

Oceanographic conditions in wintering grounds affect arrival date and body condition in breeding female Magellanic penguins

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ABSTRACT: Overwintering conditions often impact an individual animal's breeding performance in the following season. These so-called carry-over effects have been demonstrated in birds, including penguins. We studied carry-over effects in Magellanic penguins *Spheniscus magellanicus*, a species of conservation concern, breeding at Punta Tombo, Argentina, and wintering from northern Argentina to southern Brazil. We characterized oceanographic conditions in the penguins' wintering grounds from 1982 to 2012 using principal component analysis on weekly sea surface temperature (SST) anomalies. The first principal component represented a weak Rio de la Plata plume and warm SST. The Rio de la Plata plume carries cool, productive, low-salinity water north from the river mouth through the penguins' wintering area. The plume is stronger (extends farther north) when winds blow from the southwest than when winds blow from the northeast. When the Rio de la Plata plume was weak in late winter, females arrived earlier to breed and were in better condition, likely because prey was concentrated in a smaller plume area closer to Punta Tombo. Females that arrived earlier laid eggs earlier, and females laid larger eggs when they arrived earlier and were in better condition. In contrast, body condition of breeding males did not vary with winter conditions. The effects on individual females varied, likely reflecting in part individual foraging ability. A weaker Rio de la Plata plume probably increased prey encounter rates closer to breeding colonies in winter, directly and indirectly improving female body condition, increasing egg size, and resulting in earlier arrival and egg laying.

KEY WORDS: Carry-over effect · *Spheniscus magellanicus* · Magellanic penguin · Arrival date · Body condition · Egg-laying date · Egg size

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INTRODUCTION

Conditions experienced by an animal in one season can impact its performance in a subsequent season, and these delayed effects are termed carry-over effects (Harrison et al. 2011). A carry-over effect occurs when an individual's previous experiences explain a measurable amount of variation in its current physiological condition, which may affect its fitness (survival or reproduction) (O'Connor et al. 2014). Intrinsic quality affects an individual's susceptibility to carry-over effects (Harrison et al. 2011). For example, individuals that can access habitat with sufficient

resources are likely to enter the next season in better condition than individuals that cannot find good habitat or are excluded from resources by dominant individuals (Fretwell & Lucas 1969). Such effects on individuals may determine their ability to breed, and reproductive output if they breed, and therefore have population consequences (Harrison et al. 2011).

Carry-over effects from winter to the following breeding season are the most frequently studied delayed effects (Harrison et al. 2011). Winter conditions often affect breeding performance in seabirds. Common eiders *Somateria mollissima* that arrived at their breeding grounds earlier in the spring laid eggs ear-

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lier (Hanssen et al. 2016). Female Cassin's auklets *Ptychoramphus aleuticus* that ate higher-quality prey in the pre-breeding season laid larger eggs earlier than females that ate lower-quality prey (Sorensen et al. 2009). Little penguins *Eudyptula minor* laid eggs earlier if they started a breeding season in better body condition than their mean condition (Salton et al. 2015).

Seabirds are central-place foragers while breeding, returning to their nests after foraging to incubate eggs or feed chicks (Orians & Pearson 1979). During the nonbreeding season, however, seabirds are not constrained by a need to return frequently to their nests. Some seabirds travel over large areas searching for dispersed prey during winter (Dias et al. 2015). In contrast, other seabirds concentrate over continental shelves (Goyert et al. 2016) or close to oceanic features such as frontal zones or ice edges (Bost et al. 2009a, Divoky et al. 2016). Migration between distant breeding and wintering areas may be costly. For example, in a partially migratory seabird, the European shag *Phalacrocorax aristotelis*, migrants bred later and had lower reproductive success than residents (Grist et al. 2017). Furthermore, colony reproductive success in Atlantic puffins *Fratercula arctica* decreased with migration distance (Fayet et al. 2017).

Characterizing oceanographic conditions over the wintering grounds of wide-ranging seabirds is complex, but understanding dominant oceanographic patterns can give insights into which factors influence seabird foraging success. Averaging sea surface temperature (SST) or chlorophyll over the winter range of a wide-ranging seabird ignores gradients and spatial variability that indicate important features such as fronts that concentrate prey. A species' wintering range may include multiple oceanographic features, such as upwelling, frontal zones, or ice edges (González Carman et al. 2016). The features' variances over time may be correlated with each other, complicating analyses that attempt to use these multiple features to explain an aspect of seabird biology. Principal component analysis (PCA) can identify spatial patterns and their relative strengths over time. PCA is widely used in oceanography and atmospheric sciences (where it is often called empirical orthogonal functions)

to describe dominant spatial patterns (Rivas 2010). Climatic and oceanographic patterns derived from PCA include the North Atlantic Oscillation and the Pacific Decadal Oscillation. These indices represent the variance or strength of the patterns over time, and explain variability in seabird abundances, survival, breeding success, or timing (Sandvik et al. 2005, Dorresteijn et al. 2012).

We sought to test whether oceanographic conditions in the wintering grounds affected the breeding biology of Magellanic penguins *Spheniscus magellanicus*. The Magellanic penguin is classified as Near Threatened by the IUCN (www.iucnredlist.org) because of population declines. The species breeds in southern Argentina and migrates seasonally to the shelf waters of northern Argentina, Uruguay, and southern Brazil, a distance of at least 1000 km (Boersma et al. 2013, Stokes et al. 2014). Magellanic penguins may migrate more than 3000 km through several distinct marine environments (Acha et al. 2004) to reach their wintering grounds, where adults spend up to 4 mo (Stokes et al. 2014).

We used PCA to identify dominant patterns in SST anomalies from the seasonal means in the winter range of the Magellanic penguin off the Atlantic coast of South America (Fig. 1). Although we did not know beforehand what oceanographic features would explain the most spatial variability in the PCA, we expected that frontal systems, upwelling,

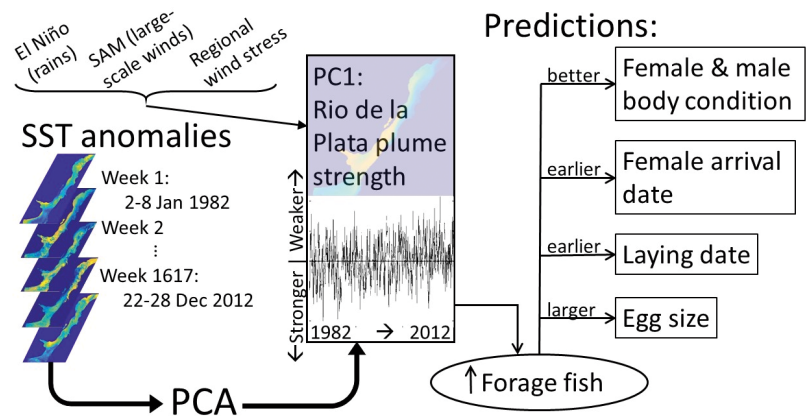


Fig. 1. Analyses of the effects of oceanographic conditions in wintering grounds on breeding Magellanic penguins. Step 1 (left): Using PCA on weekly SST anomalies, we found that the dominant spatial pattern in the Magellanic penguin's wintering area in the South Atlantic Ocean was related to the strength of the Rio de la Plata plume (center). We tested for relationships between the plume and large-scale and regional climatic indices. Step 2 (right): We predicted that in years when the plume was strong, forage fish would be more abundant in the wintering grounds, with positive effects on Magellanic penguins at the start of the breeding season. We tested our predictions of the plume effects with our long-term data set on Magellanic penguins

or the La Plata River (Rio de la Plata) plume would be important (Acha et al. 2004, Garcia & Garcia 2008). We predicted that the variance of the pattern would affect penguins because it reflects important oceanographic variability that likely affects penguins' prey.

