

Long-term changes in the breeding seasonality of Peruvian seabirds and regime shifts in the Northern Humboldt Current System

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ABSTRACT: In the highly productive Northern Humboldt Current System, 3 seabird species, the Guanay cormorant *Phalacrocorax bougainvillii*, the Peruvian booby *Sula variegata* and the Peruvian pelican *Pelecanus thagus*, commence breeding in austral spring, coinciding with the lowest availability of their prey, the Peruvian anchovy *Engraulis ringens*. This strategy ensures the matching of increased prey availability when young achieve independence in summer. This pattern was observed during the last decade when anchovy was abundant. However, over the last century, the abundance of anchovy has varied widely due to contrasting interdecadal regimes in oceanographic conditions and fishing activity. We hypothesized that these regime shifts affected the abundance and availability of prey and may have conditioned the breeding seasonality of seabirds. We examined the timing and magnitude of the onset of breeding using dynamic occupancy models and related these parameters to the seasonality of oceanographic conditions, abundance of anchovy and fishing pressure. During a regime of lower anchovy abundance (1977–1990), cormorants showed the highest flexibility, adjusting the timing of breeding from spring to winter and skipping reproduction in the worst conditions. Boobies showed the lowest flexibility, maintaining the same magnitude and timing of onset of breeding in spring. Pelicans showed intermediate flexibility, foregoing breeding during the worst conditions, but maintaining the onset of breeding in spring. The 3 species used sea surface temperature as a cue for the initiation of breeding. Furthermore, given their better diving abilities, cormorants could monitor prey availability changes associated with the reversion in the seasonality of the oxycline depth.

KEY WORDS: Onset of breeding · Environmental cues · Oxycline depth · NHCS · Northern Humboldt Current System · *Phalacrocorax bougainvillii* · *Sula variegata* · *Pelecanus thagus*

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INTRODUCTION

Birds have evolved to breed seasonally, partially as an adaptation to match breeding with optimal foraging conditions, which in most cases are predictable and restricted to a few months in the year. Seasonal

breeding is a life history trait that was acquired by the interaction of birds with the local environment on a long-term scale (Baker 1938). Although seasonal breeding is limited to a particular period in the year, birds exhibit some plasticity in the timing of breeding; from days to months (Reed et al. 2009). More-

over, seasonal breeding may be influenced by food availability; birds can skip annual reproduction as a consequence of food scarcity or relax breeding seasonality when food is abundant all year long (Lofts et al. 1966, Jenouvrier et al. 2005). During the last decades, plasticity in the timing of breeding has drawn attention, because as consequence of increased temperature due to climate change, some species of birds have advanced their timing of breeding to match the period of higher energy requirements and optimal foraging conditions (Crick et al. 1997, Walther et al. 2002, Parmesan & Yohe 2003).

Climate change can trigger sudden changes in ecosystems and disrupt differentially seasonal breeding in birds, depending on species-specific plasticity and their use of environmental cues (Durant et al. 2004, Visser 2008, Anderson et al. 2013). However, it is not the unique event causing disruption of breeding seasonality; other events at regional scales, such as El Niño in the Pacific Ocean, can cause failure of nesting and high mortality rates among young individuals (Duffy 1990).

In the Pacific Ocean, along with El Niño, interdecadal regime shifts are associated with major and sudden changes in ecosystems (Chavez et al. 2003). For example, in the North Pacific, a shift from cooler to warmer conditions occurred during the 1970s and was related to the Pacific Decadal Oscillation (Mantua et al. 1997). This regime shift caused an earlier seasonal peak in the abundance of zooplankton. Consequently, seabirds living in the area showed mixed responses; for example, Cassin's auklets *Ptychoramphus aleuticus* did not change their timing of breeding, with a consequent mismatch of breeding with the peak of zooplankton abundance. In contrast, rhinoceros auklets *Cerorhinca monocerata* advanced their timing of breeding (Bertram et al. 2001).

In the South Pacific Ocean during the 20th century, at least 3 different interdecadal regimes were reported for the Northern Humboldt Current System (NHCS) off Peru. These regimes impacted the abundance of small pelagic fish and consequently the seabird populations. In the NHCS, Peruvian anchovy *Engraulis ringens* and sardine *Sardinops sagax* are the dominant small pelagic fish (Salvatteci et al. 2014), with high abundances sustained by an extremely productive coastal upwelling system (Chavez et al. 2008). In turn, anchovy is the main prey of the most abundant seabirds: the Guanay cormorant *Phalacrocorax bougainvillii*, the Peruvian booby *Sula variegata* and the Peruvian pelican *Pelecanus thagus*. Although the dates of the interdecadal regime shifts are not precise because estimations are not based on *in situ* oceanographic

data (Alheit & Niquen 2004), the decades pre-1970s and post-2000 were characterized by intense near-coastal upwelling and high productivity that enhanced anchovy abundance. Conversely, the intermediate period was characterized by weaker near-coastal upwelling and relatively low productivity, which led to reduced anchovy habitat and benefited other species such as sardine, which increased in abundance and spread toward the continental shelf (Alheit & Niquen 2004, Bertrand et al. 2004, 2011, Swartzman et al. 2008). Moreover, in the NHCS, fisheries intensified the effects of interdecadal regime shifts. The rise of the industrial fishery during the 1960s resulted in reduced availability of forage fish to seabirds, even though anchovy was more abundant than ever before (Duffy 1983b). As a consequence, the seabird populations decreased from ~20 million individuals in the early 1960s to ~3 million individuals by the end of the decade. During the 1970s, a fully developed industrial fishery and a change of regime induced a collapse of anchovy stocks and a consequent decrease of seabird populations down to ~2 million individuals (Jordan 1963, Tovar Serpa et al. 1987, Tsukayama & Palomares 1987). At present, seabird populations fluctuate between ~2 and 3 million individuals, despite the recovery of anchovy stocks after 1990 (Gutiérrez et al. 2007).

