# A bird-eye view on the spatio-temporal variability of the seasonal cycle in the Northern Humboldt Current System : the case of Guanay cormorant, Peruvian booby and Peruvian pelican

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*To the all hard working women*

*Aves estercolarias de las islas,*
*multiplicada voluntad del vuelo,*
*celeste magnitud, innumerable*
*emigración del viento de la vida,*
*cuando vuestros cometas se deslizan*
*enarenando el cielo sigiloso*
*del callado Perú, vuela el eclipse.*
*Oh lento amor, salvaje primavera*
*que desarraiga su colmada copa*
*y navega la nave de la especie*
*con un fluvial temblor de agua sagrada*
*desplazando su cielo caudaloso*
*hacia las islas rojas del estiércol.*

*Yo quiero sumergirme en vuestras alas,*
*ir hacia el Sur durmiendo, sostenido*
*por toda la espesura temblorosa.*
*Ir en el río oscuro de las flechas*
*con una voz perdida, dividirme*
*en la palpitación inseparable.*
*Después, lluvia del vuelo, las calcáreas*
*islas abren su frío paraíso*
*donde cae la luna del plumaje,*
*la tormenta enlutada de las plumas.*

*El hombre inclina entonces la cabeza*
*ante el arrullo de las aves madres,*
*y escarba estiércol con las manos ciegas*
*que levantan las gradas una a una,*
*raspa la claridad del excremento,*
*acumula las heces derramadas,*
*y se prosterna en medio de las islas*
*de la fermentación, como un esclavo,*
*saludando las ácidas riberas*
*que coronan los pájaros ilustres.*
*(Phalacro-corax XXII, Canto General. Pablo Neruda)*

# Abstract

The Northern Humboldt Current System (NHCS) is a place of a high biological activity due to an intense coastal upwelling. It supports one of the biggest forage fish populations, the Peruvian anchovy, and the world-leading monospecific fishery in terms of landings. The NHCS also hosts large, although variable, seabird populations, composed among others by three guano-producing sympatric species: the Guanay cormorant (*Phalacrocorax bougainvillii*), the Peruvian booby (*Sula variegata*) and the Peruvian pelican (*Pelecanus thagus*), which all feed primarily on anchovy.

In this work we reviewed the fluctuations of these three seabird populations, focusing on the seasonal cycle of their breeding, to address the following questions: How different are the seasonality of reproduction among species? To what extent may they be plastic in space and time? What from the natural environment and the anthropogenic activities impact more the breeding of seabirds?

We addressed these questions using the monthly occupancy of breeders (1) in >30 Peruvian sites between 06°S and 18°S and from 2003 to 2014; and (2) in one site during three decadal periods (1952-1968, 1972-1989, 2003-2014). We also used environmental covariates from satellite and at-sea monitoring such as oceanographic conditions, prey abundance, availability and body conditions, and fisheries pressure covariates. We used multiseason occupancy models to characterize the seasonality of breeding and relate it with environmental covariates. We also used functional principal component analysis for classifying the differences in seasonality among sites, and random forest regression for analyzing the relative contribution of covariates in the variability of the seasonal breeding.

We found that in average seasonal breeding mainly started during the austral winter/ early spring and ended in summer/ early fall, this pattern being stronger in boobies and pelicans than in cormorants. The breeding onset of seabirds is timed so that fledging independence occurs when primary production, prey conditions and availability are maximized. This pattern is unique compared with other upwelling ecosystems and could be explained by the year-round high abundances of anchovy in the NHCS.

The average seasonal breeding may differ among nesting sites. Seabirds breed earlier and are more persistent when colonies are larger, located on islands, within the first 20km of the coast, at lower latitudes and with greater primary production conditions. These results suggest that in the NHCS, the seasonality of breeding is more influenced by local environmental conditions than by large-scale environmental gradients. These results provide critical information to a better coordination of guano extraction and conservancy policies.

Seabirds may also adapt the seasonality of their breeding to drastic ecosystem changes caused by regime shifts. We found that the three study species exhibited a gradient of plasticity regarding the seasonality of their breeding. Cormorants showed a greater plasticity, modulating the timing

and magnitude on their breeding seasonality. This is probably authorized by the greater foraging flexibility offered its great diving capacities. Fixed onset and magnitudes of breeding in boobies may be related to their specific foraging strategy and/or to changes of prey items when anchovy stock was low. We also suggested that boobies may adapt other fecundity traits as growth rate of chicks to lower abundance of anchovy.

The specific differences in the adaptation of seasonal breeding allow seabirds to take profit differently from local prey conditions or to face differently regime shifts. Further researches, implementing a large-scale capture-recapture methodology in parallel with monthly census, are proposed in order to fulfill gaps in the basic knowledge on vital traits (adult survival, first age at reproduction, and juvenile recruitment) which are critical parameters to evaluate the dynamic of a population.

# Résumé

Le Système Nord du Courant de Humboldt (SNCH) est le lieu d'une forte activité biologique due à un upwelling côtier intense. Il abrite l'une des plus grandes populations de l'anchois du Pérou soumis à la plus grande pêcherie monospécifique au monde. Le SNCH héberge aussi de grandes, quoique variables, populations d'oiseaux, composées entre autres de trois espèces sympatriques productrices de guano : le cormoran guanay (*Phalacrocorax bougainvillii*), le fou péruvien (*Sula variegata*) et le pélican péruvien (*Pelecanis thagus*), qui se nourrissent toutes principalement d'anchois. Dans ce travail, nous examinons les fluctuations de ces trois populations d'oiseaux marins, en nous concentrant sur le cycle saisonnier de leur reproduction, pour aborder les questions suivantes : Dans quelle mesure les saisonnalités de reproduction diffèrent elles entre espèces ? Dans quelle mesure sont-elles plastiques dans le temps et dans l'espace ? Qu'est ce qui, des conditions environnementales et des activités anthropogéniques affecte le plus la reproduction des oiseaux marins ?

Nous abordons ces questions en utilisant des données de présence de reproducteurs (1) dans plus de 30 sites péruviens répartis entre 06°S et 18°S, et entre 2003 et 2014 ; et (2) dans un site, pendant trois périodes décennales (1952-1968, 1972-1989, 2003-2014). Nous utilisons aussi des covariables environnementales d'origine satelitale ou de campagnes à la mer décrivant les conditions océanographiques, l'abondance, l'accessibilité et la condition des proies, ainsi que des covariables décrivant la pression de pêche. Nous utilisons des modèles d'occupation multi-saisonniers pour caractériser la saisonnalité de la reproduction et la relier aux covariables environnementales. Nous mettons également en œuvre des analyses en composantes principales fonctionnelles pour classifier les différences de saisonnalité entre sites, et des forêts aléatoires de régression pour analyser la contribution relative des covariables à la variabilité de la saisonnalité de reproduction.

Nous mettons en évidence qu'en moyenne, la reproduction démarre au cours de l'hiver austral / début de printemps et prend fin en été / début d'automne, ce patron étant plus marqué chez les fous et pélicans que chez les cormorans. La reproduction est calée dans le temps de telle sorte à ce que les jeunes prennent leur indépendance lorsque les conditions de production primaire, d'abondance et d'accessibilité des proies sont maximales. Ce patron est unique en comparaison avec les autres écosystèmes d'upwelling et peut être expliqué par les fortes abondances absolues de proies disponibles tout au long de l'année dans le SNCH.

La saisonnalité de reproduction diffère entre les sites de nidification. Les oiseaux se reproduisent plus tôt et avec de plus fortes probabilités lorsque les colonies sont plus grandes, situées sur des îles à moins de 20 km des côtes, aux plus basses latitudes, et présentant une production primaire plus élevée. Ces résultats suggèrent que dans le SNCH, la saisonnalité de la reproduction est davantage influencée par les conditions environnementales locales que par les gradients environnementaux de grande échelle. Les oiseaux marins adaptent aussi la saisonnalité de leur reproduction aux changements drastiques causés dans l'écosystème par les changements de

régime. Nous montrons que les trois espèces ont un gradient de plasticité de leur saisonnalité de reproduction. Les cormorans font preuve de la plus grande plasticité, en modulant la date te l'amplitude de la saisonnalité de leur reproduction. Cela est probablement permis par leur plus grande flexibilité de fourragement offerte par leurs excellentes capacités de plongée. Les dates et amplitudes fixes observées chez les fous peuvent être liées aux spécificités de leur stratégie de fourragement et à des changements de proies lorsque le stock d'anchois est bas. Nous suggérons aussi que les fous peuvent adapter d'autres traits de fécondité, comme le taux de croissance des poussins, lorsque l'abondance d'anchois est réduite. Les différences spécifiques dans les adaptations de la saisonnalité de reproduction permettent aux oiseaux de profiter différemment des conditions locales de proies, et de faire face aux changements de régime avec des stratégies différentes. Une méthodologie de capture-recapture de grande échelle en parallèle des comptages mensuels est proposée pour que les recherches futures permettent de combler des lacunes de connaissance sur les traits vitaux (survie adulte, âge a la première reproduction et recrutement des jeunes) qui sont des paramètres essentiels pour évaluer la dynamique d'une population.

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# Résumé executif

## Introduction

Le Système Nord du Courant de Humboldt (SNCH) est le lieu d'une forte activité biologique due à un upwelling côtier intense. Il abrite l'une des plus grandes populations de petits poissons pélagiques, l'anchois du Pérou, et la plus grande pêcherie monospécifique au monde. Ces grandes abondances d'anchois sont aussi à la base de l'alimentation des principaux prédateurs supérieurs comme les oiseaux et mammifères marins. Le SNCH héberge de grandes, quoique variables, populations d'oiseaux, composées entre autres de trois espèces sympatriques productrices de guano: le cormoran guanay (*Phalacrocorax bougainvillii*), le fou péruvien (*Sula variegata*) et le pélican péruvien (*Pelecanus thagus*), qui se nourrissent principalement d'anchois.

Le SNCH connaît une très forte variabilité environnementale, à une grande variété d'échelles spatio-temporelles. Dans sa composante spatiale, il y a des différences remarquables entre les eaux côtières et les eaux au large de la côte. Les eaux côtières sont froides, avec une forte production près de la surface qui épuise l'oxygène rapidement dans la colonne d'eau. Les eaux du large sont plus chaudes, moins productives et plus oxygénées. En conséquence, l'intensité d'upwelling et l'oxygène disponible sont des processus très structurants des habitats des organismes vivants dans cet écosystème. Cette structuration est soumise à une grande variabilité temporelle aux échelles saisonnières, interannuelles, décennales, centennales et millénaires. Ces fluctuations peuvent avoir des répercussions importantes sur la distribution et l'histoire de vie des espèces, comme la reproduction notamment.

En sus de la variabilité climatique naturelle, le système et aussi soumis à une forte pression anthropique. Concernant les oiseaux par exemple, il existe des évidences qu'avant la découverte de l'Amérique, les populations locales utilisaient leurs excréments (« guano ») pour améliorer les cultures. Au XIXème siècle, la redécouverte au niveau international des propriétés du guano crée une industrie d'exploitation très importante pour l'économie du pays. L'exploitation intensive conduisit à un rapide épuisement des stocks et un défaut de renouvellement du guano. Suite à l'effondrement de l'exploitation de guano, des efforts de conservation et d'aménagement de l'habitat des oiseaux furent déployés. Ces efforts, en conjonction avec une fluctuation climatique favorisant l'anchois, résultèrent en une rapide augmentation des populations d'oiseaux et la récupération de l'industrie d'exploitation de guano. Cependant, à partir des années 1950, la façon dont les humains exploitent l'écosystème côtier connut un changement radical. Le développement rapide d'une pêcherie industrielle à l'anchois convertit les humains de commensaux des oiseaux, au travers de l'exploitation du guano, à des compétiteurs directs pour l'accès au poisson fourrage. Cette forte pression compétitive associée à des conditions climatiques adverses comme les évènements El Niño, produisit des fluctuations drastiques du nombre d'oiseaux producteurs de guano. Aujourd'hui, les populations d'oiseaux producteurs de guano sont aussi devenues source d'attraction touristique. L'Etat péruvien se préoccupe donc de la santé de ces populations, non seulement vis-à-vis des effets d'évènements ponctuels comme El Niño qui ont été relativement bien documentés, mais aussi et

surtout vis-à-vis de l'impact global des variabilités d'origine climatique et anthropogénique qui sont moins bien connues.

La reproduction est un processus clé du cycle de vie, susceptible d'être affecté en premier lieu par les effets du changement climatique et des fluctuations environnementales. La reproduction chez les vertébrés est l'une des phases du cycle de vie demandant les plus forts apports énergétiques. Pour cette raison, la reproduction est généralement saisonnière et synchronisée avec la période où l'abondance de ressources est maximale dans l'écosystème. L'intégration des fluctuations saisonnières de signaux environnementaux comme la lumière, la température ou la pluie est utilisée pour anticiper la période où les ressources seront les plus abondantes. On sait d'autre part que le changement climatique risque d'affecter ces cycles saisonniers et donc de remettre en question la valeur de ces indices environnementaux pour le déclenchement de la reproduction. Des risques de décalage ou « mismatch » entre la reproduction et l'abondance des ressources peuvent apparaître (Visser, Both & Lambrechts 2004) et entraîner des échecs de reproduction à court terme, et des diminutions de population à long terme (Both *et al.* 2006).

Dans le SNCH, le cycle saisonnier est décrit comme modéré, avec une grande influence de l'intensité de l'upwelling, de la lumière utilisée pour la photosynthèse et de la profondeur de l'oxycline. En hiver, on observe un intense upwelling et une faible profondeur de l'oxycline mais moins de lumière ce qui limite la production primaire. Au printemps, il y a moins d'intensité d'upwelling, mais plus de lumière et moins de stratification dans la colonne d'eau ce qui permet une production supérieure. Cette production perdure jusque la fin de l'été (Echevin *et al.* 2008). Si la saisonnalité des conditions océanographique est bien décrite, on dispose de peu d'informations sur le cycle saisonnier des organismes vivants comme les oiseaux marins dans le SNCH. Dans ce travail, nous examinons les fluctuations de ces trois populations d'oiseaux marins, en nous concentrant sur le cycle saisonnier de leur reproduction, pour aborder les questions suivantes: Les oiseaux producteurs du guano ont-ils des cycles saisonniers? Dans quelle mesure les saisonnalités de reproduction diffèrent-elles entre espèces ? Dans quelle mesure sont-elles plastiques dans le temps et dans l'espace ? Qu'est ce qui, des conditions environnementales et des activités anthropogéniques, affecte le plus la reproduction des oiseaux marins ?

La thèse est organisée en un chapitre introductif (chapitre 1) qui fournit une vue d'ensemble sur le fonctionnement du SNCH et trois chapitres centraux (chapitres II, III, IV) prenant la forme de trois publications.

Dans le chapitre II, on analyse la saisonnalité de la reproduction des oiseaux, les différences entre espèces, les conditions environnementales pendant les périodes reproductives et non reproductives et on discute sur les stratégies d'adaptation des cycles reproductifs aux conditions de l'environnement.

Dans le chapitre III, on analyse la variabilité dans le temps et dans l'espace de la saisonnalité moyenne de reproduction pour les trois espèces. On examine les relations entre la date et l'amplitude de la reproduction et les forçages environnementaux, les processus d'attraction sociale, et la pêche à l'échelle des colonies. Nous discutons sur les échelles auxquelles les oiseaux répondent pour adapter leur reproduction.

Dans le chapitre IV, on analyse la date et l'amplitude de la reproduction dans une colonie pendant trois décennies contrastées. Ces trois périodes décennales se différencient en termes de productivité de l'écosystème et de pression anthropique. On analyse les différences entre espèces dans la date et

l'amplitude de la reproduction. On discute sur les possibles causes et conséquences des changements observés et on interprète la variabilité observées entre les espèces d'oiseaux en termes traits d'histoire de vie.

Finalement dans le chapitre de conclusion (chapitre V), on propose une synthèse des avancées acquises par la thèse, et les directions futures à envisager pour cette thématique de recherche.

**Données**

**Données sur les oiseaux**

Grâce à l'exploitation commerciale du guano par le gouvernement péruvien, des programmes de suivi et de comptage des oiseaux marins furent mis en place dès le début du XXème siècle afin d'estimer la quantité de guano à extraire. Ces programmes aboutirent notamment à la mise place de gardiens permanents dans chacune des plus grandes colonies d'oiseaux, localisées dans des îles proches de la côte et presqu'îles (06°S jusque 18°S). Chaque mois, les gardiens font un comptage des oiseaux présents dans les colonies par une méthode graphique qui consiste à dessiner les tâches de présence d'oiseaux sur une carte standardisée. Le calcul de l'abondance des oiseaux est obtenu en multipliant la densité d'oiseaux par mètre carré par l'aire occupée. Si les oiseaux sont très dispersés ou dans des falaises, le comptage est réalisé directement, sans extrapolation. Les oiseaux sont comptés par espèces, par état reproducteur, et les œufs, poussins et jeunes sont aussi comptabilisés.

Ce protocole, mis en œuvre depuis l'année 1952, est toujours en cours aujourd'hui. Malheureusement, comme ces données servent surtout pour des usages ponctuels liés à l'extraction du guano, leur archivage n'a pas fait l'objet d'une attention particulière. Par conséquent, un travail préliminaire à cette thèse a consisté, dans le cadre du projet de recherche TOPINEME, à récupérer, digitaliser et compiler les archives encore existantes, la plupart sous forme papier. Dans le cadre de cette thèse, nous avons corrigé et validé ces données existantes, aboutissant à deux séries temporelles distinctes. Une première base de données consiste en une série mensuelle des comptages pour la période 2003-2014 dans 31 colonies d'oiseaux. Une seconde série de données mensuelles concerne une seule colonie, l'ile Pescadores (11.78°S, 77.23°W), et couvre trois décennies contrastées. Pour la période 1952-1968, elle consiste en des données mensuelles de présences-absences des reproducteurs ; pour la période 1977-1990, elle consiste en des pourcentages d'oiseaux en reproduction ; et pour la période 2003-2014, elle regroupe de véritables comptages.

Les comptages réalisés par les gardiens souffrent d'un certain nombre de biais notamment dus à la différence d'expérience entre les gardiens et l'utilisation d'une densité constante du nombre de nids par mètre carré et par espèce, quelles que soient les campagnes et les colonies. Pour cette raison, nous avons choisi de travailler pour cette thèse l'information de présence - absence de reproducteurs.

La série temporelle couvrant toutes les colonies de 2003-2014 a été utilisée pour développer les chapitres II et III. La deuxième série temporelle concernant la seule île de Pescadores pour trois périodes entre 1952 et 2014 a été utilisée pour le chapitre IV.

**Données sur les conditions océanographiques**

Nous avons utilisé des données satellites et des données recueillies pendant les campagnes scientifiques réalisées par l'IMARPE (Institut de la Mer du Pérou) pour représenter les conditions océanographiques autour des colonies de reproduction d'oiseaux. Les données satellites documentent les conditions superficielles de température superficielle de la mer (SST, °C), les concentrations de Chlorophylle-a superficielles (Chlo, mg m$^{-3}$) et un Index d'Upwelling (UI). SST et Chlo ont été obtenus à partir du satellite MODIS de Juillet 2002 à Décembre 2012. UI a été calculé à partir de composantes de la vitesse du vent obtenues à partir de QuikSCAT, disponibles de Juillet 1999 à Novembre 2009.

Pour représenter les conditions verticales dans la colonne d'eau du SNCH, un paramètre critique est la profondeur de la zone de minimum d'oxygène. La zone minimum d'oxygène est très superficielle et la profondeur à laquelle l'oxygène dissous est égal à 2 ml.l−1 ($Z_{2ml}$) marque la limite de distribution des espèces aérobies comme l'anchois (Bertrand *et al.*, 2010). On a utilisé $Z_{2ml}$ pour représenter la limite verticale de la répartition des anchois. Les mesures d'oxygène in situ proviennent de bouteilles Niskin et des sondes CTD (conductivité, température et profondeur) échantillonnées pendant les campagnes scientifiques conduites par l'IMARPE depuis 1960. De ces campagnes à la mer, nous disposons aussi de données de SST et de Chlorophylle in situ. La résolution des données à la base est mensuelle et avec une résolution spatiale de 0,1 ° × 0,1 °, s'étalant tout le long de la côte péruvienne.

Pour le chapitre II, nous avons utilisé une climatologie pour chaque paramètre, calculée comme une moyenne pour chacun des 12 mois de l'année des mesures faites dans un rayon de 100km autour des colonies. Pour SST, Chlo et UI la climatologie est basée sur des données satellites de 2002 à 2009, et pour $Z_{2ml}$ des données recueillies in situ de 1960 à 2010.

Pour le chapitre III, nous avons construit une climatologie pour chacune des colonies avec la même base de données et les mêmes critères que pour le chapitre II.

Pour le chapitre IV, nous avons construit une climatologie de SST, Chlorophylle et $Z2ml$ pour chacune des périodes concernées par les données sur les oiseaux (1952-1968, 1977-1990 et 2003-2014) avec les données recueillies in situ par l'IMARPE, sur la zone comprise entre 06°S et 14°S.

**Données sur l'anchois**

L'importance économique de l'anchois pour le Pérou implique un intense effort de suivi réalisé par l'IMRAPE, notamment pour estimer ses abondances et sa condition corporelle. La biomasse et la distribution des populations sont évaluées par l'IMARPE avec des campagnes scientifiques acoustiques depuis 1983. Chaque année l'IMARPE fait entre deux et quatre campagnes acoustiques le long de la cote péruvienne (03°S -18°S). Ces campagnes sont composées de transects de ∼ 200 nm de long, parallèles entre eux (séparés par ∼ 15 nm), et perpendiculaires à la côte. Des échosondeurs scientifiques Simrad travaillant à des fréquences de 38 et 120 kHz sont utilisés pour estimer les biomasses (Gutiérrez *et al.* 2007; Simmonds *et al.* 2009). Un échantillonnage extensif au chalut pélagique complète les évaluations acoustiques pour l'identification des espèces. Le 'nautical-area-backscattering coefficient' (NASC, en m2

.mn−2), un indice de biomasse de poisson (Simmonds and MacLennan, 2005), est enregistré à chaque unité élémentaire d'échantillonnage geo-référencée (ESDU, acronyme en anglais) de 1 mille nautique. Une telle campagne, couvrant tout le littoral péruvien, peut durer de deux à trois mois.

Pour le chapitre II notre objectif était de mettre en relation les données sur l'anchois avec des données mensuelles sur les oiseaux. Pour cette raison, nous avons restreint notre aire d'intérêt à 06°S -14°S et 40km au large de la côte pour homogénéiser la zone d'échantillonnage qui peut se faire pendant un mois. Pour cette aire, nous avons extrait cinq descripteurs: (i) le NASC d'anchois moyen, utilisé comme un indice de biomasse régionale d'anchois ($s_A$); (ii) le NASC d'anchois moyen uniquement pour les ESDU avec présence d'anchois, utilisé comme un indice de biomasse locale ($s_A+$); (iii) le pourcentage d'ESDU avec de l'anchois, utilisé comme un indice d'occupation spatiale (ISO).

Par ailleurs, dans le chapitre II, nous avons utilisé des variables pour décrire l'état physiologique et de reproduction de l'anchois: (i) un facteur d'état corporel (FBC, g cm$^{-3}$) calculé à partir du poids éviscéré et de la longueur totale; et (ii) un indice gonado-somatique (GSI), calculé à partir de la proportion de la masse des gonades par rapport à la masse corporelle totale (Buitrón *et al.*, 2011). Ces données proviennent d'échantillonnages des anchois débarqués par les pêcheurs dans les ports entre 6º - 14ºS et de 2002 à 2012.

Pour le chapitre IV, notre objectif était de décrire la saisonnalité dans la biomasse d'anchois entre différentes périodes. Nous avons utilisé deux sources de données pour cela. Tout d'abord trois descripteurs acoustiques :(i) l'indice de biomasse régionale d'anchois ($s_A$); (ii) l'indice de biomasse locale ($s_A+$); (iii) et l'indice d'occupation spatiale (ISO). Ces indices ont été pris pour chaque campagne acoustique dans l'aire de 8ºS et 15ºS et 100 km au large de la côte .Nous avons calculé ces mesures pour deux périodes:1985-1990 (associée à la période 1977-1990) et 2000-2011 (associée à la période de 2003 à 2014). Nous avons également calculé pour ces deux périodes la profondeur moyenne et la hauteur des bancs d'anchois pendant la journée et la nuit à partir de données acoustiques. Le deuxième jeu de données consiste en la biomasse mensuelle d'anchois estimée par un modèle d'évaluation des stocks qui inclut l'information acoustique et les débarquements (Oliveros-Ramos & Peña 2011). À partir des biomasses mensuelles estimées depuis 1953 à 2014, nous avons construit une climatologie pour chacune des trois périodes qui correspondent aux données sur les oiseaux (1952-1968, 1977-1990 et 2003-2014).

**Données sur la pêcherie**

Une autre variable d'importance à confronter avec la saisonnalité de la reproduction des oiseaux est l'activité de la pêcherie d'anchois. Le long de la côte péruvienne, ~ 20 grands ports industriels reçoivent les débarquements d'anchois. La plupart des débarquements sont réalisés dans les ports entre 4°S and 15°S (Arias Schreiber 2012). L'IMARPE fait des suivis journaliers des débarquements par port.

Dans le Chapitre III nous avons mis en relation les débarquements dans les ports proches de cahque colonie (rayon de 100 km autour de la colonie). Pour chaque site de reproduction, les débarquements ont été cumulés par an et moyennés sur 2003 - 2014 pour représenter la pression de pêche. Nous avons inclus également la distance entre chaque site de reproduction et le port le plus proche dans un rayon de 100 km.

Dans le Chapitre IV notre but était de caractériser la pression de pêche au cours des trois périodes décennales pour lesquelles nous disposions de données sur les oiseaux (1952-1968, 1977-1990 et 2003-2014). Nous avons utilisé les débarquements d'anchois mensuels dans les principaux ports situés entre 09°S et 15°S pour faire des moyennes mensuelles, divisées ensuite par le quota annuel global. A partir de moyennes mensuelles, nous avons construit des climatologies de la pression de pêche pour les trois périodes.

## Méthodes

La méthodologie principale pour modéliser les présence/absences saisonnières de reproducteurs dans les colonies en fonction de covariables environnementales pour les Chapitres II, III et IV repose sur des modèles d'occupation multi-saisonniers. Aussi dans le Chapitre III nous avons inclus des analyses fonctionnelles et des analyses des forêts aléatoires.

## Modèles de dynamique d'occupation

La stratégie de reproduction saisonnière et le 'timing' de la reproduction sont des paramètres importants de la dynamique des populations. Les méthodes les plus utilisées pour mesurer ces paramètres sont par exemple des modèles qui suivent une population par des comptages pour tracer des fluctuations et tendances par le biais de séries temporelles. D'autres modèles s'intéressent à la croissance des populations et se basent sur les paramètres de mortalité et de recrutement. D'autres méthodes ne suivent pas les populations mais les individus par des méthodes de capture-recapture. Ces modèles s'intéressent au timing, à la productivité et à la survie individuelle et les résultats sont extrapolés à l'ensemble de la population. Dans notre cas d'étude, les données sur les oiseaux dont nous disposons sont des comptages par colonies. L'utilisation des méthodes classiques pour étudier la saisonnalité et le timing de reproduction ne sont pas envisageables parce un comptage ne permet pas un suivi individuel. D'autre part, et comme mentionné plus haut, les comptages sont affectés de biais importants, rendant les données de présence-absence de reproducteurs beaucoup plus robustes.

La méthode qui s'adapte le mieux pour modéliser les présence-absence de reproduction dans les colonies sont les modèles de dynamique d'occupation. Le principe des modèles de dynamique d'occupation est basé sur l'approche de métapopulation. Le concept de métapopulation a été formalisé comme un assemblage de sous-populations des espèces qui se déplacent et éventuellement peuvent coloniser des espaces, et être localement éteintes avec des probabilités différentes (Levins 1970). L'approche de métapopulation peut correspondre parfaitement à notre cas parce que spatialement, l'habitat occupé par les colonies d'oiseaux a une structure éparse; et temporellement, les colonies ne sont pas occupées par les reproducteurs en permanence, donc il y a une fragmentation dans le temps aussi. Le modèle de dynamique d'occupation qu'on utilise ici est un modèle multi-saisonnier (Mackenzie *et al*., 2003) où la dynamique de colonisation et d'extinction dans les colonies est modélisé comme un processus markovien du premier ordre et l'unité de pas de temps est le mois. Trois paramètres sont estimés par les modèles d'occupation multi-saisonniers : la probabilité de commencement de la reproduction ($\gamma$), la probabilité de

fin de la reproduction (ε) et la probabilité d'occupation des sites par les reproducteurs (ψ), dérivée des deux précédentes. Le commencement de la reproduction (γ) est défini comme la probabilité que le site inoccupé le mois t ait été occupé le mois t + 1. La fin de la reproduction (ε) est définie comme la probabilité que le site occupé le mois t ait été inoccupé en t + 1. On considère une occupation quand il y a présence d'œufs ou de poussins dans le nid.

Dans le chapitre II, nous avons modélisé le cycle saisonnier moyen de la reproduction pour toutes les colonies sur la période 2003-2012. L'estimation des paramètres mensuels de γ, ε and ψ été faite par une approche fréquentiste, avec maximum vraisemblance pour estimer les trois paramètres (Barbraud *et al.* 2003; MacKenzie *et al.* 2003). Les modèles d'occupation multi-saisonniers sont aussi très flexibles, car ils permettent de modéliser la dynamique de l'occupation par une relation logistique avec les covariables environnementales. Dans le troisième chapitre nous avons testé l'effet des variables environnementales et de l'abondance, biomasse et conditions physiologiques de l'anchois.

Dans le chapitre III et IV, nous avons utilisé aussi des modèles de dynamique d'occupation multi-saisonniers mais avec une approche Bayésienne qui utilise des algorithmes de simulation de chaîne de Markov (MCMC) pour estimer les paramètres. Nous avons utilisé une approche Bayésienne car elle permet au modèle de converger même quand les données sont dispersées, ce qui était notre cas après avoir désagrégé la saisonnalité de la reproduction dans l'espace et dans le temps. Dans le chapitre III nous avons désagrégé les données spatialement, construisant la dynamique de reproduction saisonnière par île et par espèce. Dans le chapitre IV, nous avons désagrégé les données temporellement, construisant une saisonnalité par période (1952-1968, 1977-1990, and 2003-2014) et par espèce. Un des facteurs à contrôler dans l'approche Bayésienne est l'information a priori. Dans les deux chapitres nous avons utilisé l'information des paramètres de γ, ε and ψ résultant du chapitre II. Dans le chapitre III spécifiquement, nous avons travaillé à partir des paramètres γ, ε and ψ par colonie pour expliquer la variabilité spatiale en utilisant deux autres méthodes : les analyses fonctionnelles pour classifier les différences de saisonnalité et les forêts aléatoires de régression pour analyser la contribution relative des covariables dans la variabilité de la reproduction saisonnière.

**Analyse fonctionnelle**

Dans le chapitre III, les estimations de début de la reproduction et d'occupation des sites par les reproducteurs étaient constituées par des courbes de saisonnalité pour chaque colonie. Nous avons identifié qu'une des méthodes les plus puissantes pour explorer et analyser des courbes dans leur intégralité est l'analyse des données fonctionnelles (FDA, acronyme en anglais, Ramsay et Silverman, 1997). Le principe des méthodes FDA considère que les données formant une courbe sont dans une fréquence d'observation assez fine pour considérer la courbe comme une fonction continue $X = \{X(t); t \in (tmin, tmax)\}$.

Dans notre cas, nous avons représenté la variabilité des courbes de reproduction saisonnière dans une fonction de dimension réduite avec une analyse fonctionnelle en composantes principales (FPCA). L'objectif de FPCA, de manière similaire à l'analyse en composantes principales standard, est de trouver un ensemble de fonctions orthogonales $\{ui, i = 1, ..., p\}$ dont la combinaison linéaire $X_j(t) \approx \sum_{k=1}^{p} \beta_{jk} u_k(t)$ permet de synthétiser la variabilité originale des courbes (Bjornstad *et al.*, 1998).

