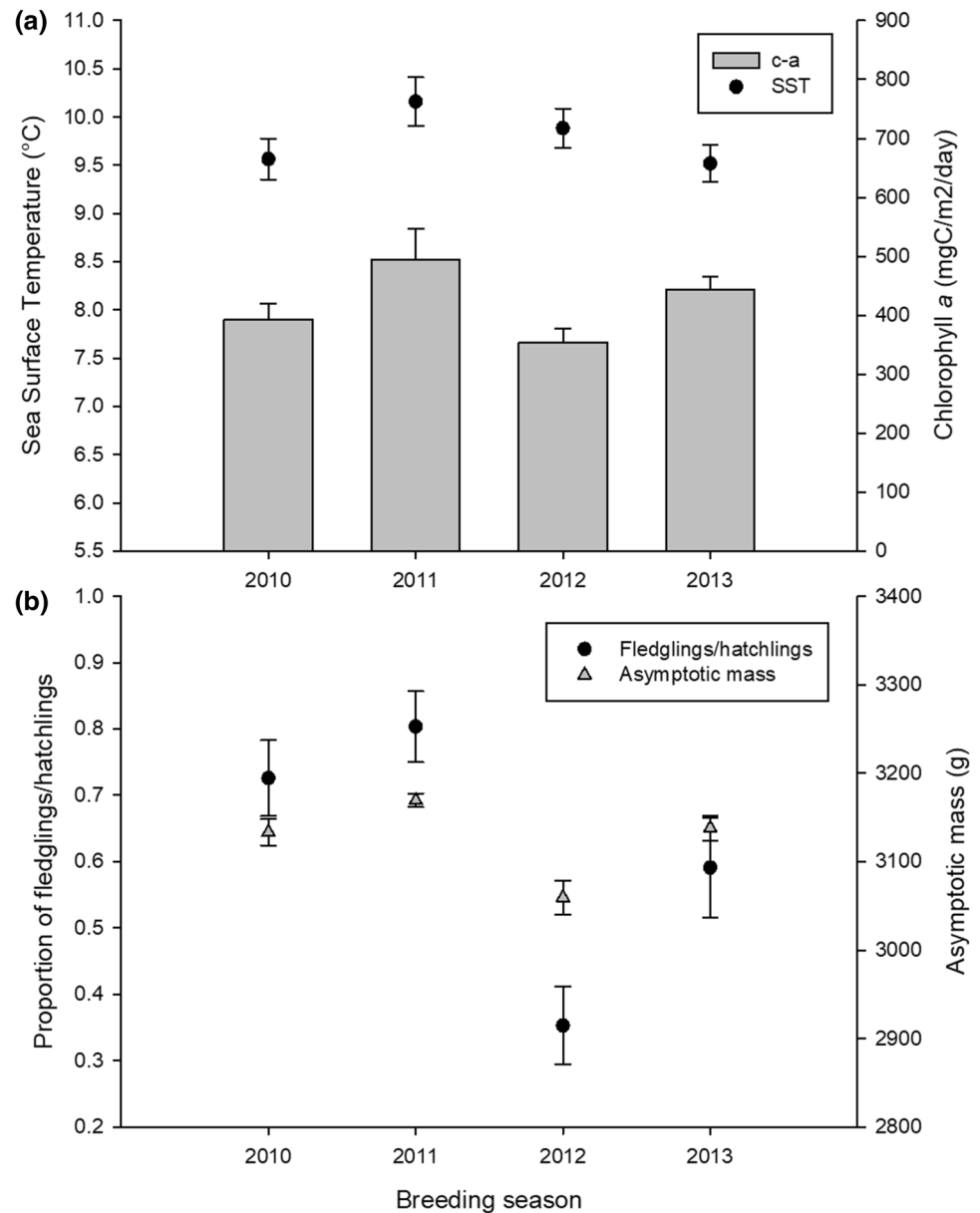
and nestling diet during four breeding seasons, we identified the key factors involved in nestling success. During those four breeding seasons, nestling growth and mortality differed drastically. One important variable that influenced nestlings was the quality of the parents, especially males. In 2012, the breeding success was the lowest of the breeding seasons we studied, and in 2011 it was the highest. Also, nestling mortality and asymptotic mass were lower in 2012 than in the other breeding seasons. *C-a* and SST appeared to be good indicators of nestling performance only in the extreme breeding seasons (favourable and unfavourable—2011 and 2012), but it failed to predict survival/condition of nestlings in “intermediate” breeding seasons. Nonetheless, the estimated proportion of low/high quality prey items in the diet of nestlings was the key factor that was related to nestling growth/survival.