In contrast to the North Pacific, little is known about the effects of interdecadal regime shifts on the seasonal breeding of these 3 seabird species in the NHCS. So far, we know that the 3 species have a marked seasonal breeding (Vogt 1942, Nelson 2005), and during the last decade (2003–2014), breeding began mainly in spring and terminated mainly in autumn. The onset of the breeding season coincided with the lowest primary and secondary production, and the independence of fledglings coincided with the highest primary and secondary production during the year (Passuni et al. 2016).

In this study, we extended the temporal coverage of our previous work to investigate how past regime shifts in the NHCS off Peru may have modified the breeding seasonality of the most abundant seabirds through changes in the seasonality of potential environmental cues used for timing breeding. We used a long-term dataset of presence/absence of breeding cormorants, boobies and pelicans on Isla Pescadores, covering 3 periods (1952–1968, 1977–1990 and 2003–2014) and coinciding with different regimes in the NHCS, to address 3 main questions: (1) Has the seasonality of the main environmental components, i.e. anchovy productivity and fishing pressure, changed

with those regime shifts? (2) Are there any changes in the timing and magnitude of the breeding seasonality of seabirds with regime shifts and do they differ among species? (3) Do the relationships between the onset of breeding and the environmental variables differ between periods?

MATERIALS AND METHODS

Study area and seabird data

The study was conducted on Isla Pescadores (11° 46' 22.8" S, 77° 15' 36" W, 16.45 ha, maximal altitude 50 m). The island is arid and uninhabited except by 1 or 2 wardens in charge of the protection and monitoring of seabird colonies. Isla Pescadores has been monitored since 1952 as part of a public program (AGRORURAL, www.agrorural.gob.pe) to record monthly abundance of breeding and non-breeding individuals in the most important colonies of cormorants, boobies and pelicans. Although the program includes more than 30 colonies, only Isla Pescadores has data available almost continuously since 1952 (Supplement 1 at www.int-res.com/articles/suppl/m597p231_supp.pdf): 1952–1968, 1977–1990 and 2003–2014.

The data series for 1952–1968 includes monthly presence/absence of breeders for each species. Individuals were considered breeders if they were observed incubating eggs, brooding or feeding chicks. The data series for 1977–1990 comprises mainly monthly percentages but also presence/absence of breeders by species. The most recent data series of 2003–2014 includes monthly counts of breeders by species. Therefore, for the last 2 periods, we converted abundance and percentage data to presence/absence data to obtain similar information for all 3 periods.

Oceanographic data

We used monthly oceanographic data collected by IMARPE and international cruises available in the World Ocean Database 2013 (Supplement 2) to build climatologies (monthly averages over years) coinciding with the 3 periods defined above. Oceanographic covariates were sea surface temperatures (SST; °C), surface chlorophyll *a* concentrations (chl *a*; mg m⁻³) and oxycline depths ($Z_{2\text{ml l}^{-1}}$; m). Chl *a* and SST reflected the annual variations of productivity in the ecosystem. $Z_{2\text{ml l}^{-1}}$ is the depth at which dissolved oxygen concentration is 2 ml l⁻¹ and is a proxy of the

upper limit of the oxygen minimum zone (Bertrand et al. 2010). $Z_{2\text{ml l}^{-1}}$ is also a good indicator of the vertical accessibility of forage fish to seabirds. Climatologies were built considering the main nesting sites of seabirds and their foraging range (Supplement 2). Differences between periods for oceanographic variables were tested with Kruskal-Wallis tests.

Anchovy data: abundance and catches

To explore the availability and abundance of anchovy, we used acoustic survey data (Supplement 3). We estimated regional abundance (s_A), local abundance (s_{A+}), spatial occupation index (ISO), depth and school height of anchovy schools. Although acoustic data were our most direct data to represent the availability of prey, these data were not available at a monthly scale. Therefore, we used anchovy production (in million tons, 10⁶ t) from an integrated assessment model (Oliveros-Ramos & Peña 2011) as a measure of potential anchovy abundance available to seabirds and the fishery. Anchovy production is the increase in population biomass due to somatic growth and birth rate without considering natural and fishing mortality and was estimated at monthly time steps. Anchovy production was built using acoustic estimates of biomass and anchovy length structure from scientific surveys and fishery landings between 7° and 18° S and from the coast to 100 km offshore. Differences between periods for anchovy abundance were tested with a Kruskal-Wallis test.

To represent fishing pressure, we used (as a covariate) the monthly landings of anchovy from industrial fisheries divided by the yearly quota. We built climatologies (monthly average over years) of the fishing pressure for the periods 1952–1968, 1977–1990 and 2000–2014.

Data were available from articles already published for the periods 1952–1968 and 1977–1990 (Tsukayama & Palomares 1987, Oliveros-Ramos & Peña 2011), and for the recent period they were provided by IMARPE (www.imarpe.gob.pe/imarpe/detallereport.php?id_seccion=I0131020101000000000000).

Modeling seabird seasonal breeding

We used dynamic occupancy models (MacKenzie et al. 2005) to make inferences about the occurrence of breeders as a dynamic process of onset (colonization) and termination (local extinction) of breeding

events using the monthly presence and absence of breeders for the 3 study periods (1952–1968, 1977–1990 and 2003–2014). Occupancy models were fitted using a Bayesian approach with JAGS (Plummer 2003) through jagsUI in R 3.1.3 (www.r-project.org). The algorithm used to generate pseudo-random number sampling in JAGS is a type of Markov chain Monte Carlo. We used 4 Markov chains with 100 000 iterations for each chain, with 1000 iterations to adapt, and we discarded the first 50 000 iterations as burn-in. We assessed model fit using the Gelman-Rubin diagnostic \hat{R} (Brooks & Gelman 1998). Model convergence was reached when \hat{R} for all parameters was <1.01 . We considered model parameters as significant when their posterior distribution did not overlap 0.