Nous avons gardé les deux premières composantes principales fonctionnelles et leurs scores ($\beta_{jk}$) qui résument la majeure partie des sources de variations dans les courbes. Les scores des composantes principales sont ensuite reliés à des covariables environnementales avec une analyse multivariée plus conventionnelle comme les forêts aléatoires.

### Forêts aléatoires de régression

Toujours dans le chapitre III, la réduction de la dimensionnalité des courbes avec une FPCA nous a permis de résumer la répartition spatiale de la synchronisation de la reproduction. Cette information, contenue dans les scores de FPCA, a été mise en relation avec des covariables géographiques, d'attraction sociale dans les colonies, et de pêche d'anchois en utilisant un modèle de forêt aléatoire de régression (Breiman 2001). Les modèles de forêt aléatoire ont été utilisés à la place des modèles classiques de régression en raison de leur meilleure performance pour détecter les effets d'interaction non-linéaire, leur faible sensibilité à des données dispersées et leur faible sensibilité à la multicolinéarité due à un grand nombre de covariables (Cutler *et al*., 2007) .

Les forêts aléatoires sont une méthode qui permet en même temps la construction de modèles précis et la production de mesures d'importance des variables prédictrices (Breiman, 2001). Nous avons utilisé les forêts aléatoires pour classer l'importance des covariables dans le timing et amplitude de la reproduction saisonnière des oiseaux. Les forêts aléatoires procèdent à une classification basée sur la construction d'un grand nombre d'arbres décisionnels à partir de sous-échantillons tirés au hasard à partir du jeu de données initial. Les arbres sont construits par des partitions successives du jeu de données en groupes homogènes. Dans le cas des forêts aléatoires, une deuxième source d'aléatorisation consiste à n'utiliser qu'un sous-échantillon des covariables à chaque partition. La prédiction faite à partir de l'arbre est contrastée avec la partie de l'échantillon qui n'a pas été utilisée pour sa construction. L'importance de chacune des variables est ensuite évaluée par cette erreur de prédiction. Plus la variable est importante, plus l'erreur de classification sera importante lorsqu'elle est retirée. Une faiblesse des forêts aléatoires est le biais qui tend à donner plus d'importance à des variables continues. Nous avons procédé à une correction de ce biais par la procédure PIMP qui contraste la prédiction initiale des arbres à une prédiction faite à partir des variables réponse permutées (Altmann *et al*., 2010). Si l'importance des variables augmente dans le cas de la prédiction avec des variables réponses permutées, alors les covariables n'aident pas à la prédiction et leur importance est donc minorée.

### Résultats

Dans le chapitre II, nous avons décrit la saisonnalité de reproduction moyenne des trois espèces d'étude, au cours de la dernière décennie (2003-2012) et l'avons mise en relation avec les conditions océanographiques, l'abondance, la disponibilité et la condition biologique de l'anchois. Nous avons examiné la pertinence pour notre cas d'étude de deux hypothèses classiques sur le cycle saisonnier de reproduction des oiseaux: i) les oiseaux ont une contrainte énergétique surtout au début de la reproduction pour initier la ponte des œufs, ii) les oiseaux ont une condition énergétique suffisante pour pondre des

œufs et utilisent les signaux environnementaux surtout pour s'ajuster à des conditions optimales des proies au moment de l'élevage des poussins.

Nous trouvons dans notre cas d'étude, qu'en moyenne, la reproduction démarre au cours de l'hiver austral/début de printemps, et se termine en été/début d'automne. Cette saisonnalité est davantage marquée chez les fous et les pélicans que chez les cormorans. Le début de reproduction se produit principalement lorsque l'upwelling est intense, mais la productivité du système n'est pas encore à son maximum annuel, et lorsque l'anchois est relativement moins disponible et en faible condition physiologique. L'abondance et l'accessibilité de l'anchois augmente au fur et à mesure de l'élevage des poussins et sont maximales lorsque les poussins atteignent le stade de jeune.

Ces résultats suggèrent que la période de reproduction est calée dans le temps de telle sorte que les juvéniles rencontrent des conditions optimales à leur prise d'indépendance, plutôt que soumise à des contraintes énergétiques liées à la ponte.

La période de reproduction est ajustée pour favoriser le stade juvénile. Cette configuration est unique en comparaison avec les autres écosystèmes d'upwelling où les oiseaux ajustent leur cycle de telle sorte que les conditions optimales des proies se produisent pendant l'élevage des poussins. Ces résultats pourraient être expliqués par les abondances d'anchois relativement hautes toute l'année dans le SNCH.

Dans le chapitre III, nous avons examiné la variabilité spatiale de la saisonnalité de reproduction (en temps et en amplitude) entre les 30 principaux sites de nidification du SNCH, sur la période 2003-2014. Cette variabilité spatiale est examinée en fonction de caractéristiques géographiques globales (ex. latitude), de conditions océanographiques locales, de phénomènes d'attraction sociale (taille des colonies), et de la pression de pêche locale. On teste l'hypothèse selon laquelle ce sont les caractéristiques géographiques de l'habitat à grande échelle (par exemple la latitude), ou à petite échelle (par exemple la productivité autour des îles, ou l'attraction sociale exercée par les oiseaux) qui sont les principaux responsables du timing et de l'amplitude de la reproduction.

En général pour les trois espèces, les oiseaux se reproduisent environ un mois plus tôt et avec une plus forte probabilité quand les colonies sont plus grandes, situées sur des îles, dans les 20 premiers kilomètres de la côte, aux latitudes les plus basses, et présentant des productivités primaires plus élevées. Les résultats montrent que les différences de saisonnalités de reproduction entre les colonies sont influencées en premier lieu par les phénomènes d'attraction sociale et de production primaire, puis par les facteurs géographiques. Ces résultats sont surtout visibles pour le cormoran et le fou.

Ces résultats suggèrent que, dans cet écosystème tropical et hautement productif, la saisonnalité de la reproduction est davantage déterminée par des conditions environnementales locales que par des gradients environnementaux de grande échelle.

Par ailleurs, ces résultats de classification des sites de nidification par leur saisonnalité d'occupation peuvent être très utiles à une meilleure coordination de l'extraction du guano, de la gestion des populations et des politiques de conservation.

Dans le chapitre IV, on s'intéresse à la variabilité décennale de la saisonnalité de reproduction, pour les trois espèces, dans un site unique (Isla Pescadores, 11.78°S, 77.23°W), entre trois périodes décennales contrastées (1950-1970, 1970-1990, et >2000). Nous faisons l'hypothèse que les trois espèces ont des plasticités différentes pour adapter la saisonnalité de leur reproduction aux changements drastiques des conditions environnementales et de l'abondance et de la disponibilité des proies se produisant à l'issue d'un changement de régime, en prêtant une attention particulière aux effets du développement de la pêcherie industrielle dans le même temps.

Nous mettons en évidence que face à un même changement de régime, les oiseaux en compétition pour la même proie montrent un gradient de plasticité de la saisonnalité de leur reproduction, en modulant le timing et l'amplitude de reproduction. Les cormorans sont l'unique espèce à moduler le timing de reproduction entre périodes. Pélicans et cormorans modulent l'amplitude de leur reproduction en fonction des périodes décennales. Les fous conservent pour leur part les mêmes timing et amplitude de reproduction.

Nous discutons la possibilité que les cormorans puissent ajuster la date de leur début de reproduction grâce à leurs bonnes capacités de plongée, qui leur permet d'exploiter une plus grande fraction de la colonne d'eau en comparaison avec les deux autres espèces. La constance des dates et amplitudes de la reproduction pour les fous peut être mise en lien avec leur stratégie de fourragement particulière et/ou à leur capacité à changer de proies lorsque l'anchois est moins abondant.

## Conclusions et perspectives

En conclusion, nous avons montré que dans le SNCH, l'initiation de la reproduction chez les oiseaux marins est globalement calée dans le temps de telle sorte que les conditions de proies soient optimales pendant l'élevage des poussins et la prise d'indépendance des jeunes. Ces résultats sont très intéressants à différents points de vue. Du point de vue écologique ce résultat permet d'avancer dans la compréhension globale du fonctionnement de l'écosystème. Ces résultats sont aussi intéressants pour prendre des décisions de conservation et de gestion des populations parce qu'ils permettent de mieux coordonner les activités scientifiques et économiques. Notamment, nos résultats permettent d'identifier les périodes critiques pour une meilleure planification des activités d'extraction de guano et que les visites touristiques aux colonies soient mieux régulées.

Nous avons montré par ailleurs que la saisonnalité de reproduction est aussi un trait hautement adaptatif dans l'espace et le temps, qui permet de tirer le meilleur parti des conditions de proies locales et de faire face aux conditions des différents régimes. Cette plasticité doit être au coeur des recherches sur les scenarios de changement climatique étant donné que c'est une clé adaptative des oiseaux pour surmonter la sensibilité de leurs populations à des conditions environnementales adverses.

Nous recommandons de poursuivre et développer la recherche sur les traits d'histoire de vie des trois espèces d'oiseaux, en particulier sur les traits liés à la fécondité. Une approche plus intégrée, mettant en

place une méthodologie de capture-recapture à grande échelle en parallèle avec les recensements mensuels, permettrait de fournir des informations non biaisées sur la survie adulte, l'âge à la première reproduction, et le taux de recrutement des juvéniles par exemple qui sont des paramètres critiques pour évaluer la dynamique d'une population.

# Preface

*A sea of plenty…*

Being a site of year-round wind-driven intense coastal upwelling, the coastal ocean off the coasts of Peru (Northern Humboldt Current System, NHCS hereafter) is the place of a high biological activity and a rich ecosystem (e.g. Chavez et al. 2008). The NHCS supports one of the biggest forage fish populations, the Peruvian anchovy, and the world-leading monospecific fishery in terms of landings (over 5 million tons annually since the early 1990s and up to 16 million tons in the 1970s). It also hosts huge, although variable, seabird populations, including the sympatric, guano-producing, Guanay cormorant (*Phalacrocorax bougainvillii*), the Peruvian booby (*Sula variegata*) and the Peruvian pelican (*Pelecanus thagus*), which are the most abundant seabirds in the Peruvian coastal region (Murphy 1936; Jahncke, Checkley & Hunt 2004). These species feed almost exclusively on Peruvian anchovy *Engraulis ringens* (Jahncke *et al.* 2004).

*… under great climatic and anthropogenic pressures*

The NHCS experiences very high environmental variability at a variety of spatiotemporal scales, from intraseasonal to interdecadal fluctuations (Duffy 1983d). Above the natural climatic variability, the system also experienced a radical change in the way humans exploited the coastal ecosystem. Until the 1950's they were essentially seabirds' commensals, exploiting the guano. From there, the rapid development of an industrial anchovy fishery converted humans into direct competitors for seabirds. This strong competitive pressure caused by the fishery, together with adverse climatic conditions such as El Niño events produced drastic fluctuations in the number of guano producing seabirds from c. 16 - 25 million individuals in the 50', down to 0.5 million individuals in 80's to 2 - 4 million individuals in the recent years. If the effects of punctual El Niño events on seabird populations have been relatively well documented (Schreiber 2002; Stenseth & Mysterud 2002), much less is known about the global impact of the climatic and anthropogenic variability of the NHCS on seabird populations (Schreiber 2002). By which mechanisms seabirds do cope with such variability? How can we explain the coexistence of those three sympatric species, all-feeding on the same prey (the anchovy Engraulis *ringens*), at high population levels? Those questions are key scientific questions in the NHCS.

*Top predators and ecosystem stability*

Within biodiversity erosion issues, the loss of megafauna (i.e. larger-bodied animals, including seabirds), termed 'trophic downgrading' may be humankind's most pervasive influence on nature (Estes *et al.* 2011). Many practicing ecologists still view large

animals as ecological passengers riding atop the trophic pyramid but having little impact on the structure below, suggesting that their disappearance imply mainly ethical and aesthetic issues. However, it became clear in the recent years that top predators in general, and seabirds in particular, belong to the complex network of interactions and regulations that makes an ecosystem, and as such have a role to play in the sustainability of the productivity of the marine ecosystems (e.g. Frederiksen *et al.* 2006). Their contributions to the system need to be quantified, goals have to be set regarding their conservation, and their needs have to be considered within the fishery management measure (for instance, establishing an ecosystem-based TAC or Marine Protected Areas). Peruvian authorities soon realized the importance of an ecosystem-based management within a system such as the NHCS where the forage fish removals by the fishery as so huge and important economically. As a consequence, understanding how seabirds may adapt to natural variability and cope with anthropogenic pressure became a key societal question too.

*Plasticity in changing environments*
Plasticity, in behavior, diet and reproductive biology, has been demonstrated to be essential for explaining the success of anchovy in the NHCS (e.g. Espinoza & Bertrand 2008). On what to feed (trophic ecology), how to forage (behavioural ecology) and how to reproduce (reproductive ecology) are key issues for the living organisms in pelagic ecosystems that may explain both niche partitioning among species, and the capacity of adaptation of each species to changing conditions through the plasticity of those characters. If their diets are all composed in vast majority by anchovy, some behavioral aspects may explain how guano-producing seabird niche segregate: pelicans forage at night (Zavalaga *et al.* 2011) while boobies and cormorants forage during daylight. Boobies are good flyers but may access only superficial anchovy aggregations (plunge-diving strategy, <10m). Cormorants are poorer flyers, but excellent divers (>60m) and use massive collective strategies for localizing fish aggregations (e.g. Compass-raft, Weimerskirch *et al.* 2010). Owing to the remarkable climatic variability of the Humboldt system (Chavez *et al.* 2008), the abundance as well as horizontal and vertical distribution of anchovy may vary greatly among years. Consequently, one hypothesis for explaining the coexistence of boobies, cormorants and pelicans at high population levels is that the climatic variability of the system provides conditions that may favor alternately the different foraging strategies, resulting in alternately high demographic parameters, sufficient for maintaining high population levels of the three species. The reproductive ecology is probably the least known aspect of those species

*A bird-eye view on the variability of the NHCS*
Thanks to the commercial exploitation of guano, guardians protect most seabird breeding colonies (>30 sites) since the 1960's. Guardians are also in charge of reporting each

month the sizes of the breeding population in each colony, with the aim of forecasting guano production. If many of those papers-sheets censuses have been lost, part of them could be retrieved and digitalized in 2012 (IRD-IMARPE collaboration), and we propose here to make a scientific use of this exceptional and opportunistic dataset to address the following questions: how different or similar are the seasonality of reproduction among species? To what extent may they be plastic in space and time? What from the natural environment and the anthropogenic activities impact more the breeding of seabirds?

To address those questions, the thesis is organized into (1) one introductive chapter providing an overview of the NHCS functioning, (2) 3 central chapters, taking the form of 3 publications, which analyze the seasonality of seabird breeding, its variability over space and different time scale, and its relationship with the climatic and anthropogenic forcing affecting of the system, and (3) one conclusive chapter providing a synthesis of the findings provided by the thesis and the future directions to envisage for these research questions.

# *Chapter I: General introduction*

Passuni , Giannina.

### 1. The Northern Humboldt Current System (NHCS): general features

The Eastern Boundaries Upwelling systems (EBUS) are among the most productive marine ecosystems in the world (Chavez & Messié 2009). There are four major EBUS: the Humboldt Current system in the South Pacific, the Canary Current system in the North Atlantic, the Benguela Current system in the South Atlantic and the California Current system in the North Pacific (Figure 1, Bakun *et al.* 2015). While the EBUS encompass only ~ 0.3% of the world surface of oceans, they sustain about 20% of the world's fish catches (Pauly & Christensen 1995), contributing significantly to securing food and livelihood security in many developing countries .
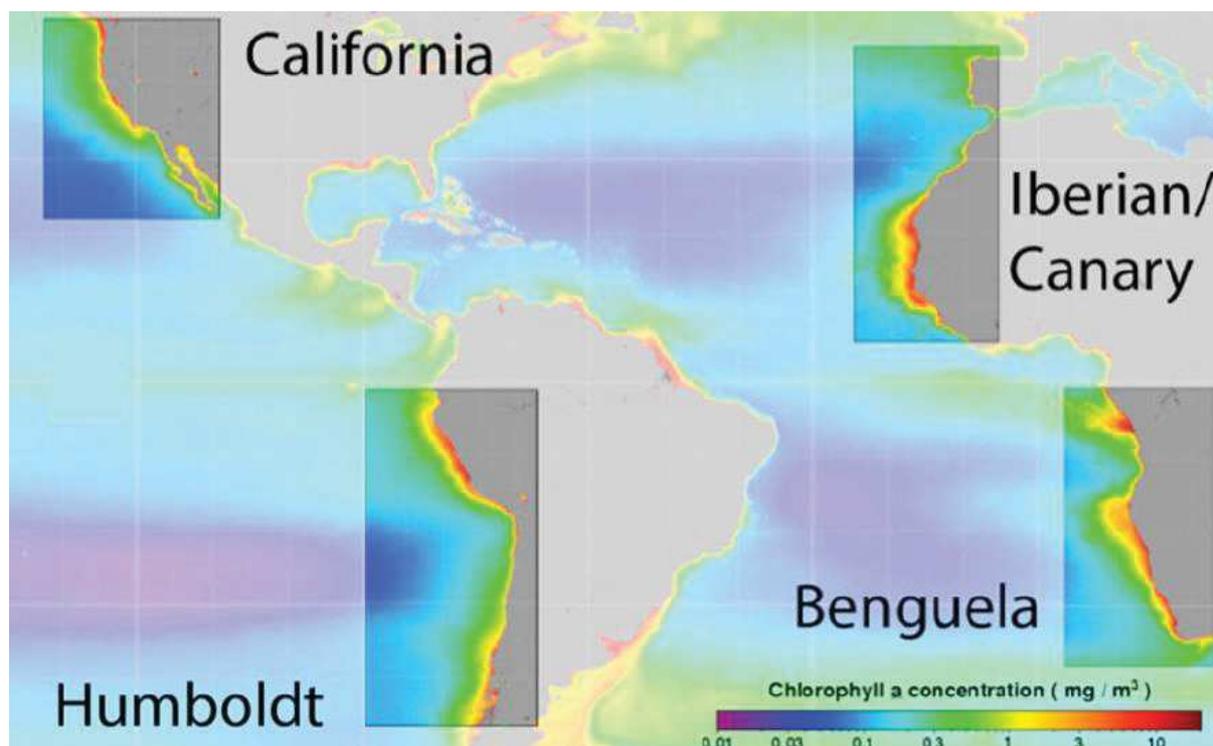


Figure 1.1. EBUS localization and their chlorophyll-a annual average concentrations. Source Bakun *et al.* 2015.

The EBUS are characterized by regular trade winds that, combined with the earth's rotation, generate coastal upwelling of nutrient-rich deep waters to the surface which fuels primary production supporting a highly productive food web (Fréon *et al.* 2008). In comparison with the other three EBUS, the Humboldt Current System (HCS) has the weakest trade winds and moderate levels of primary production. Yet, it hosts the highest forage fish production mainly with the Peruvian anchovy (*Engraulis ringens*) (Figure 1.2) that in turn sustains important populations of marine mammals (sea lions and fur seals), seabirds and a large industrial fish meal fishery (Chavez *et al.* 2008). Several hypothesis have been proposed to explain this specificity of the HCS one being a maximal shelf retention of ichthyoplankton and food in the northern HCS (NHCS) (Brochier, Lett & Fréon 2011).
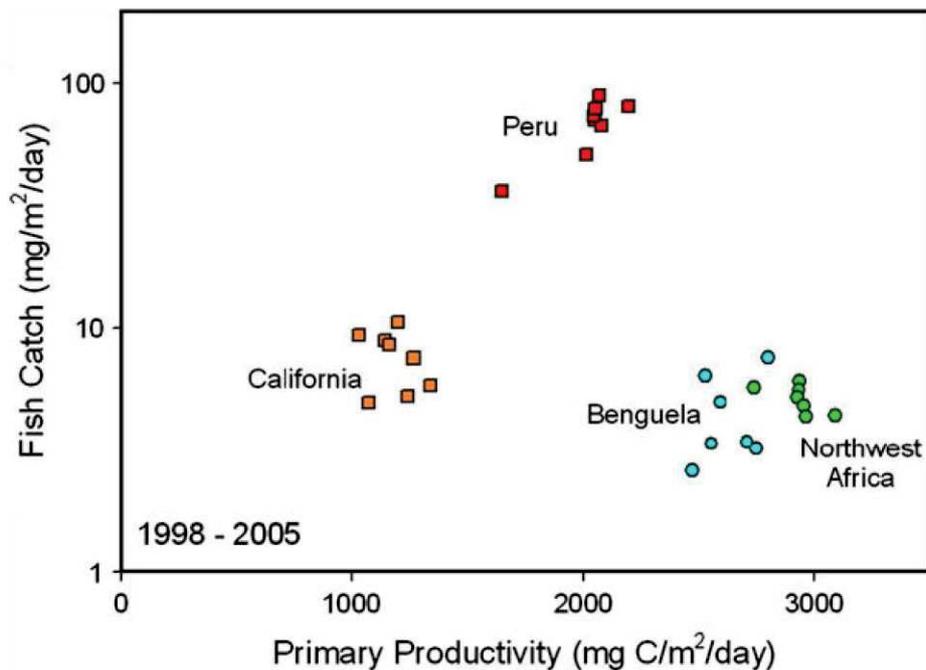
Figure 1.2. Fish catch versus primary productivity for the four main eastern boundary coastal upwelling ecosystems for the years 1998–2005. It was assumed that the reported fish catches (Fish and Agriculture Organization, FAO) were made within 100 km from the coast. The catches were then normalized by area. Primary productivity was estimated from satellite remote sensing of chlorophyll and the Behrenfeld and Falkowski (1997) model. Even during the El Niño year of 1998 Peru fish catch still exceeded that from the other areas by several fold. Is Peru exceedingly efficient in the transfer of primary production to fish or are Benguela and Northwest Africa exceedingly inefficient? Source Chavez *et al.* 2008.

The first description of the relationships between the physical and biological components in the NHCS was proposed by Vogt in 1942, based on his empirical observations of the food chain sustaining seabird populations and human activities. Although most of the elements on the Vogt's representation were hypothesized (Figure 1.3, Vogt 1948), it was already clear that seabirds depend heavily on anchovy in this system.

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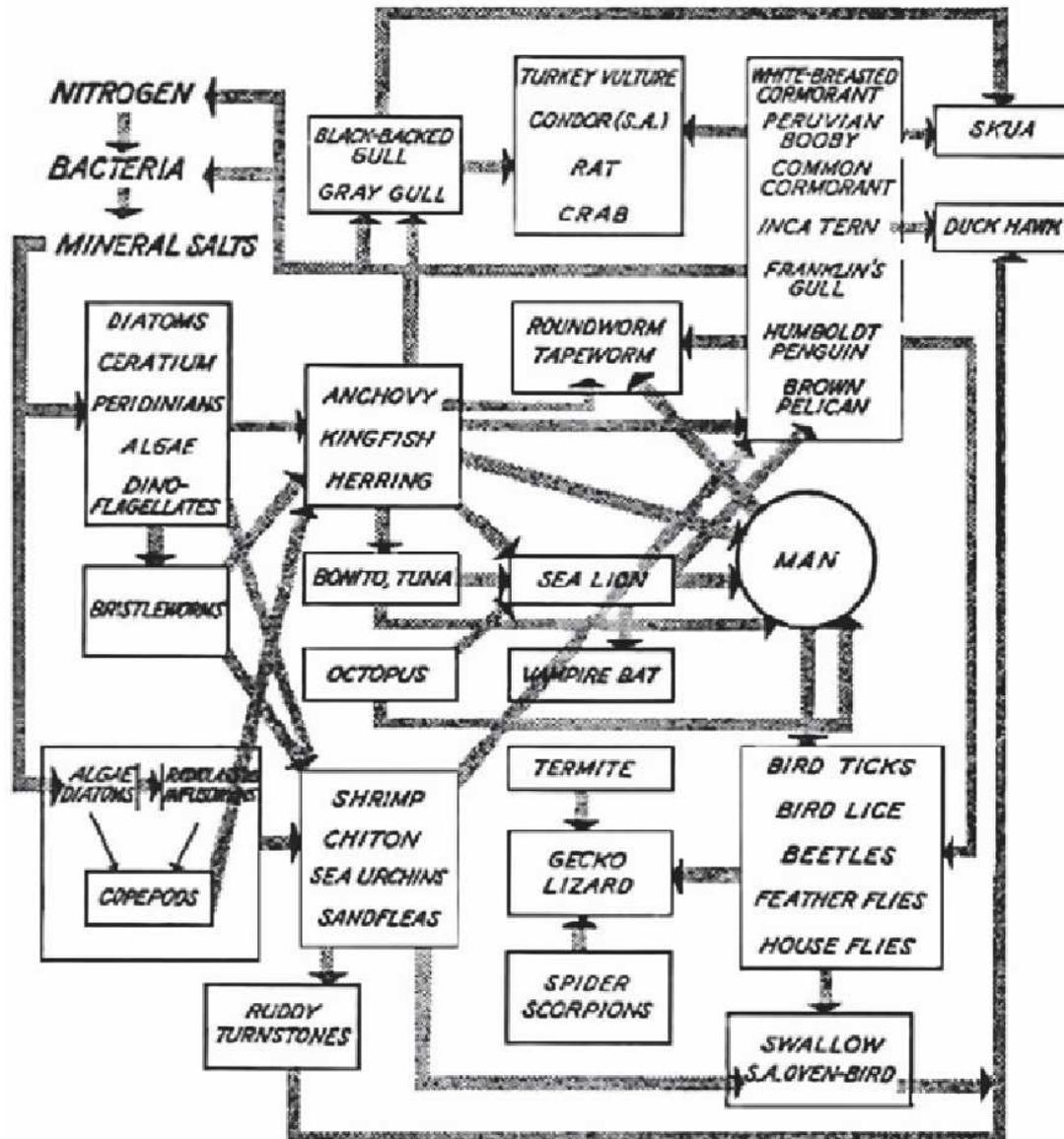


Figure 1.3. First ''ecosystem-based" diagram for the northern Humboldt Current System developed when seabirds were the focus of management Source Chavez 2008 and reprint from Vogt 1948.

This static view of the ecosystem structure mustn't hide the fact that the relationships in marine ecosystems may more variable, and the connectivity among components larger than in terrestrial ecosystems (Link 2002). For instance, oceanographic and biological components in the NHCS interact at different time and spatial scales (Bertrand *et al.* 2004, 2008). This is an evidence for a bottom-up transfer of the behaviors and spatial structuring (Frontier 1987;

Russell *et al.* 1992): physics structures the oceanscape and drives the distribution of particles and passive organisms (plankton); then, because living organisms have to meet their prey, they tend to track their distribution (e.g. Frontier *et al.* 2008) and by the succession of predator–prey relationships, the spatial structuring originally driven by physical forcing tends to be transmitted along the trophic levels of the ecosystem (Fig. 1.4, Bertrand *et al.* 2005).
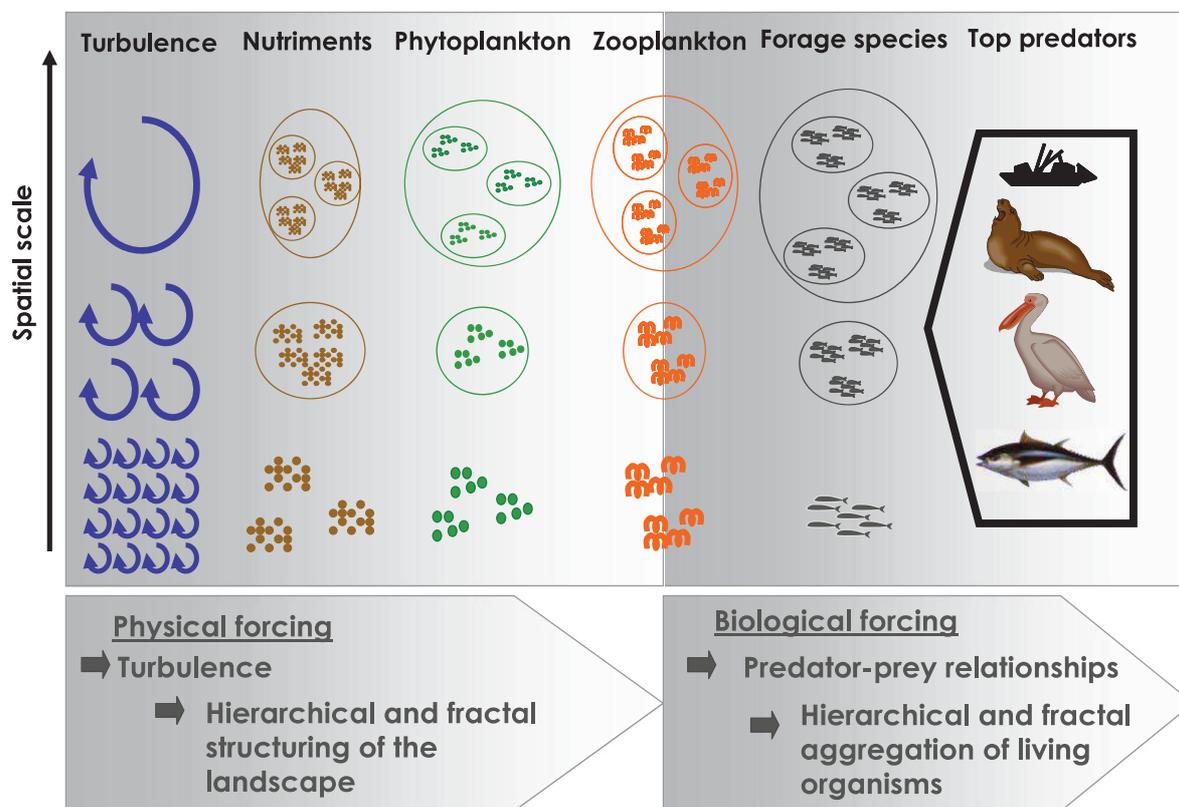


Figure 1.4. Schematic representation of the concept of bottom-up transfer of behavior and spatial structuring.

The physical forcing structures the pelagic landscape by introducing turbulence in the water mass. The dissipation of this turbulence is fractal by nature and generates a hierarchical structuring of the water mass. The inert particles (nutriments) and part of living organisms (phytoplankton and most of the zooplankton) are passively organized in space by this physical forcing. Then, biological interactions such as predator–prey relationships transmit to a certain extent this spatial structuring along the trophic chain. (Source, Bertrand *et al.* 2005).

For more in depth information of the physical forcing at high frequency level and predator prey relationship see the doctoral thesis recently presented: (Ballon 2010; Grados Paredes 2011; Boyd 2012; Salvatteci 2013; Espinoza 2014; Grados 2014; Hernandez *et al.* 2014; Alegre 2015). Hereafter we provide basic elements on the oceanography and ecology of the NHCS that will be used for interpreting the breeding of seabirds.

## 1.1. NHCS oceanography

### *1.1.1. Currents and water masses*

The boundaries of the HCS are determined in the south by the intersection of west wind drift with the South American continent and in the north by the cool upwelled waters colliding with warm tropical waters forming the Equatorial Front. The HCS is not uniform and can be divided into three zones: 1) a northern highly productive year-round Peru upwelling system (Northern Humboldt Current system, 4°S-16°S), 2) a lower productivity and rather large ''upwelling shadow" in northern Chile and southern Peru (16°S-°S), and 3) a productive seasonal upwelling system in central-southern Chile (27°S-42°S, Montecino & Lange 2009). We focus our review on the Northern Humboldt Current system (NHCS), off the coast of Peru (4°S-16°S), where most of the three studied seabird species breed.

The oceanic circulation in the NHCS results from the interaction of a basin-scale atmospheric system combined with regional effects caused by the land-sea boundary. The main atmospheric force at the basin-scale is the area of high atmospheric pressures that drives winds equatorward along the coasts of Chile and Peru called the Southeastern Pacific Subtropical Anticyclone (Strub *et al.* 1998). At the regional scale, along the Peruvian coast, the Andes mountains force the south-east trade winds to blow northward (Gunther 1941; Strub *et al.* 1998).

