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Jocelyn Champagnon, Jean-Dominique Lebreton, Hugh Drummond, David J. Anderson. Pacific Decadal and El Niño oscillations shape survival of a seabird. *Ecology*, 2018, 99 (5), pp.1063-1072. 10.1002/ecy.2179 . hal-02008360

HAL Id: hal-02008360

<https://hal.science/hal-02008360>

Submitted on 5 Feb 2019

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Pacific Decadal and El Niño oscillations shape survival of a seabird

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How to cite : Champagnon Jocelyn, Lebreton Jean-Dominique, Drummond Hugh, Anderson David J. 2018. *Pacific Decadal and El Niño oscillations shape survival of a seabird*. *Ecology* 99:1063–1072. doi: 10.1002/ecy.2179

Understanding and modeling population change is urgently needed to predict effects of climate change on biodiversity. High trophic-level organisms are influenced by fluctuations of prey quality and abundance, which themselves may depend on climate oscillations. Modeling effects of such fluctuations is challenging because prey populations may vary with multiple climate oscillations occurring at different time scales. The analysis of a 28-yr time series of capture–recapture data of a tropical seabird, the Nazca Booby (*Sula granti*), in the Galapagos, Ecuador, allowed us to test for demographic effects of two major ocean oscillations occurring at distinct time-scales: the inter-annual El Niño–no Southern Oscillation (ENSO) and inter-decadal oscillations. As expected for a tropical seabird, survival of fledgling birds was highly affected by extreme ENSO events; by contrast, neither recruitment nor breeding participation were affected by either ENSO or decadal oscillations. More interesting, adult survival, a demographic trait that canalizes response to environmental variations, was unaffected by inter-annual ENSO oscillations yet was shaped by the Pacific Decadal Oscillation and small pelagic fish regime. Adult survival decreased during oceanic conditions associated with higher breeding success, an association probably mediated in this species by costs of reproduction that reduce survival when breeding attempts end later. To our knowledge, this is the first study suggesting that survival of a vertebrate can be vulnerable to a natural multidecadal oscillation.

INTRODUCTION

Climate change is predicted to reduce biodiversity during the 21st century, with an increase in species extinction rates (Thomas et al. 2004, Bellard et al. 2012). An important challenge is to understand how anthropogenic forcing affects natural oscillations in climate and how species react to natural and forced oscillations (Jenouvrier 2013). These oscillations result from large ocean-atmosphere interactions around our planet, with heat exchange between air and sea generating quasi-periodic oscillations on several time scales (Namias and Cayan 1981), leading to complex effects on ecological systems (Stenseth 2002). Effects of climate oscillations on marine and terrestrial ecological systems are expected to be diverse and important (Stenseth et al. 2003, Almaraz and Amat 2004). For example, during El Niño–no Southern Oscillation (ENSO) warm events, anomalously warm waters in the Eastern Tropical Pacific reduce productivity in upwelling ecosystems (Barber and Chavez 1983, Hays et al. 2005) and affect the spatial and demographic dynamics of fish populations and their upper trophic-level predators (Alheit and Niquen 2004, Velarde et al. 2004, Ancona et al. 2011). In contrast, these same events enhance plant productivity on land that can cascade upward through the food web in terrestrial ecosystems (Holmgren et al. 2001).

Vital rates such as survival, recruitment, and fecundity of upper trophic-level species are influenced by inter-annual climate oscillations such as ENSO and the North Atlantic Oscillation (Stenseth 2002, Crespin et al. 2006, Cubaynes et al. 2011), but responses of these species to inter-decadal oscillations have seldom been studied (Edwards et al. 2013, Hatch 2013, Tompkins et al. 2017). Inter-decadal oceanic oscillations are still poorly understood and their mechanisms are widely debated (MacCall 2009). Nevertheless, they cause large changes to marine ecosystems (Alheit et al. 2009), such as alternative regimes of sardines and anchovy abundance observed across the major upwelling areas of the world (Lluch-Cota 2013). Demographic and behavioral responses of high trophic-level predators to these regime shifts have been suggested (Lusseau et al. 2004, Baker et al. 2012, Hatch 2013, Anchundia et al. 2014, Tompkins et al. 2017) but, to our knowledge, never documented in detail, in particular for survival rates. Seabirds, mammals, and reptiles have complex life cycles with delayed maturity and intermittent reproduction that are not easily amenable to demographic analysis (deYoung 2004). Moreover, detecting effects of climate oscillations on vital rates of long-lived marine vertebrates requires long-term data sets of marked individuals that are scarce (Edwards et al. 2013).

We used a long-term data set to evaluate how vital rates of a long-lived seabird vary with large-scale oceanographic oscillations that occur at two distinct time scales. The Nazca Booby *Sula granti* is relevant as a biological model because it is endemic to the Eastern Tropical Pacific ecosystem (Friesen et al. 2002) and feeds offshore on pelagic fish whose stocks are sensitive to climate oscillations (Anderson and Ricklefs 1987, Anderson 1989, Zavalaga et al. 2012). The Eastern Tropical Pacific is characterized by patchy and unpredictable prey for seabirds (Weimerskirch 2007) combined with high inter-annual variability of primary production due to the ENSO (Pennington et al. 2006).

We applied multi-event models (Gimenez et al. 2012) to 28 yr of capture–recapture data from a population of Nazca Boobies breeding on an uninhabited island of the Galápagos archipelago (Anderson 1989, Friesen et al. 2002, Townsend and Anderson 2007) to test for separate effects of short-period ENSO and of decadal oscillations on vital rates. Longlived vertebrates are expected to allocate the finite resources they acquire among competing fitness components (Stearns 1976). Thus, under occasional harsh environmental conditions, annual breeding participation of adults and survival of newly independent juveniles are expected to decline, whereas annual adult survival, a demographic trait that buffers environmental variations, should remain unaffected (Gaillard and Yoccoz 2003, Nevoux et al. 2010). Accordingly, we predicted that during the poor, short-term environmental conditions of strong ENSO warm events survival and recruitment of juveniles should decline and adults should skip reproduction more frequently (Cubaynes et al. 2011).