In a Bayesian framework, one of the more critical points is the selection of priors. We used informative priors after a comparison of posteriors (Supplement 4). We used the deviance information criterion (DIC, Spiegelhalter et al. 2002) to choose the suitable model to express onset of breeding. We selected the model with the lowest DIC with a minimum difference of 5 units between models. Four groups of occupancy models were built for each species: (1) null models, where onset and termination were constant through months and the 3 periods, (2) models where onset and termination of breeding varied between periods, (3) models where onset and termination of breeding varied between months regardless of periods, (4) models where onset and termination of breeding varied between months and periods.

We adapted the dynamic occupancy models to vary between months (t) by defining the occurrence of breeders in Month 1 ($z_{i,1}$) for year i as a Bernoulli trial process: $z_{i,1} \sim \text{Bernoulli}(\psi_1)$. In later months, the occurrence of breeders ($z_{i,t}$) in year i was modeled as a Bernoulli process with a success parameter that depended on 2 factors, the occurrence of breeders in the previous month ($z_{i,t-1}$) and on the value of either an onset of breeding (γ_{t-1}) or a termination (ε_{t-1}) of breeding according to the relationship:

$$z_{i,t} | z_{i,t-1} \sim \text{Bernoulli} [z_{i,t-1} \times (1 - \varepsilon_{t-1}) + (1 - z_{i,t-1}) \times \gamma_{t-1}] \quad (1)$$

The probability of onset of breeding events (γ_{t-1}) was defined as the probability that a site unoccupied by breeders in month $t - 1$ (i.e. $z_{i,t-1} = 0$) was occupied by breeders in month t . The probability of termination of breeding events (ε_{t-1}) was defined as the probability that a site occupied by breeders in month $t - 1$ (i.e. $z_{i,t-1} = 1$) was unoccupied by breeders in month t . Occupancy models were developed to produce un-

biased estimates of occurrence when the probability of detecting species is <1 (MacKenzie et al. 2005). However, in our case, given the absence of vegetation on Isla Pescadores, the large size of conspicuous nesting seabird colonies and the permanent presence of wardens, we considered that probability of detection was equal to 1.

Modeling the effect of covariates

We worked only with the onset of breeding and dropped the termination of breeding after we noticed the low identifiability of termination (Supplement 5). After having defined the most suitable model to represent the onset of breeding, and within the same framework of occupancy modeling, we evaluated at a monthly scale the effect of oceanographic and prey covariates over the onset (γ_t) of breeding events using a logistic regression. The functional linear relationship between the *logit*-transformed parameter was $\theta_{t-1} = \gamma_{t-1}$ and the covariate x_i was $\text{logit}(\theta_{t-1}) = \beta_0 + \beta_1 x_{t-1}$, where β_0 and β_1 were, respectively, the intercept and slope parameters to be estimated. The intercept and slope parameters were indicated with mean \pm SD and their significance level with f . We considered the relation as significant when $f > 0.95$.

RESULTS

Seasonality of oceanographic conditions among interdecadal regimes

The oceanographic conditions presented a moderate to strong seasonality during the 3 periods. SST patterns remained similar, but chl a and Z_{2ml-1} changed in timing (Fig. 1a–c). For the 3 interdecadal periods, the warmest waters ($\sim 21^\circ\text{C}$) were recorded at the end of summer (March), whereas the coldest waters ($\sim 17^\circ\text{C}$) were observed during winter and early spring (July–October) (Fig. 1a). The average SSTs for the 3 periods were similar (mean \pm SE; $18.2 \pm 2.2^\circ\text{C}$ for 1952–1968, $18.3 \pm 2.2^\circ\text{C}$ for 1977–1990 and 17.9 ± 2.4 for 2003–2014, $\chi^2 = 1.01$, $p = 0.60$), although slightly warmer fall (April–June) and spring (November–December) were observed during 1977–1990 compared with the other periods. Z_{2ml-1} was the oceanographic parameter that exhibited the strongest interdecadal changes in seasonal variability (Fig. 1b). During 1952–1968 and 2003–2014, the oxycline (>40 m) was deeper in winter (July–September),