In the NHCS, the near-surface layer (<25m) is dominated by two wind-driven equatorward currents: the Peru Current (PCC) and the Peru Oceanic Current (POC) (Wyrtky 1967; Chaigneau *et al.* 2013) (Fig.1.5). The PCC flows close to the coast up to 90km from the coast and the POC flows farther offshore more than180 km from the coast (Chaigneau *et al.* 2013). PCC is mainly wind-driven but also reinforced, through geostrophic adjustment, by the cross-frontal temperature and density gradient due to the upwelling (Chaigneau *et al.* 2013). PCC extends from the surface down to the upwelling depth (Echevin *et al.* 2011). In the North of Peru, there are the influence of the Equatorial Undercurrent (EUC) centered along the equator (Philander 1983) and one of its branches flows southeastward to reach the Peruvian coast at 5°S (Kessler 2006; Collins, Mascarenhas & Martinez 2013). Below the thermocline (subsurface layers) and further south, are found the primary (pSSCC) and secondary Southern Subsurface Countercurrents (sSSCC) that flow eastward and enter the NHCS at 5°S and 7°S, respectively (Figure 1.5, (Chaigneau *et al.* 2013).

Below subsurface currents, the poleward subsurface circulation is mainly composed by the Peru-Chile Undercurrent (PCUC) and a weaker secondary poleward flow, the Peru-Chile Countercurrent (PCCC). PCUC is a key element in the NHCS because it advects a relatively warm, salty, nutrient-rich, oxygen-poor, and weakly stratified water mass of near-equatorial origin (Silva & Neshyba 1979) to the extratropical regions. PCUC constitutes the main source of the coastal upwelled waters in NHCS promoting an intense primary productivity (Huyer, Smith & Paluszkiewicz 1987; Chavez *et al.* 2008; Albert *et al.* 2010). PCUC flows along the Peruvian continental shelf and upper slope from 5°S off Peru to 45°S off Chile (Silva & Neshyba 1979) and extends from the coast to 200 km offshore with a depth of 20 and 300 m depth (Echevin *et al.* 2011) (Figure 1.5).

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Finally, below the PCUC, at 500m, the Chile-Peru Deep Coastal Current, a deep equatorward near-coastal current transports relatively fresh and cold Antarctic Intermediate Water northward (Chaigneau *et al.* 2013; Pietri *et al.* 2014).
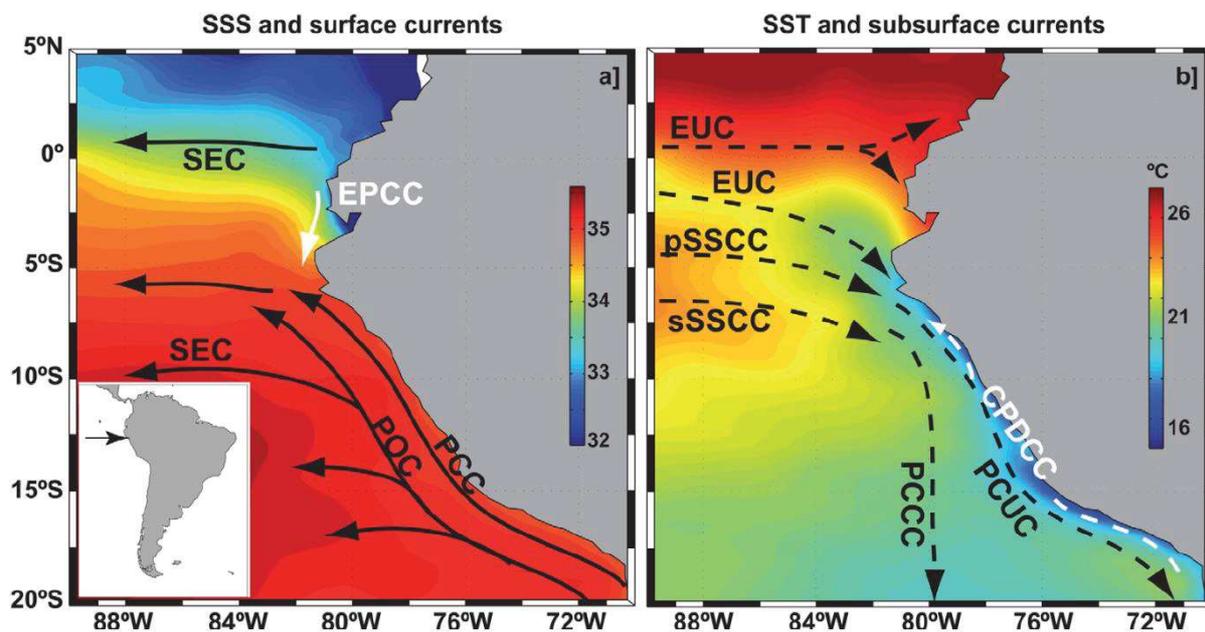


Figure 1.5. Sea surface properties and oceanic circulation scheme of the NHCS. Sea-surface salinity (SSS, color shading) and surface circulation, right panel. Sea-surface temperature (SST, color shading in °C) and subsurface circulation, left panel. The newly defined Ecuador-Peru Coastal Current (EPCC) and Chile-Peru Deep Coastal Current (CPDCC) are indicated by white arrows. Surface currents. SEC: South Equatorial Current; EPCC: Ecuador-Peru Coastal Current; POC: Peru Oceanic Current; PCC: Peru Coastal Current. Subsurface currents. EUC: Equatorial Undercurrent; pSSCC: primary (northern branch) Southern Subsurface Countercurrent; sSSCC: secondary (southern branch) Southern Subsurface Countercurrent; PCCC: Peru-Chile Countercurrent; PCUC: Peru-Chile Undercurrent; CPDCC: Chile- Peru Deep Coastal Current. Source Chaigneau *et al* 2013.

In the NHCS, the action of currents delineates six types of water masses. Four water masses near the surface are described as the cold coastal waters (CCW), the subtropical surface waters (STSW), the equatorial surface waters (ESW), and the tropical surface waters (TSW) (Bertrand *et al.* 2004; Pietri *et al.* 2014); the Eastern South Pacific Intermediate Water (ESPIW) is found at mid-depth (50-400 m), and the Antarctic Intermediate Water (AAIW) occupies the deeper depths (≈500 m) (Figure 1.6, Ayón *et al.* 2008b; Pietri *et al.* 2014). From all of them, the CCW (Zuta & Bustamante 1978) is the water mass that dominates off the Peruvian coast. CCW is a cool and salty water mass transported by the PCUC and upwelled near the coast. However, the oligotrophic STSW (Wyrtky 1967) a warmest and saltiest water mass in NHCS, can dominate the Peruvian coast during El Niño events.
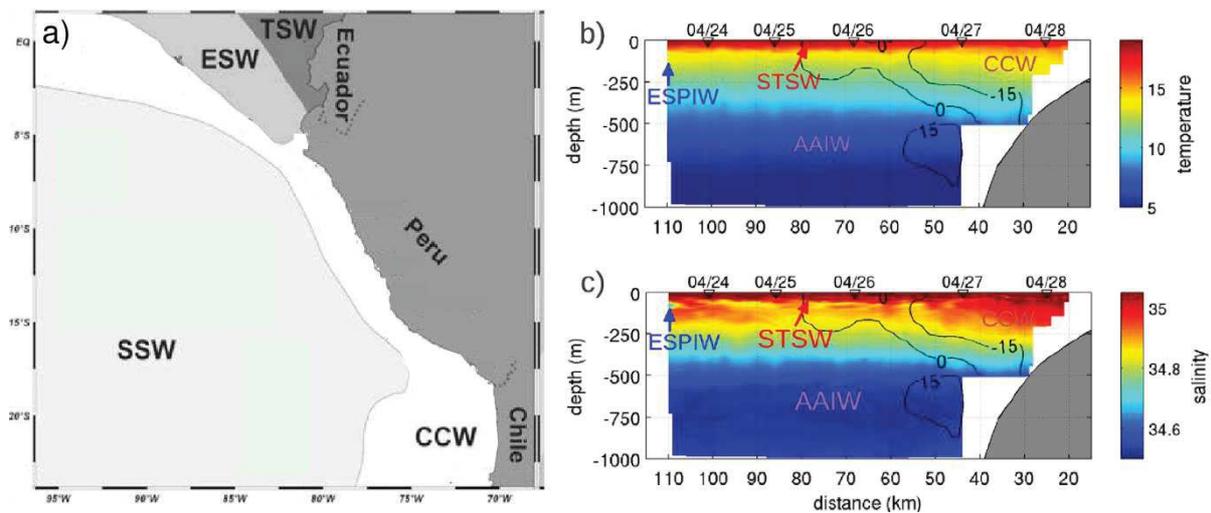
Figure 1.6. Schematic distribution of characteristic surface water masses: a) latitudinal distribution of surface water masses along the Peruvian Coast (Ayon et al 2008), vertical distribution of water mass based on b) Salinity and c) temperature from the fourth section of a glider deployment (at 14 ° S). Source Pietri et al 2014. Cold coastal waters (CCW), the subtropical surface waters (STSW), the equatorial surface waters (ESW), and the tropical surface waters (TSW), the eastern south Pacific intermediate water (ESPIW) and the Antarctic intermediate water (AAIW).

The oceanographic dynamic and the biochemical processes determine the temporal variability of nutrients in the NHCS. Higher concentrations of inorganic nutrients such as nitrates ($NO^{3-}$, 0.0–35.0 µM), phosphates ($PO4^{2-}$, 0.2–4.0 µM) and silicates ($SiO_2^{4+}$, 0.0 – 30.0 µM) (Zuta & Guillén 1970; Calienes, Guillen & Lostaunau 1985; Graco *et al.* 2007) are found near the coast associated to CCW, particularly in major local upwelling centers such as Paita (5°S), Punta Aguja (6°S), Chimbote (9°S), Callao (12°S) and San Juan (15°S) (Zuta & Guillén 1970). Off the coast (>100km) concentrations of nutrients decrease almost to zero in oceanic waters. The vertical distribution of nutrients results from the physical and biological processes such as circulation, upwelling, biological (incorporation by phytoplankton and excretion) and biogeochemical (nitrate reduction, remineralization) processes. In surface layer, the phytoplankton blooms can totally deplete nutrients. Nitrates and silicates can be depleted during phytoplankton blooms while phosphorus is always present in excess (Graco *et al.* 2007). In the case of the intermediate layers, there are high nitrate concentrations by the strong effect of ESW, particularly between 100 and 300 m (Zuta & Guillén 1970). In the deep layer, higher values of silicates and phosphates are associated with the horizontal transport, the interaction with benthos and the high rates of remineralization of organic matter (Graco *et al.* 2007).

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### 1.1.2. Oxygen Minimum Zone (OMZ)

The OMZ correspond to subsurface oceanic zones (50-100m), with ultra-low values of O2 concentration (Morrison *et al.* 1999; Karstensen, Stramma & Visbeck 2008) compared with ''classical O2 minimum zones'' found at intermediate depths (1000–1500 m) (Wyrtki 1962). The OMZ in the NHCS is one of three most intense (<20 mmol kg-1 or <0.5 mL L$^{-1}$), permanent and large ($2.18 \pm 0.66 \times 10^6$ km$^3$) of the global ocean (Paulmier & Ruiz-Pino 2009; Chavez & Messié 2009). The OMZ of the NHCS is thick (~500 m) and attains its shallowest upper boundary depth (25–50 m) off the coasts of Peru and northern Chile (Strub *et al.* 1998) (Figure 1.7, Fuenzalida *et al.* 2009).

This OMZ is maintained by the combination of significant rates of biological production and decomposition of sinking organic material and weak circulation systems in the shadow zone of the southern Pacific subtropical gyre (Chavez & Messié 2009).
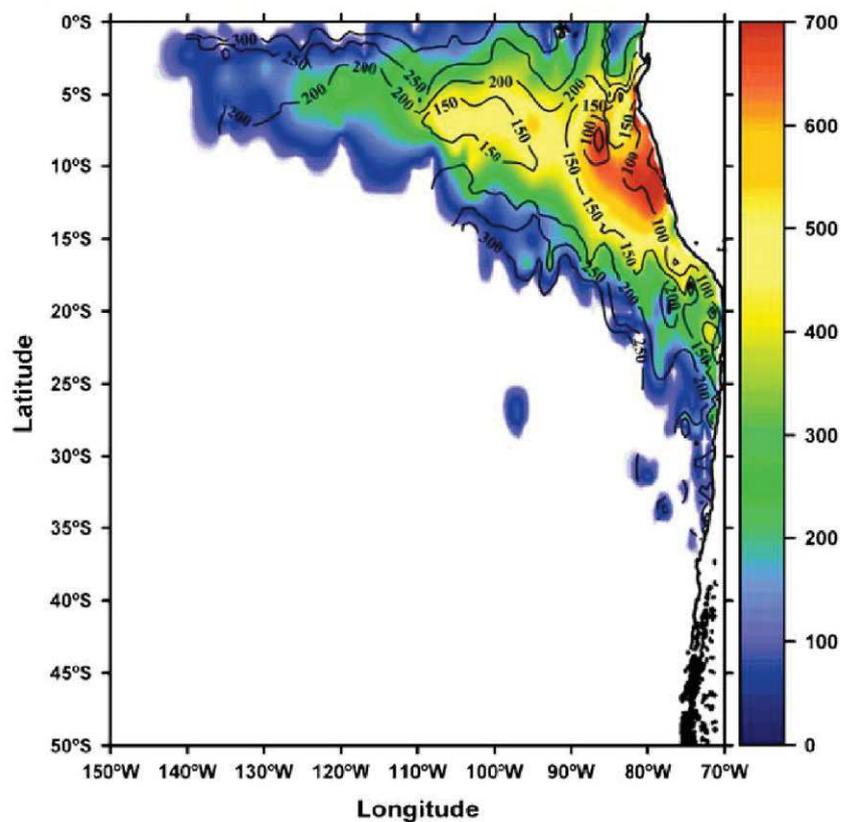


Figure 1.7. Oxygen Minimum Zone (OMZ, < 20μmolkg$^{-1}$) thickness (m) in the south-eastern Pacific. Thickness is colour-coded according to the color bar on the right-hand side of the figure. The upper boundary of the OMZ is shown in black contour lines with 50 m intervals. Source Fuenzalida *et al.* 2009.

## 1.2. Biological components of the NHCS

In this section, we describe the principal components of the trophic web in the NHCS: primary producers (phytoplankton), secondary producers (mesozoooplancton and macrozooplancton), forage fish (anchovy and sardines), and top predators (seabirds, marine mammals and fisheries).

### 1.2.1. Primary and secondary producers

The upwelling of subsurface waters provides an year-round supply of nutrients to the surface, supporting a highly productive phytoplankton bloom (Echevin *et al.* 2008). This phytoplankton bloom includes microplankton (diatoms) and nanoplankton (dinoflogelates and coccolithophores) (Ochoa *et al.* 1999). From the two groups, diatoms are dominating the coastal upwelling and responsible for the high primary production (Echevin *et al.* 2008). Primary production can be measured in terms of chlorophyll-a, one of the main photopigments of diatoms. Average chlorophyll-a concentrations decrease from ~10 mg/m3 at the coast (25-50km) to ~1 mg/m3 ~300 km offshore. There is also a latitudinal difference with maximum nearshore values of chlorophyll-a encountered from 5°S to 9°S (Echevin *et al.* 2008). Dinoflagellates are distributed mainly offshore in less turbulent water masses (Sanchez Ramirez 2000), although some species are commonly found near the coast. Therefore they can be used as indicators of water masses (Sanchez Ramirez 2000): *Protoperidinium obtusum* for CCW; *Ceratium breve*, *Ornithocercus steinii*, *Ornithocercus thumii* and *Amphisolenia thrinax* for ESW; and *Ceratium praelongum* and *Ceratium incisum* for SSW.

In the NHCS, the high primary production in upwelling areas fuels an elevated secondary production of zooplankton. Zooplankton groups can be classified into mesozooplankton (0.2 - 20 mm) and macrozooplankton (20 - 200 mm). For mesozooplankton, three regional groups can be described (Santander 1981): (1) a continental shelf group dominated by copepods (*Acartia tonsa* and *Centropages brachiatus*); (2) a continental slope group characterized by siphonophores, bivalves, foraminifera and radiolaria; (3) and an oceanic group composed by a great variety of copepods (Santander 1981). There is a clear north–south pattern, with high biovolumes mainly between 4°S and 6°S and again poleward of 14°S. Perhaps one of the reasons of these higher concentrations is the narrowest continental shelf (18 – 28 km) in front of these areas and the influence of the ESW, which hosts larger species and higher diversity (Ayón *et al.* 2008a). Macrozooplankton is likely the most abundant zooplankton group by biomass in the NHCS. They form very dense swarms that are able to remove most of the diatoms biomass, exerting a local top-down control on primary production (Antezana 2010). The macrozooplankton biomass also increases across the continental shelf and slope, and toward the offshore area (Ballon 2010). This macrozooplankton fraction is dominated by euphausiids such as *Eucalanus* spp. Euphausids and large copepods are considered as indicators of CCW (Ayón *et al.* 2008b) and constitute a very common item in the diet of forage fish (Figure 1.8, Antezana 2010) (Espinoza *et al.* 1999; Espinoza & Bertrand 2008;

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Antezana 2010). Other group that can be considered as secondary producer is the galatheid crab *Pleuroncodes monodon* (Ayón *et al.* 2008b). In the NHCS, *Pleuroncodes monodon* exhibits a complete pelagic life cycle (Gutiérrez *et al.* 2008). *Pleuroncodes* competes for space and food with important pelagic fish stocks and is a food source for top predators (Gutiérrez *et al.* 2008) as seabirds and mammals (Jahncke, Garcia-Godos & Goya 1997a; Zavalaga, Paredes & Arias-Schreiber 1998).

Vertically, the habitat available for zooplankton is limited due to the shallow oxygen minimum zone (OMZ). The OMZ acts as an effective barrier for zooplankton and other organisms as jumbo squid (Alegre *et al.* 2014), but it also offers increased food supply and refuge for species adapted to live there and perform diel vertical migration ascending at dusk and a descent at dawn (Ayón *et al.* 2008a; Escribano, Hidalgo & Krautz 2009). About 75% of the macrozooplankton biomass performs diel vertical migration and inhabits the OMZ during the day (Ayón *et al.* 2008a; Escribano *et al.* 2009; Bertrand, Ballón & Chaigneau 2010) and various species of euphausiids of the genera Eucalanus are adapted to hypoxia and occupy the OMZ during the day and night (Antezana 2009, 2010; Escribano *et al.* 2009).
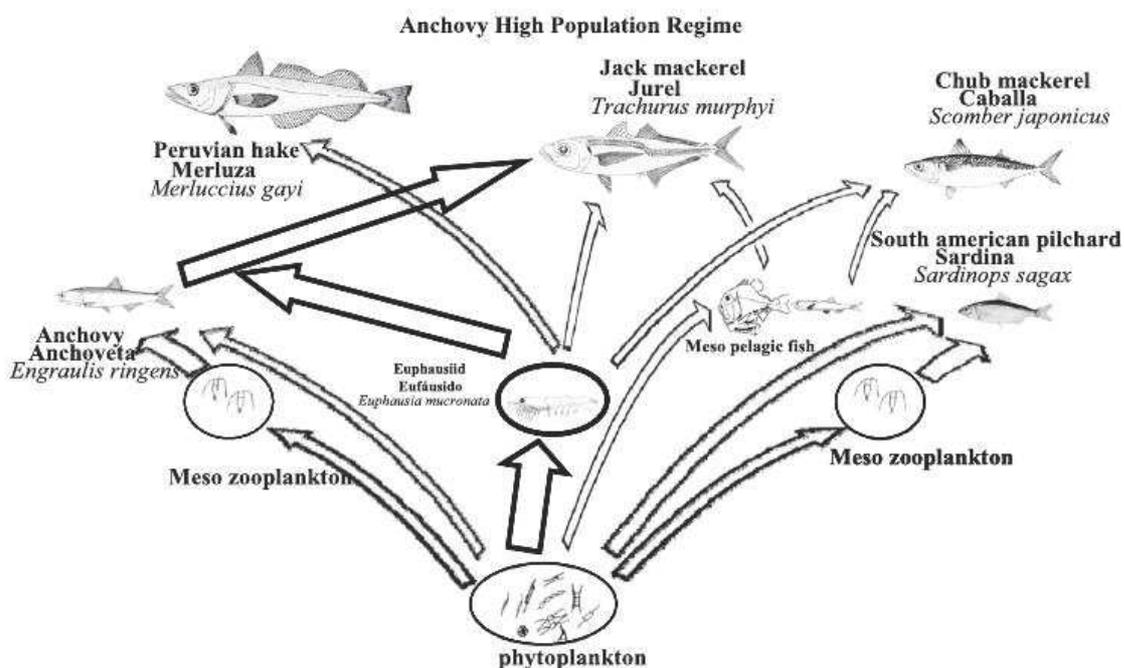


Figure 1.8. Simplified food web of NHCS, centered on euphausiid *Euphausia mucronata* during a period of high biomass of anchovy *Engraulis ringens*. Thickness of the arrows indicates the relative flow of biomass between components. Souce Antezana 2010.

### 1.2.2. Forage fish

Forage fish commonly refers to small pelagic fish (10-30cm), swimming in dense schools, mainly preying on phytoplankton and zooplankton and foraged by larger predators. In the NHCS, two species are considered as the most important by their abundance and trophic position: the Peruvian anchovy (also called anchoveta) and the Chilean sardine (Figure 9).

The Peruvian anchovy (*Engraulis ringens*) is the main species of the family Engraulidae in the NHCS (Figure 1.9). Anchovy has a maximum life span of 4 years and may reach a maximum size of 20 cm. It grows fast, reaching adult size (>12cm) and maturity after only one year. Anchovy is also flexible for reproduction, since they are able to spawn all year-round, with peaks between July and October over the whole latitudinal range off Peru (Buitrón & Perea 2000; Mori, Perea & Espinoza 2011). Anchovy distribution ranges between 4°S–42°S, the distribution range is closely associated to recently-upwelled nutrient-rich waters of the CCW (Swartzman *et al.* 2008). Following the variability of the distribution of the CCW, anchovy is concentrated at distances between 20 and 100 nm from the coast, depending on the year (Simmonds *et al.* 2009). The occurrence of this species in such large biomasses in the NHCS long appeared as a paradox: how a fish which (i) performs very small migrations and cannot escape adverse conditions, (ii) is mainly distributed in shallow dense aggregations and then theoretically easily accessible to predators (fish, cephalopods, birds, mammals and fishers), and (iii) is very slow in its avoidance reactions to predators, can achieve such enormous biomass in a relatively short time. Several reasons may explain this apparent paradox. First, the very high concentration of plankton prey within a thin layer of water allows sustaining, even locally, very large aggregations of anchovy (Ayón *et al.* 2008b). Vertically, CCW have also a shallow oxycline (<10m), which does not affect small-size anchovies but allows them to escape from predation by larger fish (Bertrand *et al.* 2010). Other adaptive strategies of anchovy include the ability to track and concentrate within refuge areas when conditions are adverse (Bertrand *et al.* 2004), and to spatially distribute its population over a large temperature range (Gutiérrez *et al.* 2008). Anchovy mainly feeds on zooplankton (98%) and phytoplankton (2%) and zooplankton constitutes by far the main item in term of energy supply (Espinoza & Bertrand 2008).

The Chilean sardine (*Sardinops sagax*) belonging to the Cupleidae family, is the only species of the genus *Sardinops* and distributes in the Indo-Pacific Ocean (Figure 1.9). In the NHCS, sardines were very abundant and distributed farther offshore than anchovy along the Peruvian coast during the 1980s (Alheit & Niquen 2004), but became almost completely absent from the NHCS since the early 2000s (Gutiérrez *et al.* 2007). The crash of the sardine population can be attributed to the synergetic effects of trophic structure and oxygen content, and these environmental effects were most likely aggravated by overfishing (Bertrand *et al.* 2011). The Chilean sardine distribution is more associated with the relatively warm conditions of the STSW than with the cold conditions of the CCW, concentrating at distances centered on the shelf break at 40 and 60 nm from the coast (Swartzman *et al.* 2008). The sardine is a larger fish than the Peruvian anchovy, reaching a maximum size of 30 cm. Therefore, it has a higher demand of oxygen than anchovy and is more affected by a shallow oxycline, avoiding such

areas (Bertrand *et al.* 2011). Sardines can efficiently filter-feed phytoplankton and small zooplankton but their main prey items are small copepods and euphausiids (Espinoza *et al.* 2009).

Other forage fish includes the longnose anchovy (*Anchoa nasus*) which is distributed mainly north of 9°S and occasionally found until 12°S (Bouchon 2007).
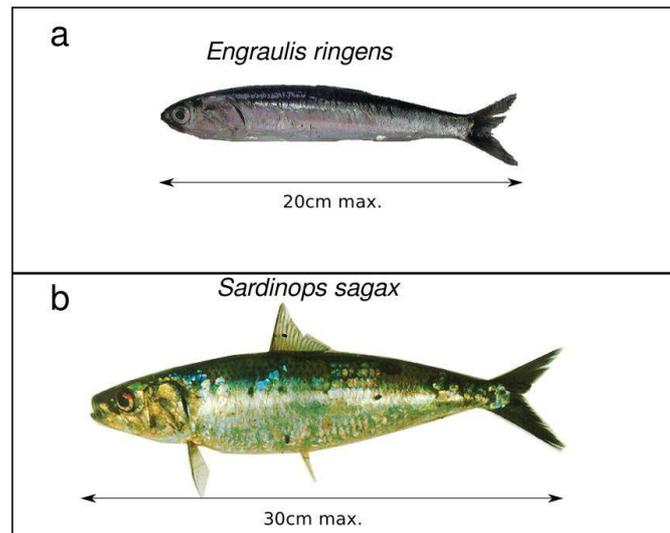


Figure 1.9. Peruvian anchovy (a) and sardine (b).

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### 1.2.3. Seabirds and mammals

In the NHCS, the main top predators relying on secondary production are seabirds, marine mammals, and fishermen.

Twenty seabird species were identified as commonly breeding in the NHCS along the Peruvian coast (Table 1, Figure 1.10) and depending on anchovy as forage fish. However some other species which are seasonal migrants can be observed from October to March (Duffy 1981; Anguita & Simeone 2015).

Amongst the most abundant species are the so-called guano-producing seabird species: Guanay cormorant (*Phalacrocorax bougainvillii*), Peruvian booby (*Sula variegata*) and Peruvian pelican (*Pelecanus thagus*). A detailed description of their biology, population distribution and habitats is provided in the following sections and their reproduction is the core subject of this thesis.

Other seabirds highlighted in NHCS are Humboldt penguin nowadays listed as concern (3000-5000 individuals), Peruvian diving petrel listed as endangered (13 000 pairs) and Peruvian Tern listed as endangered (less than 1000 pairs) (International & Conservancy 2007).

Table 1. List of the seabird species observed near the coast in NHCS. References: [1] (Murphy 1936), [2] (Tovar Serpa 1969), [3] (Figueroa & Stucchi 2008), [4] (Stucchi *et al.* 2011), [5](Reserva Nacional Sistema de Islas 2009), [6] (Duffy 1981).

| Spanish name | English name | Scientific name | Reproducing in NHCS | References |
|---|---|---|---|---|
| | Phalacrocoracidae | | | |
| Cushuri o cuervo de mar | Neotropic cormorant | *Phalacrocorax olivaceus (brasilianus)* | R | 2, 4,5 |
| Guanay | Guanay cormorant | *Phalacrocorax bougainvillii* | R | 1, 2, 3, 4, 5 |
| Chuita | Red-legged cormorant | *Phalacrocorax gaimardi* | R | 2, 4, 5 |
| | Sulidae | | | |
| Piquero | Peruvian booby | *Sula variegata* | R | 1, 2, 3, 4, 5 |
| Camanay | Blue-footed booby | *Sula nebouxii* | R | 2, 4, 5, 6 |
| Piquero de Nasca | Nazca' booby | *Sula granti* | R | 3, 4 |
| Piquero Enmascarado | Masked booby | *Sula dactylatra* | | 3, 4 |
| Piquero Pardo | Brown booby | *Sula leucogaster* | | 4 |
| | Pelecanidae | | | |
| Pelícano | Peruvian pelican | *Pelecanus thagus* | R | 1, 2, 3, 4, 5 |
| | Hydrobatidae | | | |

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| | | | | |
|---|---|---|---|---|
| Golondrina de la tempestad | Wedge-rumped storm petrel | *Oceanodroma tethys* | R | 2 |
| Golondrina de la tempestad de Elliot | Elliot's storm petrel | *Oceanites gracilis* | | 4 |
| | Sooty Storm-petrel | *Oceanodromus markhami.* | | 6 |
| Golondrina de Mar Acollarada | Hornby's storm petrel | *Oceanodroma hornbyi* | | 4, 6 |
| Golondrina de Mar Negra | Black storm petrel | *Oceanodroma melania* | | 4, 6 |
| | Laridae | | | |
| Gaviota gris | Grey gull | *Larus modestus* | | 4 |
| Gaviota capucho gris | Grey-headed gull | *Larus cirrocephalus* | | 5 |
| Gaviota peruana | Belcher's gull | *Larus belcheri* | R | 2, 3, 4, 5, 6 |
| Gaviota de Sabine | Sabine's gull | *Xema sabini* | | 6 |
| Gaviota dominicana | Kelp gull | *Larus dominicanus* | R | 2, 3, 4, 5, 6 |
| Gaviota de Franklin | Franklin's gull | *Larus pipixcan* | | 4, 6 |
| Gaviota de Galápagos | Swallow-tailed gull | *Creagrus furcatus* | | 4, 6 |
| | Sternidae | | | |
| Zarcillo | Inca tern | *Larosterna inca* | R | 2, 3, 4,5 |
| Gaviotin comun | Common tern | *Sterna hirunda* | | 2, 6 |
| Charrancito peruano | Peruvian tern | *Sternula lorata* | R | 2, 6 |
| Charran patinegro | Sandwich tern | *Thalasseus sandvicensis* | | 6 |
| Charran ártico | Arctic tern | *Sterna paradisaea* | | 6 |
| | Procellariidae | | | |
| Petrel gigante sureño | Southern giant petrel | *Macronectes giganteus* | | 4 |
| Petrel Damero | Cape petrel | *Daption capense* | | 4 |
| | Pelecanoididae | | | |
| Potoyunco | Peruvian diving petrel | *Pelecanoides garnotii* | R | 4, 5, 6 |
| | Stercorariidae | | | |
| Skua chileno | Chilean skua | *Stercorarius chilensis* | | 6 |
| | Rynchopidae | | | |
| Pico tijera | Black skimmer | *Rynchops niger* | | 6 |
| | Spheniscidae | | | |
| Pingüino de Humboldt | Humboldt penguin | *Spheniscus humboldtii* | R | 1, 2, 3, 4, 5 |

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Figure 1.10. Most common seabird species that depends on forage fish included a) Cushuri (*P. olivaceous*), b) the Guanay cormorant (*P. bougainvillii*), c) the Red-legged cormorant (*P. gaimardi*), d) Peruvian booby (*S. variegata*), e) the Blue-footed booby (*S. nebouxii*), f) the Humboldt penguin (*Spheniscus humboldti*), g) the Peruvian pelican (*Pelecanus thagus*), h)

and the Inca tern (*Sterna inca*). The i) Kelp gull (*Larus dominicanus*) is a common species that feed on eggs, chicks and regurgitates of guano seabirds breeding in sympatry.