We proceeded in 2 steps: first we characterized the oceanographic conditions in the penguins' wintering grounds, and then we tested for effects of the oceanographic conditions on penguin breeding biology. We give the results of the oceanographic analysis here to make the 'Introduction' and the 'Materials and methods' less abstract and easier to follow. We found that the dominant spatial pattern in SST anomalies was associated with the Rio de la Plata plume and refer to it hereafter as the Rio de la Plata Plume Index (PPI; Fig. 1; see 'Results').

Winds have a larger effect on the northward extent of the Rio de la Plata plume than rain, even in El Niño years with high rainfall (Möller et al. 2008, Piola et al. 2008). After finding that the dominant pattern was the plume, we predicted that when the alongshore wind stress was from the southwest (positive) over most of the region, the Rio de la Plata plume would extend farther north (the PPI would be negative). When the wind stress was from the northeast over most of the region, we expected the plume to be smaller and restricted to the southern part of the region (positive PPI). We also investigated links between the SST-anomaly pattern and large-scale climatic indices, the southern oscillation index and the southern annular mode, because we were interested in linking the pattern to larger-scale climatic processes (Fig. 1). Finally, we examined fisheries landings as an index of prey availability to wintering penguins (Sherley et al. 2013), to explain how the oceanographic pattern affects penguins (Fig. 1). We predicted that a stronger plume would increase prey available to penguins and fisheries, and landings would be higher when the plume was strong (i.e. the PPI was negative).

The Rio de la Plata plume spreads cool, low-salinity, high-nutrient water over the continental shelves of Uruguay and southern Brazil in the winter (Braga et al. 2008) and provides good habitat for forage fish (Checkley et al. 2017). We therefore predicted in the second step of the study that when the Rio de la Plata plume was strong, penguins would have more prey in the winter and would experience positive carry-over effects in the next breeding season. Specifically, we predicted that when the plume was strong: (1) penguins (females and males) that recently arrived at the breeding colony would be in better body condi-

tion, (2) breeding females would arrive earlier at the colony, (3) females would lay eggs earlier, and (4) females would lay larger eggs (Fig. 1).

MATERIALS AND METHODS

Study site and species

We studied Magellanic penguins at a breeding colony at Punta Tombo, Argentina (44.045° S, 65.223° W), which declined from 314 000 active nests in 1987 to 201 000 in 2014 (Rebstock et al. 2016) and continues to decline (D. Boersma unpubl. data). Breeding adults return to Punta Tombo from their wintering grounds in September and October and females lay one 2-egg clutch (Boersma & Rebstock 2014). Magellanic penguin females are capital breeders early in the season, fasting from their arrival to egg laying and through the first long incubation shift. Carry-over effects are expected in capital breeders (Harrison et al. 2011). The females' fasts last up to 1 mo (occasionally longer) until the males return from foraging and relieve their mates. Males may also fast for a month or more before they leave the colony to forage after females have laid the eggs (Boersma et al. 1990).

Magellanic penguins breeding along the Atlantic coasts of Argentina and the Falkland/Malvinas Islands are migratory and generally spend winters in the continental-shelf waters of northern Argentina, Uruguay, and southern Brazil, between about 40 and 23° S (Fig. 2) (Pütz et al. 2000, Stokes et al. 2014). A small proportion of the population winters near the Peninsula Valdés (Jehl 1974, Pütz et al. 2007, Stokes et al. 2014), approximately 41 to 43° S. Off northern Argentina in winter, Magellanic penguins were found in waters with low turbidity and surface temperatures higher than 9°C, often in feeding flocks with other seabirds (Jehl 1974). Magellanic penguins at breeding colonies north of about 45° S feed predominantly on Argentine anchovy *Engraulis anchoita* (Wilson et al. 2005). The largest stock of anchovy in the region migrates from the penguins' northern breeding range in summer to the penguins' wintering range in winter (Costa et al. 2016).

Penguins swim rapidly (50–90 km d⁻¹) at the beginning of the northbound migration in the austral autumn and swim more slowly (13–45 km d⁻¹) in presumed foraging areas (Stokes et al. 1998, Pütz et al. 2000, 2007, Skewgar et al. 2014). Penguins tracked with satellite transmitters reached their wintering grounds in late April to late May (Stokes et al. 1998,

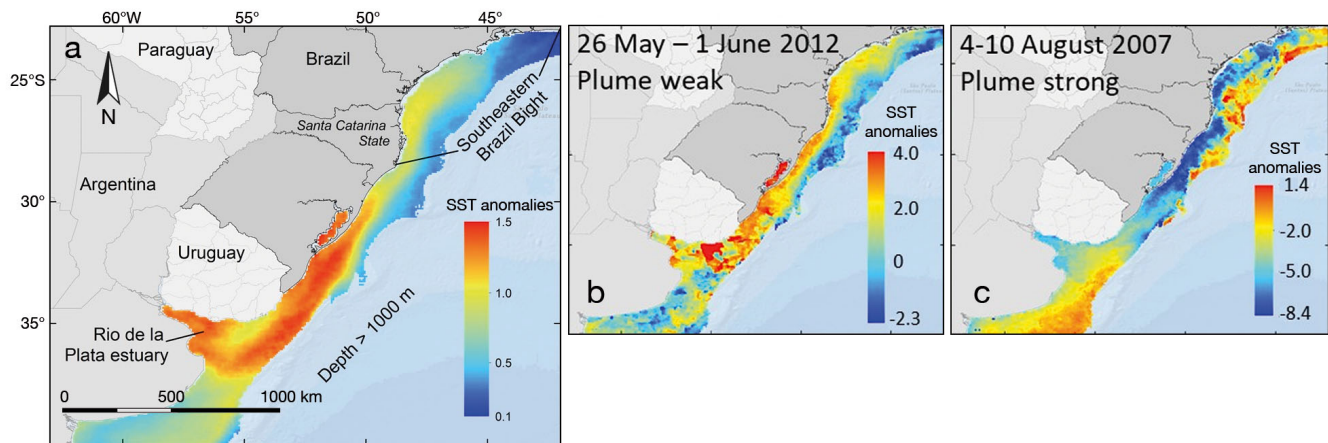


Fig. 2. (a) First principal component of sea surface temperature (SST) anomalies (Plata Plume Index, PPI) in the wintering range of Magellanic penguins in the Atlantic Ocean. All SST anomalies are positive (warm). (b,c) Examples of SST anomalies for 2 weeks when the PPI was strongly positive and strongly negative. When the PPI is positive (b), the plume is weak and contracted, and anomalies in the plume area are warm, whereas when the PPI is negative (c), the plume is strong and extended, and SST anomalies are cool. Note the different scales in the 3 panels