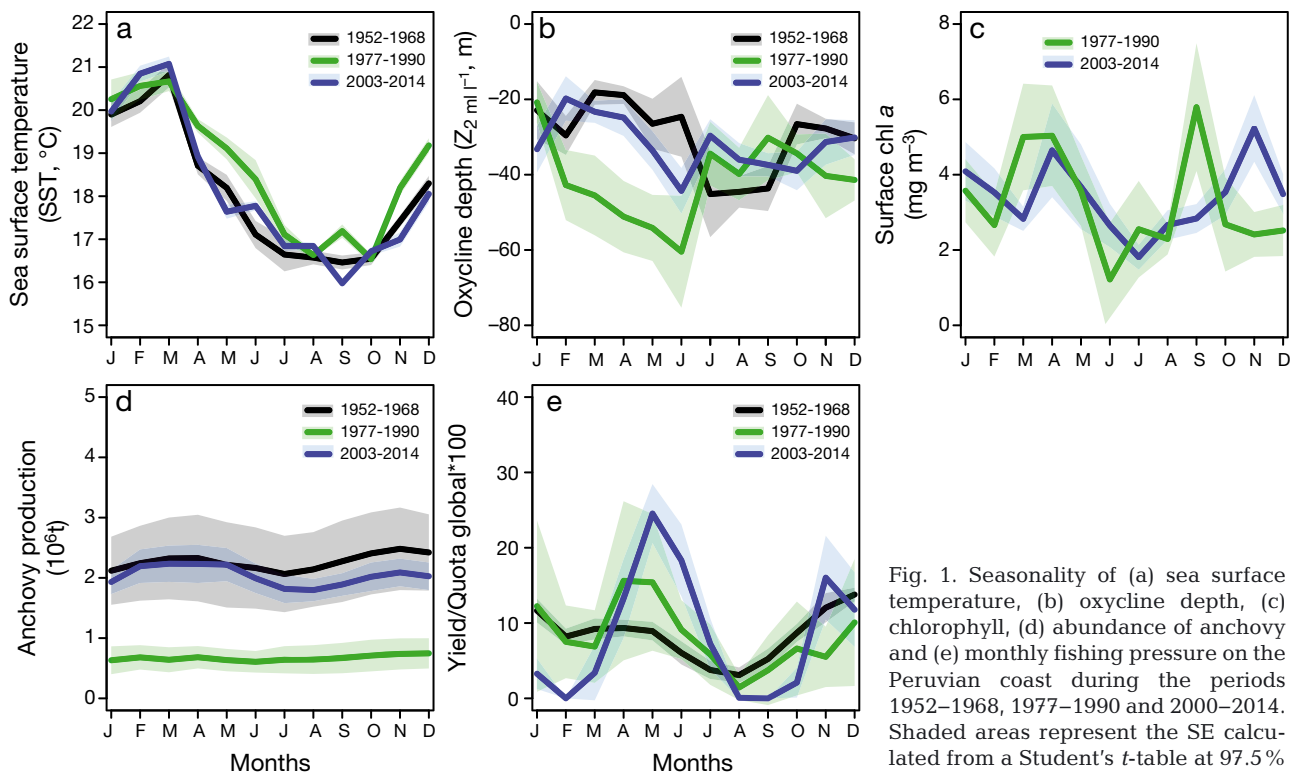


Fig. 1. Seasonality of (a) sea surface temperature, (b) oxycline depth, (c) chlorophyll, (d) abundance of anchovy and (e) monthly fishing pressure on the Peruvian coast during the periods 1952–1968, 1977–1990 and 2000–2014. Shaded areas represent the SE calculated from a Student's *t*-table at 97.5%

whereas during 1977–1990 it was deeper in summer and autumn (February–June). Also, $Z_{2ml\ l^{-1}}$ was in general much deeper during 1977–1990 (mean \pm SE; 41.3 ± 10.8 m) than in the other periods (29.9 ± 9.5 m for 1952–1968 and 31.9 ± 7.0 m for 2003–2014, $\chi^2 = 7.96$, $p = 0.02$). For chl *a*, there were 2 peaks in the year of similar intensity (>4 mg m^{-3}). There was a common peak for 1977–1990 and 2003–2014 in autumn (March–April), but the second peak was in early spring in 1977–1990 (September) and later in 2003–2014 (November, Fig. 1c). The averages of chl *a* were similar for the 2 periods (mean \pm SE; 3.2 ± 3.4 mg m^{-3} for 1977–1990 and 3.2 ± 3.5 mg m^{-3} for 2003–2014, $\chi^2 = 59$, $p = 0.48$).

Seasonality of anchovy availability and fishing pressure among interdecadal regimes

Monthly anchovy production showed a weak seasonality during 1952–1968 and 2003–2014 and a lack of seasonality during 1977–1990 (Fig. 1d). During 1952–1968 and 2003–2014, a weak semi-annual cycle emerged with a lower production of anchovy during June–August and December–January and higher production during November–December and February–May. These 2 peaks in the year were of similar

magnitude during 1952–1968 but not during 2003–2014, when the February–May peak prevailed. Average values of anchovy production showed significant differences between periods ($\chi^2 = 31.13$, $p < 0.001$), being much weaker during 1977–1990 (mean \pm SE; 2.3 ± 1.3 Mt for 1952–1968, 0.7 ± 0.3 Mt for 1977–1990 and 2.0 ± 0.4 Mt for 2003–2014). These differences in anchovy production between periods were consistent with acoustic data. During 1977–1990, anchovy were less abundant and formed denser and deeper schools in smaller favorable habitat (mean \pm SE; $s_A = 1.8 \pm 1.3$, $s_{A+} = 4.1 \pm 0.7$, school depth = 14.6 ± 2.6 m and ISO = 41.1 ± 26.8) while during 2003–2014, anchovy were more abundant and formed shallower schools that spread in a larger favorable habitat ($s_A = 2.7 \pm 0.9$, $s_{A+} = 5.5 \pm 0.8$, school depth = 12.6 ± 3.8 m and ISO = 49.6 ± 12.5).

Fishing pressure (percentage of monthly landings of anchovy from global quota) had a weak seasonality during 1952–1968, a moderate seasonality for 1977–1990 and a strong seasonality for the period 2003–2014. (Fig. 1e). For the 1952–1968 period, fishing pressure was lower in winter and constant during the rest of the year; in 1977–1990, fishing pressure was higher during summer and autumn, and in 2003–2014, fishing seasons were restricted to April–July and November–December.

Seasonality of breeding seabirds among interdecadal regimes

In general, the 3 species presented clear breeding seasonality during the 3 periods, with onset during austral spring, except for species-specific changes in magnitude and timing of the monthly probability of onset of breeding after regime shifts (Fig. 2).

A notable exception to the onset of breeding in austral spring is the timing of breeding for cormorants during 1977–1990 and 2003–2014. Cormorants presented differences in the seasonal onset of breeding among interdecadal periods (Table 1). The onset of breeding occurred in 2 main peaks, one in austral winter and another in austral spring (Fig. 2a–c), but depending on the interdecadal period, one of the peaks predominated over the other in terms of length or magnitude. During 1952–1968, the spring peak (September–November) was clearly predominant over the winter peak (May–August). In contrast, during 1977–1990, the spring peak was considerably reduced while

the winter peak (June) remained at the same level as in the previous period. During 2003–2014, the winter peak remained predominant over the spring peak, and the magnitude of the 2 peaks increased compared to 1977–1990 but did not reach the levels observed during 1952–1968 (Fig. 2a–c).