Pinnipeds and cetaceans also feed on forage fish in the NHCS. Two species of pinnipeds are important by their numbers: the South American sea lion (*Otaria flavescens*) and the South American fur seal (*Arctocephalus australis*) (Figure 1.11, Majluf 1989). Fur seals mostly occur from 6°S-17°S and their presence is linked to the flow of the PCC (Majluf & Trillmich 1981). In the NHCS, they reproduce between October and December with 90% of all births occurring during a period of 40 days. Females give birth to a single pup almost every year, but due to high mortality, only one out of every 3-4 pups survive to one year of age (Majluf 1989). Fur seal populations have experienced high variability due to harvesting, competition with fisheries, by-catch in fishing gear and El Niño events. The current size of the population is estimated to ~14 000 individuals along the Peruvian Coast (Cárdenas-Alayza 2012). The main food item for fur seals in Peru is adult anchovy, ~40% of the diet, (Majluf 1989). They take other small pelagic schooling fish, but do so only when availability of adult anchovy is low (Majluf 1989). South American sea lions occur within a broad latitudinal range along the South American coastline, and are continuously distributed along the Peruvian coast (Majluf & Trillmich 1981; King 1983). Sea lions are seasonal breeders between January and February but they have been observed pupping and mating throughout the rest of the year. Sea lions off Peru feed mostly on small pelagic fish but are more opportunistic feeders than fur seals. Sea lions are also competing with fishermen and are commonly observed taking fish from small-scale fishing gears and for this reason, they are regularly killed by fishermen when encountered at sea (Majluf 1989). Before 1910, sea lion population was large enough to feed an industry exploiting their fur and oil. Sea lions were considered competitors of seabirds by feeding on anchovy and then a 'plague to exterminate'. Industry of sea lion hunting exploited in particular pups and females. Hunting intensity was such that 36 500 sea lions were hunted per year during 1939-1941. Only in 1957-1958, the government banned sea lions hunting in response to their low abundance; consequence of hunting and El Niño events. In 1961, only 8000 sea lions remained along the Peruvian coast. In 1984, sea lion population had recovered to 35 000 individuals but never recuperated pre-hunting era population levels (Cushman 2003).

Four species of cetaceans have been reported feeding on forage fish: the Bryde's whale (*Balaenoptera edeni*), the Dusky dolphin (*Lagenorhynchus obscurus*), the Common dolphin (*Delphinus delphis*) and the Bottle nose dolphin (*Tursiops truncatus*), but very little is known about their ecology in the Peruvian waters (Figure 1.11, Majluf 1989).

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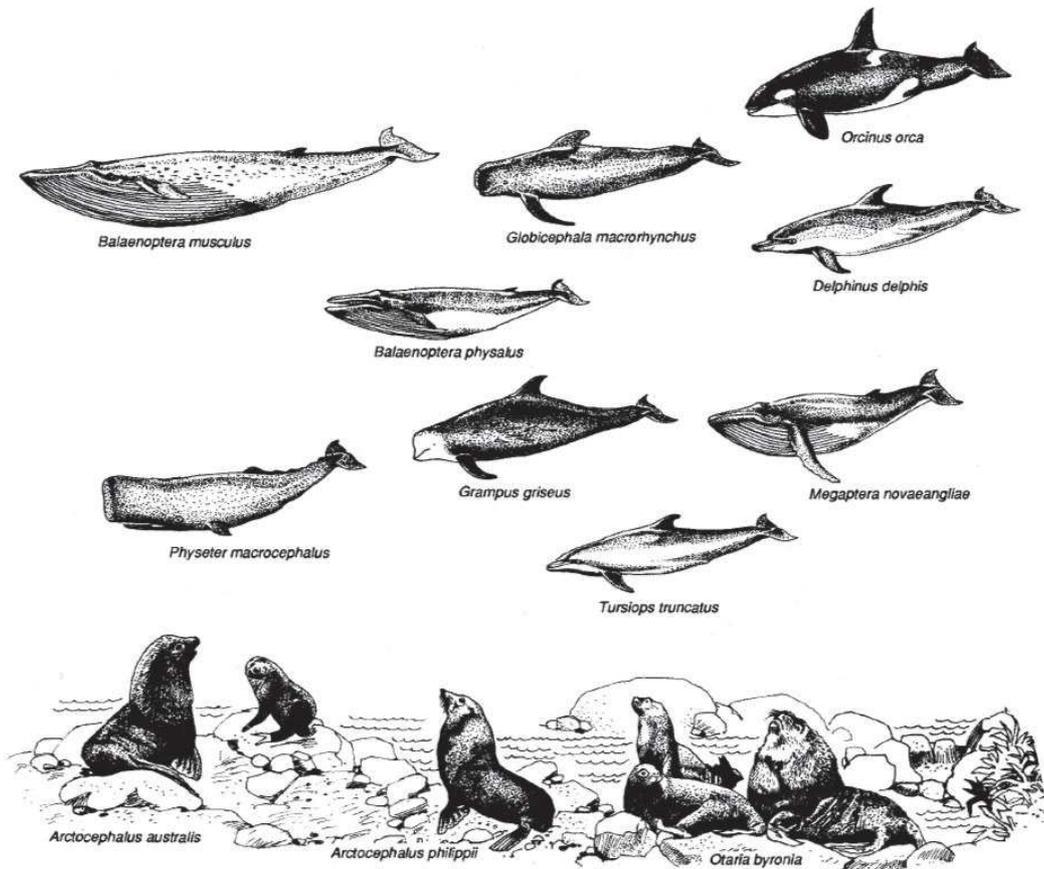


Figure 1.11. Main marine mammal species occurring in the NHCS. Source Majluf 1989.

## *1.3.* **Fish meal fishery**

The NHCS sustains large populations of small pelagic fish that supports the world's largest monospecific fisheries (Chavez *et al.* 2008). The Peruvian anchovy (*Engraulis ringens*) is the top landed species with more than 7 million tonnes in 2011 (FAO 2014). In second place, sardine (*Sardinops sagax*) was a target species from 1976 to 1999, but since 2000 sardine catches declined and fleet catches are composed of ~ 95% of anchovy.

Most of the fleet is composed by purse seiners, with a hull made of steel, ranging from 30 to 900 tons of holding capacity (HC), mostly owned by large fishing companies. Yet, since 1999 a semi-artisanal fleet of purse-seiners with hulls made of wood and ranging from 30 to 110 tons HC is developing (Figure 1.12) (Fréon *et al.* 2008)

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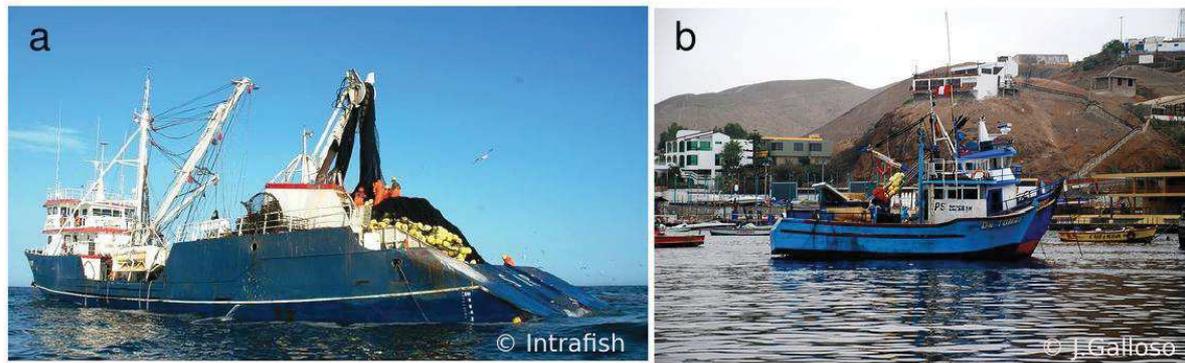


Figure 1.12. Purse-seiners used to catch anchovy, a) "industrial" purse seiner with a steel hull and b) "artisanal" purse-seiner with a wooden hull.

Fisheries of anchovy for fishmeal production started in the 1950s. In only one decade anchovy landings increased from 6 331 T in 1951 to 303 000T in 1960. The fleet also increased from 321 units in 1958 to 2030 units in 1965 (Castillo 1966). During the 1960s the fishing fleet grew steadily dominating the worldwide fish landings, with a peak harvest of 12MT per year in 1970 accounting for 20% of the world catches (Figure 1.13) (Chavez *et al.* 2008). Simultaneously, the Peruvian government became interested in the profits of the fishery, neglecting the guano industry. In 1964, with the support of FAO, the Instituto del Mar del Peru (IMARPE) was created to conduct research and provide advices for the anchovy fishery management.

The Peruvian government was interested in getting a maximum profit from the anchovy fishery without endangering the resource renewal. For that, they hired in 1966 Milner Schaefer, one of the most renowned experts in fisheries science, to evaluate the anchovy stock. Some of his suggestions to the anchovy stock management were: an annual global quota of 7.5 MT as the maximum sustainable yield (MSY), a minimum size of anchovy to be caught (12 cm in average per catch), fishing closures during anchovy spawning. However if anchovy consumption by the largest top predators as seabirds was excluded from models, 9.5MT of anchovy could be caught (Cushman 2003). Following the maximum profit of the fishery, anchovy consumption by the seabirds was excluded and the MSY was set to 9.5 MT (Figure 1.13). Neverthless, Schaefer models were calculated based only in anchovy recruitment during successful years, leaving out the effects of El Niño events.

The strong 1972-1973 El Niño, combined with the situation of overcapacity and overfishing, produced the collapse of the anchovy stock (Hilborn & Walters 1992). As a consequence in 1972, the military government decided to reduce the fishing and fish meal processing capacity, and to forbid the building or renewal of fishing vessels (Aranda 2009). In 1973, only 1.5 MT of anchovy were caught (Figure 1.13) and the Peruvian government expropriated fishmeal companies and created the national company Pesca Peru. Progressively during 70's, the private industrial fishery turned its attention to sardine and incremented its catch (Fréon *et al.* 2008), until sardine became the most important pelagic fishery during the

1980s (Alheit & Niquen 2004). Sardine catches reached a peak harvest of 3MT in 1985 (Figure 1.13) (Fréon *et al.* 2008). Anchovy began to recover and became highly abundant again in the 1990s (Niquen 2000; Gutiérrez *et al.* 2007; Bertrand *et al.* 2011) due to favorable long-term environmental conditions (Chavez *et al.* 2003). In contrast, sardine abundance and catches gradually decreased during this period, probably as a result of unfavorable environmental conditions and overfishing (Bertrand *et al.* 2004, 2011). The Peruvian government during the 90's, introduced a neo-liberal economy and the private sector found optimal conditions to invest again in vessels and to modernize and build fishmeal factories(Cushman 2003). By the end of the 1990's, the anchovy stock recovered rapidly although a strong El Niño occurred in 1997-98 that marked the collapse of the sardine stock which has not yet recovered (Bertrand *et al.* 2004)( Fig.1.13). In the 2000s, the investment and capacity of the fishing industry increased, and annual landings of anchovy ranged from 5 to 9MT (Fréon *et al.* 2008; Aranda 2009)( Figure 1.13). One of the most visible effects of overcapacity on fishing activity was a reduction in the annual number of fishing days for completing the global catch quota. The fishing season of the Peruvian anchovy decreased from ∼ 350 days in 1987 to ∼ 50 days in 2006 (Fréon *et al.* 2008). In 2009, the government implemented individual vessel quota allocations (IVQs) in the anchovy fishery. The introduction of the IVQs had an immediate effect, lengthening the annual fishing season and reducing the total number of operating fishing vessels (Tveteras, Paredes & Pena-Torres 2011).
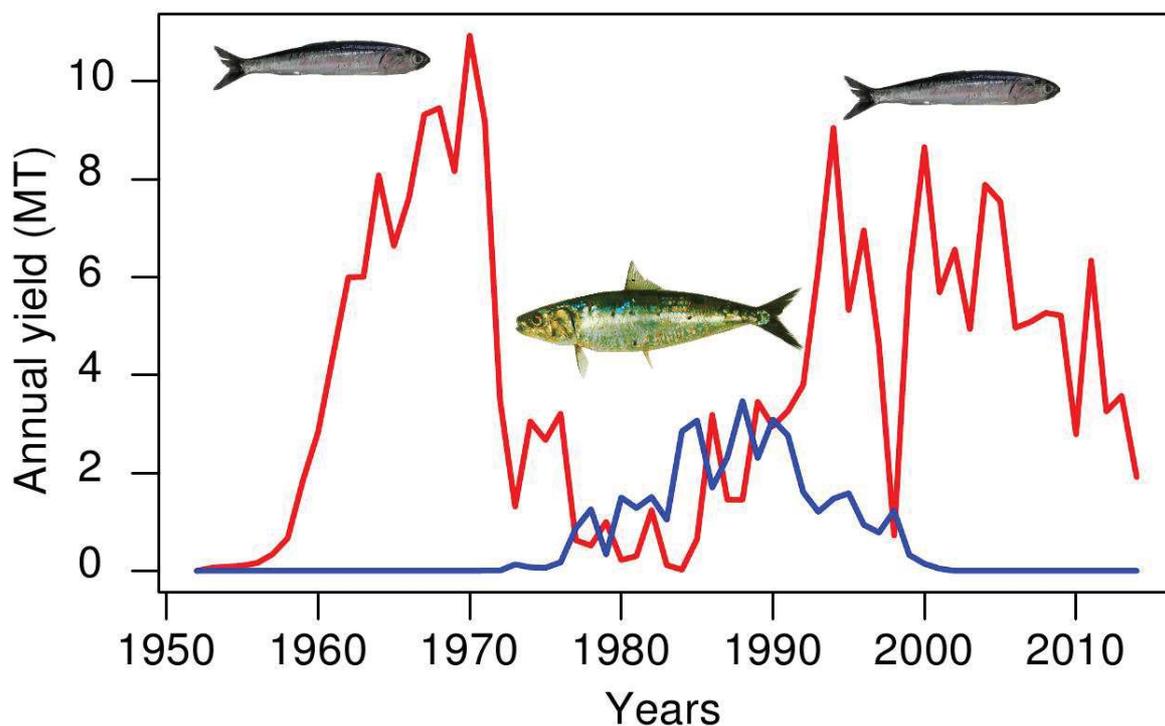


Figure 1.13. Time series of annual yield (MT) of anchovy and sardine in the NHCS. Source of data,  IMARPE.

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### 1.4. Guano harvesting industry

Seabird population dynamics in Peru are closely linked to the development of the country. An excellent analysis of the importance of seabirds in the history of Peru was proposed by Robert Cushman in *"The Lords of Guano: Science and the Management of Peru's Marine Environment, 1800-1973"* published in (2003). This excellent narrative is the main basis of the description provided below, that focuses on the events (as a time line) that help to understand the high variability of seabird population over the last two centuries.

Since pre-colonial times, seabirds have been linked to anthropogenic activities. In the history, seabirds were 'lethally' related to human when eggs or adults were hunt by artisanal fishermen (they considered cormorants as a great delicacy) (Cushman Murphy 1936); they were also 'non-lethally' related to humans, through the exploitation of their guano as fertilizer, or as competitors with fisheries for anchovy consumption. Garcilaso de La Vega (1539-1616) reported that, during the pre-hispanic period, native population of the valleys of Southern Peru used seabirds manure called *huanu piscup* as fertilizer for corn crop. The word *huanu* was changed to guano in Spanish to designate the manure from seabirds. Also, the name of the most important seabird producing guano, the guanay Cormorant, originates from this word. Cormorant together with booby and pelican are the more important seabirds in guano production. The knowledge of using guano as fertilizer was kept during Spanish colonization but was not exploited at large scales (internationally) until 1800's when the presence of great deposits of guano was reported and published internationally by Alexander von Humboldt and Justus von Lieblig.

In 1840's historical deposits of guano began to be exploited industrially, giving high profits to the Peruvian government. However the seabirds nesting in colonies were considered by the workers more as a nuisance than the source of guano, and some populations declined because of human disturbance as documented by Coker for the Peruvian pelican (Coker 1908).

After having exhausted the historical guano deposits, the development of an extensive culture of cotton in the Peruvian coast demanded more guano than what was produced. The Peruvian government hired Robert Coker, a young scientist, for finding ways to increase the guano production and to identify other marine resources to exploit. Robert Coker recommended the creation of the 'Compania Administradora del Guano' (CAG, 1909 - 1963) that was in charge of the protection of seabirds and had the monopolistic commercialization of guano. To ensure the protection of seabirds, Coker recommended establishing a closed session of guano extraction during the peak of the breeding season (November to March) and a long-term rotation (minimum 1 year) between the tenths of guano-producing colonies.

A private Peruvian company exploiting guano from the main colonies hired Henry Forbes (1911-1913) to have a concurrent opinion. Henry Forbes recommendations were similar to R. Coker concluding that omitting El Niño 1911, the most important cause of seabird decline was the exploitation of guano without rotation and the lack of closed session during the breeding season that he estimated being from September to May (Forbes 1913, 1914). Later, under the management of the CAG Robert Cushman (1919-1925) and William Vogt (1939-

1941) were hired as expert ornithologists. R. Cushman reported massive mortalities of seabirds during the extreme El Niño events of 1925 linked probably to oceanographic conditions and disease (Cushman Murphy 1923, 1925). W. Vogt reported that guano production was limited by the anchovy abundance. Some of their suggestions were taken into account, like the interest of the conservation of the three seabird species (cormorants, boobies and pelicans) and not only cormorants, because they have different niches and their numbers can only increment the amount of guano (Vogt 1942). These policies gave results and 14 new colonies located on headlands became active first in the south Peruvian coast and then in the north. The maximal retribution of this practice was reached in 1955-1956 when 33 million of seabirds (Figure 1.14) nested in 52 active colonies, producing more than 300 000 metric tons of guano (Figure 1.15 and 1.16). Also, their advices led to the implementation of systematic guardianship, and the regular report of seabirds abundance in each of the breeding colonies (Tovar Serpa, Guillen & Nakama 1987).
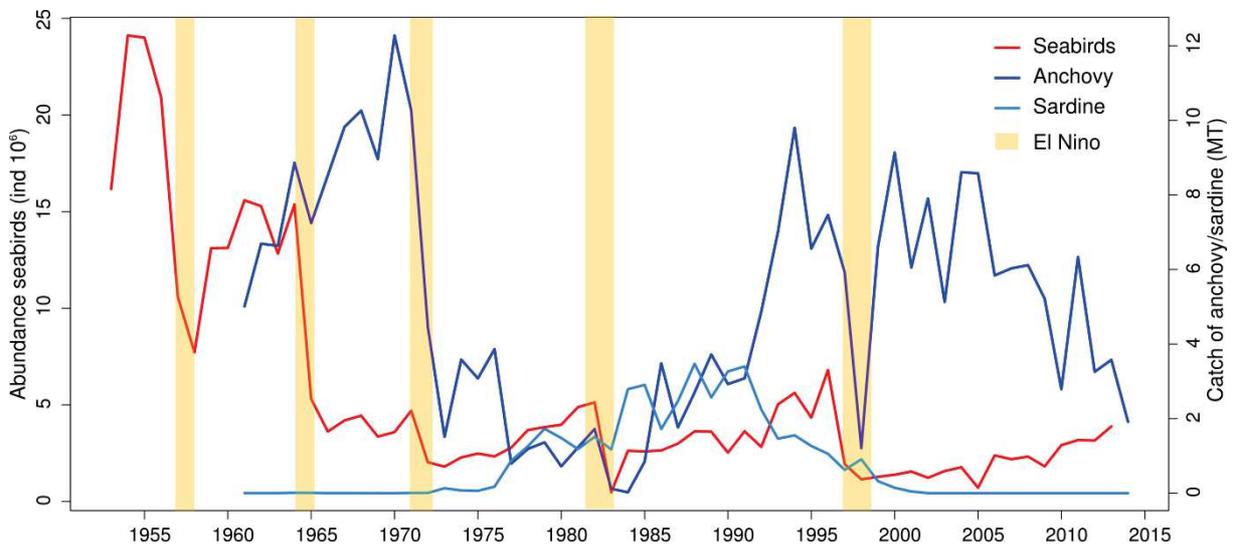


Figure 1.14. Abundances of seabirds (cormorants, boobies and pelicans) from 1952 to 2014, and catch of anchovy and sardine. Years when strong El Niño events occurred are marked by orange bars. Data source AGRORURAL and IMARPE.

However at the peak of maximal abundance of seabirds (Cushman 2003) the industrial fishery was developing and the competition for anchovy between fishers and seabirds began to be important. Seabird populations decreased due to strong El Niño event of 1957-58, cormorants decreased from 30 million to 3.1 million, boobies from 4.2 million to 160 000 and pelicans from 1.3 million to 20 000. Most of seabirds migrated during 1957 but many of them never returned (Figure 1.14). In contrast, the El Niño 1957-1958 did not affect significantly the fishery that was still increasing its fishing power, through the use of echo localization to search for anchovy schools for instance. The use of echosounders made the fishery much less dependent on flocks of seabirds to localize fish schools, and increased the efficiency of vessels in terms of searching time. The number of vessel to capture anchovy grew by 600% during 1956-1958.

Figure 1.15. Map of the main seabird colonies during 1956. Source: 48 Memoria del Directorio de la Compania Administradora de Guano.

Seabird populations recovered up to 17 million individuals in the 1960. (Figure 1.14), yet, the guano production could only fulfill 25% of the fertilizer demand from national agriculture (Cushman 2003). Therefore most of the fertilizer required was imported synthetic fertilizer and policy for seabird conservation by CAG lost importance. In 1963, CAG was reorganized into Corporacion Nacional de Fertilizantes (CONAFER) with the objective of developing in Peru the production of synthetic fertilizer. By 1963, the fishing industry had completely

developed. It had the capacity to catch and process 13 MT.y$^{-1}$ of fresh anchovy when only 8 MT.y$^{-1}$ was fished. Given this situation, an advisory table was created to manage and regulate the fishery. CONAFER was excluded of the advisory table. By the end of CAG in 1963, 45 colonies were still active, all with guardianship (Tovar Serpa *et al.* 1987).

The end of CAG seabird management and the orientation of the state policy towards anchovy fishery sealed the fate of seabirds. During 1967-1971 seabird numbers decreased to 4 million (Figure 1.14) and anchovy quotas and catches increased up to 14 MT in 1972. The anchovy fishery became at that time one of the most important of Peru revenues (2% of the gross domestic product). The final stroke was the 1972-1973 El Niño that led the seabird population to decrease to 2 million of individuals (Figure 1.14). As a consequence, lower quantities of guano were produced (Figure 1.16) and guano extraction became a minor economic activity.
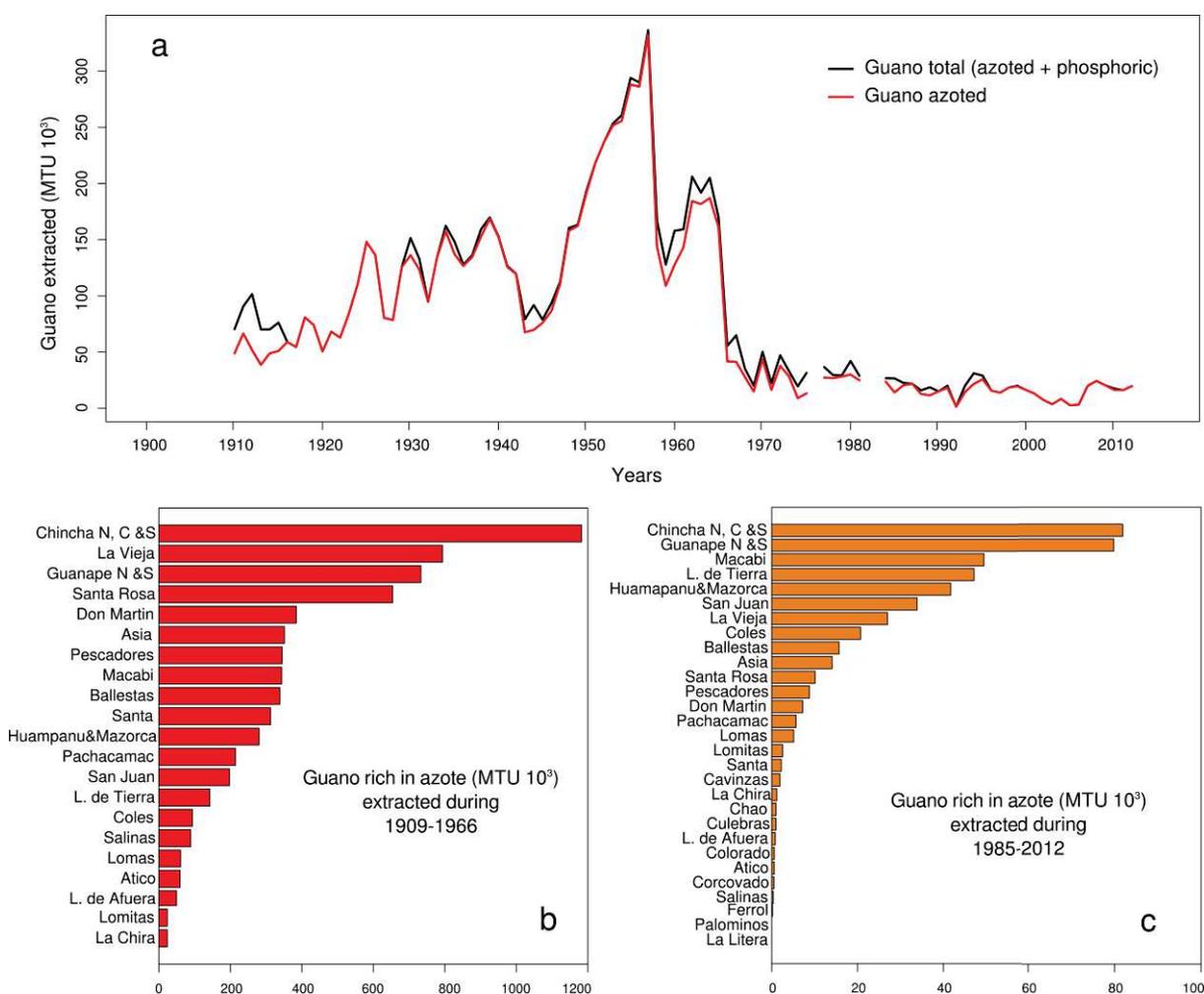


Figure 1.16. a) Guano extracted per year during the last century in the main seabird colonies (Data source AGRORURAL), b) Guano extracted by nesting site from 1909-1966, period of large abundance of anchovy and under the CAG administration and c) guano extracted during 1985-2012, period of less abundance and posterior recuperation of anchovy but not of seabirds. Data source for b and c were Cushman 2003 and AGRORURAL *pers.com.*

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In 2003, under the international development of the organic agriculture, the Peruvian government became interested again in guano exploitation and created Proabonos (nowadays AGRORURAL) to exploit guano for exportation to organic farmers in northern hemisphere countries and local agriculture. AGRORURAL together with Peruvian Environmental office (SERNANP) are nowadays the institutions in charge of seabird protection and guano harvesting. Also, the renewed interest in charismatic species like seabird and other large animals living in coastal islands motivated the Peruvian government to establish the National Reserve of Guano Island, Islets and Headland (Reserva Nacional Sistema de Islas 2009). The National reserve includes most of the important nesting colonies of seabirds (22 islands and islets and 11 headlands, Figure 1.17).
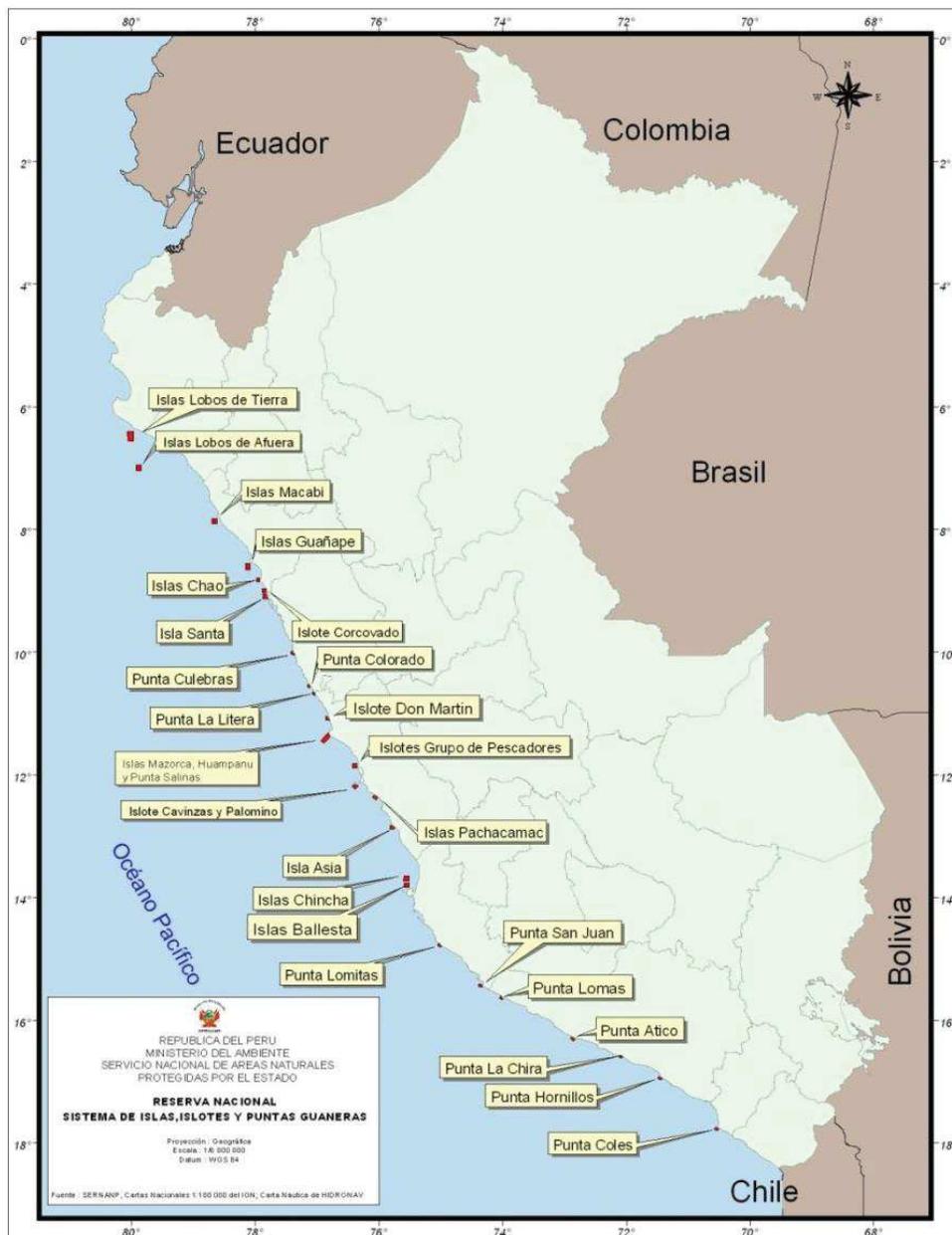


Figure 1.17. Map of the main seabird colonies during 2009, when the National Reserve of Guano Island, Islets and Headland was created. Source AGRORURAL.

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## 2. Temporal dynamics in the NHCS

The ocean dynamics involve processes and patterns linked with different spatio-temporal scales (Figure 1.18, Haury, McGowan & Wiebe 1978). The NHCS is a highly fluctuating ecosystem with several bottom-up forcing processes, causing fluctuations at millennial, centennial, decadal, interannual and seasonal scales (Chavez *et al.* 2003; Echevin *et al.* 2008; Salvatteci 2013; Salvatteci *et al.* 2014). Although the frequency varied between time processes, the main characteristic of regimes from seasonal to milenial scales were cool "La Niña-like" productive regimes and warm less productive "El Niño-like" regimes. We describe in this section the main forcing processes in the NHCS that may influence the seasonal reproduction of seabirds (cormorant, booby and pelican).
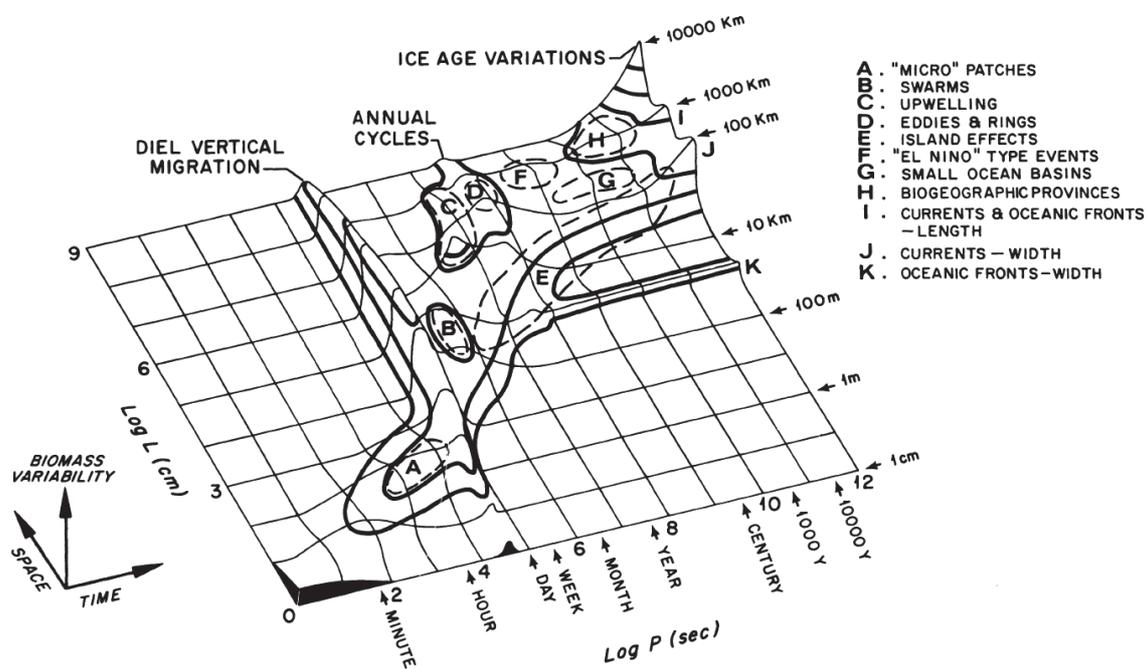


Figure 1.18. Stommel's diagram showing how population or "biomass variability" is linked to the oceanic process in time-space scales. It represented a conceptual model of the time-space scale of zooplankton biomass variability and the factors contributing to this scales. I, J, K, are bands centered about thousands and tens of kilometers in space scale with time variations between weeks and geological time scales. Source Haury *et al.* 1978.