2014, Pütz et al. 2000), and reached the mouth of the Rio de la Plata (Fig. 2) by mid-May (Pütz et al. 2000, Stokes et al. 2014). The timing of penguin strandings in autumn and winter support this migration timing. Penguins begin stranding in Rio Grande do Sul state, southern Brazil, in June each year (García-Borboroglu et al. 2010, Mäder et al. 2010). Banded penguins that previously bred at Punta Tombo have been found dead in northern Argentina, Uruguay, and southern Brazil in July and August (Stokes et al. 2014).

Return migration speed

Data on the return (spring) migration are sparser and restricted to penguins that were oiled, rehabilitated, and released (Boersma 2012, Ruoppolo et al. 2012). We used tracking data from 6 adult penguins released in northern Argentina in August 2007 with Argos satellite tags (ST-20 PTTs, Telonics, packaged by Sirtrack). Tags were programmed to transmit for 36 h on and 36 h off. Tracks of the penguins were published in Boersma (2012); here we estimated migration speeds to determine when penguins leave their wintering grounds to return to Punta Tombo. Three of the penguins swam south to the latitudes of breeding colonies, 700–1400 km from their release sites. Two penguins did not swim south and 1 did not reach the breeding latitudes while its tag was transmitting (Boersma 2012); these 3 penguins may have been young pre-breeders but were in adult plumage. Because we were interested in the return migration,

we calculated migration duration and swimming speed using only the periods when penguins swam rapidly southward.

SST anomaly PCA (Plata Plume Index, PPI)

To characterize the winter habitat of Magellanic penguins, we performed a PCA on the SST anomalies for the wintering area, 40° to 23°S, from the coast to the 1000 m isobath (Fig. 2). The seasonal cycle of warming and cooling dominates SST variability in the region (Rivas 2010). We used anomalies from the seasonal cycle to characterize interannual variability.

For the PCA, we used the Coral Reef Temperature Anomaly Database (CoRTAD), a dataset of SST and SST anomalies from the US National Oceanic and Atmospheric Administration (NOAA) (Selig et al. 2010, Casey et al. 2015). The CoRTAD dataset was created by averaging daytime and nighttime data from the Pathfinder satellite AVHRR sensor at approximately 4 km resolution. Each week of data from January 1982 through December 2012 (1617 wk) was averaged to define the annual cycle, using a harmonic analysis that included annual and semi-annual cycles. SST anomalies were then calculated by subtracting the 31 yr weekly means from the SST for each pixel (4 × 4 km location) and week.

We excluded pixels representing water deeper than 1000 m because Magellanic penguins generally migrate over the continental shelf (Pütz et al. 2000, 2007, Stokes et al. 2014). We used the 2 min resolu-

tion topo_8.2.img bathymetry dataset (Smith & Sandwell 1997), accessed through the 'satbath' command in MATLAB R2016a (MathWorks). We also excluded 4034 of 31 414 pixels in water <1000 m deep because they were missing SST data in at least 25% of the weeks (fewer than 1213 SST observations). The 25% cut-off was a compromise between too few pixels (incomplete spatial coverage) and too few observations (spatial pattern not representative of the study period). We calculated the number of pixels with at least n observations, where $n = 1$ to 1617, and plotted the number of pixels against n . We chose 25% because it was near a breakpoint in the number of pixels. Pixels that were excluded based on this criterion included many coastal pixels and some pixels at the offshore southern edge of the wintering region.

The PCA uses a space-by-time matrix (Fig. 1): SST anomalies are arranged so that rows represent space (latitude and longitude) and columns represent time (weeks). The principal components returned are thus spatial patterns, and the loadings represent a time series for each principal component or pattern. The first principal component is the pattern that explains the most variance in the SST anomalies, and generally, only the first few principal components have physical interpretations as spatial patterns. The time series for each spatial pattern of SST anomalies indicates the strength and sign of that pattern for each week. When a week in the time series has a high absolute value, the pattern is strong (positive and negative anomalies are strong). The sign of the time series value indicates the sign of the anomalies. When the time series is negative, the pattern is reversed. For each week that the time series is negative, positive anomalies in the pattern become negative and negative anomalies in the pattern become positive. When the time series is near 0, the anomalies are weak and the pattern is weak or undetectable. The principal pattern showed the extent and strength of the Rio de la Plata plume (the PPI; see 'Results').

We calculated 2 temporal averages from the PPI based on migration timing, representing early winter (May and June) and late winter (July and August), because the response variables are annual events: body condition, arrival dates, egg-laying dates, and egg size. We tested early-winter and late-winter means separately because we expected conditions immediately before return migration to have stronger effects than conditions earlier in the winter (Sorensen et al. 2009, Soldatini et al. 2016). We also calculated monthly means for comparison with regional wind stress, the southern oscillation index

(SOI), and the southern annular mode (SAM, also called the Antarctic oscillation) (Fig. 1).

We calculated along-shore wind stress from 40° to 22.9°S and from the coast to approximately 500 km offshore (730 km in the Southeastern Brazil Bight). We used monthly gridded QuikScat scatterometer data, resolution 0.25° latitude \times 0.25° longitude, processed by Remote Sensing Systems (www.remss.com) from July 1999 to November 2009. We calculated the alongshore wind stress, with positive values indicating the component of wind blowing approximately from the southwest (from 215°, where north = 0°).

Maps of monthly means showed that wind stress changed from predominantly southwest to northeast at various latitudes within the penguins' wintering area. We identified the latitude where the alongshore wind stress shifted from southwest to northeast (the wind-reversal latitude) each month by calculating a running mean of wind stress over each degree of latitude, averaging from south to north. If the mean wind stress was from the southwest over the entire region, we used the northern edge of the region, 22.9°S, as the wind-reversal latitude (May 2004, 2006, and 2008). If the mean wind stress was from the northeast over the entire region, we used the southern edge of the region, 39.1°S, as the wind-reversal latitude (August 2001). We regressed monthly means of the PPI for the winter months (May–August) on the wind-reversal latitude at 0, 1, and 2 mo lags. Plume waters reach the Southeastern Brazil Bight in 25 to 49 d (Pimenta et al. 2005), so we did not expect wind to influence the plume at longer lags. We included year as a linear variable to account for any temporal trends.