Boobies presented no difference in seasonal onset of breeding between periods (Table 1). The onset of breeding occurred in spring (between September and November) with similar magnitude during the 3 periods (Fig. 2). Likewise, pelicans presented no dif-

Table 1. Models used to test time variation in probabilities of breeding onset (γ) and breeding termination (ε) in Guanay cormorants, Peruvian boobies and Peruvian pelicans. Models with the minimum deviance information criterion (DIC) were selected (indicated in **bold**). p : period; t : month

| Model | DIC | | |
|---|---------------|----------------|---------------|
| | Cormorant | Booby | Pelican |
| Model constant through months and periods (γ, ε) | 397.24 | 458.62 | 222.84 |
| Model with a period effect (γ_p, ε_p) | 389.01 | 460.76 | 220.84 |
| Model with a month effect (γ_t, ε_t) | 367.47 | 423.772 | 188.10 |
| Model with month and period effects ($\gamma_{t,p}, \varepsilon_{t,p}$) | 361.98 | 433.57 | 190.47 |

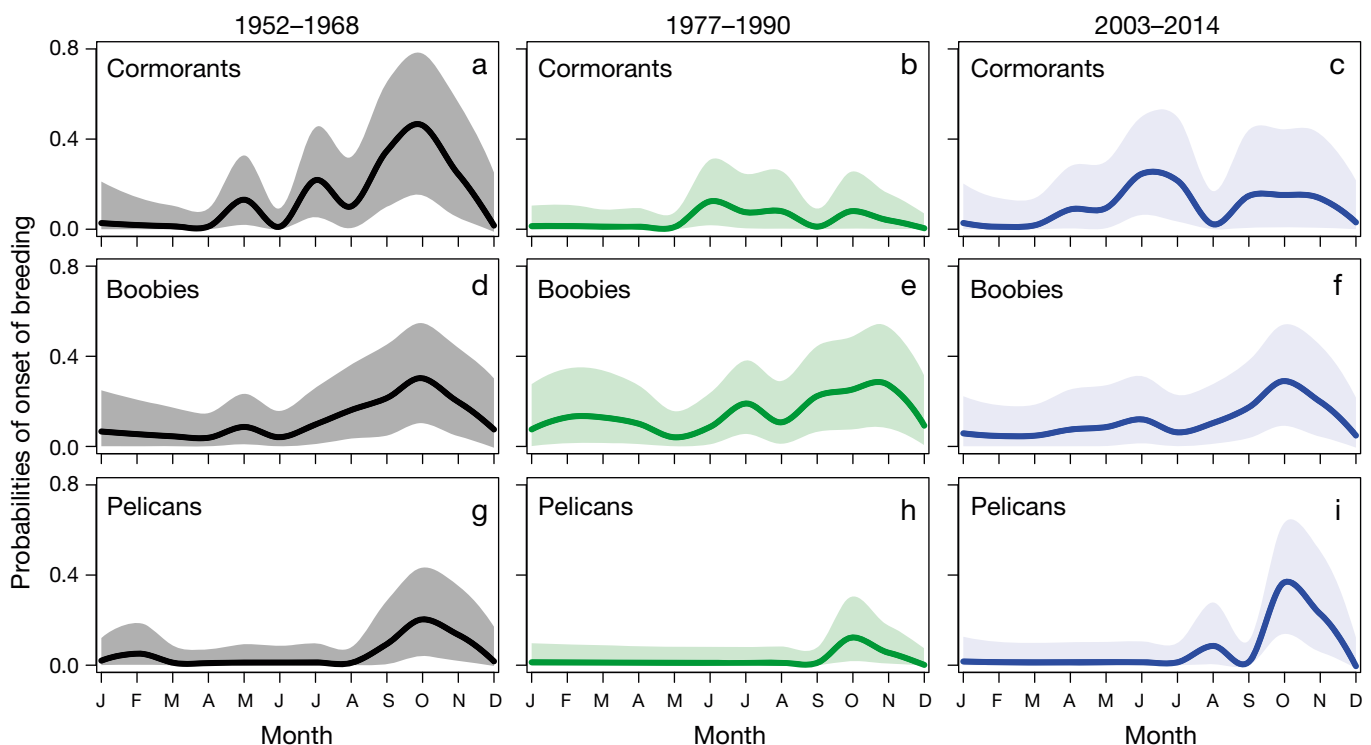


Fig. 2. Monthly average estimates of probability of the onset of breeding during the periods 1952–1968, 1977–1990 and 2003–2014 for (a–c) Guanay cormorants, (d–f) Peruvian boobies and (g–i) Peruvian pelicans. Shaded areas represent the 5% and 95% quantiles of the posterior distribution of monthly probability of the onset of breeding. Breeding onset probabilities were slightly smoothed using a loess model with a span value of 0.45

ference in seasonal onset of breeding between periods (Table 1). Pelicans had a similar timing of onset of breeding in spring (between September and November, Fig. 2g–i). However, probabilities of onset of breeding had different magnitudes between periods; the lowest probabilities were recorded during 1977–1990 and the highest during 2003–2014 (Fig. 2).