In contrast, low environmental quality over multidecadal periods exceeding the lifespan of the organism limits the utility of reproductive restraint. Seabirds do breed during these long-term poor conditions, perhaps because death will often come before good conditions return. On the other hand, an individual born during poor conditions may outlive them given sufficient longevity. Even if selection should favor observation of a limit in investment on reproductive effort (Goodman 1974), the limit should be higher, and survival lower, during multidecadal resource scarcity than during poor conditions on an inter-annual scale. Thus, we predicted reduced reproductive success with constant or lower adult survival during these prolonged poor conditions.

MATERIALS AND METHODS

Nazca Boobies were studied at the breeding colony at Punta Cevallos, Isla Española, Ecuador (1°23' S, 89°37' W). During the 28 breeding seasons (October–May) from 1984–1985 to 2011–2012, 14,298 fledglings and 2,150 after first-year adults (AFY) were individually banded with metal leg bands and recaptured annually during two independent surveys. In band resight surveys, individuals were captured during 5–10 consecutive nights at the onset of each breeding season, except 1988–1989 (Huyvaert and Anderson 2004). In nest surveys, breeders were identified, except in the 1986–1987 to 1990–1991 breeding seasons, and their sex was determined on the basis of sexually dimorphic voices (Nelson 1978), which match chromosomal sex determination (Maness et al. 2007).

Longitudinal data collected at the individual level enable models to estimate demographic parameters with several sources of uncertainty, including imperfect detection of individuals (Gimenez et al. 2012). The multi-event model (Pradel 2005) that we used also accounts for uncertainty in state assignment to an individual. It distinguishes between an individual's actual state of the life cycle (e.g., breeding a given year), and the events that are observed and reflect to some extent its underlying state (e.g., seen during band resight survey this given year; see detection probability paragraph for use of this feature of the model).

During the pre-breeding period of 2–6 year, Nazca Boobies remain at sea and are, thus, unobservable (Conn and Cooch 2009, Maness and Anderson 2013). Our models considered that pre-breeders may appear at the colony for the first time and recruit (first breeding attempt) in the same year, or may attend the colony for some years before recruiting, as described for the Common Guillemots *Uria aalge* (Crespin et al. 2006). Breeding participation was taken into account by modeling the possibility of an adult skipping breeding in any given year. Thus, members of each sex had four possible states that may change annually: pre-breeder absent from the colony (PBabs, an unobservable state except as a nestling in its first year), adult pre-breeder present at the colony (PBpres), breeder (Br), and nonbreeder with previous breeding experience (NB).

Multi-event models consider three types of parameters: initial state probabilities, transition probabilities, and detection probabilities (Pradel 2005). The initial state probabilities were the probabilities of being in one of the eight biological states at first capture (for each sex, either PBabs, PBpres, Br, or NB). For individuals banded as fledglings, the initial state was PBabs male or PBabs female, the probability set by the sex ratio at fledging. For AFY individuals, age was unknown; the models estimated the probability of AFY being in one of those three states (PBpres, Br, or NB) at banding, multiplied by the estimated sex ratio for each state (PBpres, Br, NB).

Transition probabilities were defined by the probabilities that an individual in a given state and in a given year would survive and change to another state in the following year. Transition probabilities were then the product of the annual survival probability times the probability of changing from one state to another (movement among states probability). Five probabilities of movement among states were estimated for each sex (Fig. 1). These included three pre-recruitment or recruitment probabilities: $p_{\text{PBabs} \rightarrow \text{PBpres}}$ was the annual probability of PBabs returning to the colony for the first time but without breeding, $p_{\text{PBabs} \rightarrow \text{Br}}$ was the annual probability of recruiting directly (breeding the first time it returns to the colony), and $p_{\text{PBpres} \rightarrow \text{Br}}$ was the annual probability of recruiting indirectly (breeding after spending at least one year at the colony). In addition, we estimated the annual probability of a breeder skipping breeding ($p_{\text{Br} \rightarrow \text{NB}}$) and the annual probability of breeding again after skipping the previous year ($p_{\text{NB} \rightarrow \text{Br}}$).

Finally, detection probability corresponded to the probability that a bird was observed depending on its state. It was estimated by the model based on observations. For each breeding season, a given individual could be observed (1) as a fledgling at the time of banding, (2) at the colony during the annual band resight survey (sex is not always recorded during those operations), and during the annual nest survey as (3) a breeding male or (4) as a breeding female, or it could be not observed. Uncertainty appeared on the state of an individual seen during a given band resight survey if it was not also observed during the nest survey of the same year. It might actually be a breeder (Br), a pre-breeder present at the