We tested links between the Rio de la Plata plume and 2 large-scale climatic indices, the SOI and SAM. The SOI is the normalized sea-level pressure difference between Tahiti and Darwin, Australia. Negative values correspond to El Niño conditions and positive values to La Niña. Precipitation in southeastern South America increases during El Niño events, increasing outflow of the Rio de la Plata to the continental shelf in the penguins' wintering area (Piola et al. 2008). We used monthly means of SOI from the NOAA National Centers for Environmental Information, <https://www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/>. The SAM is the first principal component of atmospheric pressure anomalies south of 20°S around the globe. When the SAM index is negative, sea level pressure is lower and westerly winds are stronger north of 40°S than farther south (Rivas 2010), and SST is high off southern Brazil between 25° and 35°S

(Soares et al. 2014) and low on the Argentine shelf (Meredith et al. 2008). The anomalies are reversed when the index is positive. We used monthly means of SAM from the NOAA National Weather Service Climate Prediction Center, www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao.shtml. We regressed monthly means of the PPI on monthly means of the SOI and SAM for winter months (May–August). We included year as a linear variable to account for temporal trends and tested for correlations at 0 to 3 mo lags (SOI or SAM leads winter PPI by 1–3 mo).

Fish stocks

We expected that any effects of the SST patterns on penguins would be mediated by their prey. Prey availability, which is sometimes measured from commercial fisheries catches, affects breeding performance of seabirds (Furness 2007, Sherley et al. 2013). The diet of Magellanic penguins during the non-breeding season is not well known, but a recent stable isotope study indicated that Argentine anchovy, Brazilian sardine *Sardinella brasiliensis*, and squid (*Loligo* spp. and *Illex* spp.) are important in the winter (Silva et al. 2014). We used catches of Argentine anchovy and Brazilian sardine as proxies of food availability to the penguins during winter.

We used monthly landings of anchovy from January 1989 to December 2010 from the Argentine Ministry of Agriculture, Livestock, and Fisheries (www.agroindustria.gob.ar/sitio/areas/pesca_maritima/desembarques/). Mar del Plata (38.0°S, 57.5°W) accounted for 84.5% (1995) to 99.9% (2007, 2009) of the landings. We regressed landings on the PPI and year for the winter months (May–August) at 0 and 1 mo lags. Landings were square-root transformed to make the regression residuals normal.

We used annual landings of Brazilian sardine in Santa Catarina state, Brazil, 1982–2000, from Cergole et al. (2002). Santa Catarina is the southern-most state within the sardine's range. Because only annual landings were available, we calculated means of the PPI for May through August. We assumed that any effects of the plume on landings were due directly or indirectly to the extent of the plume in winter because the Rio de la Plata plume does not generally reach the range of the Brazilian sardine in summer and spring (Pimenta et al. 2005). We regressed sardine landings on the winter PPI means and year. We did not transform landings because the regression residuals were normally distributed.

Effects of wintering-area oceanographic conditions

We tested whether oceanographic conditions in winter influenced a penguin's body condition at arrival to the breeding colony at Punta Tombo, Argentina. Body mass and fat mass are the most common measures of body condition used for detecting carry-over effects (Harrison et al. 2011). We weighed and measured unmarked penguins from 20 to 27 September 1998 to 2009, to determine body condition near arrival. We sexed penguins by comparison with mate or by bill depth (Boersma & Davies 1987), and used 264 males and 177 females, with 24–51 penguins measured per year. We defined body size as the first principal component of 4 measurements: bill depth, bill length, flipper length, and foot length. To adjust body mass for size, we regressed mass on body size using simple linear regression and used the residuals as an index of body condition (Hood et al. 1998). Although we did not use individually marked penguins, the chance of finding and measuring the same individual more than once was low because there are several hundred thousand adult penguins and we did not use the same place or nests each year to reduce the chance of measuring the same penguins. Mortality, variance in arrival date, and high fidelity to breeding areas and nests further reduce the chance of remeasuring a penguin. Moreover, even if we had remeasured several of the same individuals in a subsequent year, it would have had only a small effect on the degrees of freedom and would not have affected our results or conclusions. Our results ($F = 6.9$) would still be significant at $\alpha = 0.01$ with between 9 and 10 degrees of freedom in the denominator, compared to the 173 degrees of freedom we used. Pseudoreplication could not be a problem in this analysis. We regressed the body condition index on May–June and July–August means of the PPI, and included date measured (day in September) because after arrival, penguins fast at the colony and lose weight until they return to sea to forage for 2 wk or more while the mate incubates the eggs (Fowler et al. 1994). We did not include year in the regression because there was no significant increase or decrease over time in body condition (simple linear regression: $F_{1,175} = 0.7$, $p = 0.40$). Because early and late winter effects were in opposite directions, we standardized the early- and late-winter PPIs and re-ran the regressions to compare coefficients for early and late winter.

To test whether winter oceanographic conditions impacted female arrival dates at the breeding colony, we checked all nest sites daily each season in 1 of our study areas where all individuals were banded. We

used the first sighting of each female anywhere in the colony or adjacent beaches for the date the female arrived. We used nests that we first checked on or before 25 September in a given season because the earliest egg laid in our 35 yr study was 26 September (Boersma et al. 2013), and used years when at least 24 nests met all criteria. A total of 1048 nests met the criteria in 1984, 1985, 1989–1992, 1995, 1996, and 1998–2009. We used 354 females with 1–15 yr of arrival dates per female (mean = 3 yr). We converted arrival date to days since 1 September and square-root transformed the days to make the regression residuals normal. We used mixed-effects models with female ID as a random effect. Fixed effects were May–June and July–August means of the PPI, and year as a linear variable.

To test if egg-laying dates varied because of the winter oceanographic conditions, we used the female arrival dataset. We used mixed-effects models with female ID as a random effect. Fixed effects were May–June and July–August means of the PPI, female arrival date, and year as a linear variable. We also tested a mixed-effects model with female ID and year as partially crossed random factors (unbalanced design). The conclusions were the same for both models, and the likelihood-ratio test comparing the 2 models was not significant ($\chi^2_1 = 0.2$, $p = 0.69$). This is not surprising, as year and the PPI are confounded. We report results from the simpler model, using only female ID as a random effect.