Effects of environmental conditions on breeding seasonality

SST was negatively related to the onset of breeding for the 3 species and the 3 periods (Table 2, Fig. 3a–c). Relationships between Z_{2ml}^{-1} and the onset of breeding differed among periods and species (Table 2, Fig. 3d–f). They were positive during the 3 periods for cormorants (Fig. 3d), but differed among periods for boobies, being positive during 1952–1968 and 2003–2014 and negative during 1977–1990 (Fig. 3e). Likewise, relationships between Z_{2ml}^{-1} and the onset of breeding of pelicans differed among periods, being negative during 1952–1968 and 1977–1990 and positive during 2003–2014 (Fig. 3f). Chl *a* was negatively related to the onset of breeding for cormorants, but positively to the onset of breeding for boobies during 1977–1990 and 2003–2014 (Table 2, Fig. 3g,h). Meanwhile, relationships between chl *a* and onset of breeding for pelicans differed between periods: positive during 1977–1990 and negative during 2003–2014 (Fig. 3i).

There were strong positive relationships between anchovy production and the onset of breeding for all 3 species for 1952–1968, which weakened during

1977–1990 and became negative during 2003–2014 (Fig. 3j–l, Table 2). Fishing pressure was positively related to the onset of breeding of the 3 species during 1952–1968 (Table 2). Afterwards, there was some evidence for negative relationships between fishing pressure and the onset of breeding for the 3 species during 1977–1990 and 2003–2014.

DISCUSSION

Similar to other biological components of the NHCS, seabird populations experienced large inter-decadal changes with regime shifts. Our study showed that during the 3 periods, breeding of the 3 seabird species remained seasonal, as previously stated (Passuni et al. 2016), but the timing and magnitude of the probability of onset of breeding events varied among periods and species. These differences in timing and magnitude of onset of breeding events between species are discussed in relation to the oceanographic and prey changes resulting from the regime shifts.

Environmental variability of the NHCS at the decadal scale

In the NHCS, the decadal regime shift during the early 1970s strongly affected the thermocline and oxycline depths, with shallow values in the 1960s, a deepening during the 1970s, a maximum depth during the 1980s and back to shallow conditions during the 1990s–2000s (Bertrand et al. 2011). Our results

Table 2. Summary of model outputs relating sea surface temperature (SST), depth of the oxycline (Z_{2ml}^{-1}), chl *a*, anchovy secondary production and fishing pressure to the probability of onset (γ) of breeding in 3 species: Guanay cormorant, Peruvian booby and Peruvian pelican. Values are mean \pm SD of the slope parameters, with the parameter *f* (i.e. the proportion of the posterior distribution with the same sign as the mean) in parentheses. To consider a slope significant (indicated in **bold**), *f* must be >0.95 . –: chl *a* data not available from 1952–1968

| | Cormorant | | | Booby | | | Pelican | | |
|--------------------|--|--|--|--|--|--|---|--|--|
| | 1952–1968 | 1977–1990 | 2003–2014 | 1952–1968 | 1977–1990 | 2003–2014 | 1952–1968 | 1977–1990 | 2003–2014 |
| SST | -1.82 ± 0.84 (0.99) | -1.76 ± 1.00 (0.97) | -1.51 ± 0.76 (0.99) | -2.05 ± 0.94 (1.00) | -0.98 ± 0.54 (0.97) | -2.39 ± 0.94 (1.00) | -0.29 ± 0.71 (0.64) | -2.96 ± 1.67 (0.98) | -2.36 ± 1.09 (1.00) |
| Z_{2ml}^{-1} | 0.18 ± 0.71 (0.60) | 0.62 ± 1.00 (0.73) | 2.06 ± 1.16 (0.98) | 0.17 ± 0.77 (0.59) | -1.44 ± 0.67 (0.99) | 3.17 ± 1.34 (1.00) | -1.24 ± 1.16 (0.86) | -1.57 ± 1.49 (0.86) | 2.64 ± 1.52 (0.98) |
| Chl <i>a</i> | – | -3.07 ± 1.44 (1.00) | -1.07 ± 1.22 (0.81) | – | 0.11 ± 0.63 (0.58) | 0.95 ± 1.23 (0.78) | – | 2.47 ± 2.34 (0.86) | -1.10 ± 1.63 (0.75) |
| Anchovy production | 4.16 ± 2.07 (0.98) | 1.06 ± 2.34 (0.67) | -2.09 ± 1.99 (0.85) | 4.63 ± 2.12 (0.99) | 2.24 ± 2.27 (0.84) | -1.89 ± 2.00 (0.83) | 3.86 ± 2.35 (0.97) | 2.56 ± 2.38 (0.86) | -1.56 ± 2.20 (0.76) |
| Fishing pressure | 1.14 ± 0.94 (0.90) | -1.23 ± 1.08 (0.88) | 0.38 ± 0.40 (0.83) | 1.83 ± 1.01 (0.98) | -1.50 ± 0.68 (0.99) | -0.30 ± 0.47 (0.74) | 3.43 ± 1.38 (1.00) | -0.82 ± 1.44 (0.41) | -0.98 ± 0.69 (0.94) |