Effects of breeding parameters on nestlings

As we expected from our predictions, parental body conditions were positively related to nestling growth, but not to their survival. So, parents that started the breeding period in poor condition had fledglings with low mass. This was consistent with the Prudent Parent Hypothesis where there is low parental investment in nestlings when the parents' condition is poor (Stearns 1992). Nonetheless, we do not know how parents' condition changed as the breeding season passed. If we had those data, we could have determined if they maintained their condition or even improved their condition at the cost of nestling condition, or if their condition became even worse because they invested more than they could afford to invest in nestlings. In Adélie penguins (*Pygoscelis adeliae*), adults regulate their condition according to environmental factors, and this impacts the amount of food delivered to their nestlings (Ballard et al. 2010). This strategy is consistent with penguin breeding biology, which is to ensure their own survival first (Culik 1994; Watanuki et al. 2002). The attributes of the parents were also linked to the mass of the young at the time of independence in Magellanic penguins (Reid and Boersma 1990; Scioscia et al. 2010), but not for Chinstrap penguins (*Pygoscelis antarcticus*) (Moreno et al. 1997).

Male condition was more influential for nestlings than was female condition, especially for growth rate constants and asymptotic body size of nestlings. Magellanic penguins are moderately sexually dimorphic [on average males are 20% heavier than females (Gandini et al. 1992)]; the larger body mass of males could make a difference in the amount of food they provided to nestlings. In fact, in Magellanic penguins, nestling diet is more similar to that of the male parent than to the female parent in those colonies with a more diverse diet, like the one in this study (Ciancio et al. 2018). It was also possible that the more influential physical

Fig. 4 a Mean \pm SE chlorophyll *a* during each breeding season (2010 to 2013) (grey bars), and mean \pm SE Sea Surface Temperature—SST (red squares) are shown for each breeding season studied. The oceanic values were estimated for the known foraging sites of Magellanic penguins. Total values for chlorophyll *a* were: 2010 = 18,066.44 mgC/m²/day, 2011 = 22,764.54 mgC/m²/day, 2012 = 16,287.87 mgC/m²/day and 2013 = 20,404.33 mgC/m²/day. Mean values for SST were: 2010 = 9.56 °C, 2011 = 10.04 °C, 2012 = 9.99 °C, 2013 = 9.52 °C. **b** Magellanic penguin nestling survival (black circles) and asymptotic mass (grey triangles). Mean values \pm SE are shown

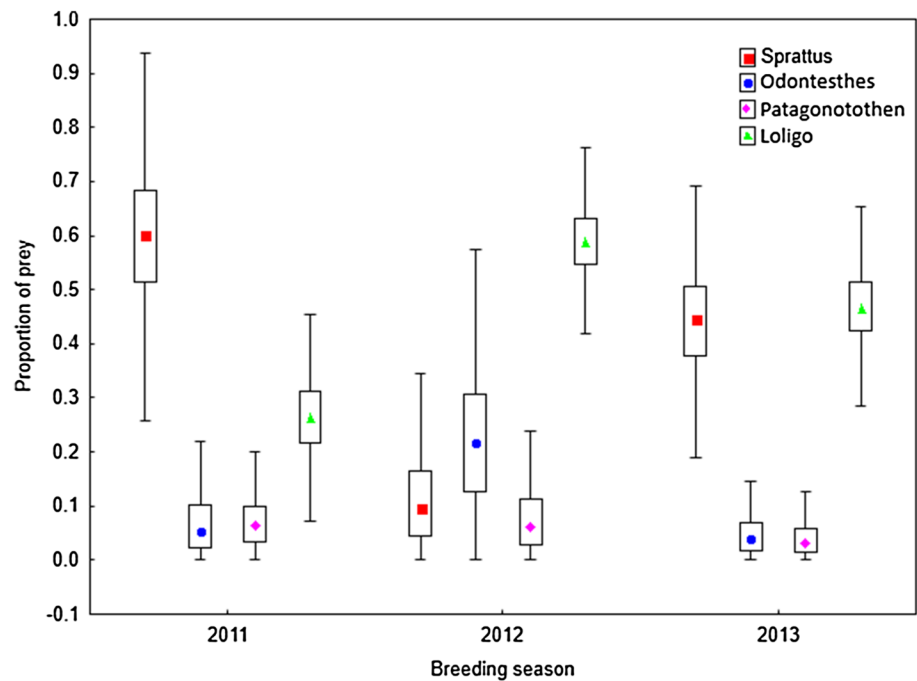


condition of males compared to females on nestling growth was because they seemed to forage at higher trophic levels than females and, therefore, males may have provided more high quality items to nestlings than did females (Forero et al. 2002). Nonetheless, other work on Magellanic penguins that breed in northern colonies found no difference between the sexes in their isotopic niches (Yorio et al. 2017).