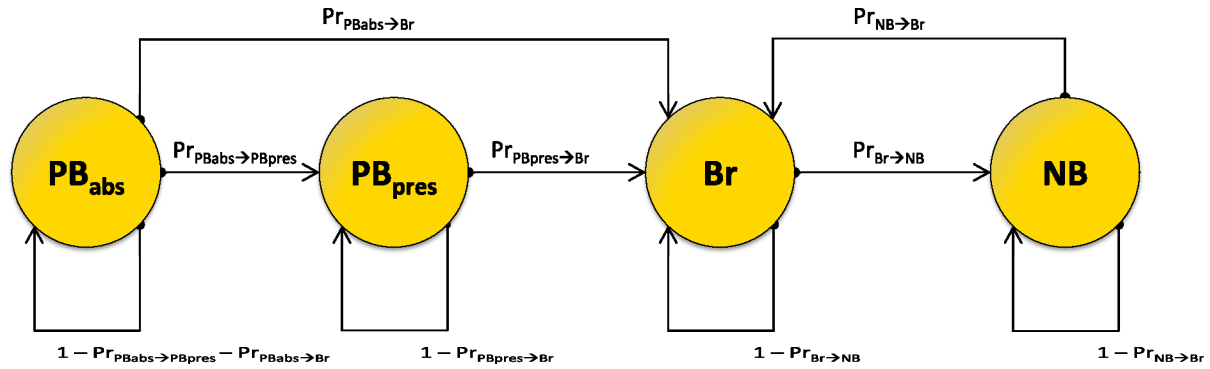


FIG. 1. Schematic representation of the states considered in the models and the probabilities of changing from one state in a given year to another in the following year (movement among states probabilities). $Pr_{PB_{abs}}$, pre-breeder absent from the colony; $Pr_{PB_{pres}}$, adult pre-breeder present at the colony; Br , breeder; NB , nonbreeder with previous breeding experience. $Pr_{PB_{abs} \rightarrow PB_{pres}}$ was the annual probability of PB_{abs} returning to the colony for the first time but without breeding, $Pr_{PB_{abs} \rightarrow Br}$ was the annual probability of recruiting directly (breeding the first time it returns to the colony), $Pr_{PB_{pres} \rightarrow Br}$ was the annual probability of recruiting indirectly (breeding after spending at least one year at the colony), $Pr_{Br \rightarrow NB}$ was the annual probability of a breeder skipping breeding, and $Pr_{NB \rightarrow Br}$ was the annual probability of breeding again after skipping the previous year.

colony (PB_{pres}), or a nonbreeder (NB). To accommodate this uncertainty, a parameter was introduced to estimate the probability of breeding but missing from the nest survey. An individual captured at the colony during a band resight survey and later identified as a breeder during a nest survey in the same breeding season was coded as breeder. The event matrix related the events to the states PB_{abs} , PB_{pres} , Br , and NB for each sex independently, leading to 10 different parameters (Table 1).

Constraints were needed to make parameters identifiable (Lebreton et al. 2009); these constraints expressed biologically reasonable assumptions. First, for initial state probabilities, a constraint on the fledgling sex ratio of 0.5 was based on molecular sexing of a subset of fledgling Nazca Boobies (Maness et al. 2007, Maness and Anderson 2013). Second, we considered survival probabilities to differ only between first-year (FY) birds and older (AFY) birds. To estimate movement among states probabilities, pre-recruitment and recruitment probabilities were allowed to vary with age until birds were four years old. The fifth age class included birds ≥ 5 yr old. In addition, no FY bird has ever been observed to return to the colony, so $Pr_{PB_{abs} \rightarrow PB_{pres}}$ for FY birds was assigned a value of zero. Similarly, “direct” ($Pr_{PB_{abs} \rightarrow Br}$) or “indirect” ($Pr_{PB_{pres} \rightarrow Br}$) probabilities of recruitment of one-year and two-year-old birds were set at zero. Finally, no nest survey was conducted in the 1986–1987 to 1990–1991 seasons, so the probability that an individual is breeding but not observed during the nest survey was set at 1 for those years (i.e., breeders were detected during band resight survey only). Detection probability for PB_{pres} , Br , and NB were set at zero in 1988–1989, a period with no fieldwork.

Goodness-of-fit (GOF)

No optimal GOF currently exists for multi-event models, although such tests exist for models that do not incorporate uncertainty regarding state at the time of each event. As the best approximation available, we tested the fit of the JollyMove model using program U-CARE version 2.3 (Choquet et al. 2009a), treating events as states known with certainty. Details of the method of testing GOF are available as supplementary materials (Appendix S1). The goodness-of-fit procedures provided an estimate of overdispersion \hat{c} , which takes into account heterogeneity that is not considered by our general model (Choquet et al. 2009a). It corrects the variance of estimates and adjusts model selection based on QAIC (Akaike information criterion corrected for overdispersion)

TABLE 1. Event matrix linking states (first column) to events (top row).

States	Captured as		Seen during band	Seen as male during	Seen as female during
	Not seen	fledgling	resight survey	nest survey	nest survey
PBabs ♂	$1 - p_{PBabs} \text{ ♂}$	$p_{PBabs} \text{ ♂}$	0	0	0
PBpres ♂	$1 - p_{PBpres} \text{ ♂}$	0	$p_{PBpres} \text{ ♂}$	0	0
Br ♂	$1 - p_{Br} \text{ ♂}$	0	$p_{Br} \text{ ♂} \times S_{\text{♂}}$	$p_{Br} \text{ ♂} \times (1 - S_{\text{♂}})$	0
NB ♂	$1 - p_{NB} \text{ ♂}$	0	$p_{NB} \text{ ♂}$	0	0
PBabs ♀	$1 - p_{PBabs} \text{ ♀}$	$p_{PBabs} \text{ ♀}$	0	0	0
PBpres ♀	$1 - p_{PBpres} \text{ ♀}$	0	$p_{PBpres} \text{ ♀}$	0	0
Br ♀	$1 - p_{Br} \text{ ♀}$	0	$p_{Br} \text{ ♀} \times S_{\text{♀}}$	0	$p_{Br} \text{ ♀} \times (1 - S_{\text{♀}})$
NB ♀	$1 - p_{NB} \text{ ♀}$	0	$p_{NB} \text{ ♀}$	0	0
Dead	1	0	0	0	0

Notes: S is the probability for a breeder (Br) to be seen during annual band resight survey only (i.e., without being observed during the following nest survey). Each p_x is the probability of observing an individual in a particular state. Detection probability of pre-breeder absent from the colony (p_{PBabs}) was set at 0 because they were only detected when banded as fledglings and never recaptured in that state. p_{PBpres} , adult pre-breeder present at the colony; NB, nonbreeder with previous breeding experience.