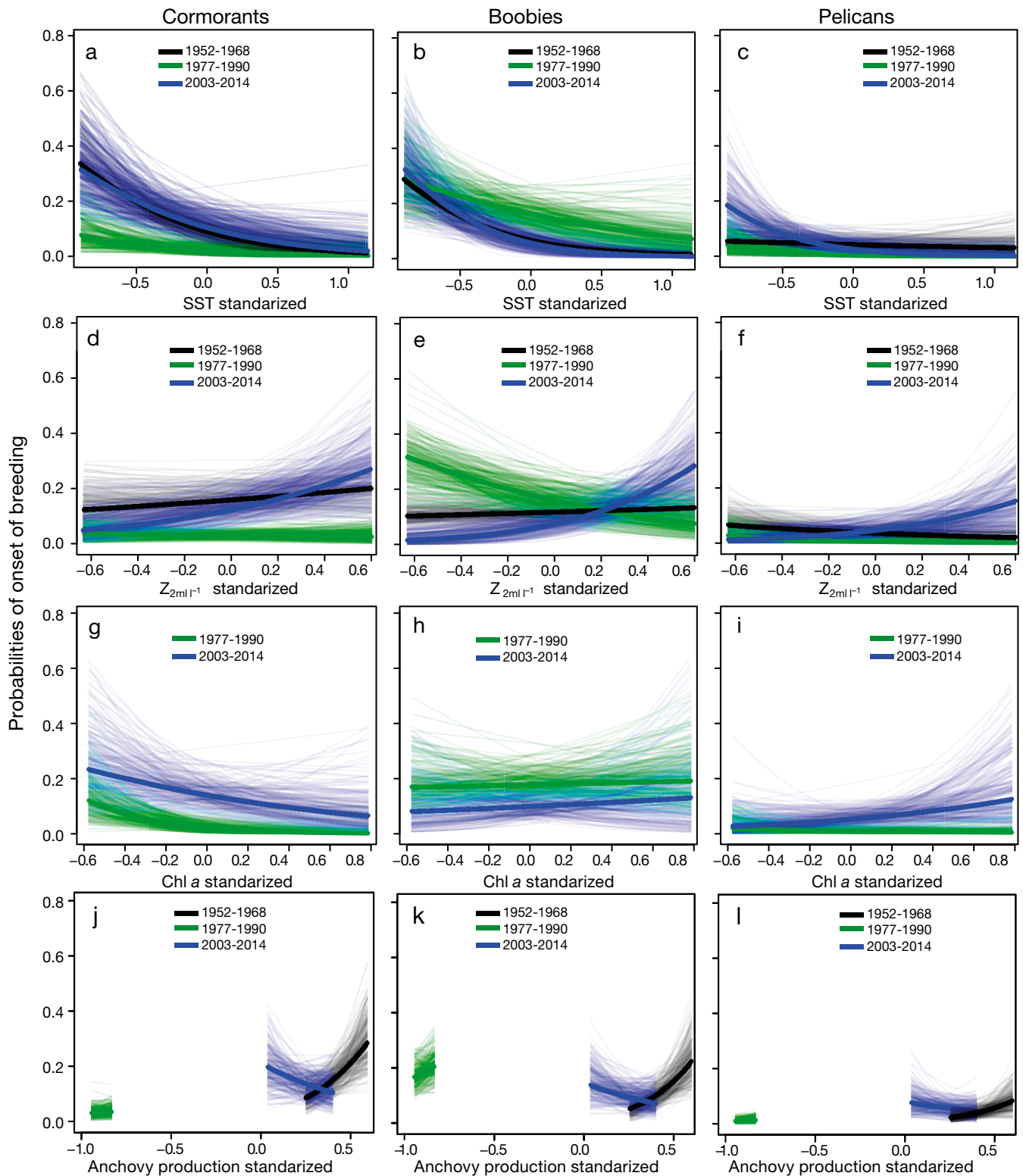


Fig. 3. Modeled probabilities of breeding onset as a function of the standardized mean of (a–c) sea surface temperature (SST), (d–f) oxycline depth $Z_{2m|l-1}$, (g–i) chl a and (j–l) anchovy abundance during the periods 1952–1968, 1977–1990 and 2003–2014 for Guanay cormorants (left column), Peruvian boobies (middle column) and Peruvian pelicans (right column). The functional relationships were obtained from the models with time and period effects for each species. Thin lines represent the 200 simulations, while solid lines represent the medians of these simulations

revealed that the 1970–1990 period had a reversal of the oxycline seasonal dynamics compared to 1952–1968 and 2003–2014. During 1952–1968 and 2003–2014, the oxycline was deeper in winter and shallower in summer, while the reverse was observed during 1977–1990. Reversion in oxycline depth patterns may have consequences on the community of the NHCS, as oxycline depth affects available vertical habitat for pelagic species. This reversion of the oxycline can be related to previous studies that found that most life was concentrated in a shallow layer during periods with a shallower oxycline, boosting up the energetic transfer from phytoplankton to zooplankton and fish. In contrast, during periods with a deeper oxycline, this energetic transfer was less efficient (Ayón et al. 2011, Bertrand et al. 2011).

Interdecadal differences in anchovy abundance were remarkable, with higher anchovy abundance during 1952–1968 and 2003–2014 than during 1977–1990. Indeed, the 1960s was the decade with the highest anchovy abundance (Tsukayama & Palomares 1987). During the periods 1952–1968 and 2003–2014, the relatively cold coastal water arising from the near-coastal upwelling expanded offshore, thus increasing the habitat favorable to anchovy and leading to a higher recruitment success of anchovy. In contrast, during 1970–1990, the warmer offshore Surface Subtropical Water approached closer to the coast, providing habitat favorable to sardine (Swartzman et al. 2008). Moreover, the lack of seasonality in anchovy abundance during 1977–1990 may be related to the effects of recurrent El Niño events, which, combined with the low abundance of the adult stock and an intensive fishery, was not conducive to successful reproduction of anchovy (Jordan 1976, Oliveros-Ramos & Peña 2011).

Effects of regime shifts on the magnitude of the onset of seabird breeding

The lower magnitudes of the onset of breeding observed in cormorants and pelicans during the period 1977–1990 following the 1970s regime shift suggest that these species were less likely to breed at Isla Pescadores. Lower breeding probability on Isla Pescadores was probably mainly caused by the low abundance and aggregation at the regional level of the main prey (anchovy) during the 1977–1990 period (Tovar & Guillen 1987, Guillen 1992). Lower prey accessibility due to the deepening of the oxycline depth may be an additional factor, particularly for pelicans, which feed by surface seizing (Duffy

1983a, Zavalaga et al. 2011), but less likely for cormorants since their diving capacities surpassed the deepening of the oxycline that limits anchovy habitat during less productive and low-oxygen periods (Weimerskirch et al. 2012).