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## 2.1. Millennial and centennial variability

The NHCS is a high variability system, including at millennial and centennial scales. At millennial scale, fluctuations were evidenced between periods of anchovy dominance or oceanic species (e.g. sardine) dominance (Figure 1.19, Salvatteci 2013). Periods of anchovy dominance were related with high production considered as "La Niña-like" productive regimes. Periods of oceanic species dominance were characterized by Walker circulation, low SST, weak OMZ, low export production and low abundance of anchovy and other fish. Most of these characteristics are consistent with a 'El Niño-like' mean conditions in the Tropical Pacific (Feldberg & Mix 2002; Koutavas 2002). It is important to highlight that periods of anchovy dominance are characterized by productivity but not by temperature.

For example at centennial scale, the Little Ice Age (1500 – 1850 AD) was dominated by 'El Niño-like' mean conditions, characterized by lower productivity, weaker OMZ and an increase in precipitation observed off the Peruvian coast (Salvatteci et al. 2014). The subsequent periods, Medieval Warm Period and the Current Warm Period, were dominated by 'La Niña-like' mean conditions, characterized by an intense OMZ and high marine productivity. The Current Warm period began with a regime shift in ca.1820 towards more productive conditions (Sifeddine et al. 2008; Gutiérrez et al. 2009). During the Current Warm Period a rapid expansion of the subsurface nutrient rich waters occurred, accompanied by oxygen depletion and higher biological productivity (Gutiérrez et al. 2009; Salvatteci 2013). Since 1900 AD, anchovy reached very high levels of productivity, actually the highest levels of productivity over the past 20 000 years (Figure 1.19, Salvatteci 2013).
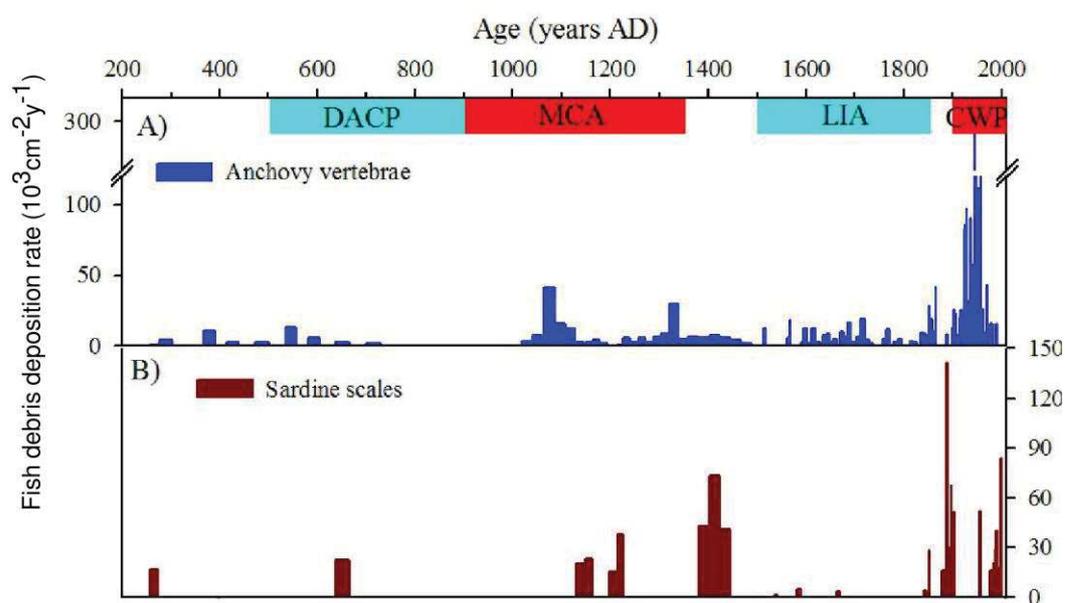


Figure 1.19. Fish debris deposition rates off Pisco, Peru for A) Anchovy vertebrate fluxes (# vertebrae.$10^3$y$^{-1}$cm$^{-2}$) and B) Sardine scale fluxes (# scales.$10^3$y$^{-1}$cm$^{-2}$). Highlighted areas indicate the Current Warm Period (CWP from ~1900 to the present), Little Ice Age (LIA, from 1500 to 1850AD), the Medieval Climate Anomaly (MCA, from 900 to 1350AD) and the Dark Ages Cold Period (500 – 900 AD). Source Salvatecci 2013.

## 2.2. Decadal variability

In the NHCS, the most important variability at decadal scales is the Pacific decadal oscillation (PDO). PDO phases have a duration of 20 to 30 years (Chavez *et al.* 2003) and similarly to millennial and centennial scales, its fluctuations range between warm 'El Niño-like' and cool 'La Niña-like' conditions due to basin wide effects on sea surface temperature and thermocline slope that affects productivity (Chavez *et al.* 2003).

Several physical mechanisms drive the PDO including (1) changes in ocean surface heat fluxes and wind-driven transport related to the Aleutian low pressure, due to both local unpredictable weather and to remote forcing from interannual to decadal tropical variability via the "atmospheric bridge"; (2) processes determining oceanic thermal inertia that integrate PDO variability on interannual and decadal time scales; and (3) decadal changes in the Kuroshio-Oyashio current system manifested as sea surface temperature anomalies along the subarctic front at about 40ºN in the western Pacific ocean (Newman *et al.* 2015). In this regard, the duration and the intensity of the decadal phases are not fixed for the entire Pacific but rather depend on the ecosystem considered. For the NHCS, three regime shifts were reported in the last century: 1970, 1985 and 2000. 'La Niña-like' conditions also called 'La Vieja'(Chavez *et al.* 2003) (1950-1970 and 1990-to the present) were characterized by the presence of a wide domain of Cold Coastal Waters (CCW) near the coast, shallower thermocline and oxycline, increased nutrient supply and consequently, higher productivity and dominance of anchovy (Figure 1.20, Bertrand *et al.* 2011).

'El Niño-like' condition or 'El Viejo' period (Chavez *et al.* 2003)(1970-1985) was characterized by a narrow CCW domain, the presence of Subtropical Surface Water (STSW) near the coast, a deeper thermocline and oxycline, weaker upwelling and lower productivity (Figure 1.20, Bertrand *et al.* 2011). The range of habitat favorable to anchovy was dramatically reduced while the habitat favorable to sardine increased and spread towards the continental shelf (Bertrand et al., 2004), causing the quasi disappearance of anchovy that cannot migrate or deepen (Alheit & Niquen 2004; Bertrand *et al.* 2011). Increased abundance of sardine during 'El Niño-like' conditions of PDO is not an obligatory characteristic of the regime given that former warm phases of the PDO did not exhibit larges abundances of sardines. (from 1925 to 1950)(Gutiérrez *et al.* 2009). Regime shifts at decadal scales are also enhanced by fisheries (Jiao 2009). The development of anchovy fisheries during 1950-60 and the consequent collapse of the anchovy stock in the 1970's, made the regime shift more catastrophic for seabirds causing a drastic reduction of populations in the late 1960's (Duffy 1994).
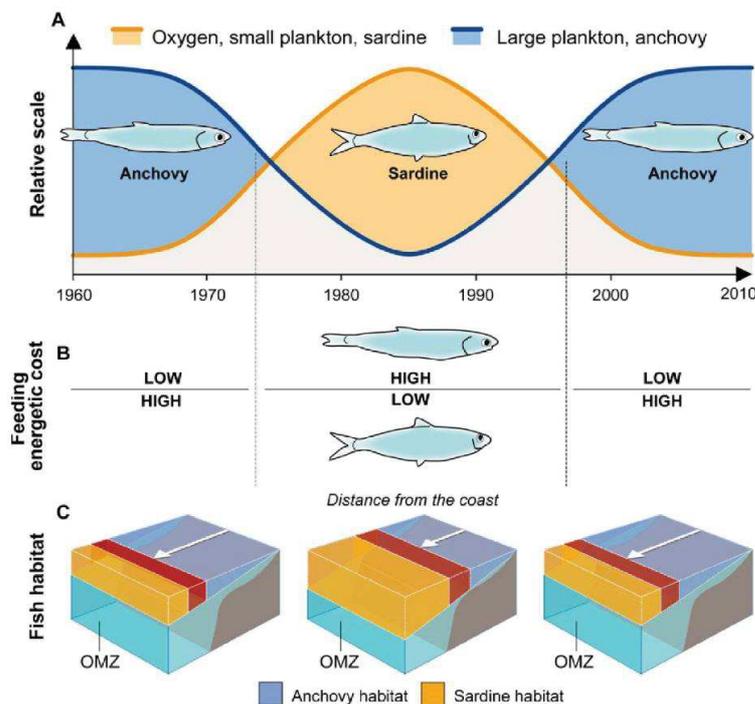
Figure 1.20. Conceptual model of decadal changes in anchovy and sardine populations in the southeastern tropical Pacific. Schematic representation of a) the temporal changes in abundance of large plankton and anchovy (blue) and small plankton and sardine (orange) during 1960-2010. b) Energetic costs of feeding on dominant plankton size-spectra for anchovy and sardine according to the scenarios from a. c). Schematic of the available habitat for anchovy (blue shaded area) and sardine (red shaded area). Source, Bertrand *et al.* 2011.

## 2.3. Interannual variability

The principal cause of interannual variability in the NHCS is related to the Southern Oscillation (ENSO) that produce positive (El Niño) and negative (La Niña) sea-surface temperature anomalies (SST) in the equatorial and eastern Pacific (Chavez, Messié & Pennington 2011).

The physical mechanism of ENSO is associated to a periodic instability of the ocean-atmosphere dynamics in the Pacific Ocean. In normal situations, the earth rotation creates trade winds at the equator that blow relentlessly from east to west, pushing sea water towards the west side of most ocean basins. As a consequence the surface water is warmer in the west and cooler in the east of ocean basins. The warmer surface in the west injects heat and moisture into the atmosphere causing towering cumulonimbus clouds and rain. The now-drier air then travels east before descending over the cooler eastern tropical Pacific. The pattern of air rising in the west and falling in the east with westward moving air at the surface is referred to as the Walker Circulation (Figure 17). El Niño (EN) condition occurs when trade winds are relaxed or reversed, allowing the warmer than normal water to move into the central and eastern tropical Pacific Ocean. Kelvin waves of "downwelling" are formed in the center of Pacific Ocean (180°E) and propagate to the east toward the American continent

modifying the current dynamics, what has as immediate consequences an increase of sea level and deepening of thermocline. As a consequence of the deepening of the thermocline, the upwelling is weakened and inefficient in terms of nutrient enrichment (Barber & Chavez 1983). La Niña (LN) condition occurr when trade winds are reinforced. Then, "upwelling" Kelvin waves form in the center of the Pacific Ocean (180°E) and propagate to the east toward the American continent modifying the current dynamics, and displacing the thermocline to shallower depths. As a consequence, the upwelling of subsurface waters is more efficient and brings nutrient towards the surface, making the cold coastal waters to expand (Bertrand *et al.* 2008) (Figure 1.21).
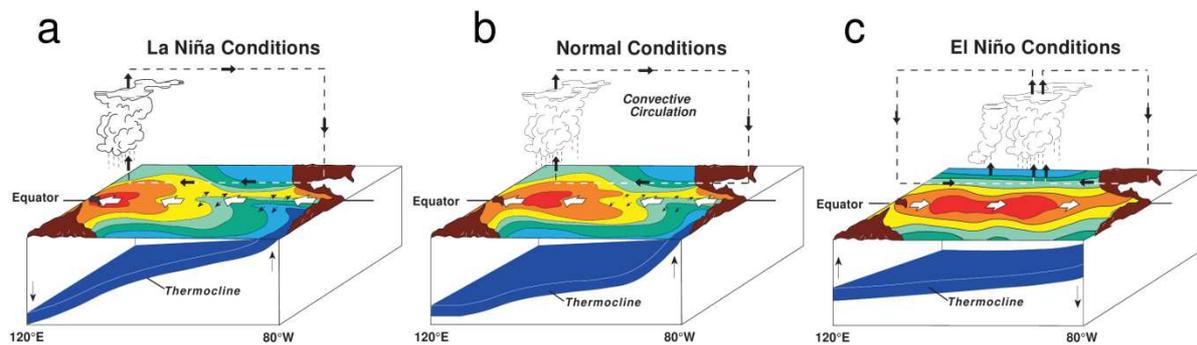


Figure 1.21. Schematic representation of a) La Niña, b) Normal conditions and c) El Niño conditions in the Pacific Ocean. Source: NOAA / PMEL / TAO Project Office.

Different indices are used to measure ENSO: index based on sea level pressure in equatorial ocean (Equatorial Southern Oscillation Index), index based on SST (NOAA's official Oceanic Niño Index) and also index based on winds (http://www.cpc.ncep.noaa.gov/data/indices/). For monitoring ENSO in general, the SST-based index is the most widely used. The SST-based index is divided by zones according to where data on SST anomalies are observed: El Niño 1+2, El Niño 3, El Niño 4 and El Niño 3.4.
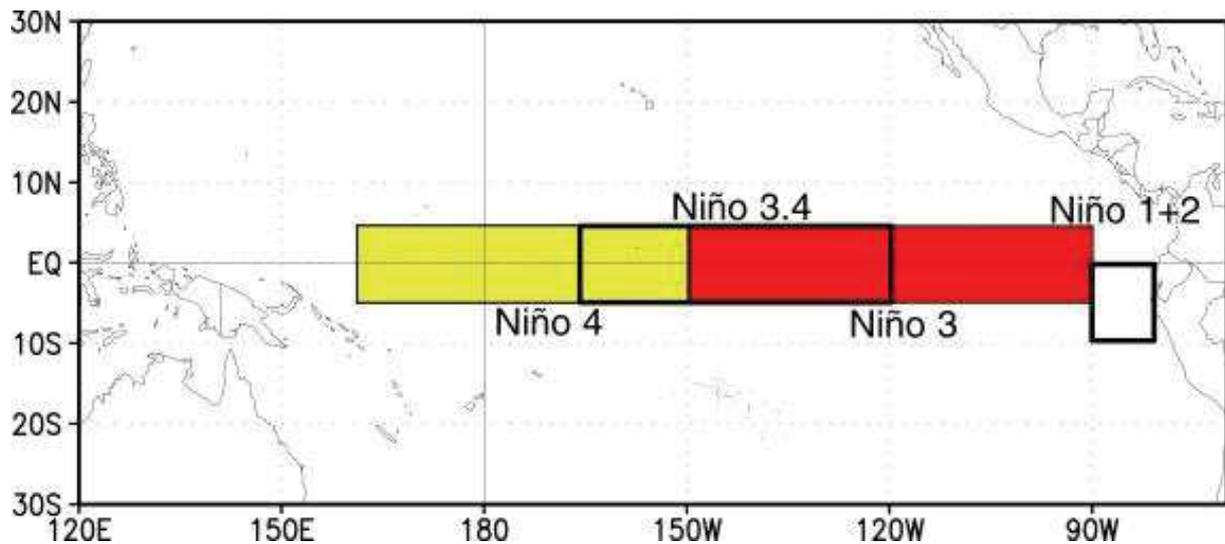
Figure 1.22. Graphical representation of El Niño regions based on sea surface temperature data collected in the eastern and central tropical Pacific Ocean. Source: http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/nino_regions.shtml.

The area El Niño 1+2 (80W-90W and 0S-10S) is the closest to NHCS, then the most representative of the conditions in the Peruvian coastal ecosystem (Figure 1.22). We used the SST anomalies larger than 0.4°C with persistence up to 5 months (Trenberth 1997) to identify El Niño events and monthly anomalies larger than -1°C with persistence up to 5 months to identify La Niña events (Trasmonte & Silva 2008) (Figure 1.23).
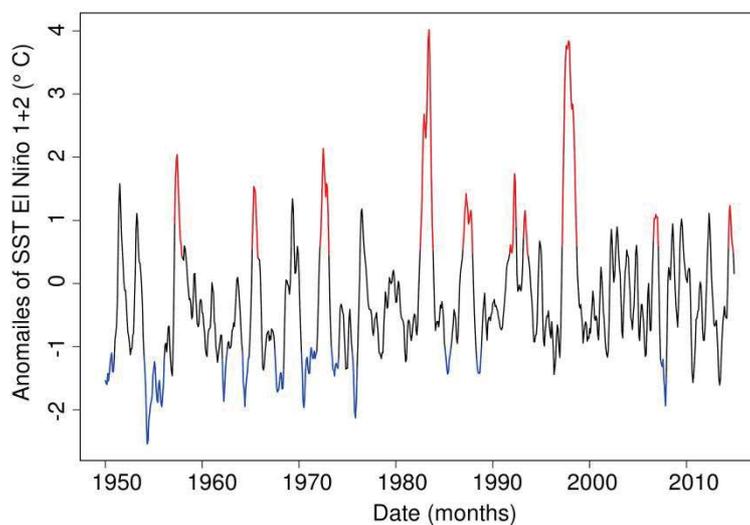


Figure 1.23. Time series of the SST anomalies in the El Niño 1+2 are. Red portions of the line refer to EN conditions according to Trenberth 1997 and portions in blue refer to LN conditions according to Trasmonte and Silva 2008. Source of time series: http://www.cpc.ncep.noaa.gov/data/indices/ersst3b.nino.mth.81-10.

LN and EN events condition the spatial organization of living organisms by modifying the volume of their favorable habitat. Under EN, the extent of cold and nutrient rich waters (CCW) is reduced and the presence of other water masses as STSW with higher SST

increases at the coast (Bertrand et al. 2004). During these conditions, anchovies concentrate closer to the coast if remaining CCW refuge areas exist, and deeper in the water column beneath the warm and less productive surface waters, as for instance during the El Niño 1997-98 (Bertrand et al. 2004). Under these conditions, anchovy first deepens, then concentrated into few residual, very coastal upwelling cells (Gutiérrez et al. 2007) and fishermen make lower catches and briefer trips (Bertrand et al. 2008). Low availability of anchovy during EN conditions forces the other top predators such as seabirds to increase their diving effort and/or to migrate to areas with higher prey availability; extreme EN events may induce heavy chicks and adults mortalities (Jordan 1964; Tovar Serpa 1981; Apaza & Figari 1999).

LN consequences over the biological components of the ecosystem were scarcely commented or reported as opposed to EN (McPhaden 2002). In the NHCS, under LN conditions the upwelling is strong, CCW extend until more than 100 nm offshore (Bertrand *et al.* 2004). Primary productivity is generally enhanced with an increased presence of diatoms (Tam *et al.* 2008) and then secondary production thrive under these conditions (McPhaden 2002). Very few data were published on the effects of these events on seabirds and none for NHCS, although it was observed that during LN years, seabird population increased (Agrorural *com. pers.*).

## 2.4. Seasonal variability

In upwelling systems, seasonality is triggered mainly by wind regimes that control the inputs of nutrients in the system (Valiela 1995; Romero *et al.* 2002; Bograd *et al.* 2009). Input of nutrients can prompt primary production that can be traced all the way up the food web. The Humboldt Current System (HCS) has a marked seasonal cycle controlled by the upwelling of nutrients (Montecino & Lange 2009). Even though the seasonality of the upwelling is not homogeneous over the entire range of the HCS, in the NHCS, the upwelling is year-round and only the strength of it is modulated between seasons (Echevin *et al.* 2008). The upwelling is strongest during the austral winter and weakest during the summer. Differing from other EBUS, the strongest phase of the upwelling is less productive, so in winter the primary productivity is lower than in spring and summer (Echevin *et al.* 2008). In addition to the upwelling input, the oxycline depth was described in the last decade as other major factor shaping the habitat of living organisms in the NHCS (Bertrand *et al.* 2010, 2011). Moreover the NHCS is located at lower latitude than the other EBUs, with lower variability in the photoperiod. Therefore the seasonality in the NHCS oceanographic components can be considered as low to moderate (Montecino & Lange 2009) and its effects over the biological component were considered for long time as less evident than interannual variability and less studied.

In the Chapter 3, 4 and 5 we develop extensively the seasonal variability of oceanographic and biological component NHCS and its effect on the breeding seasonality of seabirds.

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## 3. Biology of pelican, boobies and cormorants in the NHCS

### 3.1. On the Pelecaniforms: current classification and evolution

The Guanay cormorant (*Phalacrocorax bougainvillii*, Lesson 1837), the Peruvian pelican (*Pelecanus thagus*, Molina, 1782) and the Peruvian booby (*Sula variegata*, Tschudi 1843) belong to the Pelecaniform order. Pelecaniforms share general morphological traits including four webbed toes (steganopodes), salt gland enclosed completely within the orbit and naked gular skin forming a pouch (except for tropicbirds), and life traits history as piscivory (Nelson 2005).

Within the traditional classification, Pelecaniforms are a monophyletic group composed of 6 families: Phaetontidae (3 species of tropicbirds), Fregatidae (5 species), Pelecanidae (7 species of pelicans), Anhingidae (4 species of darters), Phalacrocoracidae (28 species of cormorants and shags) and Sulidae (10 species of boobies and gannets) (Cracraft 1985; Hackett *et al.* 2008). However, more recent evidence suggested that Pelecaniformes could be a polyphyletic group where Phaetontidae could be considered as a separate group (Kennedy & Spencer 2004; Hackett *et al.* 2008) or a paraphyletic group where Pelecaniformes could be a part of a larger clade including shorebirds, hammerkop, ibises and herons (Hedges & Sibley 1994). Furthermore, the families composing the Pelecaniforms order are considered as monophyletic, particularly for the group of families Phalacrocoracidae, Anhingidae and Sulidae (Cracraft 1985; Smith 2010). Sulidae and Phalacrocoracidae are closely related, based on behavioral evidence: the sexual displaying ritual is common to the two groups (Nelson 2005).

Cormorants (Phalacrocoracidae) are heavy-bodied, deep-feeding, flat- and tree-nesting birds with indifferent or labored flight (Siegel-Causey 1988). The cormorants and shags contain more than half the species within the Pelecaniforms and are widely viewed as being most closely associated to the darters and anhingas (Anhinga), gannets (Morus), and boobies (Sula) (Siegel-Causey 1988). Phalacrocoracidae is probably a polyphyletic group because the traditional division of shags (Leucocarbo) and cormorants (Phalacrocorax) by their plumage pattern and morphological characteristics are not consistent with the behavioral taxonomy and the genetic classification (Kennedy, Gray & Spencer 2000). We adopted the more recent classification proposed by (Kennedy et al. 2000), that simplified the classification including all the members of the family in the genus Phalacrocorax. The phylogenetic similarity of Guanay cormorants with other species of the genera is a subject of discussion because some classifications situated Guanay cormorant closely related to Cape cormorant by their morphological characteristics (Siegel-Causey 1988), but phylogenetically and biogeographically it is closer to cormorants from New Zealand: Chatham Island shag, Campbell shag and Bronze shag (*Phalacrocorax onslowi, Phalacrocorax campbelli and Phalacrocorax chalconotus*) (Kennedy *et al.* 2000).

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Boobies and gannets are characterized by their torpedo-shape body adapted to plunge diving in marine ecosystems. The Sulidae are considered as a monophyletic group but there are still discussions about the position of *Papasula abotti* (Friesen & Anderson 1997). Between the boobies, the Peruvian and Blue-footed boobies are considered sister species (Friesen & Anderson 1997), which seems to have diverged during the Pleistocene (1.1-0.8MYA) (Patterson, Morris-Pocock & Friesen 2011). Divergence of Peruvian from Blue-footed boobies was driven by local adaptation to cold coastal waters in the NHCS (Friesen & Anderson 1997). Blue-footed and Peruvian boobies may be nearing the end of the speciation process with reproductive barriers well established. However, Peruvian and blue-footed boobies hybridize infrequently (Taylor, Zavalaga & Friesen 2010a), potentially due to strong premating reproductive isolation (Taylor *et al.* 2012).

Pelicans are characterized by their long beak and large throat pouch. Traditionally, at least 7 species of pelicans are considered, where Peruvian pelican (*Pelecanus thagus*) is only one of the 6 subspecies of Brown pelican (*Pelecanus occidentalis*) (Nelson 2005). However, recently Peruvian pelican have been considered as a separate species because it is significantly larger than any Brown pelican subspecies, it exhibits plumage differences and it is endemic of the HCS (Nelson 2005). In addition, recent genetic work supports the species status of the Peruvian pelican and dates the divergence of this species from the Brown pelican at 0.75 MYA (Kennedy *et al.* 2000).

The oldest record of Pelicaniformes dates of the Eocene (50-30 million years ago, MYA), fossils belong to Pelegornithidae, a common ancestor between Pelecaniformes and Procelariiformes (Olson 1985), and Plotopteridae, flightless diving birds that may be the common ancestor of cormorants (Warheit 1992; Smith 2010). Plotopteridae and Pelegornithidae probably diversified during late Eocene coinciding with world decline of ocean bottom temperatures and went extinct during later Oligocene (22-15 MYA) coinciding with warmer waters and El Niño-like scenarios (Warheit 1992).

The earliest Sulidae and Phalacrocoracidae fossils date of the late Eocene (35 and 39 MYA, respectively) (Olson 1985) and the oldest fossil register of pelican comes from early Miocene (20MYA) (Olson 1985). Genetically, the split between Sulidae and Phalacrocoracidae can be dated to 42MYA (Friesen and Anderson 1997). According to fossil register, during the Mid-Miocene period (18 to 7 MYA) there was a high diversity of Sulidae (Warheit 1992) that resulted into differentiated genus as Sula and Morus that splitted around 15-10MYA (Olson 1985). During late Miocene (7 to 4 MYA), the diversity of Pelecaniformes in general and Sulidae in particular declined probably associated with the decrease of the sea level and El Niño like situations. The evidence suggested that only three lineages of Sulidae (Morus, Sula and Papasula) survived the decline of late Miocene and are now diversifying again (Friesen & Anderson 1997).

Fossil registers of boobies and cormorants are available in the NHCS. Two species of Phalacrocoracidae fossils were identified during the latest Miocene-early Pliocene (9-2 MYA), *Phalacrocorax aff. bougainvillii* (a big cormorant, possible related to *P. bougainvillii*) and Phalacrocorax sp. (a smaller cormorant) (Urbina & Stucchi 2005). At least 6 species of

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Sulidae have been described. They cohabited during the late Miocene-early Pliocene (9-2 MYA), *Sula spp*, *Sula aff. variegata* (possibly related to *S. variegata* and *S. nebouxii*), *Sula magna* (the largest species in the genera), *Sula sulita* (the smallest species in the genera), a specie of gannet *Morus peruvianus* (Stucchi & Devries 2003).

## 3.2. Morphology of the guano-producing seabirds

Guanay cormorants have different plumages at the young and adult phases. The adult plumage is dark with glossed blue-green on the head, neck, back, wings and tail. The underparts are white from the base of the foreneck to dark for the undertail coverts. There are white filoplumes above the eye and others scattered about the neck. The eye is dark brown with a white corneal ring surrounded by an olive-green orbital ring. The facial skin is red, turning to orange above the eye. The bill is brown/black or yellowish, faintly pinkish or blue and the gular sac is brownish. The legs and feet flesh is pink (Nelson 2005). There is no marked sexual dimorphism between sexes but males are slightly heavier than females. Young and immature are markedly duller than post-breeding adult, brown beneath (Figure 1.24).



Figure 1.24. Guanay cormorant, a) adult in ventral view, b) adult in dorsal view.

Boobies also have different plumages between adults and young. Adults have white head, neck and underparts, brown wings and back and variegated feathers. Their bills are purplish-blue, sometimes almost pinkish, their facial skin is dark-grey and the iris is red. Their legs and feet are bluish-gray. There are no color difference between sexes or breeding and pre-breeding adults. However, there are sexual dimorphism in size and call. Females are slightly heavier than males, and males and females can be differentiated by vocalizations: males whistle and females grunt (Zavalaga *et al.* 2009). Young and immature are dinghy grey to buff or light fuscous below with feathers of breast and belly broadly bordered by white after large, sub-terminal brownish area. Head and neck are finely streaked ash. Wings and back are duller, darker in adults due to narrower white borders of the feathers of dorsal plumage. Their

irises are yellowish-grey becoming light brown during the second year and then red (Figure 1.25). They probably acquire the adult plumage through 2 incomplete molts (Nelson 2005).
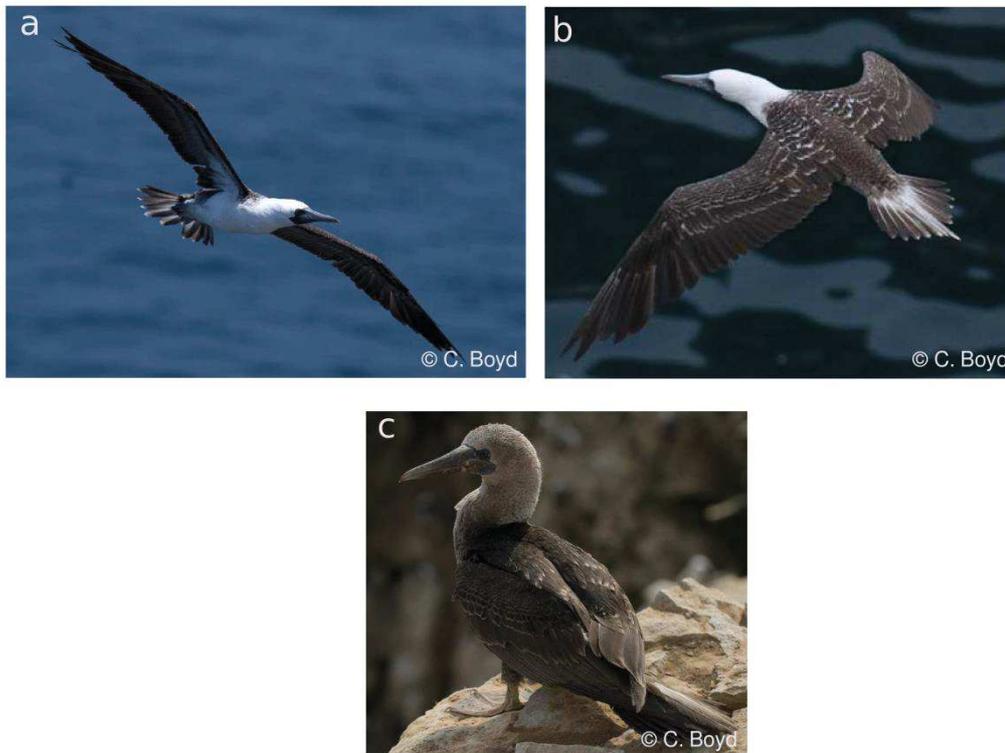


Figure 1.25. Peruvian booby, a) adult in ventral view, b) adult in dorsal view and c) young of Peruvian booby.