Model selection

We started with a general model including year, age, and sex main effects and interactions for all parameters (that is, for transition and detection probabilities). This model is closest to the Jolly-Move model, to which goodness-of-fit tests apply. Then we fitted constrained models as follows. First, we ran a reduced general model including constraints that make most parameters identifiable (following Crespin et al. 2006; see Appendix S2). From this reduced general model, we performed a multi-step model selection using the minimum QAIC model as a starting point for the next step (Lebreton et al. 1992). Because our first objective was to assess the effect of climatic covariates on survival, we were interested in detecting time-dependence in survival (Doherty et al. 2012). So, we modeled first survival, then detection probability, and finally movement among states. At the end of the selection process, several effects were examined again. Details of the selection procedure are available as supplementary materials (Appendix S2). We used E-SURGE version 1.9 (Choquet et al. 2009b) to fit all 39 models. Following Lebreton and Pradel (2002), we repeated each model at least 10 times with random initial values to ensure convergence to a global maximum likelihood, requiring long run times (approximately 70 h for each model). Model selection led to a preferred model for which some of the parameters presented residual temporal variation, which we attempted to model using climatic covariates.

Explanatory variables

Integrated analysis of distinct data sets from different spatiotemporal scales has been recommended for modeling pelagic fish populations (Bertrand et al. 2004) or seabirds as environmental indicators (Frederiksen et al. 2007). Accordingly, we considered both physical and low trophic-level data at global and local scales (see temporal trend of each variable in Appendix S3; Stenseth et al. 2003): (1) The Pacific Decadal Oscillation (PDO) was implicated in large-scale and long-term changes in Pacific ecosystems (Chavez 2003, Alheit and Niquen 2004, Lindegren et al. 2013). We obtained monthly values, smoothing them with a 12-month filter from the onset of the Nazca Booby breeding season (October; data available online).⁶ (2) Annual mean ENSO conditions (hereafter Ni-no3) were estimated by monthly sea surface temperature anomalies (SSTA) over the Ni-no3 region (5° S–5° N and 150°–90° W), smoothed with a 12 month filter from October. Annual values reflect the duration of ENSO warm or cool events. SSTA values were obtained from the LDEO/IRI Data Library, available online.⁷ (3) Because ENSO warm events peak

⁶ <http://jisao.washington.edu/pdo/PDO.latest>

⁷ http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOIv2/.monthly/

⁸ <http://www.science.oregonstate.edu/ocean.productivity>

over December–February (Cai et al. 2014), we averaged monthly sea surface temperature anomalies for those three months across the Ni-no3 region; this yields a measure of the intensity of ENSO during the breeding period (hereafter, Ni-no3DJF). (4) The consequences of the ENSO for local oceanographic conditions were estimated from sea surface temperature anomalies over the breeding period (October–May, the period during which we were sure that birds were present around the colony; hereafter SSTA_br). For each month, we averaged nine values in the 2° x 2° block between 0.5° S and 2.5° S and 87.5° W and 89.5° W, matching known foraging areas of chick-rearing Nazca Boobies from Isla Espa-nola (Zavalaga et al. 2012). (5) We included information on net marine primary production (NPP; mg C·m⁻²·d) on the same local 2° x 2° block described above and averaged over the breeding period. Those data were available only for 1998 onward, which are for 15 of 28 yr (provided by Oregon State University; available online).⁸ Values were obtained from SEAWIFS for the period 1997–1998 to 2006–2007 and completed by MODIS data for the seasons 2007–2008 to 2010–2011 (following the linear regression for the 66 months where SEAWIFS and MODIS data were both available; July 2002 to December 2007: R² = 0.81, t = 16.533, P < 0.0001). (6) The annual composition of the diet of Nazca Boobies in 14 of 28 breeding seasons (1985–1986; 1992–1993 to 1994–1995; 1999–2000 to 2005–2006; and 2009–2010 to 2011–2012) was expressed as the proportion of total items that were sardines (*Sardinops sagax*) or flying fishes (*Exocoetidae* spp.). This proportion showed a nearly qualitative change (Appendix S3) from sardines (high quality diet) to flying fish (low quality diet) around 1997 (Tompkins et al. 2017). Proportional data were transformed on a logit scale.

Because testing the influence of many variables on demographic parameters could lead to problems of collinearity and spurious results due to type I error (Grosbois et al. 2008), we summarized the seven explanatory variables using a standardized principal components analysis (PCA), using the first two principal components as covariates in the capture-recapture analysis, following the recommendations of Grosbois et al. (2008). Missing data (on diet and NPP) were handled using the R package missMDA (Josse et al. 2011), thus providing PCA values for all years. For better interpretation of the first two axes, we conducted a post-PCA varimax rotation of –22.25° (Kaiser 1958).

Testing the effect of principal components on demographic parameters

TABLE 2. Summary of modeling survival, detection, and movement among states probabilities for Nazca Boobies in the colony at Isla Española.