Two non-exclusive mechanisms may explain this lower breeding probability: either the seabirds emigrated from Isla Pescadores or they were there but skipped breeding. Limited available data on the mean proportion of breeders on Isla Pescadores (AGRO-RURAL unpubl. data) evidenced that a great proportion of adult cormorants skipped breeding during the 1977–1990 period (proportion of breeding cormorants during 1977–1990 was 47%, compared to 60% during 2003–2014). Cormorants may skip breeding as an extreme adjustment of breeding effort in order to minimize future fitness costs as has been reported for other seabirds, including other cormorant species, during years of low prey abundance (Nur & Sydeman 1999, Reed et al. 2015). An alternative reason for desertion of colonies on Isla Pescadores is emigration of breeders to other colonies with higher abundance of anchovy. Although information is lacking on the dispersal between colonies at the individual level, there were reports of higher concentrations of the 3 seabird species around 8° S associated with concentrations of anchovy after the El Niño of 1982–1983 (Guillen 1992). Additionally, maximum abundances of cormorants on Isla Pescadores (AGRO-RURAL pers. comm.) were lower in 1977–1990 ($\approx 195\,500$ individuals) than in 2003–2014 ($\approx 730\,000$).

In contrast to cormorants, boobies had similar probabilities of breeding during all periods. This suggests that breeding seasonality of boobies was affected relatively little by changes in oceanic regimes, prey abundance and accessibility. The lower effect of regime shifts on the magnitude of breeding onset in boobies compared to cormorants and pelicans is further supported by the larger population decrease of cormorants (up to 85%) and to lesser extent pelicans (22%) from 1952–1968 to 1977–1990 than that of boobies (7%) (Barbraud et al. 2017). Several non-exclusive hypotheses could explain lower sensitivity of boobies. First, due to their smaller size, boobies (Supplement 6) probably need less prey for maintenance requirements than cormorants and pelicans (256 g wet weight anchovy d^{-1} for boobies, 320 g d^{-1} for cormorants and 620 g d^{-1} for pelicans, Bertrand et al. 2012). In addition, species with smaller body size are able to more efficiently exploit low-density fish schools (Piatt 1990). Second, the foraging strategy of boobies may be more advantageous than that of cor-

morants during the low abundance of anchovy. Boobies, contrary to cormorants, leave colonies solitarily to search for prey and rely on personal information based on memory to forage (Weimerskirch et al. 2010), which may facilitate locating prey schools at low abundance. Boobies can travel larger distances to forage on fish than cormorants and pelicans (Zavalaga et al. 2011, Weimerskirch et al. 2012). Moreover, boobies may rely more on marine mammals such as southern sea lions *Otaria flavescens* to detect prey concentrations than cormorants or pelicans do (Duffy 1983a), which may facilitate locating foraging patches when prey abundance is low.

The interspecific differences in the magnitude of probabilities of onset of breeding during different regimes in the ecosystem can also result from differences in species-specific life history traits. Boobies have notably lower chick growth, and longer chick rearing and post-fledging periods than cormorants and pelicans (Supplement 6; Duffy & Ricklefs 1981, Nelson 2005). During a food shortage, slower growth and longer time of chick rearing may be seen as an adaptation (Schreiber 1994), and during 1977–1990, boobies may have had fewer immediate energetic constraints than the other 2 species, enabling the maintenance of breeding activities.

Effects of regime shifts on the timing of the onset of breeding

For the 3 periods and species, the onset of breeding in spring or winter was systematically related to lower SST. Seabird species may use low SST during winter and early spring as a precursor of primary production (Afan et al. 2015). In the NHCS, lower SST is a cue of favorable upwelling conditions and a precursor of primary and secondary production later in the year (Zuta & Guillén 1970). Another cue followed by the 3 species could be the abundance of anchovy regardless of fisheries and natural mortality, at least before the mid-1960s when intensive fisheries of anchovy began. Indeed, high anchovy abundance in spring coincided with the onset of breeding during 1952–1968, but this relationship disappeared after the crash of anchovy stocks during the 1970s.

Timing of the onset of breeding appeared more flexible in cormorants. The onset of breeding typically occurred in spring in 1952–1968 and probably also between 1915 and 1941 (Vogt 1942). However, it was also reported that during years with unusual climate conditions, such as 1954, the onset of breeding occurred in winter (Graves et al. 1955). The onset of

breeding in winter became prevalent during 1977–1990 and remained equally important as onset in spring during 2003–2014. This longer period of onset of breeding was similar to the mean seasonal breeding pattern found in the last decade for the entire Peruvian coast (Passuni et al. 2016).

Therefore, cormorants may use other alternative cues apart from SST to fine-tune reproduction. One of these cues can be oxycline depth. Unlike boobies and pelicans, the onset of breeding was positively related to oxycline depth regardless of the period considered. We speculate that the change in timing of the onset of breeding in cormorants may be partly explained by the reversion in seasonality of the oxycline depth during 1977–1990. Since cormorants can dive, they could time reproduction using oxycline depth as a cue so that fledglings meet optimal conditions when becoming independent (i.e. lower oxycline depth and better availability of anchovy), as suggested by Passuni et al. (2016).

The relation between anchovy production and onset of breeding was not consistent enough over the different periods to be considered as an environmental cue. Non-consistency may be due to the differential fishing pressure among periods that disrupted the probable relationship between seasonality of anchovy production and onset of breeding. During the 1950s, a persistent high abundance of anchovy and low intensive fishery spread along the year may have resulted in a weak seasonality of production of anchovy concomitant with the onset of breeding of seabirds. After the 1970s, the ‘race for fish’ generated by a fleet overcapacity of up to 72% produced short fishing seasons and anchovy removals that were very concentrated in time (Fréon et al. 2008), probably disrupting the relationship between anchovy production and onset of seabird breeding.

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