Pelicans have a great diversity of plumage between young and adults, breeders and non-breeders. Adult pelicans have a pale ashy or silvery gray body plumage. The feathers of the back, rump, lesser and median wing coverts and scapulars are edged with blackish brown, producing a striped appearance. The ventral surface is smoky brown and finely streaked with white, the flanks and sides of breast with silvery white shaft-stripes. The neck is brown, with white feathers on the back of the head and bordering the gular pouch. Pelicans have a pale straw-colored and occipital crest that is more prominent in Peruvian pelican than Brown pelican (Nelson 2005). The legs and feet of adults are lavender-gray, sometimes with a greenish overlay on the tarsus (Figure 1.26). The bill is grayish and the lavender stripes of the pouch are more brightly colored than those of Brown pelican. Pelican have variations in colors of the neck feathers, the iris, the naked skin around the eye, the bill and the pouch. These variations can be the consequence of different stages of breeding what is not fully understood in the case of the Peruvian pelican. Yet at least 3 distinct types of plumages during breeding have been described in details (Cushman Murphy 1936). Like Guanay cormorants, Peruvian pelicans do not have sexual dimorphism but males are probably slightly heavier than females. Immature and young pelicans are brown with white breast, some buff on the upper side of the wings. The head and neck are brown without lateral stripe. The bill is green at the base and top with orange sides. The pouch is orange-yellow. In Brown pelicans,

the adult plumage is acquired probably during the 3rd or 4th year. Females generally assume adult plumage at younger ages than males (Nelson 2005).
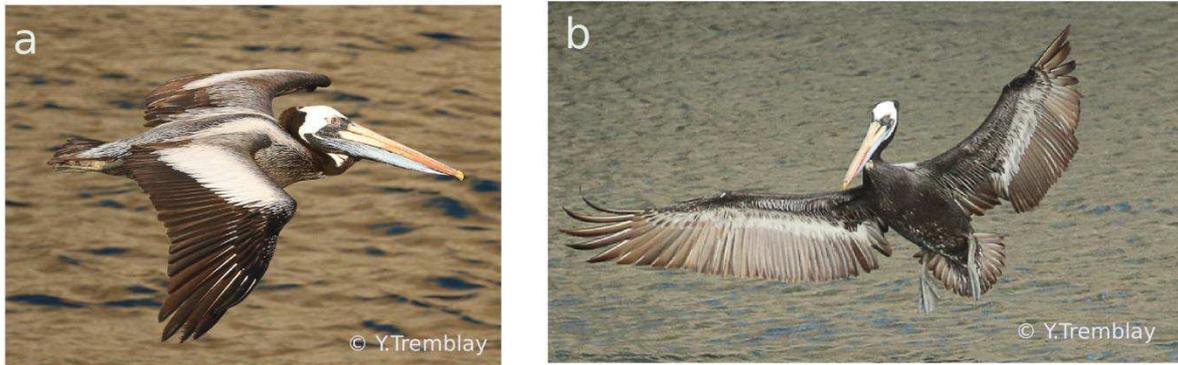


Figure 1.26. Peruvian pelican, a) adult in dorsal view, b) adult in ventral view.

In summary, pelicans are heavier and bigger than cormorants and boobies. Cormorants are heavier than boobies and boobies had longer wings than cormorants. Compared with Brown pelican, Peruvian pelican is larger and heavier.


## 3.3. Distribution range


The Guanay cormorant, the Peruvian booby and the Peruvian pelican are endemic species of the Humboldt Current System. Nesting colonies have been observed between Isla Lobos de Tierra (6°S) in Peru and Isla Mocha (38°S) in Chile (Murphy 1936). During exceptionally strong El Niño events specimens of boobies and cormorants have been recovered as far as the Gulf of Guayaquil in the North (3°S) and Islas Chiloe in the South (42.67°S) (Jordan 1958; Jordan & Cabrera 1960). The three species are associated to the coastal islands and headlands with a maximum distance from the coast of 60 km for Isla Lobos de Afuera. Colonies of boobies were exceptionally reported farther from the coast at 62km (Hormigas de Afuera) (Murphy 1936).

The populations of the three species appear to be genetically panmictic across their geographic range, suggesting high gene flow between colonies that may reduce loss of genetic diversity during population decline and increase the ability to colonize new areas during population expansion (Taylor *et al.* 2010b, 2011; Jeyasingham *et al.* 2013). A 1-year ringing experiment seems to support this high gene flow hypothesis (Jordan 1958; Jordan & Cabrera 1960): rings were recovered farthest from the nesting colony during autumn for boobies (April-June) and cormorants (June-July), suggesting migrations of at least 2000 miles during Autumn (Figure 1.27).
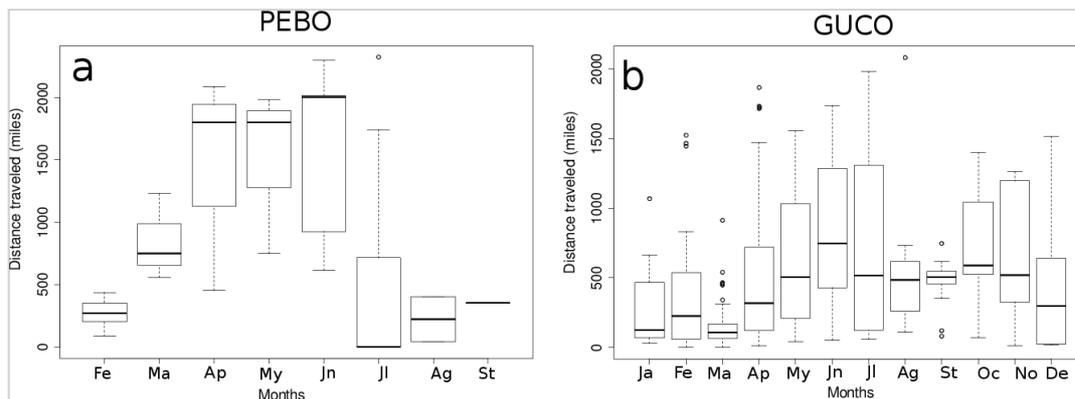
Figure 1.27. Monthly distance travelled in miles by a) Guanay cormorant and b) Peruvian booby. Data source Jordan 1958; Jordan & Cabrera 1960.

### 3.4. Reproduction

In general terms, the three seabird species breed annually and were reported laying eggs in any month of the year but more frequently during spring and summer (Nelson 2005). The three species also had altricial hatchling brooded by both parents and in case of pelicans chicks are gathered into crèches (Nelson 2005).

While the three species cohabit in coastal islands and headlands, they form monospecific colonies (Duffy 1983a), expressing different yet overlapping preferences for nesting places. Cormorants and pelicans prefer nesting in open ground and boobies prefer nesting in cliffs. Cormorants prefer the coolest slopes and pelicans the warmest flat surfaces. Competition between cormorants and boobies is expressed only passively through the occupation of nesting space, while pelicans exhibit active aggressive interactions and nest usurpations (Duffy 1983).

Courtship in cormorants begins with nest claim by males and the display of reproductive behavior, by extending the head upside and down along the spine. A development of erect crest feathers is also reported, but not observed in all cases. Nests of cormorants may be active in any month, yet laying peaks occur from November to January (Nelson 2005). The number of egg laid is 2 ±1 and a maximal of 5 eggs were reported (Cushman Murphy 1936). In normal environmental conditions there is no brood reduction. Chicks recently emerged are black and become covered in the following days with an even mixture of black and white down (Figure 1.28). The complete breeding cycle takes c. 4 months (Table 2). There is scarce information about basic breeding biology for example about reproductive success, growth rates, etc. (Nelson 2005).

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Figure 1.28. Guanay cormorant, a a) recently emerged chick b) and chicks of 2-3 weeks. Peruvian booby, adults with two chicks of 2-3 weeks. Peruvian pelican, d) adults with several chicks in a "crèche".

Courtship in boobies begins with the attendance of nest by male and 'sky-pointing' behaviour, simultaneously spreading and swiveling wings until pair has formed. After pair formation, the couple waits for 3 weeks or more before egg-laying. The nest of boobies is made of debris and pebbles. Boobies nest in cliffs and slopes in open ground. For boobies, incubation begins with the first egg, the clutches may be replaced but the time interval is not known. Clutch size is of 1.5 (1-2) eggs. Egg-laying has been reported mainly from September to February and principally from November to December (Nelson 2005). The incubation care is shared by male and female but male stay at the nest more time. The first days chick have the eyes closed. Between weeks 2 and 3, chicks get well covered with down and they become able to regulate temperature, then the brooding phase ends. The primary tail feathers probably emerge in the week 6 and by the week 13 chicks are clear of down. Chicks reach average adult weight by the week 7-8, and then decreases by the week 11 due to feather growth and wing exercising before fledging (Galarza Ninaya 1968). Fledgings begin to fly at 14 weeks and keep returning to the nest to be fed for 4 to 6 weeks approximately (Table 2). Young independence was reported mainly from January to April, yet may occur throughout the year (Nelson 2005). Breeding success of the three seabird species has not been quantified formally. Yet, it is know that at least 70% of bobbies eggs hatch, the remaining being lost by

predation from gulls. High success of reproduction was mentioned with most of hatching fledged, in absence of human disturbance (Galarza Ninaya 1968).

Table 2. Approximate duration of the main breeding stages (in days) from pre-laying attendance to the independence of fledglings for cormorants, boobies and pelicans. Pre-laying attendance includes forming a couple and building a nest, post-fledging includes rearing of youngs by adults after fledging. [1] (Nelson 2005 mainly from Galarza Ninaya 1968), [2] (Schreiber & Burger 2002), [3] (Tovar Serpa & Cabrera Quiroz 2005).

| | Guanay cormorant | Peruvian booby | Peruvian pelican |
|---|---|---|---|
| Pre-laying attendance | 28[1] | 28[1] | 14[1] |
| Incubation period | 28[1] | 42.4 (40-48)[1] | 37[1] |
| Chick period | 56[1] | 98[1] | 80[1] |
| Post-fledging care | 30[3] | 35 30-42[1] | 30[3] |
| Total | 142 | 203 | 161 |

For pelicans, no courtship display was reported, but selection of nest by females occur in October (Murphy 1936). Nests of pelicans are made of feathers and guano that they bring in their gular sac from outside their colonies. Egg laying was reported at any month but being least during May–Sept (Nelson 2005). Clutch size was reported as 2.41±0.92 (1-6) eggs (Coker 1919; Cushman Murphy 1936; Wetmore 1945). A successful breeding cycle for pelicans lasts 18 weeks (Table 2). A detailed report of their breeding biology is provided in Nelson 2005, but is based on Brown pelican. Less studies were undertaken on the Peruvian pelican, and they are known to desert nests under disturbance (Tovar Serpa & Cabrera Quiroz 2005; Zavalaga *et al.* 2011).

### 3.5. Diet and foraging strategy and of the guano-producing seabirds species

The main prey species for the three studied seabirds is the Peruvian anchovy (*Engraulis ringens*) (Coker 1908; Jordan 1966; Jahncke *et al.* 1997a). First research on seabird diets was done examining stomach contents. An early study conducted in 1939 found that anchovy contributed 96% of the cormorant diet, and 80% of the booby and pelican diet (Vogt 1942). In the following years diet of seabirds was regularly monitored by IMARPE, analyzing pellet regurgitates of cormorants and regurgitates of boobies.

Although cormorants prefer anchovy, they may switch their diet composition, and more than 32 species of fish and mollusks have been identified as potential preys (Jahncke, Garcia-Godos & Goya 1997b). Changes in prey composition were reported to occur in association with low availability of anchovy due to El Niño events (Jahncke, Perez & Garcia-Godos

1998; Jahncke & Goya 2000) or overfishing during the 1960-1970 (Tovar Serpa & Minaya Galarza 1983). Another prey item found in significant quantities in cormorant pellets was the Peruvian silverside (*Odontesthes regia*), that may constitute up to 40% of the diet, proportions similar to those of anchovy (Jahncke *et al.* 1997b). Quantitative estimates of cormorant diet as energy intake is still controversial because it is difficult to estimate it experimentally (Tovar Serpa & Cabrera Quiroz 2005). A theoretical approach was done by Duffy & Roy 1987 and showed that in average Guanay cormorant consuming at the population scale (20 MT of anchovy in the early 1960's) less than 5 % of the anchovy stock biomass and during the peak of maximal abundance with 20 million individuals, they took up to 11 % of the anchovy (Duffy & Roy 1987).

The main prey for booby is anchovy too but diet may in periods of low availability of anchovy such as El Niño events, where anchovy may contribute to 70-80% of their diet (Jahncke *et al.* 1997a; Jahncke & Goya 2000). Other possible prey species include sardine (*Sardinops sagax*), with possibly up to 20% of the diet composition (Tovar & Guillen 1988; Tovar Serpa, Cabrera Quiroz & Guillen 1988) and other 12 species of fish and 1 squid contributing less than 10% (Tovar Serpa & Cabrera Quiroz 2005).

There were no quantitative or qualitative studies on pelican diet (Tovar Serpa & Cabrera Quiroz 2005).

Feeding methods are different for the three seabird species. Cormorants are mainly pelagic surface divers, diving on average at shallow depths (4 m) but, but able to reach up to 32 m (Weimerskirch *et al.* 2012) or 74 m (Zavalaga & Paredes 1999) depth according to authors, following the depth of dense anchovy schools. Peruvian boobies are plunge divers, throwing themselves as darters from 20-30 m heights (Tovar Serpa & Cabrera Quiroz 2005), deepening 2m in average and occasionally 10 m (Weimerskirch *et al.* 2012), for taking profit only of the shallowest anchovy schools. Peruvian pelicans capture preys by surface plunge-diving and surface-seizing up to 2m depth (Duffy 1980). Their very shallow dives are counterbalanced by a nocturnal foraging, anchovy schools being shallowest at night (Zavalaga *et al.* 2011). Peruvian pelicans also can use kleptoparasitism over boobies and cormorants (Duffy 1980) and exceptionally cannibalism on chicks by postfledging pelicans (Daigre, Arce & Simeone 2012).

Breeding boobies and cormorants perform mostly one trip per day covering on average 120 km of range within 3h duration trips (Bertrand *et al.* 2012), with exceptionally long trips lasting 6h, what has been reported to indicate food shortage (Vogt 1942).

### 3.6. Predators and parasites

Some of the main predators of eggs and chicks are Kelp gull (*Larus dominicanus*), Belcher's gull (*Larus belcheri*), Andean condor (*Vultur griphus*), Great skua (Stercorarius skua) and Turkey vulture (*Cathartes aura*) (Vogt 1942; Tovar Serpa & Cabrera Quiroz 2005). However, the low abundance of predators nowadays, and their hunting by guardians (Agrorural com pers.) prevent serious threat to colonies.

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Between the most important parasites, the presence of ticks (*Ornithodorus amblus*) in huge densities can cause desertion of breeders and abandon of eggs and chick by adults (Duffy 1983b). Ticks can be vectors of viruses but there were not reported as causing disease in seabirds (Clifford *et al.* 1980). Other parasites are present but less studied: nematodes and tapeworms in stomach and esophagus of cormorants (Avila 1945). Avian cholera may cause huge mortalities (de Lavalle 1917; de Lavalle y Garcia 1924).

## 4. Timing of breeding in birds

Reproduction in birds implies energy-demanding activities such as nest building, territory acquisition and defense against conspecifics, egg laying, incubation and chick rearing. Since breeding is energy-demanding and since resources in the environment are limited, many organisms do not maintain a fully functional reproductive system throughout the year (Murton & Westwood 1977; Clarke 1981). Generally a restricted reproduction period coincides with optimal conditions in the environment where the species breed.

### 4.1. Why birds must restrict breeding season to a particular period?

Theoretically, it can be hypothesized that energetic resources may constrain the breeding season for a restricted period of the year when fitness benefits are maximal for both parents and their offspring. In birds, two nonexclusive theories have been proposed to explain the timing of breeding.

First the 'optimal breeding time' theory (Lack 1968) suggests that adults adjust their breeding decision to match maximum food availability during the rearing of chicks. Chick rearing is one of the most energy demanding phases of the annual cycle (Drent & Daan 1980) and fitness returns may be greater for genotypes that time reproduction in this way. Basal metabolic rates during chick rearing for Starling (*Sturnus vulgaris*) have been compared to those of heavy labor by human standards (Drent & Daan 1980) (Figure 1.29). In a marine ecosystem, the cost of feeding a large brood for glaucous-winged gull (*Larus glaucescens*) was shown to increase adult foraging time, decrease adult body weight at the end of the breeding season, and decrease over-winter adult survival (Reid 1987).

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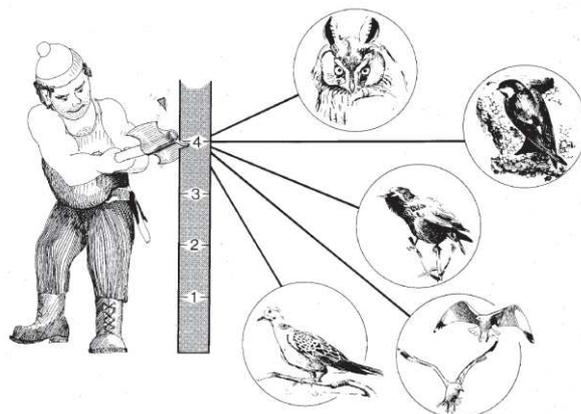


Figure 1.29. Comparison of maximum sustained working level of parent birds tending nestlings with the working level of heavy labor by human standards. Maximum sustained working level is expressed as metabolizable energy per day (DME). Examples are of *Asia atus*, *Delichan urbica*, *Sturnus vulgaris*, *Larus glaucescens* and *Streptapelia risaria*. Source Drent & Daan 1980.

Second, the 'egg-laying constraint' theory (Perrins 1970) highlights that females may be limited by body condition in the decision of beginning reproduction and it implies that reproduction is done when food is enough available to synthesize and lay eggs (Figure 1.30). Many cases were reported in terrestrial ecosystem as for Tawny Owl (*Strix aluco*) failure to breed in years of rodent scarcity (Southern 1970). In marine ecosystems, it was shown that a threshold value on body condition conditioned the decision of laying eggs for Common (*Sterna hirundo*) and Roseate (*S. dougallii*) terns (Safina *et al.* 1988) and decision of breeding for Blue Petrels (*Halobaena caerulea*) (Chastel, Weimerskirch & Jouventin 1995).
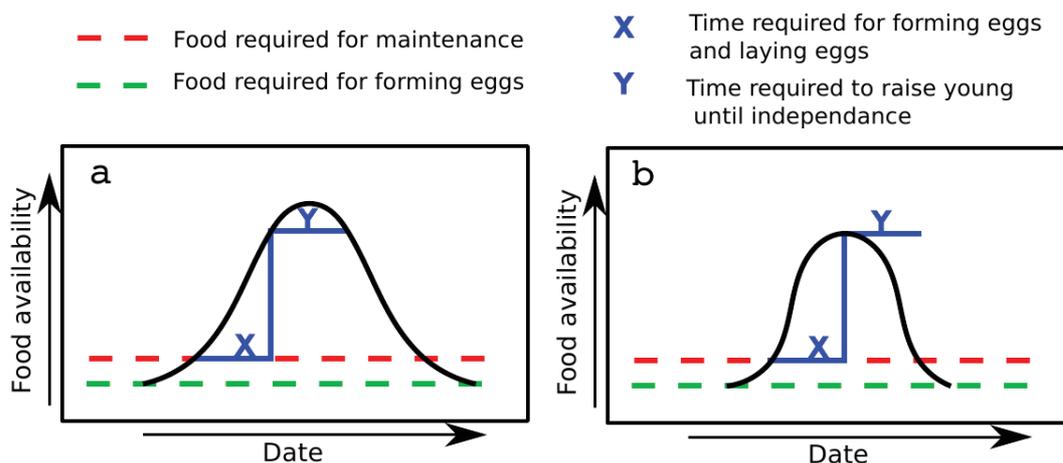


Figure 1.30. Hypothetical relationship between food supply, date of laying eggs and date of young becoming independent in two species, (a and b). The black curves show the level of food abundance against the food required for body maintenance (green) and the food required for forming eggs (red). Depending on the species, the time required from forming, laying and incubate eggs (X) varies and the amount of food availability affects the capacity to raise the young to the point of independence (Y). Redrawn from Perrins 1970.

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Females must deal with the fact that food is plentiful for only a short period of time in the environment so that it is important to take advantage of it efficiently. The two theories are not necessarily exclusive but may be complementary. Birds can be energetically constrained for laying their eggs, yet this requirement can be overcome and they can adjust the timing of breeding when resources are optimal for rearing chicks (Black *et al.* 2011).

## 4.2. Timing of breeding and mechanisms implied

The seasonal cycle is the main periodicity at the annual scale in terrestrial and aquatic systems (Valiela 1995; Bertram, Mackas & McKinnell 2001; Zhang *et al.* 2014). For several ecosystems in the world the seasonal cycle determines a more productive period during spring to summer due to relaxation of light limitation and rise of temperatures. In consequence, the most common breeding schedule in birds is the annual seasonal cycle with the exception of some long-lived seabirds as albatrosses and petrels that breed biennially due to the long duration of their reproduction activities (Hamer, Schreiber & Burger 2002). From an evolutionary point of view, animals living in an ecosystem with a marked seasonal cycle have internalized the circannual environmental rhythm within their internal clock, and can maintain annual cycles of gonadal development even in the absence of environmental stimuli (Gwinner 1996, 2003). Yet, this internalization of the circannual rhythm is usually rough in precision therefore vertebrates need external stimulus to fine-tune the time of their breeding events (Prendergast 2005; Bronson 2009). External cues can be environmental (e.g., photoperiod, food availability, temperature) or social such as behavioral interactions between conspecifics (Wingfield 1983; Tramontin, Wingfield & Brenowitz 1999).

Factors used to tune seasonal breeding can be classified by its role controlling the decision of onset reproduction as proximate factors or by its control during chick raising as ultimate factors (Baker 1938). Ultimate factors are exogenous environmental factors that result in natural selection favoring a particular time of breeding where survival of progeny and reproductive success increase. Availability of food supply can be counted as an ultimate factor as birds are raising young when food is more available. A classic example of food availability as ultimate factor of timing breeding season is the case of Great tit (*Parus major*) (Perrins *et al.* 1965). Proximate factors are early signals that allow birds to predict impending relevant changes in the environment (Baker1938). Animals prepare for changes in ultimate factors by responding to proximate factors that provide reliable information either in the long or short term about the suitability of the environment for breeding. In the classical example of Great tit, air temperature is used as a proximate factor of food availability during rearing chicks (Visser *et al.* 1998) (Figure 1.31, Durant *et al.* 2007). Other examples of birds using proximate cues to timing the seasonality of their breeding are the European starlings (*Sturnus vulgaris*) that use increase of air temperature in early spring as a cue to egg-laying (Meijer *et al.* 1999) and Spotted antbird (*Hylophylax naevioides*) that uses slight change of 1 hour in photoperiod to stimulate gonadal growth and song activity (Hau, Wikelski & Wingfield 1998).

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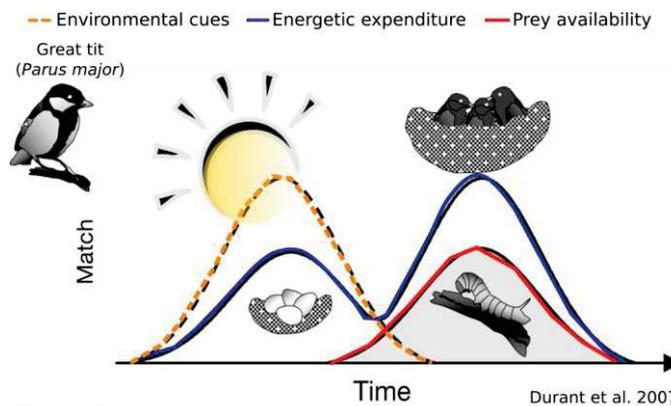


Figure 1.31. Warmer air temperature is proximate factor used by Great tit (*Parus major*) for triggering the onset of egg laying. The ultimate factor is the availability of caterpillar when chicks are reared and when birds' energetic demands are highest. Source Durant *et al.* 2007.

On a physiological point of view, internal clocks and external cues act through the neuro-endocrine systems that in turn control the maturation of reproductive organs and the development of reproductive behavior. Internal clock and external factors control the neuroendocrine cascade in the hypothalamo-adenohypophysial-adrenocortical axis. The neuroendocrine cascade begins with the secretion and release of hormones from the hypothalamus (gonadotropin-releasing hormone, GnRH). GnRH then stimulates the secretion of hypophyseal hormones such as luteinizing hormone (LH) and follicle-stimulating hormone (FSH), which in turn induces gonad growth and steroid hormone production (Murton & Westwood 1977; Ball 1993; Wingfield & Farner 1993; Hau 2001) to finally express reproductive behavior (Figure 1.32).
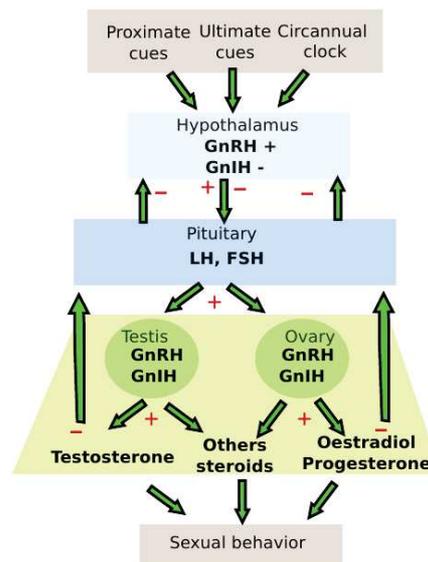


Figure 1.32. Schematic representation of the neuroendocrine cascade controlling expression of sexual behavior. Redrawn from Hau *et al*. 2001.

### 4.3. Sensitivity and adaptation of birds to proximate factors for timing the breeding

Disentangling by which mechanism birds respond to proximate factors for adjusting the timing of their breeding has been the object of intense discussions in the literature during the last decades. One of the first studies proposed that the timing of breeding was a function of the latitude of breeding colonies (Baker 1939). Using the date of egg-laying from 254 species, Baker found that the higher the latitude, the more seasonal is the breeding (Figure 1.33, Baker 1939). This hypothesis was supported by the fact that at high latitudes seasonal breeding is primarily controlled by photoperiod (Wingfield & Kenagy 1991), with brief and synchronized breeding seasons during the short spring-summer period when prey is sufficiently abundant to support high predation rates and to limit competition (Martin 1987). In contrast, in mid and low latitude ecosystems, with only slight seasonal fluctuations, most of the species may display opportunistic breeding.
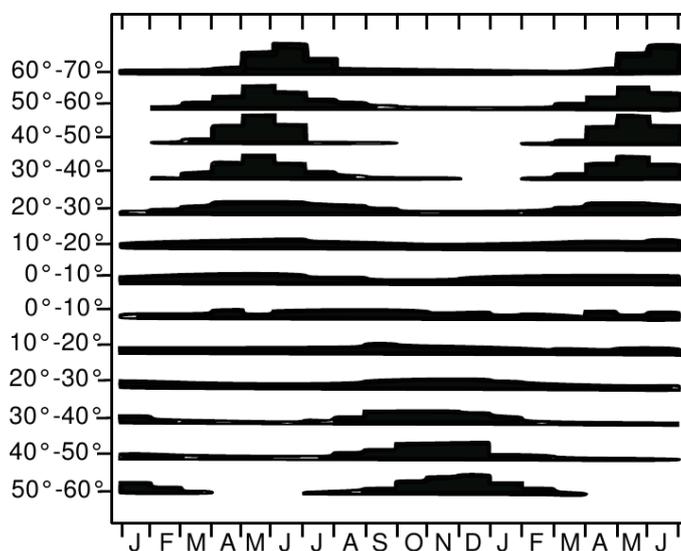


Figure 1.33. Diagram showing how many times each month occurs in the records of egg-seasons in each 10° of latitude. Graphic was done from date of egg- laying dates from 254 species of Old World birds according with its latitudinal location. Source Baker 1939.

However, some species breeding at high latitudes may display extended breeding seasons as, for instance, the Red-necked Nightjar (*Caprimulgus ruficollis*) (Camacho 2013). And some species in the tropics may display discrete breeding seasons, especially in places where large seasonal changes as raining seasons occur in the marine environment, as it is the case for sooty tern (*Sterna fuscata*)(Le Corre 2001; Jaquemet, Corre & Quartly 2007). In any case, animals are sensitive to slight differences in photoperiod but need a more flexible physiological control of life history states to cope with resource variability (Wingfield *et al.* 1992; Beebe, Bentley & Hau 2005).

Detailed classifications of the use of environmental cues have been proposed to explain the adaptation of the timing of breeding in birds in different ecosystems (Wingfield *et al.* 1992; Sharp 1996; Dall *et al.* 2005; McNamara & Houston 2008). Wingfield et al. (1992) proposed

a model to explain the timing of seasonal breeding, based on a partitioning among constancy (C, the degree to which the environment consistently remains the same over time) and contingency (M, the degree to which the environment tends to vary maximally over time). Then, the environmental information factor, Ie=M/C, reveals the extent to which birds must integrate supplementary cues (SI) to initial predictive cues (IPI) in order to optimize the timing of their breeding (Figure 1.34).
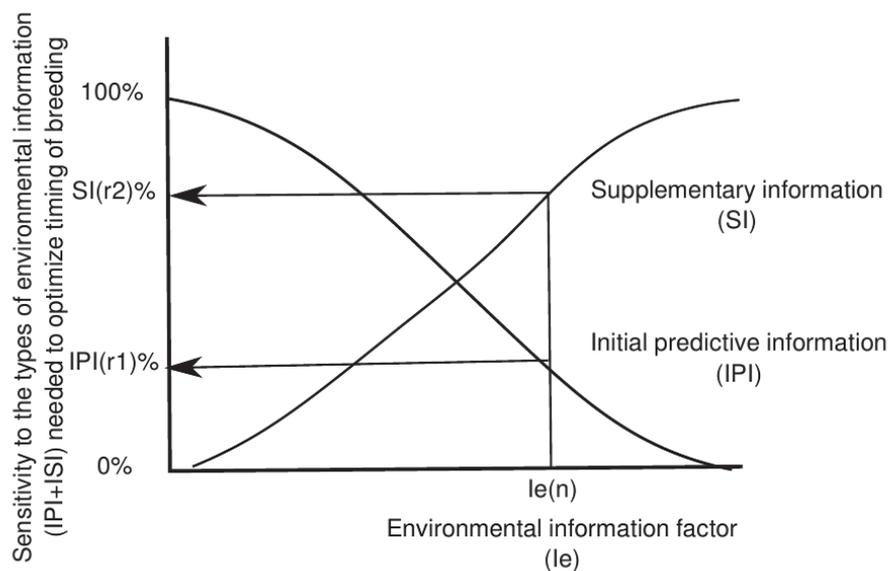


Figure 1.34. Model proposed by Wingfield et al. (1992) about the theoretical relationships between the environmental information factor (Ie) and the environmental information needed to optimize the timing of breeding, with the relative contribution of two types of environmental information (initial predictive information and supplementary information). As Ie tends towards zero, the individual respond only to predictive information. When Ie increases, supplementary information becomes important. When Ie is very high supplementary information may predominate. Source Wingfield *et al.* 1992.

Another, more comprehensive approach was proposed by Lofts & Murton (1968). They highlighted three relevant factors to the timing of breeding: (i) the minimum photoperiodic threshold ('critical day-length') required for the gonadal development, (ii) the nature of the refractory period (absolute, relative, or absent) that plays a fundamental role in determining the physiological probability of breeding at different times in a year, and (iii) the extent to which non-photic cues such as food supply, temperature and social interactions can affect the temporal flexibility of reproduction (Table 1). The photoperiod is the predominant factor regulating seasonal breeding of many species at temperate and high latitudes (Baker 1939; Lofts & Murton 1968). However, since two-thirds of the world's bird species live and breed at mid- to low latitudes where breeding may be prolonged but less predictable, other factors such as refractoriness are necessary to explain the timing of breeding (Wingfield *et al.* 1996; Hau 2001). The refractoriness is the process through which the organism becomes unresponsive to the external stimuli, primarily photoperiod for instance, producing a shutdown in the neuroendocrine cascade and the consecutive gonads collapse that occurs

immediately after breeding in single brooded species, or after the laying of the last clutch in multi-brooded birds (Dawson & Sharp 2007. Refractoriness is profoundly important for its effects on the timing of termination of breeding and the capacity for reproductive flexibility (Farner *et al.* 1983). The process of refractoriness, particularly photorefractoriness, is controlled by the septo-infundibular GnRH system of the brain that remains active and capable of responding to environmental stimuli for relative refractoriness, or switches off and becomes unable to do so in the absolute refractoriness (Ball 1993). Species with absolutely refractoriness would display more rigid periods of reproductive quiescence, with little flexibility to adjust breeding duration or timing as American Tree Sparrow (*Spizella arborea*) (Hahn *et al.* 1997). On the other side, species with relatively low refractory periods would be more flexible if they also evolved a strong sensitivity to supplementary cues whose inputs could be integrated to permit maintenance or re-attainment of reproductive competence. This is the case of the Red-winged black bird (*Agelaius phoenicus*) for instance, which is flexible in the timing of its breeding by including photorefractoriness associated to the availability of suitable vegetation (Hahn *et al.* 1997).