Steps	Survival probability		Movement probabilities among states						Detection probabilities					
	FY	AFY	PBabs return to colony	Direct recruitment	Indirect recruitment	Skip	Return after skip	Br	PBpres and NB	band resight survey only	No. identified/mathematical parameters	DEV	QAIC	ΔQAIC
General model	Sex × Y	Sex × Y	Age × Y × Sex	Age × Y × Sex	Age × Y × Sex	Sex × Y	Sex × Y	Sex × Y	State × Sex × Y	Sex × Y	838/1,010	120,482.1	44,377.4	
Reduced general model	Sex + Y	Sex + Y	(Age + Y) × Sex	(Age + Y) × Sex	(Age + Y) × Sex	–	–	Sex + Y	(State × Sex) + Y	Sex + Y	461/470	121,231.4	43,889.0	488.5
Survival	–	–	–	–	–	–	–	–	–	–	–	–	–	0.0
Detection	–	–	–	–	–	–	–	Y	Sex + Y	–	458/467	121,178.7	43,864.3	24.7
PBabs → PBpres	–	–	–	–	–	–	–	–	–	–	–	–	–	0.0
PBabs → Br	–	–	–	–	–	–	–	–	–	–	–	–	–	0.0
PBpres → Br	–	–	–	–	–	–	–	–	–	–	408/415	121,403.2	43,843.9	20.4
NB → Br	–	–	–	–	–	–	Sex	–	–	–	356/363	121,637.7	43,823.0	20.9
Br → NB	–	–	–	–	–	Sex	–	–	–	–	308/315	121,878.5	43,812.3	10.7
Adjustment	–	–	–	Age × Sex	–	–	–	–	–	–	–	–	–	–

Notes: PBabs, pre-breeder absent from the colony; PBpres, pre-breeder present at the colony; Br, breeder; NB, nonbreeder with previous breeding experience; Y, year effect; Sex, differences between male and female; Age, age effect. Additive effects tested are specified by + and interactions by ×. Model selection was based on QAIC (Akaike information criterion corrected for overdispersion). ΔQAIC indicated the change in QAIC of a given model relative to the best model of the preceding step. Only the best model for each step is presented. Complete model selection is available in Appendix S5. A dash stands for no decrease in QAIC for any model inside a step compared to the best model from the preceding step.

The first principal component (PC1) was characterized by inter-annual oscillations and PC2 by inter-decadal oscillations (see Results). After model selection procedures and following Grosbois et al. (2008), we tested the effect of temporal trend, linear and quadratic effects of PC1, and a linear effect of PC2 on transition probabilities that present residual temporal variation. For this, we performed an analysis of deviance test (ANODEV; Lebreton et al. 2012) that accounts for unexplained environmental variation. Because we had no biological hypothesis for a negative or positive effect of intermediate values of PC2, we did not test a quadratic effect of PC2 on transition probabilities. For each parameter, we tested first for a temporal trend, then for PC1 in the presence of the temporal trend if it was significant, and finally for PC2 in the presence of PC1 or the temporal trend if any of them were significant. If the temporal trend was significant, and noting that PC2 showed also a linear trend over time (see Results), a relationship between covariate and the parameter might not result from a causal relationship but instead from some other factor that would also present a temporal trend (i.e., see Coulson 2001). To prevent such spurious results we tested for detrended (residuals) PC2 (hereafter dPC2) in the presence of the temporal trend as recommended by Grosbois et al. (2008).

For PC1, we had a clear prediction of a negative effect of ENSO warm events (or both warm and cold events in case of a quadratic effect) on transition probabilities (i.e., vital rates), so we performed a one-tailed test when applying ANODEV as recommended by Lebreton et al. (2012). For PC2, we had no clear prediction, so we performed a one-tailed test only when a temporal trend was detected previously, because then we expected an effect of detrended PC2 to be coherent with the temporal trend detected. For instance, if PC2 decreases over the study period and survival increases over the same time period, higher values of detrended PC2 should also affect survival negatively. Because we conducted multiple tests on each parameter, ANODEV tests were performed with Bonferroni corrections, following Grosbois et al. (2008).

When testing an effect of a principal component on survival probabilities from season y to season $y + 1$, we tested the value of the principal component for year y (that is, oceanic conditions during the period of risk of death). On the other hand, when testing the effect of a principal component on pre-recruitment and recruitment probability (i.e., movement among states probabilities) from season y to season $y + 1$, we considered the value of the covariate during year $y + 1$, which corresponds to oceanic conditions at the time of recruitment.

RESULTS

Model selection

The GOF procedure led to the consideration of an overdispersion coefficient $c^{\wedge} = 2.82$ for model selection (see details in Appendix S4). The general model had 1,010 parameters, of which 838 were estimable. The reduced general model had a lower QAIC, reducing the number of parameters ($n = 470$) and limiting the number of non-estimable parameters ($n = 9$). All parameters were identifiable in this preferred model except first-year survival of fledglings for the years in which no fledglings were banded (1988–1989 to 1991–1992) or too few individuals were observed after banding (2008–2009 to 2010–2011). Then we proceeded to model selection from this reduced general model (Table 2; Appendix S5).

Estimates from the preferred model

The preferred model (Table 2) indicated that the survival probabilities of Nazca Boobies were year- and sex-dependent for FY and AFY. Survival of females was lower than for males (average estimated survival probability \pm SD for FY 0.49 \pm 0.22 vs. 0.58 \pm 0.22 and for AFY 0.92 \pm 0.05 vs. 0.93 \pm 0.05). The preferred model also showed year dependence for the probability of prebreeders recruiting indirectly (spending

at least one year at the colony before breeding), for each sex independently. Effects of covariates on those vital rates were then tested (see Effect of covariates).

In the preferred model, probabilities of direct recruitment for each sex and age were constant. From the average estimated probabilities of indirect recruitment, we derived the cumulative proportions of breeders across age for each sex (Appendix S6). The probability of skipping breeding was constant across years, but skipping behavior was more frequent for males (0.10 [95% CI = 0.09, 0.13]) than females (0.03 [95% CI = 0.02, 0.04]), and returning from skipping was lower for males (0.26 [95% CI = 0.22, 0.31]) than for females (0.41 [95% CI = 0.30, 0.53]).