To test if winter oceanographic conditions affected egg size, we calculated the volume of each egg in 2-egg clutches from measurements of egg length and egg width, using separate equations for first- and second-laid eggs (Boersma & Rebstock 2010). We included 103 clutches of 72 known-age females from 1991 to 2008, with 1 to 5 clutches per female (mean = 1.4). We used mixed-effects models with female ID as a random effect. We regressed total clutch volume (sum of the volumes of the 2 eggs) on May–June and July–August means of the PPI, laying date, and female mass (females weighed in September or October). We included female age and age squared as fixed effects because egg size depends nonlinearly on female age (Cerchiara et al. 2017). We used female mass instead of body condition because the first principal component of the 4 measurements only explained 41 % of the variance in this dataset. Results of the full mixed-effects model were similar whether we used female mass or the body condition index. We did not include year in the regression because there was no significant increase or decrease over time in egg size (simple linear regression: $F_{1,101} = 2.2$, $p = 0.14$).

Statistics

We used Stata 11.2 (StataCorp) for all statistical tests. We used MATLAB R2016a for the SST PCA. For all regression analyses, we report the F -statistic for the full model and t - or z -statistics for individual fixed effects. For mixed-effects models, we also present the likelihood-ratio χ^2 -statistic for random effects. We included year as a linear fixed effect in the regressions for arrival date and laying dates because we knew that both became later during our long-term study. We found no linear changes over time in body condition and egg size, so we did not include year in those models. We did not include year as a random effect or a fixed factor in any of the models because it would be completely confounded with the PPI. The PPI has only 1 value per year for the early-winter period and 1 value per year for the late-winter period. Any other effects of year would have to be included explicitly in the models, not just as the umbrella effect of 'year'.

RESULTS

Return migration speed

Three of the penguins tracked during southbound migration in August 2007 returned to the latitudes of breeding colonies while their satellite tags were transmitting, 2 penguins stayed near or north of the release site, and 1 penguin swam south but did not reach breeding colonies (see tracks in Boersma 2012). Whether a penguin swam south was not related to its body condition at release, as the penguin that was in the best condition of the 6 released and the penguin that was in the worst condition both went south. We calculated the distances, durations, and swimming speeds of the 3 return migrations (Table 1). One penguin (ID no. 53337) swam south, circled back to the north, then began swimming rapidly south for a few days until the tag stopped transmitting. We list his southbound periods separately in Table 1.

The mouth of the Rio de la Plata is approximately 1200 km from Punta Tombo, and the northern limit of the usual wintering area ($\sim 23.5^\circ$ S) is about 3000 km. At average southbound speeds of 40 km d⁻¹, these distances would take about 30 and 75 d to swim, respectively. If penguins maintain the speed of penguin 53337 in his second southbound period, however, they could cover the 3000 km distance in 30 d.

Table 1. Return migration by male Magellanic penguins released from wildlife rehabilitation centers in northern Argentina. Penguin 53337 backtracked briefly to the north, then swam south again more rapidly

Penguin ID	Distance (km)	Duration (d)	Speed (km d ⁻¹)
IF0237	1110	24.4	45.5
IF0526	735	21.2	34.7
53337 (1st southbound period)	947	23.2	40.8
53337 (2nd southbound period)	440	4.3	102.3

Plata Plume Index, PPI (SST anomaly PCA)

The first 3 spatial patterns (principal components) of the SST anomalies in the Magellanic penguins' wintering area in the South Atlantic explained 33.5, 17.7, and 5.5% of the variance in the SST anomalies. The remaining spatial patterns each explained <5% of the variance. We used only the first spatial pattern, because we assumed it would have the largest biological effect on penguins.

The principal spatial pattern (PPI) has warm (positive) SST anomalies at all pixels in the study region (Fig. 2a; note scale is always positive in panel a). When the PPI is positive, the Rio de la Plata plume is weak, with strong warm SST anomalies north to approximately 29° S, and weaker warm anomalies up to almost 24° S. The plume normally carries cool water to the Southeastern Brazil Bight; when the plume is weak, the cool water is absent and the SST anomalies are warm. The least anomalous temperatures are in the northeast, where warm, salty, nutrient-poor Tropical Water is transported along the continental slope by the Brazil Current and mixes with shelf water (de Macedo-Soares et al. 2014); the warm water is closer to average than in other parts of the region. Intermediate anomalies are found in the southwest, where cold, nutrient-rich Subantarctic shelf water is normally transported north by the Patagonian Current (de Macedo-Soares et al. 2014).

The PPI showed high-frequency (week to week) variations as well as interannual fluctuations (Fig. 3a). The May–June and July–August means showed strong interannual variations (Fig. 3b). The plume weakened over time, on average, as the monthly means of the PPI increased significantly ($F_{1,370} = 32.6$, $p < 0.0001$, $R^2 = 0.08$). The increase was still significant when using only the winter months of May–August ($F_{1,122} = 8.3$, $p = 0.005$, $R^2 = 0.06$), but not

the 2 mo means (May–June, $F_{1,29} = 2.5$, $p = 0.13$; July–August, $F_{1,29} = 2.1$, $p = 0.16$). May–June and July–August means were not significantly correlated with each other ($F_{1,29} = 3.2$, $p = 0.09$).

When southwest winds dominated over most of the penguins' wintering area (the wind stress changed from southwest to northeast farther north), the Rio de la Plata plume carried cool water farther north (the PPI was negative and the SST anomalies were cold). When the mean alongshore wind stress changed from southwest to northeast farther south, the plume was weaker (the PPI was positive, with warm SST anomalies; $F_{2,39} = 3.7$, $p = 0.04$, $R^2 = 0.11$; wind-reversal latitude: $t = 2.7$, $p = 0.01$). There was no linear temporal trend (year: $t = 0.1$, $p = 0.90$). The latitude where mean alongshore wind stress changed from southwest to northeast affected the plume strength 1 mo later (1 mo lag: $F_{2,38} = 5.3$, $p = 0.01$, $R^2 = 0.18$; wind-reversal latitude: $t = 3.2$, $p = 0.003$; year: $t = 0.3$,