## 5. Modelling the timing of breeding of seabird and its relation with environmental conditions in the NHCS

### 5.1. Seabird data: Land-based census data collection

The three studied seabird species are considered as the major guano producers in the NHCS. Consequently their populations were continuously monitored since 1952 to evaluate the amount of guano possibly produced. The methodology to evaluate the monthly abundance of seabirds was land-based census and it changed little over the years. Land based census consisted in monthly counts performed by the guardians living at each of the densest nesting sites. Every last day of month at sunrise, wardens climb to the most elevated point of the site and plot the observed patches of cormorants, boobies and pelicans on a standardized map of the site (Figure 1.35). Information on age (adult, young, chick, egg) and reproductive status (reproductive and non-reproductive individuals) are recorded for each observed patch of birds (Figure 1.35). The relative surface of each patch is estimated with a sheet of graph paper. The number of seabirds within each patch is then inferred by multiplying those surfaces by a species-specific conversion factor of individuals per m² (Figure 1.35). These conversion coefficients were estimated empirically and were modified at least twice since 1952 (Table 3). The last coefficient versions dated from 2003 (AGRORURAL personal communication). Seabirds nesting on cliffs are counted individually and added to the total.

Most of the detailed information by nesting site and by month was lost over the years because of changes of institution charged of guano extraction. Only yearly mean data were frequently used and published (Jordan & Fuentes 1966; Jahncke 1998). Detailed monthly colony data is only available since 2003, when AGRORURAL the current institution in charge of guano

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exploitation, was composed. Nowadays, AGRORURAL maintains the permanent presence of two wardens in 31 nesting sites (Figure 1.17) who are in charge of protecting and monitoring seabird colonies.
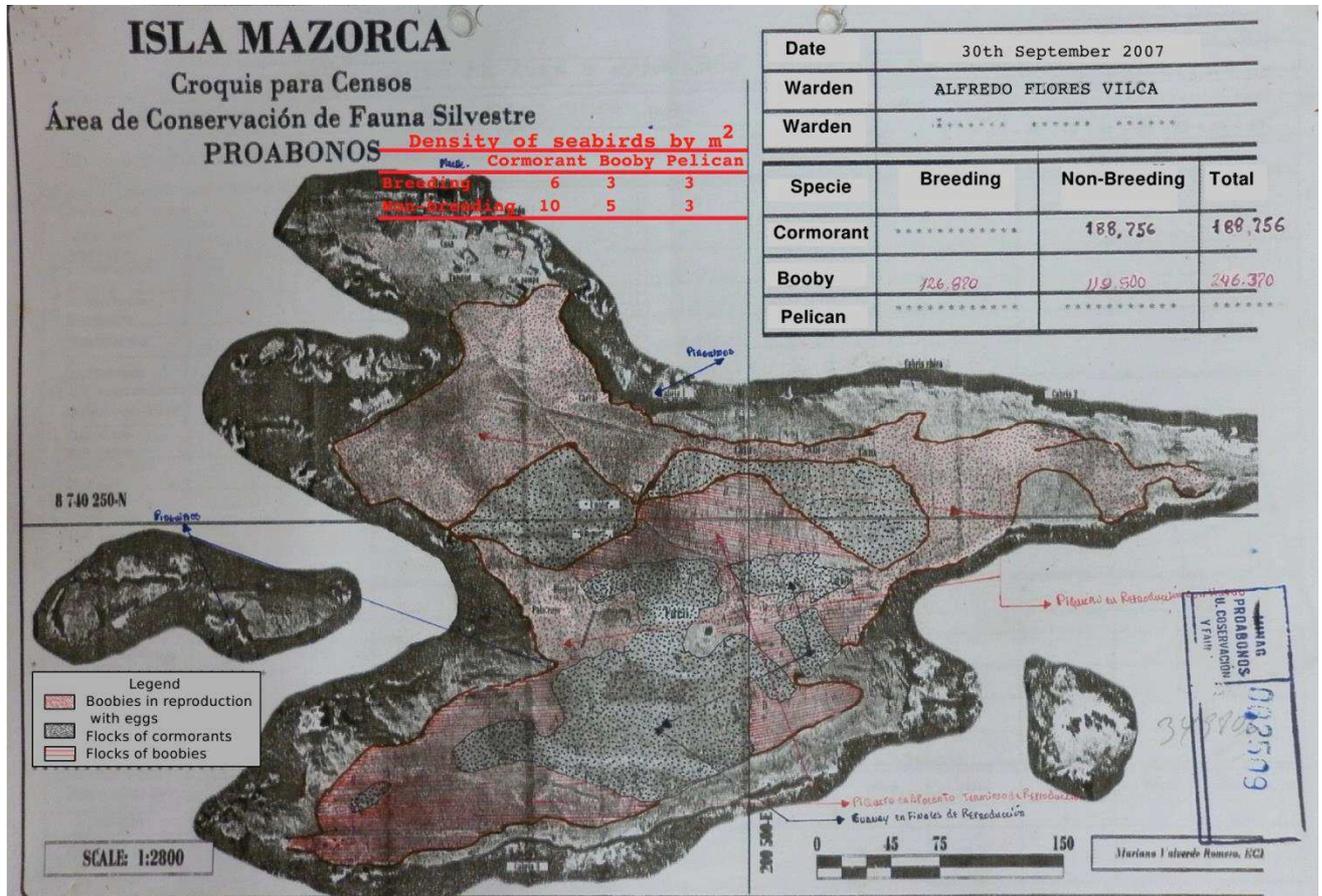


Figure 1.35. Example of an original field data sheet of the seabird census for Mazorca Island on September 2007. Information about occupied patches by species, age and reproductive status were recorded. Surface occupancy was converted to abundances by multiplying surface occupancy by a species-specific conversion factor of density (number of nests/individuals by $m^2$). Some labels were translated for better understanding.

Table 3. Conversion factor of individuals per m² used for calculating the abundance of seabirds by nesting sites. Numbers in parenthesis were those used before 2003 (Tovar Serpa & Cabrera Quiroz 2005) and those outside parenthesis are the coefficients currently used (Agrorural *com.pers*).

| | Density of individuals by m$^2$ | | |
|---|---|---|---|
| | Cormorant | Booby | Pelican |
| Breeding | 6 (7) | 3 (5) | 3 |
| Non-breeding | 10 (15) | 5 | 3 |

Although land based census data have a good resolution at spatial and temporal scales, it may have a large bias in counting (25-49% depending on the species, estimated by comparison with simultaneous aerial surveys, Sophie Bertrand *personal communication*) due in part to the use of fixed density coefficients. Also part of the bias comes from the different skills of wardens for counting, the size of the colonies and the geography of the nesting sites (flat versus slope surfaces). Differences between counts in large colonies can reach up to 33% of variation and between the counts of different wardens up to 30% (Sophie Bertrand *personal communication*). Given this high uncertainty in abundance estimates and since our main interest was about the relationship between breeding seasonality and environmental conditions, we used information on the monthly presence and absence of breeding brids at colonies as a primary dependent variable.

### 5.2. Metapopulation approach: Multiseasons site occupancy model

Unbiased abundance and trends of population were classical parameters to estimate when using classical population models (Kéry & Schaub 2012). However in our case the bias in counts can invalidate the use of counts to model the dynamic of population of seabirds. This drawback makes that we were interested in working demographic traits from other approaches.

The most robust and simple option was to work on occupancy of effective population (breeders). Occupancy of breeders was identified as the most convenient approach first because it does not involve assumptions on false positives (when breeders are present they are in great numbers) and second because there are well implemented methods to deal with occupancy data with time and space structure. We identified the metapopulation approach as the best to use in our study case.

One of the most useful methods to deal with occupancy data sampled in fragmented space is the metapopulation approach (Hanski 1998). Metapopulation concept was formalized as an assembly of subpopulations from a same species, that can go extinct and recolonized with

equal probability (Levins 1970). The metapopulation approach was subsequently used for species that live in delimited habitat patches (e.g. islands, ponds) and can migrate between them to colonize other spaces or eventually be locally extinct with different probabilities (Figure 1.36, Harrison & Taylor 1997).
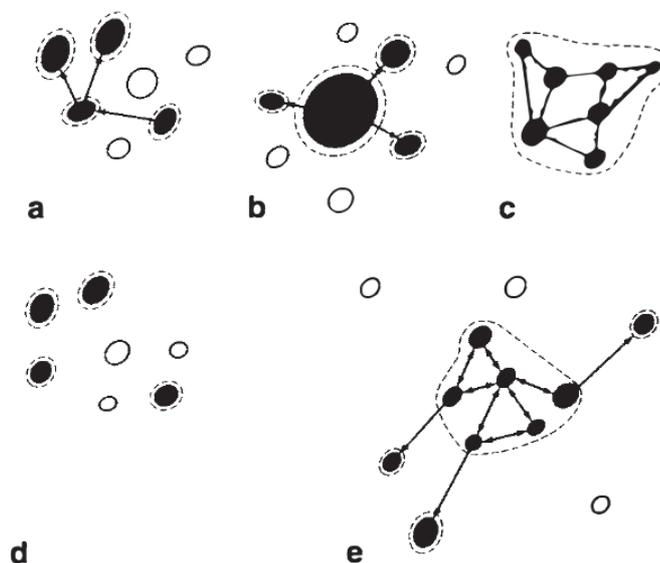


Figure 1.36. Different types of metapopulation. Filled circles represent occupied habitat patches; empty circles represent vacant habitat patches; dotted lines represent boundaries of local populations; arrows represent dispersal. a) Classic boundaries of Levins; b) mainland-island; c) patchy population; d) nonequilibrium metapopulation; e) intermediate case combining features of (a), (b), (c), and (d). Source Harrison & Taylor 1997.

The metapopulation approach can perfectly match our case because seabirds in the NHCS nest mostly on islands or headlands delimited by walls, therefore the habitat occupied has a clear spatial structure ("patchily"); and temporally, the nesting sites are not permanently occupied, so there is fragmentation in time too.

There are two classes of metapopulation approaches: i) the occupancy status of several patches within a single season and ii) the dynamic of multiple patches occupied over several season through rates of colonization and extinction.

The first approach was first viewed as a simple number or proportion of sites that are occupied. This model has two strong assumptions: lack of false positives and population closure. Population closure in the context of site occupancy models means that there is no change of state during the period of sampling. This model is also called Hierarchical single season occupancy model when it incorporates the observation process as a measure of detection that could bias the state ("true" or "ecological") process (Mackenzie *et al.* 2002).

The second approach, based on multiple seasons, includes time as a first-order Markovian process. This model is called Multiseason occupancy model (MacKenzie *et al.* 2003) and

relaxes the assumption of population closure. Closure assumption is relaxed by the introduction of colonization and extinction rates with a time passage of t+1. Multiseason occupancy model is build first from an initial occupancy ($\psi_1$) and all later months by histories of colonization ($\gamma$) and local extinction ($\varepsilon$) (Figure 1.37).
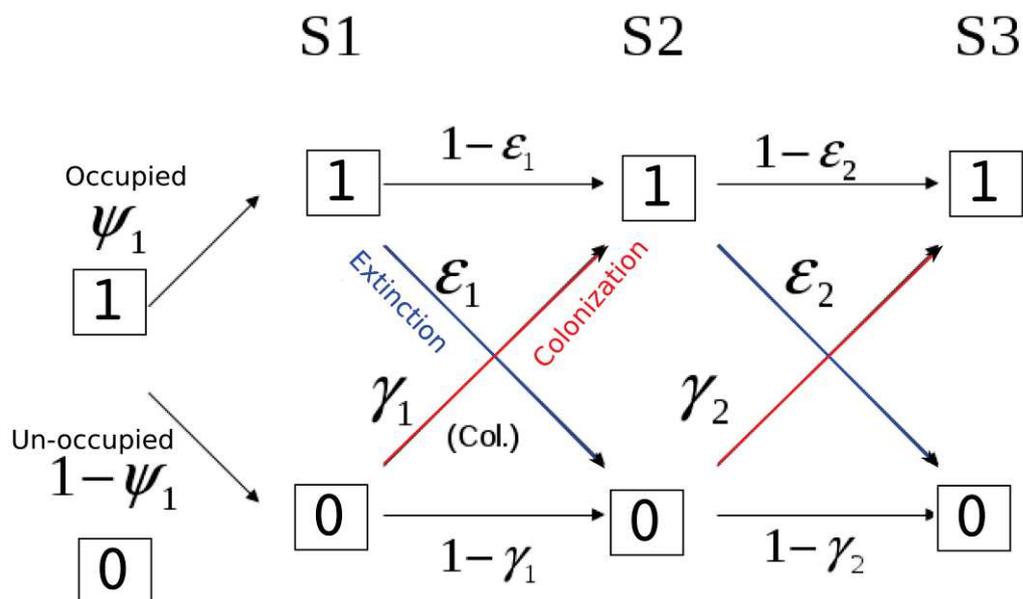


Figure 1.37. Schema of the estimation of parameters in multiseason occupancy models. $\Psi$ is the initial occupancy ($\psi=1$, or $1-\psi=0$), then in the next seasons (S1, S2 and S3) extinction (Pr(h=10) =$\varepsilon$) or colonization (Pr(h=01)=$\gamma$) parameter are estimated.

Colonization (Pr($h_t$=01)=$\gamma_t$) is defined as the probability that the site unoccupied in season t was occupied in t+1. Local extinction (Pr($h_t$=10)=$\varepsilon_t$) is defined as the probability that the site occupied in season t was unoccupied in t+1. Therefore, three parameters were estimated by multiseason occupancy models; probability of colonization ($\gamma$), probability of local extinction ($\varepsilon$) and occupancy of breeders ($\psi$) derivated from onset and termination.

We adapted these parameters to the dynamic of occupancy of nesting sites by seabirds. In our case colonization corresponded to onset of breeding that initiated with egg-laying and local extinction with the departure of seabirds from the nest due to successful breeding or nest abandon. Also, occupancy of nesting sites was a proxy of the average duration of breeding cycle.

Estimation of $\gamma$, $\varepsilon$ and $\psi$ through several seasons can be done through frequentist approach with a likelihood-based framework (Barbraud *et al.* 2003; MacKenzie *et al.* 2003); or through a Bayesian approach using Markov chain Monte Carlo simulations (MCMC) algorithms (Kéry & Schaub 2012). Any of the framework used were similar in results when data are large enough but when data is sparse Bayesian approach is advised. We used both approaches in this thesis; first we used the frequentist approach but due to its lack of convergence when data was sparse, we used Bayesian approach later.

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Multiseason occupancy models can also be considered as hierarchical when observation process (detection) is taken into account. However we do not used hierarchical models because nesting sites are desert areas without vegetation and seabirds are nesting in high numbers then the observational process is needless because we assumed that there are not false negatives and no false positives.

Multiseason occupancy models are very flexible because they allow including covariates to model the dynamic of occupation through a logistic relationship (MacKenzie *et al.* 2005). Two kinds of variables can be included: site-specific variables that remain constant over time (e.g. altitude, latitude, vegetation) and site-specific variables that may change over time (e.g. temperature, precipitation, food availability). In our case we are interested in including as site covariates: island surface area, latitude, effect of island or headland and as site-specific variables oceanographic covariates, prey covariates and fishery covariates.

# *Chapter II: Seasonality of the breeding of the Peruvian seabirds in relation with prey and environmental conditions*
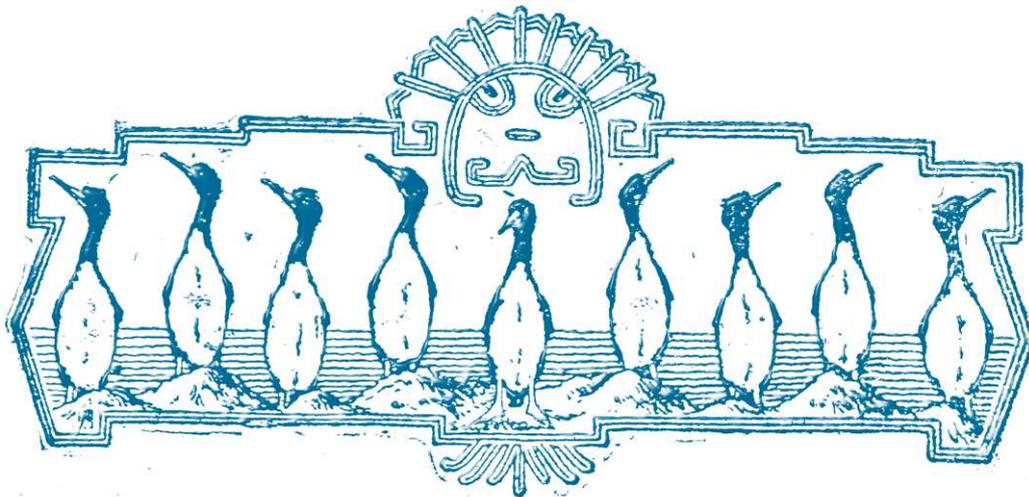
# *Seasonality in marine ecosystems: Peruvian seabirds, anchovy and oceanographic conditions*

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*Abstract.*

 In fluctuating environments, matching breeding timing to periods of high resource availability is crucial for the fitness of many vertebrate species, and may have major consequences on population health. Yet, our understanding of the proximate environmental cues driving seasonal breeding is limited. This is particularly the case in marine ecosystems where key environmental factors and prey abundance and availability are seldom quantified. The Northern Humboldt Current System (NHCS) is a highly productive, low latitude, ecosystem of moderate seasonality. In this ecosystem, three tropical seabird species (the Guanay cormorant *Phalacrocorax bougainvillii*, the Peruvian booby *Sula variegata* and the Peruvian pelican *Pelecanus thagus*) live in sympatry and prey almost exclusively on anchovy *Engraulis ringens*. From January 2003 to December 2012, we monitored 31 breeding sites along the Peruvian coast, to investigate the breeding cycle of these species. We tested for relationships between breeding timing, oceanographic conditions and prey availability using occupancy models. We found that all 3 seabird species exhibited seasonal breeding patterns, with marked interspecific differences. Whereas breeding mainly started during the austral winter/ early spring and ended in summer/ early fall, this pattern was stronger in boobies and pelicans than in cormorants. Breeding onset mainly occurred when upwelling was intense but ecosystem productivity was below its annual maxima, and when anchovy were less available and in poor physiological condition. Conversely, the abundance and availability of anchovy improved during chick rearing and peaked around the time of fledging. These results suggest that breeding timing is adjusted so that fledging may occur under optimal environmental conditions, rather than being constrained by nutritional requirements during egg-laying. Adjusting breeding time so that fledglings meet optimal conditions at independence is unique compared with other upwelling ecosystems and could be explained by the relatively high abundances of anchovy occurring throughout the year in the NHCS.

*Key words: Guanay cormorant; Peruvian booby; Peruvian pelican; Northern Humboldt Current System; oceanographic variability; prey abundance; seasonal breeding; occupancy model.*

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## 1. Introduction

For animals reproducing in fluctuating environments, breeding timing is often critical to success (Lack 1968; Cushing 1990). In birds and mammals, the intrinsic determinants of breeding timing (e.g. hormones (Prendergast 2005), energy status (Perrins 1970)) are suggested to evolve in response to bottom-up processes, such as spatial and temporal resource availability (Hamer *et al.* 2002).

Indeed, current theories propose that food availability often constrains the breeding season to a restricted period of the year when fitness benefits are maximal for both parents and their offspring. In birds for instance, Lack (1968) suggested that seasonal variation in resource availability should select for the period of chick provisioning to match environmental peaks of food availability ('optimal breeding time' theory). Chick rearing is indeed regarded as one of the most energy-costly phases of the annual cycle (Drent & Daan 1980), and fitness returns may be greatest for genotypes that time reproduction in this way. In contrast, Perrins (1970) highlighted that female nutritional requirements early on in the breeding season may select breeding timing so that egg-laying matches periods of peak resource availability ('egg-laying constraint' theory).

For seabirds of temperate and polar marine ecosystems, seasonal breeding is primarily controlled by photoperiod (Wingfield & Kenagy 1991), and the precise date of egg-laying appears to be driven by egg laying constraints (Schroeder *et al.* 2009; Shultz *et al.* 2009). In contrast, in tropical ecosystems, seasonal changes in photoperiod are small and few studies have examined the correspondence between seasonal ecosystem productivity and seabird seasonal breeding from a bottom-up perspective (Le Corre 2001, Jaquemet et al. 2007).

One major drawback in explaining why nesting cycles are timed the way they are, or why breeding timing often shows such inter-annual variability is the complexity of accurately documenting and measuring bottom-up processes (Hamer *et al.* 2002; Thompson *et al.* 2012). Indeed, one important challenge to overcome is the ability to simultaneously measure oceanographic processes, prey availability and seabird responses on appropriate temporal (year-round) and spatial scales. Ideally, a relatively large number of contrasted seasons should be monitored for robust inferences to be drawn. At present however, study durations are often too short to provide a comprehensive overview of the heterogeneity in ecosystem and trophic processes.

Here, over a period of 10 years, we studied the relationships between seasonal breeding patterns, seasonal variation in physical oceanographic characteristics, and seasonal variation in prey abundance, prey availability and prey quality for three tropical seabird species: the Guanay cormorant (*Phalacrocorax bougainvillii*, Lesson 1837), the Peruvian booby (*Sula variegata*, von Tschudi 1843), and the Peruvian pelican (*Pelecanus thagus*, Molina, 1872). Our study was carried out in the Northern Humboldt Current System (NHCS), the most equatorward region (4°-18°S) of the four major eastern boundary upwelling ecosystems worldwide (EBUE's: Benguela, Humboldt, California and Canary). EBUEs are characterized by cool and nutrient-rich upwelling waters that strongly affect sea surface temperature and chlorophyll concentration in coastal waters (Chavez & Messié 2009; Sydeman *et al.* 2014). The upwelling of the low latitude NHCS occurs year-round with

moderate seasonality in oceanographic conditions, mainly modulated by the strength of winds (Echevin *et al.* 2008). This system also encompasses an intense and shallow oxygen minimum zone (OMZ) (Fuenzalida *et al.* 2009), the upper limit of which (i.e. lower oxycline) is known to constrain the vertical distribution of prey fish species (Bertrand *et al.* 2010, 2011), affecting their availability to seabirds.

Our three study species are all endemic to the NHCS. They breed sympatrically in high numbers (global population ≈2-4 millions of individuals; Peru National Institute for the Agricultural and Rural Development-AGRORURAL *unpublished data*) and compete for prey, especially Peruvian anchovy (*Engraulis ringens*), with a large-scale fishing industry off the coast of Peru (Jahncke *et al.* 2004). These seabirds are also the main contributors of guano production along the Peruvian coast (Duffy 1994). Yet, research on the seasonality of their breeding cycle is scarce, and existing studies are mostly restricted to a single season or few colonies (Jahncke & Paz-Soldan 1998), or were conducted before the development of industrial fishing (before the 1950's, Vogt 1942). The earliest work described those seabirds as year-round breeders, with incubation peaking in the late austral spring and early summer (November-December) when local anchovy abundance was high (Vogt 1942, Appendix A, Figure A1). Further, it was suggested that these seabirds might increase their breeding frequency and adjust their egg-laying periods (Nelson 2005) in response to population decline (Jordan & Fuentes 1966) and severe ENSO events (Duffy 1990).

In this study, we merged data on seabird nesting seasons, oceanographic conditions and prey availability to address 3 major questions: (i) Is the breeding cycle of cormorants, boobies and pelicans in the NHCS characterized by marked seasonality? (ii) Are there observable differences in the nesting cycles of the three species? (iii) Do seasonal changes in oceanographic conditions and prey abundance, availability and quality affect the breeding cycle of those seabirds? Documenting seasonal breeding patterns in relation to environmental characteristics and prey availability was expected to provide us with knowledge on the determinants of breeding cycles, in light of possible egg-laying constraints and/or optimal breeding windows in those tropical species.

## 2. Materials and methods

### 2.1. Study area and species

Cormorants, boobies and pelicans occur between 3°S and 42°S (Nelson 2005, Jeyasingham et al. 2013). Breeding sites are typically situated on arid and uninhabited islands and headlands, each breeding site hosting one to several colonies. Most islands are located within a 20 km distance from the coast, except for Isla Lobos de Afuera (7°S) that lies at some 60 km from the coast (Figure 2.1). All species are considered to be annual breeders (Nelson 2005) and lay one to four eggs (cormorant: 2-4 eggs; booby: 1-4 eggs; pelican: 2-3 eggs). The length of the breeding period from egg-laying laying to chick-fledging is of ≈4.7 months for cormorants, ≈5.3months for pelicans and ≈6.7 months for boobies (Appendix B).

In the NHCS, AGRORURAL is the state institution responsible for guano harvesting in seabird colonies. AGRORURAL also ensures seabird conservation and protection through guardianship and monitoring of breeding sites. At the end of each month, one or two resident wardens from AGRORURAL perform a land-based census of the colonies for all three species at each breeding site. The wardens climb to the highest point of the island, mark observed patches of breeders (colonies) and non-breeders (flocks) on a standardized map of the site, and subsequently convert patch surfaces into an abundance index by applying a nest density factor that was pre-established for each species in the NHCS (see Appendices C and D). Individuals are considered as breeders if they are observed incubating eggs, brooding or feeding chicks (Appendix C). Colonies most often varied from thousands to tens of thousands of individual breeders (Appendix D) and counts were strongly biased because (i) wardens varied in their experience, (ii) some nesting areas, such as cliffs, were hard to monitor from the ground, and (iii) whereas nest density varied across years and sites, the nest density conversion factor was assumed constant. Comparing concomitant ground and aerial surveys (used as a reference), revealed that ground counts underestimated colony size by 25 - 49% on average, depending on the species. Given this high uncertainty in abundance estimates and since our main interest was about the relationship between breeding seasonality and environmental conditions, we used information on the monthly presence and absence of birds at colonies as a primary dependent variable (see Appendix D).

The monthly presence/absence of birds was thus determined at colonies of 31 sites (Figure 2.1) from January 2003 to December 2012 (i.e. 120 months). Using multiseason site-occupancy models (MacKenzie *et al.* 2005), we investigated the seasonality of breeding patterns in relation to oceanographic and prey parameters (considered as covariates) and nesting habitat (considered as a nuisance variable). Nesting habitat features were fixed site-specific covariates that characterized the geographical situation of breeding sites.

Oceanographic covariates were both dynamic and site-specific, reflecting the spatio-temporal variations in oceanographic conditions surrounding each breeding site during the year. Prey covariates were also dynamic (but not site-specific) and reflected the temporal variation encountered in prey abundance and condition in the NHCS throughout the year.

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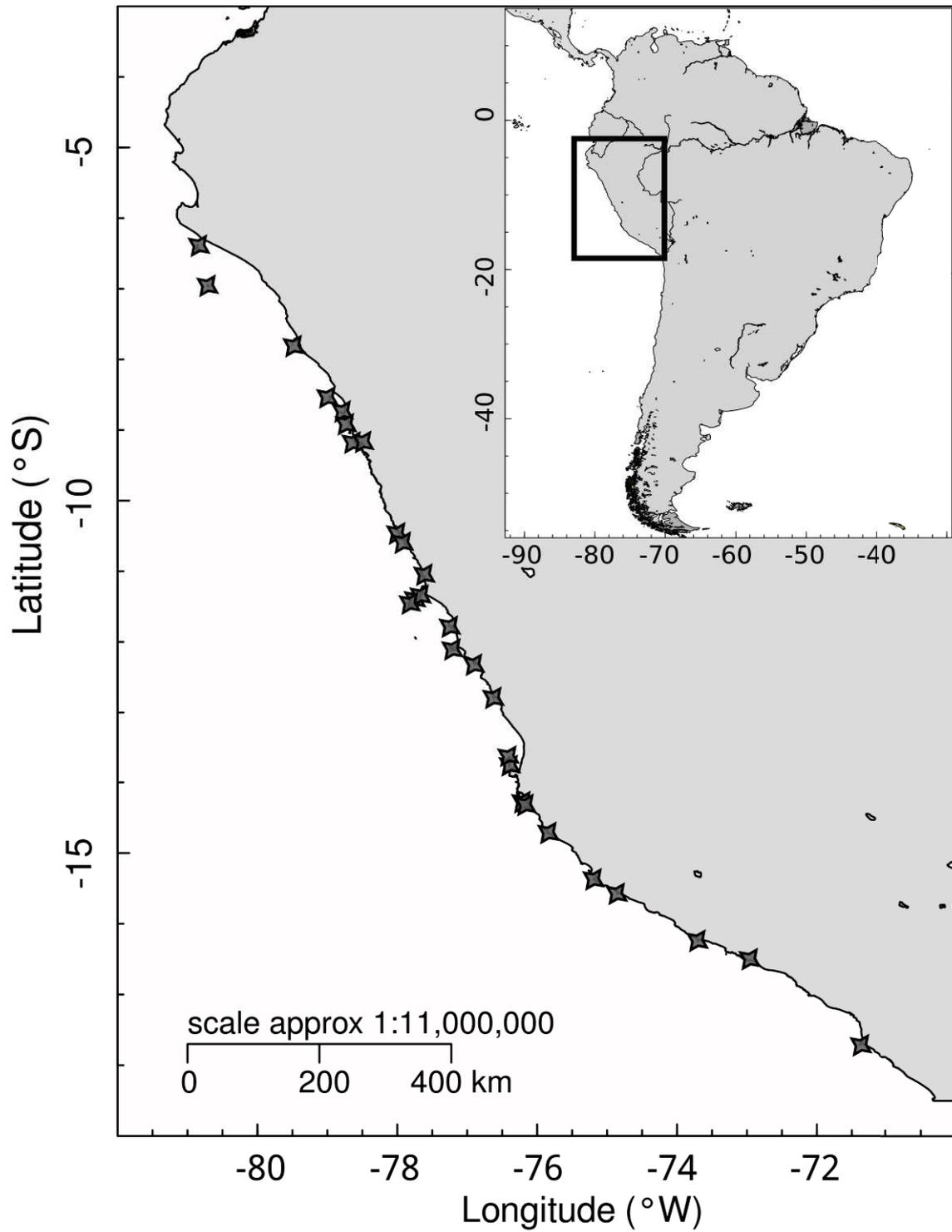


FIGURE. 2.1. Map figuring the 31 breeding sites of guano producing seabirds (Guanay cormorant, Peruvian booby and Peruvian pelican) monitored by AGRORURAL along the coast of Peru.

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## 2.2. Nesting habitat covariates

Each breeding site was described with the following geographic features: (i) whether the breeding site was an island or a headland (I/H), (ii) its log-transformed distance from the coast (DC, km, null for headlands), and (iii) its latitude (LAT).

