# MODEL DYNAMICS

## Age-structured population dynamics

Bird populations were represented with 4 age classes, including 3 juvenile classes (age-0 chicks, age-1, and age-2). Adults were lumped into a single age-3+ category.

Juvenile mortality was fixed at zero, which had the effect of lumping the mortality that occurred during a cohort’s juvenile years into the recruitment relationship. Recruitment therefore represented adult-to-adult recruitment. For juveniles:

The adult population in year *y* was calculated as:

The model allowed adult birds to skip breeding. The skipping rate, , varied by year, depending on conditions. The expected colony count, *CC*, was estimated as the number of mature adults () who didn’t skip breeding. To align the decision to skip breeding with the conditions that affected survival and reproduction of the parents, the year subscript on the skipping variable was *y-1*.

Reproduction was modeled using a Beverton-Holt equation, based on the colony count, *CC*, and also allowing productivity (p) and carrying capacity (c) to vary by year as a function of environmental conditions:

## Covariates

Past studies have suggested that all three species of birds are dependent on anchoveta biomass. Anchoveta and bird populations are affected by El Niño events. In addition to a reduction in upwelling which affects primary productivity, during El Niño events the oxygen minimum layer sinks deeper, possibly making it easier for anchoveta to escape from avian predators. In addition, it is theorized that disturbance from fishing can scatter the anchoveta schools, making them less accessible to foraging seabirds; we use fishing mortality (F) as a proxy for fishing pressure.

*Anchoveta biomass*. We used time series for anchoveta spawning stock biomass from a model by Carl Walters that used a fitted population dynamics model plus a set of empirically-derived recruitment deviations from the model.

*Fishing mortality*. The fishing mortality timeseries, F, also came from the Walters model [we need to clarify exactly which time series we’re using).

*El Niño events*. We used a nearshore NOAA sea-surface temperature El Niño index called EN\_ICEN (documentation [here](http://www.met.igp.gob.pe/publicaciones/2014/ElNino_v2_27_03_2014_7.pdf)), which varies from about -3 (strong La Niña) to 3.5 (strong El Niño). We assumed that the main impacts on breeding birds--including desertion of the colony, loss of chicks or, in severe events, adult mortality--would occur during late chick rearing, when adults are most stressed. Assuming that in general the main breeding season occurs in August-November in a given year *y*, we used an index of the average monthly values from May-July in calendar year *y+1* as our index of El Niño conditions.

Note: We have not (yet) tried using oxygen minimum layer (ULOMZ) as a covariate, because the EN\_ICEN timeseries we have is twice as long as the ULOMZ time series. We are hoping to get access to more ULOMZ data, which may prove to be a better predictor of anchoveta availability.

## Assessing the influence of covariates

To assess the influence on bird populations of the covariates 1) an El Niño index (*EN*), 2) the anchoveta spawning stock biomass (*A*), and 3) the anchoveta fishing mortality rate (*F*), the model included a linear response to those covariates in each year in four parameters: the Beverton-Holt productivity parameter ; the Beverton-Holt carrying capacity parameter, the adult survival rate *;* and the skipping rate:

1. The Beverton-Holt productivity parameter was modeled as:

where is the average value of the Beverton-Holt productivity parameter, *p*; is the El Niño index in year y; is the anchoveta spawning stock biomass (estimated by the Walters model) in year *y*; and and are fitted coefficients. On the assumption that bad conditions occurring at any time during the juvenile years could cause mortality in the juvenile cohort, we used the worst conditions experienced during the cohort’s juvenile years (y to y+2) in equation 5; this meant using a moving window that contained the maximum value of the El Niño index, the maximum value of fishing mortality, F, and the minimum spawning stock biomass of anchoveta.

1. The Beverton-Holt carrying capacity parameter, c, was allowed to vary in response to anchoveta abundance, *A*:

We used the number dying at the largest observed population size as a prior for mean carrying capacity, , with an uninformative prior (mean 0, standard deviation 1) for.

1. The adult survival rate was modeled as:

where , , and were fitted. We used a prior for the average adult survival rate, equal to (1 – the base adult mortality rate), and uninformative priors (mean 0, standard deviation 1) for, and .

1. The skipping rate was calculated as:

🡺Clarify the timing for the manuscript

where the mean skipping rate, , and the parameters , and were fitted, using uninformative priors (mean 0, standard deviation 1) for , and . The mean skipping rate is unknown but presumed to be low. We set the prior for the mean skipping rate at 10%. Furthermore, to reduce the flexibility of the model and prevent the skipping rate from being overly sensitive to the value of the El Niño index when the index was in negative territory (i.e., good conditions), we set all El Niño index values to zero if they fell below the threshold of 1;

## Fitting

We fitted the average values and coefficients as just described, as well as the initial adult population size*,* .

, and were fitted in log space to avoid negative values, and was bounded above by the maximum number of offspring per female for the species (1.5 chicks for cormorants and pelicans, and 2 chicks for boobies). The righthand sides of equations 7 and 8 were arctan-transformed for fitting, to bound the skipping rate and the survival rates within the interval [0,1].

# DATA PROVENANCE

*Hi John*

*The data you have for 1953 through 1983 are essentially the same as those reported by Jahncke 1998 (see attached). I believe the 1953-1982 data were originally reported by Tovar, H., and D. Cabrera, Las aves guaneras y el fenomeno "El*

*Nino," Bol. Inst. Mar Peru, vol. extraordinario, 181-186, 1985. I have a paper copy of Jahncke 1998, which I can scan for you if that would be useful, but not Tovar & Cabrera 1985. (I also have a copy of Tovar 1987, but that provides data summaries, not annual counts.) According to Jahncke, the 1983 data come from Duffy et al (1987).*

*From 1984 onwards, the data you have differ from the data reported by Jahncke 1998. Jahncke took his data for 1984-1989 from Guillen (1992). Jahncke (1998) is the source publication for Jahncke's 1990-1996 data.*

*Jahncke states that the data from 1953-1989 are annual averages [based on monthly counts], whereas the  data for 1990-1996 are the average of censuses for March, July, and November.*

*It may be that Jahncke's data from 1984 onwards include non-breeding birds, whereas your data are only for the breeding colonies because Jahncke's data are generally higher.*

*It does seem fairly clear, though, that the data are based on calendar year rather than breeding year, and are averaged over some or all months. Given that breeding peaks in September-December for both the cormorants and boobies, the average for year Y is probably generally still driven by numbers of breeding birds in Sep-Dec of year Y, but it may also include numbers from Jan-Mar in year Y.*

*cheers*

*Charlotte*