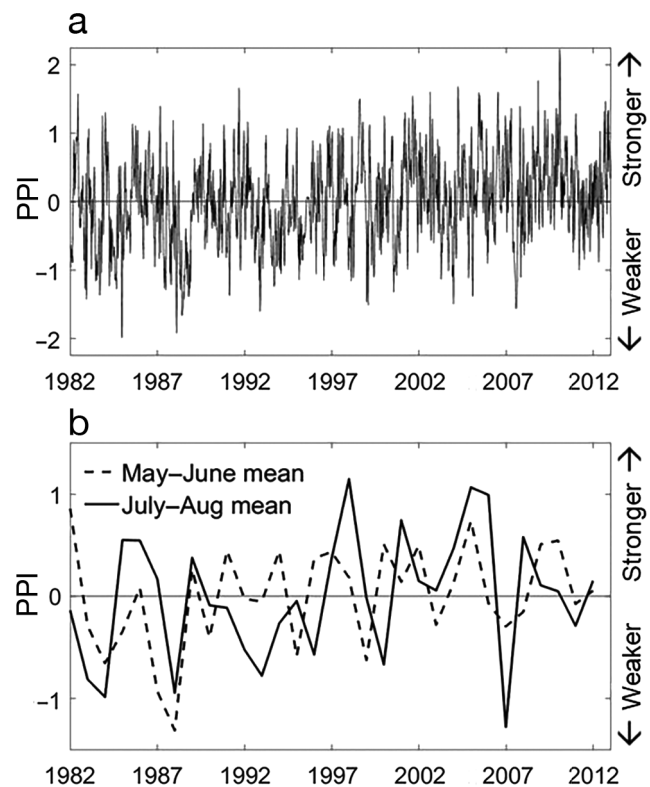


Fig. 3. (a) Weekly time series of the Plata Plume Index (PPI) shows both week to week and interannual variation. During weeks when the time series is strongly positive, the pattern is strong (see Fig. 2), SST anomalies are positive, and the Rio de la Plata plume is weak. During weeks when the time series is strongly negative, the pattern is reversed. When the time series is near 0, the pattern is weak or undetectable and the plume is near mean conditions. (b) May–June and July–August means of the PPI show strong inter-annual variation

$p = 0.75$) but, by 2 mo later, there was no significant relationship ($F_{2,37} = 0.05$, $p = 0.95$).

The strength of the Rio de la Plata plume in the winter months (May–August) did not vary with the SOI at any lag up to 3 mo ($t = 0.02$ – 1.0 , $p = 0.83$ – 0.31). The plume was weaker in winter when the SAM index was higher at a 2 mo lag ($t = 2.0$, $p = 0.046$). Year and SAM explained 8% of the variation in the PPI for May through August.

Fish stocks

There were no significant relationships between landings of anchovy in northern Argentina and the strength of the Rio de la Plata plume at 0 or 1 mo lags ($p \geq 0.80$). Year was not significant in any of the regressions, indicating no linear temporal trend ($p > 0.60$).

Annual landings of Brazilian sardine in Santa Catarina state increased when the Rio de la Plata plume was weaker in May through August (the PPI mean was higher; $F_{2,16} = 4.2$, $p = 0.03$, $R^2 = 0.26$). We found no linear trends in landings over time, as year was not significant (year: $t = 1.2$, $p = 0.27$).

Effects of wintering area oceanographic conditions

The 4 measurements of penguins (bill length, bill depth, flipper length, and foot length) accounted for 73% of the variance in body size (the first principal component). Body size explained 19% of the variation in body mass ($F_{1,439} = 105$, $p < 0.0001$). Females were in better body condition ($F_{3,173} = 6.9$, $p = 0.0002$, $R^2 = 0.09$) when the Rio de la Plata plume was strong in early winter ($t = 2.9$, $p = 0.004$), and when the plume was weak in late winter ($t = 4.0$, $p < 0.001$). The date the female was measured did not affect the body condition index ($t = 0.2$, $p = 0.88$). When we used the standardized PPIs, the t - and p -values were the same as for the unstandardized variables. The effects were about 44% stronger for late winter (regression coefficient = 0.13) than for early winter (coefficient = 0.09). For males, the strength of the Rio de la Plata plume was not significantly related to body condition in early winter ($t = 1.9$, $p = 0.06$) or late winter ($t = 0.9$, $p = 0.37$). Only the date measured affected body condition ($F_{3,260} = 5.6$, $p = 0.001$, $R^2 = 0.05$). After arrival, male body condition in the breeding colony decreased with the number of days they fasted ($t = 3.2$, $p = 0.002$).

The strength of the Rio de la Plata plume, year, and individual ID all affected female arrival dates (Wald

$\chi^2_3 = 319$, $p < 0.0001$). Females arrived earlier at Punta Tombo when the Rio de la Plata plume was weak in early winter (May–June; $z = 3.4$, $p = 0.001$) and late winter (July–August; $z = 8.1$, $p < 0.001$). The responses of individuals to the strength of the Rio de la Plata plume were not consistent (Fig. 4; likelihood-ratio test: $\chi^2_1 = 64.8$, $p < 0.0001$) and only 1 female's individual response was significant at the 0.05 level. Female arrival dates at Punta Tombo became later over time (year: $z = 15.9$, $p < 0.001$).

Year and arrival date influenced egg-laying dates (Wald $\chi^2_4 = 5951$, $p < 0.0001$), but the strength of the Rio de la Plata plume did not significantly explain any of the residual variation ($z \leq 0.9$, $p \geq 0.37$). Females laid eggs later over time ($z = 4.3$, $p < 0.001$) and when they arrived later ($z = 68.0$, $p < 0.001$). Individual ID was significant ($\chi^2_1 = 368$, $p < 0.0001$). Both arrival dates and egg-laying dates became later over time, but arrival dates changed faster (0.45 d yr^{-1}) than egg-laying dates (0.36 d yr^{-1}), thus the period between arrival and egg laying has decreased in recent years.

Egg size depended on female age and age squared, laying date, and female weight (Wald $\chi^2_6 =$

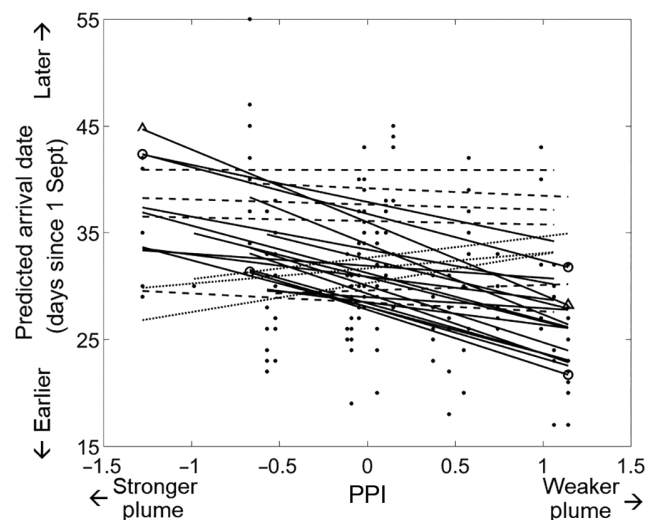


Fig. 4. Variation in the arrival dates of female Magellanic penguins in relation to the strength of the Plata Plume Index (PPI) in the wintering area: 18 females arrived earlier when the plume was weak (black dots and solid lines, slope < -1), 3 arrived later (dotted lines, slope > 1), and 6 did not vary their arrival dates (dashed lines, $-1 \leq \text{slope} \leq 1$). Each line represents the predicted arrival dates for 1 female for which we knew the arrival date in at least 8 years ($n = 27$). Lines vary in length because we had 8 to 15 years of data depending on the female. The line for 1 female whose slope was significant ($p = 0.01$) is marked with a triangle at both ends, and lines for 2 females with $p < 0.10$ are marked with circles at both ends. Results were similar for a minimum of 6 ($n = 46$ females), 7 ($n = 36$), 9 ($n = 17$), or 10 ($n = 8$) years of data per female