Thanks to two methods of detection (band resight survey and nest survey), the average estimated probability of detection for breeders over the study period was (estimate \pm SD) 0.96 \pm 0.05, but not all breeders were recorded as such. Indeed, the model could estimate the average proportion of birds breeding in a given year but not recorded as breeders (they were seen only during that year's band resight survey). This proportion differed slightly between sexes but varied greatly among years, reflecting annual differences in field-work effort (male, 0.28 \pm 0.29; female, 0.27 \pm 0.29). Probabilities of detection for prebreeders and nonbreeders were equal but differed between the sexes (average estimated probabilities for males, 0.78 \pm 0.12, and females, 0.61 \pm 0.16).

Effect of covariates

Principal component analysis of the seven explanatory variables was performed for the seasons 1984–1985 to 2011–2012, leading to 28 values of seven principal components. The first two principal components captured 85.7% of the total variance (Appendices S7, S8). PC1 was strongly correlated with SSTA_br, NPP, Ni~no3, and Ni~no3DJF, which each contributed from 23.8% to 24.9% of the variance. PC2 was mainly correlated with representation of flying fish in the diet (35.2% of the variance of PC2), followed by PDO (32.2%) and dietary representation of sardines (30.9%). There was evidence of a linear temporal trend for PC2 ($R^2 = 0.41$, $P = 0.0001$) but no evidence of either a linear or quadratic temporal trend for PC1 (Appendix S9).

With a Bonferroni correction applied to each set of three tests throughout, the critical alpha level was reduced from 0.05 to 0.017. Results of tests were presented in Table 3. Observing that survival of AFY birds showed a positive temporal trend over the study period ($F_{1,25} = 20.49$, $R^2 = 0.45$, $P = 0.0001$; $O(\text{Trend}) = 0.410$ [95% CI = 0.333; 0.486]), we tested for an effect of PC1 and detrended PC2 on survival of AFY birds in the presence of this temporal trend. We found an effect of detrended PC2 on this survival ($F_{1,24} = 7.13$, $R^2 = 0.23$, one-tailed $P = 0.0067$; $O(\text{detrended PC2}) = -0.222$ [95% CI = -0.307; -0.137]; Fig. 2). Survival during the first year of life was affected by both ENSO warm events and cold events ($F_{1,18} = 7.87$, $R^2 = 0.30$, onetailed $P = 0.0059$; $O_1 = 0.214$ [95% CI = 0.073, 0.355]; $O_2 = -1.183$ [95% CI = -1.546, -1.852]; Fig. 3).

TABLE 3. Effect of the covariates on demographic parameters that showed residual temporal variation after model selection.

Demographic components and covariates	F	df	R ²	P	One-tailed P
Survival					
FY					
Trend	1.90	19	0.09	0.185	
PC1	1.00	19	0.05	0.330	0.835
qPC1	7.87	18	0.30	0.012	0.006
qPC1 + PC2	0.60	17	0.03	0.448	
AFY					
Trend	20.49	25	0.45	<0.001	
Trend + PC1	3.43	24	0.13	0.076	0.038
Trend + qPC1	1.01	23	0.04	0.325	0.162
Trend + dPC2	7.13	24	0.23	0.013	0.007
PBabs->PBpres					
Male					
Trend	0.95	24	0.04	0.340	
PC1	0.53	24	0.02	0.532	0.266
qPC1	0.00	23	0.00	1.000	0.500
PC2	0.37	24	0.01	0.545	
Female					
Trend	5.11	24	0.18	0.033	
Trend + PC1	2.51	23	0.10	0.127	0.063
Trend + qPC1	1.42	22	0.06	0.246	0.123
Trend + dPC2	4.94	23	0.18	0.036	0.018
PBpres->Br					
Male					
Trend	1.76	25	0.07	0.196	
PC1	0.32	25	0.01	0.579	0.290
qPC1	4.61	24	0.16	0.042	0.021
PC2	4.54	25	0.15	0.043	
Female					
Trend	1.17	25	0.04	0.291	
PC1	0.89	25	0.03	0.355	0.710
qPC1	1.11	24	0.04	0.303	0.152
PC2	1.68	25	0.06	0.206	

Notes: ANODEV was used to test for a linear temporal trend (Trend), a linear effect of the first axis of the PC analysis indicative of an effect of ENSO (PC1), a quadratic effect of PC1 (qPC1), and a linear effect of the second axis of PC analysis indicative of an effect of PDO and small pelagic fish diet (PC2), on each demographic parameter. Test of detrended PC2 is noted by dPC2. Onetailed t tests were used when there was a clear prediction on the direction of the effect of the explanatory variable (see Materials and Methods for details). Significant P values after Bonferroni correction are shown in boldface type. FY stands for first-year birds and AFY for older birds. DISCUSSION

During their first year, survival of juvenile Nazca Boobies was influenced by local oceanic conditions (primary production and temperature) during breeding and by global oceanic conditions. All those variables reflect the ENSO, a climatic cycle with a period of 2–7 yr (Stenseth 2002). Adult survival was influenced by the PDO and the regime of small pelagic fish populations surrounding their breeding area. Both PDO and the pelagic fish composition shift on an inter-decadal basis (Chavez 2003, d’Orgeville and Peltier 2007, Lindegren et al. 2013), and probably also in Galápagos (Tompkins et al. 2017). Thus, our study strongly suggested that survival of Nazca boobies was influenced by climatic conditions occurring at two scales: inter-annual and inter-decadal.