Nestling survival differed among breeding seasons according to hatching asynchrony and hatching order. Hatching asynchrony and hatching order may be crucial in determining nestling performance in many species (Podlas and Richner 2013; Merklings et al. 2014; MacLeod et al. 2016), because asynchrony creates a size asymmetry between siblings that could facilitate the competition for food of the larger sibling. The “Brood Reduction

Hypothesis” predicts that in an unpredictable environment, when food abundance is low (i.e., “unfavourable” years), hatching asynchrony helped to reduce the brood through the death of the last hatched chick and allowed parents to raise other nestlings successfully. Conversely, when abundance of food was high (i.e., “favourable” years), they would be able to raise all the nestlings in the clutch successfully (Lack 1954). We found in a study where we manipulated hatching asynchrony that it had no effect on nestling mortality as predicted by the Brood Reduction Hypothesis, although it affected nestling quality (Barriounevo and Frere 2017); the same result was obtained for other *Spheniscus* penguins (Seddon and Van Heezik 1991). Contrary to our predictions, we did not find an effect of asynchrony on nestling growth, but we found an effect on

Fig. 5 Proportion of different prey items found in the diet of Magellanic penguins based on SIAR simulations for each breeding season. Squares, circles, diamonds, and triangles show the median for each prey type. Box shows the 25–75 percentiles and bars represent the non-outlier range



their survival depending on the breeding season. Nestlings that hatched in 2011 and with 1-day asynchrony survived better than those that hatched in 2012, indistinctly of the asynchrony. Apparently, 1-day asynchrony is the best option under optimal conditions compared to “unfavourable” breeding season. One-day asynchrony is approximately the average hatching asynchrony for this colony, which was 1.6 days (Barrionuevo and Frere 2017).

We also found that there was a clear disadvantage of hatching late in the “unfavourable” breeding season, regardless of how large the asynchrony was, because the last hatched nestlings in 2012 died at higher rate compared with first or last nestlings in the other breeding seasons. Also, the number of fledglings per nest was important for nestling growth; nestling that fledged from two-bird clutches had lower asymptotic mass than those that fledged from one-bird clutches, which suggested the importance of competition between nestlings and the possible constrain of food for two fledgling clutches, even in “favourable” breeding seasons. These two-fledgling clutches had earlier inflexion points in the growth curve, a potential explanation for this is that two nestlings in the nest forced parents to deliver more food, resulting in faster growth compared to one nestling clutches. In other penguin species, nestlings that grew with their siblings grew slower than nestlings that grew alone (Ainley and Schlatter 1972; Cooper 1977). On the contrary, in yellow-eyed penguins (*Megadyptes antipodes*), this difference in growth parameters between nestlings of different brood sizes was only evident when food abundance was low (Van Heezik and Davis 1990).

Climatic/oceanic variables and estimated nestling diet

Heavy rainfall is an important cause of nestling death in some colonies (Demongin et al. 2010; Boersma and Rebstock 2014; Ropert-Coudert et al. 2015). In the colony we studied, there were no burrows that could be flooded by rains, but nests that were covered poorly did not prevent nestlings from getting wet and dying of hypothermia. In fact, the breeding season with the highest nestling mortality (2012) was the breeding season with the rainiest December. During December, nestlings are relatively young, but parents begin to leave them alone in the nests and exposed to rain (Barrionuevo, personal observation). We recorded two times consecutive days of heavy rains that were followed by an 11% of nestling death in each period of days. We did not determine if they died of hypothermia, and the wet conditions in which we found these nestlings could have been a posteriori of the death.

We found that $c-a$ and SST differed among months, $c-a$ was higher in spring than in summer, which was already known, because blooms occurred during the spring in this area (Saraceno et al. 2005). SST increased as the season progressed, which coincided with an increase in the ambient temperature. Also, $c-a$ was higher in 2011 than in 2012, and SST was higher in 2011 than in 2013, which demonstrated the significant inter-annual variability in oceanic variables within the western South Atlantic (Saraceno et al. 2005).

$C-a$ and SST explained inter-annual variability in breeding investment in *Eudyptes* penguins (Dehnhard et al. 2016). Although we did not find a significant relationship between