47.9, $p < 0.0001$). The strength of the Rio de la Plata plume did not significantly explain any residual variation ($z \leq 1.3$, $p \geq 0.21$). Egg size increased with female age until females were approximately 18 yr old, then decreased with age (age: $z = 4.1$, $p < 0.001$; age squared: $z = 3.4$, $p = 0.001$). Earlier-laid eggs were larger than later-laid eggs ($z = 3.6$, $p < 0.001$). Heavier females laid larger eggs than lighter females ($z = 2.3$, $p = 0.02$). Individual ID was significant ($\chi^2_1 = 23.6$, $p < 0.0001$), suggesting that individual foraging ability varies.

DISCUSSION

We found that oceanographic conditions, specifically the strength of the Rio de la Plata plume, in the wintering grounds had direct and indirect impacts on breeding female Magellanic penguins at Punta Tombo. Contrary to our expectations, female penguins returned to the breeding colony earlier and in better condition when the Rio de la Plata plume was weak in winter (Fig. 5). Although the plume spreads high-productivity water along the coasts of Uruguay and southern Brazil, it also disperses the penguins' prey (Phillips et al. 2017) and increases turbidity when it is strong (Piola et al. 2008), making it harder for penguins to find and capture prey (Kowalczyk et al. 2015, Phillips et al. 2017). The Rio de la Plata plume strength also indirectly affected laying dates and egg sizes. When females arrived earlier they laid eggs earlier, and females laid larger eggs when they arrived earlier and were in better condition (Fig. 5).

Return migration speed

Penguins migrating south generally swam slower than penguins at the start of northbound migration. The slower speed may result from northbound penguins swimming with the prevailing currents between Punta Tombo and the mouth of the Rio de la Plata, and southbound penguins swimming against the current (Piola & Rivas 1997), or penguins foraging more southbound than northbound. Alternatively, the rehabilitated penguins that swam south may not have been returning to breed. Penguins that were oiled breed at lower rates than unoled penguins (Fowler et al. 1995, Wolfaardt et al. 2008).

Satellite-tracked African penguins *Spheniscus demersus* that had been transported about 800 km to avoid contact with an oil spill swam back to their breeding colonies at speeds of 33–47 km d⁻¹ (Barham

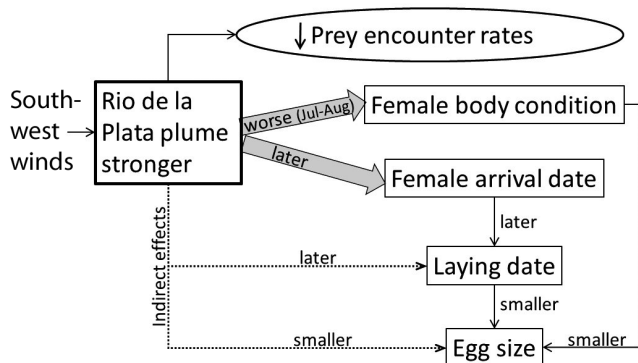


Fig. 5. Effects of winter oceanographic conditions on Magellanic penguins breeding at Punta Tombo, Argentina. Direct effects are shown with wide grey arrows, indirect effects with dotted arrows. The Rio de la Plata plume did not affect male body condition

et al. 2006), comparable to the speeds we tracked (35–46 km d⁻¹) except for 1 male's (53337) 4 d average of over 100 km d⁻¹. The fastest returns of African penguins that had been relocated or rehabilitated were 64–81 km d⁻¹ (Randall et al. 1981, Wolfaardt et al. 2008). Macaroni penguins *Eudyptes chrysolophus* returning from wintering grounds to breeding colonies averaged 58.1 km d⁻¹ for a month (Bost et al. 2009b). Our results and these examples show that penguins can sustain rapid swimming for at least a month during migration. Breeding adult Magellanic penguins can reach colonies in the northern parts of the breeding range within a month of leaving the wintering grounds. Breeders arrive at colonies from late September to mid-October, which means they likely leave the wintering grounds in late August to early September.

Plata Plume Index, PPI (SST anomaly PCA)

When the principal SST anomaly pattern is strongly positive in winter, the northward extent of the Rio de la Plata plume is reduced. Conversely, when the pattern is strongly negative, the plume extends unusually far north, up to approximately 24° S. The plume reaches ~23° S in some years, although it usually does not penetrate north of ~26° S (Campos et al. 1999). Note that variations in upwelling cannot explain the pattern. Coastal upwelling is generally restricted to the areas around capes in the Southeastern Brazil Bight during summer (Piola et al. 2008, de Macedo-Soares et al. 2014). In addition, southwest winds drive the plume farther north and predominate in winter, producing downwelling, not upwelling (Pimenta et al. 2005).

The Rio de la Plata plume is rich in phosphates and silicates from continental runoff (Braga et al. 2008) and, in winter, is associated with high concentrations of organic matter, chlorophyll *a*, and zooplankton (Muelbert et al. 2008). Chlorophyll *a* was highest in low-salinity plume water, especially north of the Rio de la Plata mouth in July (Piola et al. 2008). Higher trophic level animals, including sea turtles, albatrosses, and pinnipeds, are associated with Rio de la Plata plume fronts in fall and winter (González Carman et al. 2016). Seabirds worldwide often associate with river plumes, including the Columbia River plume in the eastern North Pacific (Phillips et al. 2017), the Changjiang (Yangtze) River plume in the East China Sea (Matsumoto et al. 2016), and the Yarra River plume in Port Phillip Bay, Victoria, Australia (Kowalczyk et al. 2015).

The PPI was correlated with regional wind stress and the SAM, but not with the SOI (Fig. 5). The plume extent responds more strongly to wind than to river input (Möller et al. 2008), and the SOI mainly affects rainfall in the region (Piola et al. 2008), whereas the SAM affects winds (Rivas 2010).

Fish stocks

River plumes provide a source of new nitrogen (mostly nitrate from outside the euphotic zone, as opposed to regenerated nitrogen in the form of ammonia and urea), enhancing primary and secondary productivity. Plumes provide important habitat for forage fish, especially anchovies, around the world (Checkley et al. 2017). The Rio de la Plata plume is an important spawning and nursery area for key prey species of Magellanic penguins, including the Argentine anchovy (Muelbert et al. 2008, de Macedo-Soares et al. 2014) and Argentine hake *Merluccius hubbsi* (Muelbert et al. 2008), especially in winter (Matsuura et al. 1992, Martins & Haimovici 2017). In addition, high Brazilian sardine catches were associated with low-salinity plume water (Sunyé & Servain 1998).