Our models estimated that 30% of the annual variation found in juvenile survival is explained by the ENSO index. ENSO warm events are associated with lower primary productivity and some studies already documented how it affects survival of juvenile seabirds (i.e., Blue-footed Boobies *S. nebouxii*; Oro et al. 2010). It is not clear why ENSO cool events, which are generally associated with higher primary production, were not correlated positively with survival of juveniles. While a negative influence of warm events on fish biomass is well documented (Bertrand et al. 2004), a positive effect of cool events is less evident, and high fish catches appear not to be related directly to higher primary productivity (Carr 2001). Nazca Booby adults forage at fish concentrations in association with other large predators, including some tunas and sharks (Au and Pitman 1986, Anderson and Ricklefs 1987) that could maim or kill Nazca Boobies (Zavalaga et al. 2012). We speculate that the foraging aggregations promoting this risk are more common during ENSO cool events if higher marine productivity supports larger concentrations of forage fish, attracting juvenile Nazca Boobies as they move northeast along their migratory route to the waters off the Central American coast (Huyvaert and Anderson 2004).

Lagged effects of climate on demographic parameters are well documented, especially in long-lived seabirds (Thompson and Ollason 2001, Barbraud and Weimerskirch 2003, Crespín et al. 2006, Sandvik et al. 2012). In this study, we did not test for a lagged effect of climatic condition on demographic parameters in order to limit the number of covariates tested. In addition, El Niño acts rapidly on the marine ecosystem in the Eastern Tropical Pacific, through a quasiimmediate impact on the trophic chain (Anderson 1989). Thus, a lagged effect of environmental conditions is less likely in this region than in other parts of the world (Ancona et al. 2011). Nevertheless, we acknowledge that considering a lagged effect might have enlarged our understanding of climatic covariate and their effects on demographic parameters.

Decadal oscillations and diet composition explained 23% of the variance found in adult survival. The conditions of the “Sardine Phase” were associated with markedly higher breeding success in this colony (Tompkins et al. 2017), good foraging success during breeding (Zavalaga et al. 2012), and with lower adult survival (this study). This result suggests a cost of reproduction in this long-lived seabird: under favorable conditions, breeding attempts will more often reach later stages of the breeding cycle, increasing breeding effort and decreasing subsequent survival as follows. Short-term survival costs of reproduction interact with heterogeneity in individual quality to determine associations between breeding and survival at the individual level in Nazca Boobies (Townsend and Anderson 2007). Survival of breeders is depressed relative to non-breeders, and in many years, failing at the nestling stage reduces subsequent survival more than failing at the egg stage, suggesting costs associated with both initiating and continuing breeding attempts (Townsend and Anderson 2007). Overlaid on this cost of reproduction, and probably obscuring it partially, is heterogeneity in individual quality: because parents producing an independent fledgling in a given breeding season do not show the reduction in survival that accompanies failing at the nestling stage (Townsend and Anderson 2007). Thus, our results are consistent with higher average effort towards reproduction (particularly, hatching success) during the Sardine Phase, depressing average adult survival.

A cost of reproduction on survival may be surprising because long-lived birds are expected to invest less in reproduction during years with few resources (Stearns 1976), and skipping breeding has been observed in Red-footed Boobies *S. sula* (Cubaynes et al. 2011) and Blue-footed Boobies (Ancona et al. 2011). Nevertheless, our results suggest that, in Nazca Boobies, skipping was uncommon in males (10% annually) and rare in females (3%), and indeed a normal amount of nest initiation was observed by Clifford and Anderson (2001) during the strong ENSO warm event in 1997–1998. In our study, climate indices had a more pronounced effect on survival (including adult survival) than on breeding parameters such as recruitment or skipping behavior, whereas theory predicts that adult survival should be more buffered than breeding parameters against environmental stochasticity in long-lived species (Gaillard and Yoccoz 2003). Associations between large-scale climate indices and adult survival have been found in some other species (Genovart et al. 2013, Oro 2014). An effect of climate variation on the demographic parameters most associated with individual fitness (i.e., adult survival) may suggest high sensitivity of those long-lived species if the climate changes toward poor conditions. Nevertheless, it is important to recognize that environmental canalization in survival of long-lived seabirds is probably common (Barbraud et al. 2012).

Effects of two simultaneous inter-annual climate oscillations have already been reported for other birds. Both ENSO and the North Atlantic Oscillation appear to affect the population dynamics of White-headed Ducks *Oxyura leucocephala* (Almaraz and Amat 2004). The 60-yr oscillation in ocean and atmospheric conditions in the North Pacific appears to affect the diet and breeding success of Black-legged Kittiwakes *Rissa tridactyla* in a 34-yr study conducted by Hatch (2013). Although potentially of great importance, responses of marine ecosystems at the multidecadal scale (>50 yr) are poorly known (Edwards et al.

2013). Evidence of many oscillations with a periodicity approaching 60 yr is accumulating: the PDO, the North Atlantic sea surface temperature (d'Orgeville and Peltier 2007), global mean surface temperature (Schlesinger and Ramankutty 1994), and global mean sea level (Chambers et al. 2012). All of these low-frequency oscillations may be signatures of a major oscillation with an astronomical origin (Scafetta 2010). Neglecting them could lead to distortions in analyses of demographic response of vertebrates to climate warming.

Longitudinal studies encompassing various cycles of such decadal oscillations are notably lacking. We are confident that our approach allowed detection of a genuine influence of low-frequency oscillations on survival of adult Nazca boobies, even with a relatively limited number of study years (28 yr) compared to cycle length. First, an analysis of PDO alone as a covariate on adult survival was also significant ($F_{1,24} = 7.13$, $R^2 = 0.24$, one-tailed $P = 0.0053$; $\theta(\text{year}) = 0.411$; $\theta(\text{detrended PDO}) = -0.209$). Second, PDO is correlated with low-frequency fluctuations in sardine and anchovy populations in the nearby Peruvian upwelling (Chavez 2003). So, PDO probably shape survival of Nazca Booby through change in diet composition that occur at low frequency. Long-term capture–recapture data allow us to detect links between environmental oscillations and vital rates (Frederiksen et al. 2014), but effects of oscillations can be confounded with effects of other factors (Grosbois et al. 2008). For instance, a temporal trend in survival over the study period might be correlated with the climatic covariate only because the latter also presented a temporal trend. The correlation between survival and the climatic covariate could have been due to their individual correlations with time (Coulson 2001). By applying the methods presented by Grosbois et al. (2008) that extract the annual variability from the detrended covariate, we were able to test effects of our covariate on survival estimates even in the presence of a trend for both survival and covariate.