c-a and asymptotic mass, the difference between 2011 compared to 2012 in *c-a* was consistent with a lower asymptotic mass and higher mortality of chicks in 2012 compared to 2011. Nonetheless, nestling growth and survival were worse in 2012 than in the other breeding seasons (2010 and 2013), although this difference was not noticeable in *c-a*, given that concentrations of *c-a* were similar between “unfavourable” and “intermediate” breeding seasons. Perhaps, *c-a* only explained variability in nestling growth/survival among breeding seasons with extreme conditions. Another explanation for this lack of a relationship between *c-a* concentrations and nestling performance between “unfavourable” and “intermediate” breeding seasons could be that the harvest of fish by commercial fisheries in 2012 put pressure on penguins’ prey, which might result in a lower than expected prey abundance than predicted by the levels of *c-a*. *c-a* is related to the biomass of fish schools in ecosystems without a fisheries (McInnes et al. 2017). We discard this possibility, because the feeding grounds for Magellanic penguins near Puerto Deseado, commercial harvest of fish that are eaten by penguins was very low (Frere et al. 1996b; Alemany et al. 2013, 2014). However, Gandini et al. (1999) found some overlap between penguin diets and fish by-catch in the shrimp (*Pleoticus muelleri*) fishery, but this was in northern colonies in the north of Golfo San Jorge, which is > 250 km away from Puerto Deseado.

We also found that the lower the SST, the higher was the asymptotic mass. Nonetheless, in 2010 and 2013, which were “intermediate” breeding seasons, SST was slightly lower than in 2012, which did not correlate to the better performance of nestlings in 2010/2013 compared to 2012. SST is related to the position of frontal zones (Park et al. 1998), which affect the distribution and abundance of zooplankton, fish, and squid (Acha et al. 2004). In some species, warmer waters are related to lower provisioning rates and lighter fledglings (Weimerskirch et al. 2001). Conversely, in other studies, warmer waters were related to higher fledgling mass and higher number of chicks per breeding pair (Pinaud and Weimerskirch 2002; Cullen et al. 2009). The relationship between SST and food availability for marine birds is complex. It may depend on the diet of the birds: if they are more piscivorous, “warm” waters would benefit them (Kitaysky and Golubova 2000), contrary to our findings.

Although *c-a* explained differences in nestling performance between extreme breeding seasons and SST was related to asymptotic mass, these oceanic variables failed to explain the performance of nestlings in breeding seasons with “intermediate” performance of nestlings. The key to understanding these relationships may lie in the type of diet. The quality of the prey items has been shown to be important in nestling growth and survival (Golet et al. 2000; Wanless et al. 2005). Van Heezik and Davis (1990) have suggested that the growth of penguin nestlings can be constrained

by food type. *Loligo* squid are food items of low energetic content, contrary to *Sprattus*, which are the most energetic prey in this ecosystem (Ciancio et al. 2007, 2015). In addition, studies of closely related African penguins (*Spheniscus demersus*) showed that squid were more difficult to digest than fish (Wilson et al. 1985), which would affect nestling growth and survival negatively. The growth curves of penguins fed on a squid diet took longer to reach a constant weight than penguins fed on a fish diet (Heath and Randall 1985). Although we did not find a significant relationship between asymptotic mass of nestlings and estimated proportion of *Loligo/Sprattus*, this was the only variable that was clearly different among breeding seasons that was consistent with nestling performance in all breeding seasons. In 2012, the estimated proportion of squid in the diet was high and the proportion of *Sprattus* was very low. Conversely, 2011 had the largest proportion of *Sprattus* in the estimated diet. In 2013, the estimated proportion of squid in the diet was also high, but there was also a large amount of *Sprattus* in the diet. In agreement with this estimated proportion of *Loligo/Sprattus*, nestling mortality and condition was not as bad in 2013 as in 2012.

Conclusions

In this study, the physical condition of parents, especially that of males, was positively related to nestling growth. Some studies of penguins found that parents were able to buffer inter-annual differences in food abundance/food quality and climatic conditions, which diminished their effects on nestling growth (Dehnhard et al. 2016) or breeding success (Scioscia et al. 2016). This occurred under particular conditions, either within “favourable” breeding seasons (Dehnhard et al. 2016) or in a colony with an above average breeding success for the species (Scioscia et al. 2016). We found that in unfavourable breeding seasons, parents did not compensate for low quality prey items, because we found marked differences in growth and survival of nestlings. We do not know if the food provisioning rate was also low during 2012 or if the poor condition of nestlings was only a consequence of too much squid in the diet. We also do not know if the parents’ condition also deteriorated during this breeding season. At Isla Quiroga, foraging effort by parents was greater than in other colonies (Sala et al. 2015), which suggested that breeding in this colony may have required increased foraging efforts during “unfavourable” seasons that affected their offspring’s fitness.

Although high/low concentrations of *c-a* were related to high/low performance of nestlings, respectively, and SST was inversely related to asymptotic mass, these oceanic variables appeared not to be reliable to estimate the condition of the nestlings, especially between “intermediate”

and “unfavourable” breeding seasons. The key factor in determining nestling growth and survival appeared to be the proportion of high compared to low quality prey in the penguin diet.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The Agrarian Council of the Province of Santa Cruz gave us the corresponding permits to work on Quiroga Island with the Magellanic Penguin (no. 491756/16).

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