The level of exploitation of the fish stocks may determine in part whether fish landings correlate with the PPI. Anchovy is considered an under-exploited stock in Brazil, Uruguay, and Argentina (Carvalho & Castello 2013). Under-exploited stock landings reflect factors besides stock size, such as fishing fleet size (Quetglas et al. 2013), which could explain why we found no relationship between anchovy landings and the PPI. In contrast, Brazilian sardine are considered overfished (Castello et al.

2009), and landings have declined continuously since the early 1970s (Gigliotti et al. 2010). The fishery collapsed in the late 1980s, and most landings shifted from north to south in the Southeastern Brazil Bight (Cergole et al. 2002). Sardine landings may more closely reflect stock size than landings of the under-exploited anchovy, and we found that Brazilian sardine landings correlated with the Rio de la Plata plume strength.

Distribution of the fish species may also help determine whether landings are correlated with the PPI. Brazilian sardine are restricted to the Southeastern Brazil Bight (Cergole et al. 2002). Catches and spawning centers of the Brazilian sardine move north and south with changes in productivity (Cergole et al. 2002, Gigliotti et al. 2010). Sardine catches in Santa Catarina state correlated positively with the PPI because sardine likely move south to Santa Catarina when the plume is weak, and waters to the north of the plume are less productive. Anchovy overlap Brazilian sardine at the northern limit of their range, but occur farther south (Matsuura et al. 1992, de Macedo-Soares et al. 2014) and the area we used for anchovy landings is south of the Rio de la Plata plume influence in winter. Sardine may be more important in penguins' diets when penguins winter farther north, likely in years when anchovy and other prey abundance is low in the southern part of the winter range.

Effects of wintering area oceanographic conditions

Females generally arrived at Punta Tombo in better body condition when the Rio de la Plata plume was weak in late winter, and arrived earlier when the plume was weak in early and late winter. Although the Rio de la Plata plume supports high primary and secondary productivity, a larger plume likely reduces the prey density and prey encounter rates (Phillips et al. 2017), and distributes prey farther north (Martins & Haimovici 2017), requiring penguins to work harder or migrate farther to find prey. Prey encounter rates may be higher when the river plume is smaller, because prey is more concentrated and turbidity is lower, making it easier for penguins to find and capture their prey (Kowalczyk et al. 2015). Southwest winds that push the plume farther north also trap the plume against the coast (Piola et al. 2008), likely reducing the dispersion of the sediments carried by the plume (Fernández-Nóvoa et al. 2017). Northeast winds force the plume farther offshore and allow dispersal of sediments (Piola et al. 2008). Penguins are

primarily visual foragers and prey capture is limited in low light (Wilson et al. 1993, Walker & Boersma 2003). Results of studies on the effects of turbidity on seabird foraging success are mixed, probably because the studies varied in turbidity and the study species' foraging habits (Henkel 2006). Litz et al. (2014) suggested that the Columbia River plume serves as a refuge for forage fish from piscivorous predators. Moderate turbidity decreased the ability of piscivorous fish to find and capture their prey, but did not affect prey capture by planktivorous fish (De Robertis et al. 2003), suggesting that turbid river plumes may generally provide refuges for forage fish. Hence, the reduced turbidity when the Rio de la Plata plume is weaker may increase foraging success by Magellanic penguins.

Females were in worse body condition when the Rio de la Plata plume was weak in early winter, even though a shorter migration should require less energy expenditure and provide more time to improve their condition before returning to the colony to breed. The high productivity associated with a stronger plume may be critical in early winter for the females to regain body condition after breeding. However, the effects of the plume were stronger in late winter than in early winter. The period immediately prior to breeding was more important than the earlier period, as in other seabirds (Sorensen et al. 2009, Soldatini et al. 2016). It is possible that females forage in separate areas in early and late winter, as in brown skuas *Catharacta antarctica lonnbergi* in the Southwest Atlantic (Krietsch et al. 2017), but this is unknown.

The Rio de la Plata plume extent did not affect male body condition. Males are larger than females, and larger penguins dive deeper than smaller penguins during the breeding season (Walker & Boersma 2003). Males had a wider isotopic niche width than females, indicating that they ate a wider variety of prey in winter (Silva et al. 2014). Whether males and females forage in separate areas in the winter is unknown. The ability to dive deeper and eat larger and more diverse prey species may enable males to maintain better body condition than females when preferred prey is not abundant. In addition, males had been fasting longer than females when we measured them, as males arrive at the colony earlier than females (Boersma et al. 1990). Females that arrived recently had lost little mass, and the winter Rio de la Plata plume explained more variation in body condition than the date we measured them. On the other hand, males that had been ashore longer had lost enough mass that date measured explained more of

the variation in body condition. The stomach contents of male and female penguins arriving at Punta Tombo at the beginning of the breeding seasons in the mid-1980s were sampled, and stomachs were often found to be empty (D. Boersma unpubl. data), suggesting that the birds were already fasting. Nevertheless, if males started their return migrations earlier than females, as in crested penguins (Thiebot et al. 2014), they would have fasted longer. Winter conditions generally affect breeding females more strongly than males in seabirds (Sorensen et al. 2009, Schultner et al. 2014), but there are exceptions (e.g. Chastel et al. 1995).

The small amount of variance that the PPI explained for breeding females has several explanations. Winter conditions likely affect survival (Reiertsen et al. 2014) and/or the probability of breeding (Crossin et al. 2012, Soldatini et al. 2016). We only considered birds that survived in suitable condition to breed. Winter conditions may affect younger penguins (Chastel et al. 1995) more than they affected breeding adults at Punta Tombo. Juvenile and younger adult Magellanic penguins winter farther from breeding colonies than breeding adults (Stokes et al. 2014) and are less experienced foragers. In addition, penguins breeding at colonies farther south must swim farther to reach wintering grounds and to return to breeding grounds than penguins from Punta Tombo, and effects of wintering area conditions can vary depending on colony location (Bogdanova et al. 2017). Finally, effects varied depending on the individual female. Some individuals are better foragers than others, because of age, experience, or intrinsic ability (Le Vaillant et al. 2016). Experienced or high-quality penguins likely forage in areas with higher prey densities than less-experienced or low-quality individuals (Harris et al. 2014).

In spite of individual variation, the strength of the Rio de la Plata plume in winter significantly affects female Magellanic penguin arrival dates and body condition in the following breeding season at Punta Tombo. The plume strength, driven by winds, likely determines forage fish locations and availability in the penguins' wintering grounds. A smaller plume keeps prey closer to breeding colonies and reduces turbidity, increasing prey encounter rates and foraging success of overwintering penguins.

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