Understanding and modeling of oceanic oscillations and their possible interactions with climate warming is at an early stage. For instance, climate simulations model ENSO only with difficulty (Bellenger et al. 2014), and the mechanisms behind low-frequency oscillations of small pelagic fishes are still under debate (MacCall 2009). Nevertheless, insight into the effects of climate warming on oceanic oscillations is beginning to emerge. A recent study concluded that the frequency of ENSO warm events will double in the next century and proposed a mechanism for forecasting them (Cai et al. 2014). Our results may be incorporated into population dynamics models to simulate the future of this booby colony under different climate warming scenarios (Jenouvrier 2013). Such studies are needed to assess vulnerability of seabirds and other taxa to climate change. Indeed, it is critical to determine which taxa are vulnerable and which aspects of their ecological and evolutionary biology determine their vulnerability (Sutherland et al. 2009).

This study represents a step forward in understanding the effect of multidecadal oscillations on marine ecosystems. To our knowledge, this is the first evidence that survival of a high-trophic-level vertebrate is influenced by environmental drivers on the scale of decades. Soon, data sets exceeding 50 yr and based on individual monitoring will be available for some seabirds (Fay et al. 2017) and it will be possible to test the effect of low-frequency oscillations over a complete period. Taking low-frequency oscillations into account is at an early stage but is absolutely necessary in the context of global warming. Failing to consider low-frequency oscillations among the possible causes of fluctuations in tropical seabirds (Anchundia et al. 2014) could lead to strong bias in reporting responses to regional climate warming.

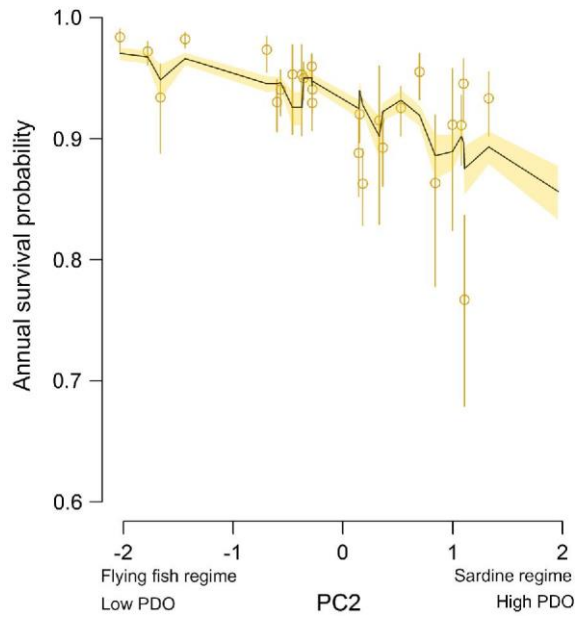


FIG. 2. Annual survival estimates of after first year (AFY) male Nazca Boobies. Regression lines and 95% CI from the model with temporal trend and detrended effect of PC2 (incorporating pelagic fish diet and Pacific Decadal Oscillation [PDO]). Values from the preferred model before fitting the climatic covariate are presented by the circles with their 95% CI. A similar pattern was observed for female Nazca Boobies with an average reduction of 0.67% in survival compared to male.

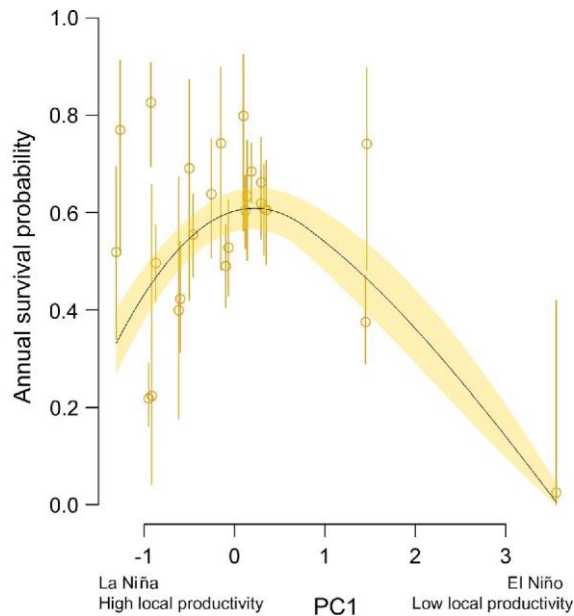


FIG. 3. Annual survival estimates of male Nazca Boobies during their first year. Regression lines and 95% CI come from the model with a quadratic effect of PC1 on survival of Boobies during their first year. Values from the best model after model selection (with time dependence on survival of first-year birds) are presented by the circles with their 95% confidence intervals in grey. Two non-estimable values from this model were discarded. A similar pattern was observed for female Nazca Boobies with an average reduction of 21% in survival compare to male.

ACKNOWLEDGMENTS

J. Champagnon received a postdoctoral grant from AXA Research Fund. We thank the Galápagos National Park Service for permission to work in the Park; the Charles Darwin Research Station, TAME Airline, and Doris Welch (Ecoventura) for logistical support; the National Geographic Society and Wake Forest University for research funding; and many field workers and colleagues for assistance in producing our long-term databases. This material is based upon work supported primarily by the National Science Foundation under Grant Nos. DEB 93045679, DEB 9629539, DEB 98-06606, DEB 0235818, DEB 0842199, and DEB-1354473 to D. J. Anderson.

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SUPPORTING INFORMATION

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