## 2.3. Oceanographic covariates

Oceanographic covariates (Appendix E) were remotely sensed by satellite and included Chlorophyll-a concentrations (Chlo, mg m$^{-3}$), Sea Surface Temperatures (SST, °C), an Upwelling Index (UI) obtained from wind speed components. In addition, vertical profiles of dissolved oxygen concentrations acquired from research vessels of the Instituto del Mar del Peru (IMARPE) allowed us to determine dissolved oxygen concentrations (DO, ml l$^{-1}$) close to the surface (0-5 m) and the depth of the oxycline, defined as the depth where dissolved oxygen is equal to 2 ml l$^{-1}$ ($Z_{2ml\,l^{-1}}$, m). Oxycline depth is a proxy of the upper limit of the oxygen minimum zone (Bertrand et al. 2010), and is associated with the limit of vertical anchovy distribution. Chlo, SST, UI and DO reflected annual variations in ecosystem productivity. A climatology profile (monthly averages over all years) for each covariate was computed within a 100km-radius around each colony using data from 2002-2012 for Chlo and SST, data from 1999-2009 for UI, and data from 1960-2010 for DO and $Z_{2ml\,l^{-1}}$. This range encompassed the maximum-recorded foraging ranges of the three species during breeding: ≈63 km for cormorants (S. Bertrand, unpublished data), ≈90 km for boobies and ≈83 km for pelicans (Zavalaga et al. 2011; Bertrand et al. 2012).

## 2.4. Prey covariates

Acoustic data were collected 2-4 times a year during routine acoustic biomass estimation surveys performed along the Peruvian coast by IMARPE. In general, the survey design consisted in parallel cross-shore transects of ~100 nautical miles long and ~15 nautical miles between transects (Gutiérrez et al. 2007; Simmonds et al. 2009) (Appendix F). Surveys were performed by research vessels equipped with 38 and 120 kHz Simrad split beam scientific echosounders (EK500 and EK60) mounted on the hull. The echosounders were calibrated with a standard sphere (Foote et al. 1987). Nautical-area-backscattering coefficients (s$_A$ or NASC) were recorded in each georeferenced elementary distance sampling unit (ESDU = 1 nautical mile) (Simmonds & Maclennan 2005). Here, we only considered the s$_A$ attributed to anchovy by applying a -65 dB volume threshold on backscattering strengths, and by identifying echoes from associated catches during fishing trawls (Gutiérrez et al. 2007; Simmonds et al. 2009).

We analyzed the acoustic surveys from 1999-2011, a period with abundant anchovy and collapsed sardine stocks (Bertrand et al. 2011). For each survey, we sub-sampled the area

between latitudes 6ºS and 14ºS to cover most of the breeding sites. The sampling ranged from the coast to 40 km offshore both in order to cover the core area of anchovy abundance (Bertrand *et al.* 2011) and the average distance of foraging for cormorants and boobies (Weimerskirch *et al.* 2012). From this subsample we determined (i) regional anchovy abundance, *i.e.* the monthly average $s_A$ per ESDU; (ii) local anchovy density, *i.e.* the monthly average $s_A$ per ESDU when anchovy were present ($s_A+$); and (iii) anchovy spatial distribution, *i.e.* the monthly spatial occupation index (ISO) computed as the percentage of ESDU where anchovy was present. For acoustic surveys conducted over two months, we calculated averages based on the month with the most data. In a few cases, the numbers of days were similar for the two months, and the information was then split for each month (Appendix F, Table F1). We built regional climatologies (monthly averages over 1999-2011) for the three indices ($s_A, s_A+$, ISO). However the months of January, April and May were not surveyed and only two surveys were performed in June and July (Figure E2).

To describe the physiological condition of anchovy we used: (i) a Body Condition Factor (BCF, g cm$^{-3}$), defined as the ratio between eviscerated weight and the third power of the total length; and (ii) a Gonado-somatic Index (GSI), defined as the proportion of gonad mass relative to total body mass. The detailed methodology for data collection and for calculating these physiological indices is described elsewhere (Buitrón et al. 2011, see Appendix G). Climatologies (monthly averages over all years) of the two indices (BCF, GSI) were computed from monthly reports of the North-central anchovy stock (6º - 14ºS) from 2002-2012 (Figure G1). We used the North-central stock because most seabird colonies were situated within this area.

## 2.5. Modeling seabird seasonal breeding and its relationship with oceanographic and prey covariates

Multiseason occupancy models are dynamic models allowing making inferences (i) on the occurrence of events at a collection of sites, and (ii) on how changes in occurrences are driven by colonization and local extinction (MacKenzie et al. 2005). We used the monthly presence and absence of breeders (Table D2) in breeding sites (which contain one or several colonies) as a dynamic process of onset and termination of breeding events (colonization and local extinction). We estimated three parameters using multiseason occupancy models. First, we determined (1) the occupancy probability of a breeding site ($\psi$) during the first month of the breeding season. Second, we determined changes in occupancy as (2) the onset probability ($\gamma$) and (3) termination probability ($\varepsilon$) of breeding events. The occupancy of a breeding site ($\psi$) was defined as the probability of a breeding colony being present on the site. The onset probability of breeding events ($\gamma$) was the probability that a breeding site without breeders in month $i$ was colonized in month $i +1$. The termination probability of breeding events ($\varepsilon$) was the probability that a breeding site with breeders in month $i$ was deserted by breeders in month $i +1$. Models were fitted using maximum likelihood techniques using the PRESENCE software 6.1 (MacKenzie *et al.* 2005). Occupancy models were developed to produce unbiased estimates of occurrence when the probability of detecting a

species (p), given its occurrence at a particular site, was <1 (MacKenzie *et al.* 2005). In our case however, given the absence of vegetation, the large size and conspicuousness of nesting colonies, and the permanent presence of wardens on the study sites, we considered that p = 1.

We used a 2-stage approach in model selection procedures:

First, we compared *a priori* models to evaluate whether (i) the onset and termination of breeding obeyed a first order Markovian dynamic ($\gamma \neq \varepsilon$) or not ($\gamma = \varepsilon$), (ii) the probabilities of breeding onset and termination varied monthly ([$\gamma(m)$ $\varepsilon(m)$], $m$=1:12), were full time dependent over the 2003-2012 period ( [$\gamma(i)$ $\varepsilon(i)$], $i$=1:120), or were constant ([$\gamma(.)$ $\varepsilon(.)$]), and (iii) the probabilities of onset and termination of breeding depended on nesting habitat covariates (I/H, LAT, DC). We modeled the influence of the geographical covariates on the onset and termination of breeding events using the *logit* function (Appendix H). Models were ranked based on Akaike's information criterion (AIC). The lower the AIC, the better the fit of the model and two models with a difference in AIC < 2 were assumed to be of similar predictive power (Burnham & Anderson 2002).

Second, based on the above-selected models, we modeled the influence of monthly variations in oceanographic and prey covariates on the onset and termination of breeding events using a *logit* function. We used the first axis of a principal component analysis (PCA) on the climatology of oceanographic variables instead of the original variables, to limit the number of covariates in the analyses and control for variable interdependence. For climatology of anchovy covariates, we did not perform a PCA and each covariate was modeled individually because data points were insufficient and unbalanced (7 points for acoustic data and 12 points for physiological covariates). In order to optimize convergence of the maximum-likelihood routine, covariates were standardized ($s_A$, $s_A$+, ISO, BCF and GSI). We tested the effects of oceanographic and prey covariates on the onset and termination of breeding events using an analysis of deviance (ANODEV, Appendix H), and quantified how much of the temporal variation in onset and termination of breeding events was accounted for by each covariate model using $R^2$ (Grosbois *et al.* 2008). We also tested the effects of oceanographic and prey covariates with time lags up to three months in order to test the hypothesis that changes in onset and termination of breeding events may be a response to earlier changes in environmental conditions.

## 3. Results

### 3.1. Seasonal onset and termination of breeding events

The probabilities of breeding onset and termination were best represented by a first order Markovian process (Table I1). For all three species, models where breeding varied monthly had lower AIC than full time and constant models (Table I2). For cormorants, breeding onset occurred almost throughout the year, initiating in April and reaching a maximum in October, before subsequently declining. The seasonality in breeding onset for boobies and pelicans was more pronounced than for cormorants (Figure 2.2). In boobies and pelicans, breeding onset was rather restricted to a period between July and October, reaching a maximum in

September for boobies (Figure 2.2). Breeding termination probabilities were consistent with the duration of the main breeding stages from pre-laying attendance to the independence of fledglings (Figure I2). For the three species, these probabilities were particularly high from December to April, reaching a maximum in March for cormorants, in January for boobies, and in April for pelicans. Breeding termination probabilities declined after May, except for a peak in June for boobies and pelicans. In the rest of the paper we only focus on breeding onset models as the relationships between breeding termination, oceanographic and prey covariates (see Table I4, I5 and I6) were inverse to those obtained for breeding onset.

Site covariates influenced the magnitude of breeding onset probabilities (Table I3) without changing the nesting cycle patterns described above. For cormorants and boobies, breeding onset probabilities were higher on islands than on headlands. For pelicans, islands located further away from the coast had higher breeding onset probabilities. For all three species, latitude had a lower effect on breeding onset probabilities than island/headland covariates.
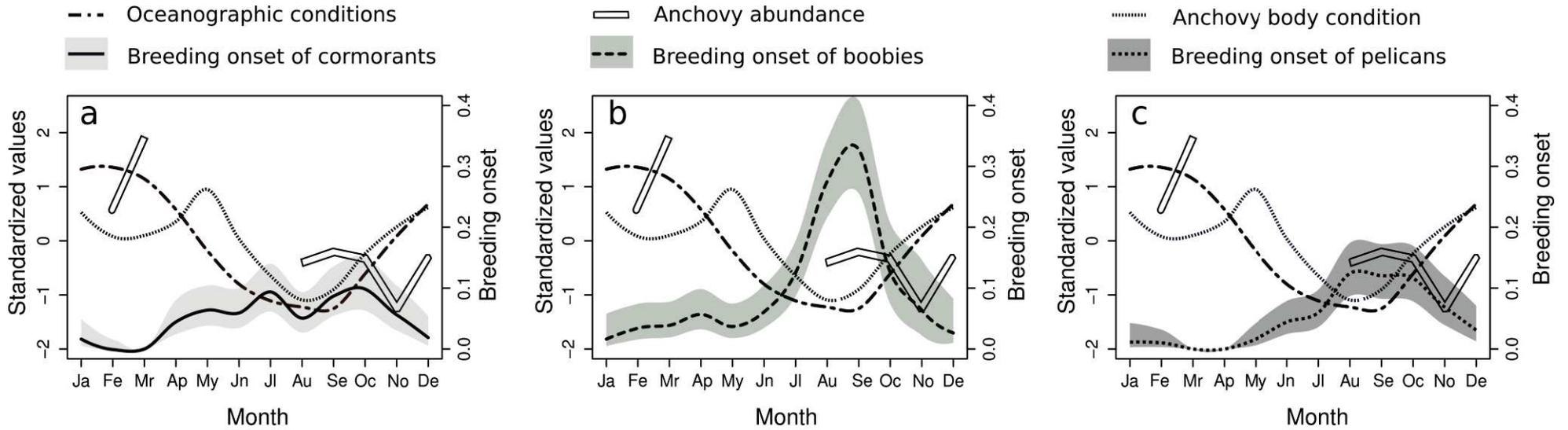
FIG. 2.2. Estimates of monthly probabilities of breeding onset for (a) cormorants (solid black line), (b) boobies (dashed line) and (c) pelicans (dotted thick line) related to oceanographic conditions (PC1, dashed lines with dots), standardized anchovy abundance ($s_A$, solid white lines) and standardized anchovy body condition (BCF, dotted thin lines). Shaded areas correspond to 95% confidence intervals. Lines of breeding onset, oceanographic conditions and anchovy body conditions were smoothed with a loess model with 0.45 of span. Effects of nesting habitat covariates on breeding onset probability.

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### 3.2. Effects of oceanographic conditions on breeding onset probability

Oceanographic covariates exhibited moderate seasonal cycles (Figure E1). We differentiated two groups of oceanographic variables exhibiting contrasted monthly patterns. One group regrouped SST, Chlo and DO with maximum values observed during austral summer (DO in January, SST in February and Chlo in March-April) and minimum values in the austral winter (DO in July, SST in September and Chlo in August). In contrast, the second group of covariates (UI and $Z_{2ml\,l^{-1}}$) reached maximum values during the austral winter (September) and minimum values in summer (UI in January and $Z_{2ml\,l^{-1}}$ in February; Figure E1). The seasonal variability of oceanographic covariates was synthesized with the first PCA axis (PC1) that represented 89.1% of the total variance (only 7.3% on the second component; Figure E2.). The seasonality of oceanographic conditions (Chlo, SST, DO, UI and $Z_{2ml\,l^{-1}}$) was related primarily to upwelling and primary production (Figure 2.3).

A higher UI associated with a deeper $Z_{2ml\,l^{-1}}$, lower SST, lower Chlo and lower DO (PC1 values $< 0$) corresponded to higher breeding onset probabilities (Figure 2.3). The relationships between onset probabilities and PC1 were consistent between species (Table 2.1). For all three species, all models including PC1 with time lags of up to two months indicated significant relationships with breeding onset ($F$-tests: all $P < 0.05$, Table I4). However, models with a one-month lag performed generally better at explaining seasonal variation in breeding onset probabilities (Table I4).

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TABLE 2.1. Summary of selected models relating oceanographic conditions (PC1), anchovy regional and local abundance ($s_A$ and $s_A+$), anchovy body condition (BCF) and the Gonado-somatic index (GSI) to the probabilities onset of breeding ($\gamma$) for cormorant, booby and pelican. Monthly termination of breeding [$\varepsilon(m)$] were not changed between models. Oceanographic conditions, body condition and the Gonado-somatic index were lagged of one month. *Notes:* The slope ($\beta$) $\pm$ SE indicates the shape of the relationship between covariates and onset of breeding. The $F$ statistic of ANODEV (noted $F_{cst/cov/t}$) and its associated p-value ($P$) test the covariate effect on onset of breeding, while $R^2$ provides a measure of the magnitude of the effect. I/H is the geographical effect that in case of pelican changes to DC.

| | | Cormorant | | | | | Booby | | | | | Pelican | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Covariables | Models | $\beta$ | SE | $F_{cst/cov/t}$ | $P$ | $R^2$ | $B$ | SE | $F_{cst/cov/t}$ | $P$ | $R^2$ | $\beta$ | SE | $F_{cst/cov/t}$ | $P$ | $R^2$ |
| Oceanographic conditions | [$\gamma$(I/H+PC1-1) $\varepsilon$(m)] | -0.23 | 0.05 | 10.67 | 0.01 | 0.52 | -0.48 | 0.05 | 34.58 | 0.00 | 0.78 | -0.51 | 0.07 | 160.82 | 0.00 | 0.94 |
| Anchovy regional abundance | [$\gamma$(I/H+$s_A$) $\varepsilon$(m)] | -0.65 | 0.16 | 7.21 | 0.02 | 0.42 | -2.57 | 0.1 | 18.11 | 0.00 | 0.64 | -0.9 | 0.16 | 9.61 | 0.01 | 0.49 |
| Anchovy local abundance | [$\gamma$(I/H+$s_A$+) $\varepsilon$(m)] | -0.4 | 0.13 | 2.69 | 0.13 | 0.21 | -1.15 | 0.11 | 15.5 | 0.00 | 0.61 | -0.75 | 0.11 | 11.52 | 0.01 | 0.54 |
| Anchovy spatial distribution | [$\gamma$(I/H+ISO) $\varepsilon$(m)] | -0.4 | 0.13 | 2.44 | 0.15 | 0.20 | -0.22 | 0.11 | 0.22 | 0.65 | 0.02 | -0.19 | 0.12 | 0.33 | 0.58 | 0.03 |
| Anchovy body condition factor | [$\gamma$(I/H+BCF-1) $\varepsilon$(m)] | -0.54 | 0.15 | 4.25 | 0.07 | 0.30 | -1.68 | 0.14 | 40.84 | 0.00 | 0.80 | -1.09 | 0.14 | 35.39 | 0.00 | 0.78 |
| Gonadosomatic index of anchovy | [$\gamma$(I/H+GSI-1) $\varepsilon$(m)] | -0.19 | 0.01 | 1.00 | 0.34 | 0.09 | -0.02 | 0.10 | 0.07 | 0.8 | 0.01 | 0.16 | 0.10 | 0.37 | 0.55 | 0.04 |

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### 3.3. Effects of prey availability and anchovy condition on breeding onset probabilities

Although the observations of anchovy abundance were limited by a lack of acoustic data in January and April-July, regional and local anchovy abundance ($s_A$ and $s_A+$) exhibited moderate seasonality (Figure F2). In contrast, no seasonality was observed in anchovy spatial distribution (ISO) (Figure F2). Thus, anchovy abundance was higher in the austral summer than in spring (Figure 2.2). Anchovy physiological condition also exhibited marked seasonality (Figure 2.2). Maximum values of body condition (BCF) were found during the austral summer (December) and in autumn (May). In contrast minimum values were found during the austral winter (August). The gonado-somatic index (GSI) exhibited a marked seasonal cycle with a maximum centered on the austral spring (September-December) and a minimum during the austral autumn (May; Figure G1).
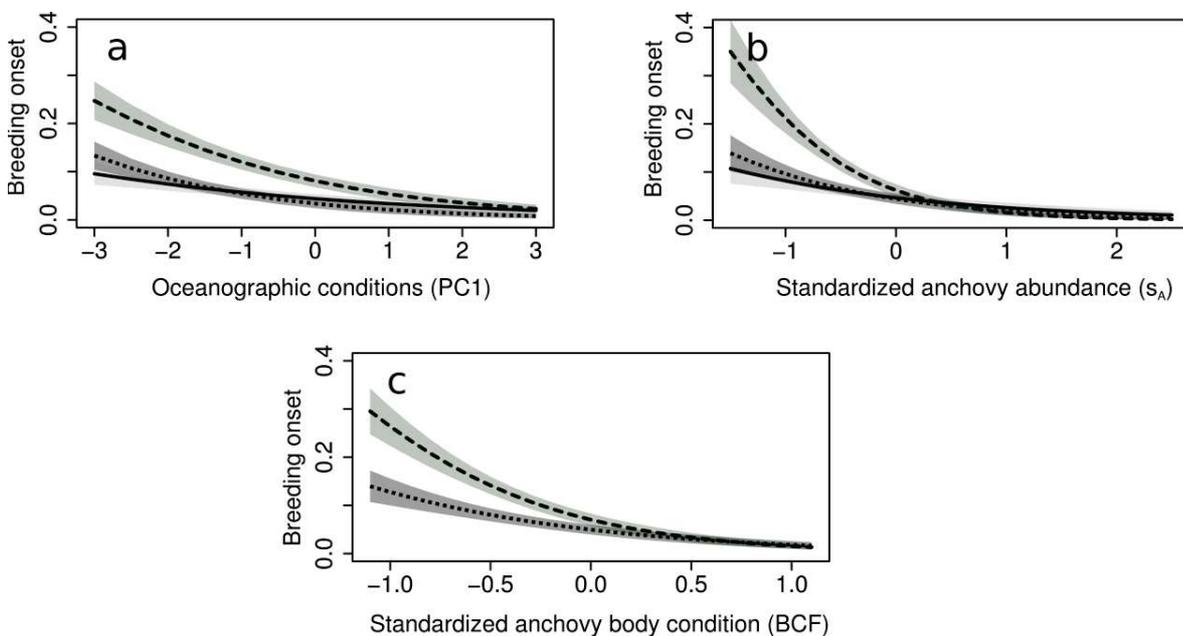
FIG.2.3. Modeled probabilities of breeding onset as a function of (a) oceanographic conditions (PC1 standardized), (b) the standardized regional anchovy abundance ($s_A$), and (c) standardized anchovy body condition factor (BCF) for boobies (dashed lines) and pelicans (dotted thick lines). The functional relationships were obtained from the selected models for each species ($P < 0.005$ and highest $R^2$). Shaded areas represent = 95% confidence intervals.

The regional abundance of anchovy ($s_A$) was negatively related with breeding onset for all three species, and the local abundance of anchovy ($s_A+$) was negatively related to breeding onset in boobies and pelicans (F-tests: all $P < 0.05$, Table 2.1, Table I5). Thus, when $s_A$ and $s_A+$ increased, probabilities

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of breeding onset decreased (Figure 2.3). Anchovy body condition (BCF) had negative effects on breeding onset for boobies and pelicans (*F*-tests: all $P < 0.05$, Table 2.1). Thus, when anchovies were in poorer physiological condition, breeding onset probabilities were higher (Figure 2.3). The gonado-somatic index (GSI) had no significant effect on breeding onset for any of the three species. Covariate models of BCF with a zero and one month lag generally best explained the seasonal variation in breeding onset probabilities (highest $R^2$,Table I6).

## 4. Discussion

Our results provide insights into the possible drivers of seasonal breeding for cormorants, boobies and pelicans in the NHCS. First, we highlighted marked differences in breeding onset between the three species. Whereas breeding onset varied seasonally for all species, cormorants had a protracted breeding season compared to boobies and pelicans. Indeed cormorants appeared to breed most of the year (except during the months of January-March), whereas boobies and pelicans mainly restricted their breeding period to the austral spring. During the austral spring, upwelling strength was intense and associated with cold sea surface temperatures and low surface chlorophyll concentrations. At this time, prey also appeared to be less available (deeper oxycline) and of poorer physiological condition (low body condition factor). Conversely, breeding mainly stopped in summer when upwelling strength was weakest and associated with warmer sea surface temperatures and higher surface chlorophyll concentrations. At this time, prey was more available to seabirds due to a shallower oxycline, with a recovery in its physiological condition (body condition of anchovy higher than during months of breeding onset). Thus, our data suggest that environmental factors had a stronger effect on breeding onset in boobies and pelicans than they did in cormorants (Figure 2.4). Furthermore, this effect seemed to occur within as much as a one-month time lag, as evidenced by the time lag between oceanographic and prey condition measures and the observed effects on breeding timing.

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| | Fall | | Winter | | | Spring | | | Summer | | | Fall |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | May | June | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Apr |
| Cormorant breeding onset | | | | | | | | | | | | |
| Cormorant independence | | | | | | | | | | | | |
| Booby breeding onset | | | | | | | | | | | | |
| Booby independence | | | | | | | | | | | | |
| Pelican breeding onset | | | | | | | | | | | | |
| Pelican independence | | | | | | | | | | | | |
| Upwelling strength | | | | | | | | | | | | |
| Primary production | | | | | | | | | | | | |
| Anchovy availability | | | | | | | | | | | | |
| Anchovy abundance | | | | | | | | | | | | |
| Anchovy condition | | | | | | | | | | | | |
| Reproduction of anchovy | | | | | | | | | | | | |

FIG. 2.4. Schematic representation of the onset (dark gray) and termination (i.e. fledging; light gray) of breeding seasons for cormorants, boobies and pelicans related to seasonal variability in environmental conditions. In the section of seasonal variability in environmental condition dark gray area indicates maximum and light gray area minimum values; 'x' indicates the lack of data.

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## 4.1. Seasonal variability in oceanographic conditions and anchovy availability

In the NHCS, two factors play a major role in the seasonality of ecosystem productivity: the upwelling strength and the pycnocline depth (Echevin *et al.* 2008). Although active throughout the year, the upwelling is strongest during the austral winter and weakest during the summer. However, the strongest phase of the upwelling is also the less productive, so that upwelling strength and primary productivity are negatively related in the NHCS (Echevin *et al.* 2008). This phase opposition, a unique feature of the NHCS in comparison with other EBUEs (Romero *et al.* 2002; Bograd *et al.* 2009), is due to light limitation in winter and a shallower pycnocline depth in spring and summer than in winter (Echevin et al., 2008). The seasonal trend in pycnocline depth is also observed in the oxycline depth (Fig. E1) given the inter-correlation of those two parameters (Bertrand *et al.* 2014). The oxycline is indeed shallower in summer constraining the vertical distribution of anchovy to a thin surface layer easily accessible to seabirds. In winter, the oxycline deepens allowing anchovy to increase their vertical distribution range, thereby reducing their availability to seabirds.

Interestingly, anchovy also varied seasonally in terms of their horizontal distribution. Anchovy biomass close to the coast was higher in summer than in winter (Fig. F2a), most likely due to the arrival of new recruits (Oliveros-Ramos & Peña 2011), and to the distribution of water masses. Indeed, anchovy horizontal habitat range is intimately linked to highly productive, cold coastal waters (Bertrand *et al.* 2004; Swartzman *et al.* 2008), which geographical distribution depends on upwelling intensity. Accordingly, anchovy habitat range is greater in winter (up to 60 km from the coast) than in summer (up to 40 km from the coast) (Swartzman *et al.* 2008).

## 4.2. Effect of nesting habitat characteristics on breeding onset

We found no effect of latitude on breeding onset for our 3 study species, as sometimes documented in seabirds (Wolf *et al.* 2009). This lack of a relationship could be explained by the relatively weak latitudinal differences in oceanographic conditions along the studied region. However, we found a preference for breeding on islands rather than on headlands for all three species, and especially outer islands for pelicans. Until the 1940s, islands were free of terrestrial predators (cats, dogs, foxes) providing safe breeding grounds for seabirds. During the early 1940s, Peruvian authorities began to fence-off coastal headlands in order to provide more nesting space for seabirds thereby enhancing guano production (Vogt 1942). This increase in secured nesting habitats resulted in an increase in the breeding populations of our three study species (Duffy 1983a). Nevertheless, our results show that seabirds still preferred to nest on islands rather than headlands, suggesting the latter may be suboptimal breeding habitat. This is indeed likely to be the case, as over the last two decades human population along the Peruvian coast has increased, and seabirds nesting on headlands have become more susceptible to egg poaching and illegal hunting (AGRORURAL; *personal communication*). In addition, the disturbance of breeding colonies by terrestrial predators may still occur in headlands, since fences are not entirely predator proof.

### 4.3. Seasonal breeding patterns in relation to oceanographic conditions and anchovy availability

The seasonal breeding pattern related to oceanographic and prey conditions described above was more evident for pelicans and boobies than for cormorants. During the study period, cormorants had an extended breeding period lasting for more than half of the year. The ability of cormorant to breed almost year-round may be linked to their feeding strategy. Indeed, while hunting, cormorants actively search for prey by pursuit-diving, and may be less sensitive to seasonal variation in prey availability (Sabarros *et al.* 2012). This hypothesis seems to be confirmed by the observation that, in the NHCS, cormorants may dive as deep as 70 m while foraging (Zavalaga & Paredes 1999), actively searching for their prey over the entire vertical range of the anchovy habitat (Weimerskirch *et al.* 2012). In contrast, boobies and pelicans do no actively seek out prey, but forage by plunging (top 10-m of the water column) or seizing prey items (top 2-m) at the surface (Duffy 1980, Weimerskirch et al. 2012).

For boobies and pelicans, breeding was mostly confined to a restricted period of the year. Our data suggest that optimal oceanographic conditions and food availability conditions did not coincide with egg laying or incubation, but rather with chick fledging. Indeed, during egg laying and incubation, the oxycline was one of the deepest in the year, the upwelling current was strong, and anchovies likely not concentrated near the coast. However, as the season progresses, primary productivity increases, and anchovies likely concentrate near the coast by the time birds are feeding chicks (December). Maxima of primary productivity, abundance, availability and prey condition may thus be optimal when chicks of boobies and pelicans become independent (January-March).

Therefore, we suggest that boobies and pelicans have adjusted their cycle so that chick fledging coincides with periods of high resource quality and availability. Our findings support the hypothesis of an 'optimal breeding time' rather than an 'egg-laying constraint', except that in this particular case, optimal food conditions are matched to support chick fledging rather than chick development as originally proposed by Lack (1968). Optimal resource availability at fledging may maximize juvenile survival by increasing the foraging success of inexperienced young. When compared to adults, foraging success is indeed often lower in juvenile seabirds as they are usually less skillful at capturing prey (Brandt 1984; Daunt *et al.* 2007). Non-exclusively, optimal prey availability after breeding could also be important for adults during molt (Green *et al.* 2009). For most bird species, including seabirds, the timing of molt and breeding are separated because those two activities are energetically expensive (Bridge 2006; Green *et al.* 2009). Unfortunately, we have little information on the duration and timing of molt for the studied species. However, patterns at the family level for cormorants and boobies and at the generic level for pelicans, suggest that the onset of molting flight feathers begins a few weeks after the young reach independence (Schreiber 1980; Bridge 2006).

By contrast, cormorants initiated breeding just after the peak of anchovy abundance in autumn, which may support the idea that those animals might have been at least partially constrained by nutritional requirements for egg laying. This hypothesis is consistent with the fact that cormorants lay the largest clutches of the three species (average clutch size: 3.1 versus 2.5 for boobies and pelicans,

Nelson 2005). On the other hand, the extended breeding period of cormorants also suggests that individuals may be able to adjust breeding timing to maximize juvenile survival as well, as is the case for boobies and pelicans. More detailed studies at the individual level are necessary to evaluate the constraints faced by cormorants to initiate breeding and to tease apart whether cormorants are able to adjust their breeding cycle to meet an optimal breeding window, all while being somewhat energetically constrained during incubation.

### 4.4. Comparison with seasonal breeding in other eastern boundary upwelling ecosystems

Seabird seasonal breeding has been documented in other EBUEs and the underlying mechanisms may differ from the ones highlighted in our study. In the Benguela Upwelling System (South Africa), Cape Gannets (*Morus capensis*) initiate breeding when upwelling strength and primary productivity are maximal. At this time, food availability is high due to the presence of dense shoals of sardines and anchovies spawning near the coast (Sabarros *et al.* 2012). In contrast, at the end of breeding, high mortality is observed in juvenile gannets that migrate from the coast of south west Africa, up the western and eastern coasts of Africa, to tropical waters following shoals of sardines (Broekhuysen, Liversidge & Rand 1961). In this ecosystem breeding timing is most likely constrained by food availability at the beginning of the breeding season. In the California Upwelling System, both winter and summer upwellings are important, but in different ways. For instance, Cassin's auklet (*Ptychoramphus aleuticus*) fledging success is associated with the summer upwelling mode, suggesting an adaptation of the breeding timing to prey availability (Ainley, Spear & Allen 1996; Black *et al.* 2011). However, in the same system, stronger winter upwelling are associated with earlier laying dates for Cassin's auklets and common murres (*Uria aalge*), suggesting that pre-laying nutritional stress may also be critical to those seabirds (Schroeder *et al.* 2009; Black *et al.* 2010; Thompson *et al.* 2012; García-Reyes *et al.* 2013). Finally, in the Southern California Bight (a sub-region of the California Current), the reproductive season, location, and breeding effort of brown pelicans appears to be linked to the availability of food resources before the breeding season (winter) (Anderson & Gress 1983) according to 'Egg-laying constraint' hypothesis. This is not the case for the Peruvian pelican.

The specific nature of the environmental cues used by seabirds to initiate breeding events remains to be determined. In the absence of egg-laying constraints, females may use environmental information available early in the season environment to fine-tune egg production annually (Noordwijk, McCleery & Perrins 1995). For seabirds of EBUEs, possible environmental cues might include changes in sea-surface temperature and/or upwelling intensity related to future prey availability (Frederiksen *et al.* 2004; Schroeder *et al.* 2009). In the NHCS, a low latitude ecosystem, possible environmental cues might also include upwelling activity or ocean surface characteristics, such as water turbulence that is known to create ephemeral oases concentrating marine life from plankton to birds (Bertrand et al. 2014). According to our data, upwelling occurrence and strength could forecast food availability for at least a month after the onset of breeding. Another, more direct, environmental cue for breeding seabirds could also be the onset of anchovy spawning that mainly occurs during the egg-laying period. The timing of anchovy spawning likely forecast anchovy availability later in the in summer and fall when recruits integrate the stock (Oliveros-Ramos & Peña 2011), at the period when most young seabirds

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become independent. These hypotheses offer exciting perspectives to test how environmental cues trigger determine seabird breeding-onset, and to better understand the consequences of interannual variability in environmental conditions on seabird reproduction.

**Acknowledgements**

## 5. Summary of appendix

Appendix A. Summary of the first report on the breeding phenology of guano-producing seabirds and food availability in the NHCS Peruvian ecosystem (adapted from Vogt (1942)).

Appendix B. Approximate duration of the main breeding stages of Peruvian seabirds.

Appendix C. Detailed description of seabird land-based census methodology.

Appendix D. Detailed description of the size of colonies of Peruvian seabirds.

Appendix E. Detailed description of oceanographic data used to build monthly climatologies and later synthesized by principal component analysis (PCA).

Appendix F. Detailed description of acoustic data used to build monthly climatologies of abundance and horizontal distribution of anchovy.

Appendix G. Detailed description of data used to build monthly climatologies of physiological conditions of anchovy.

Appendix H. Equations of the logit link for occupancy model with covariates and ANODEV test used to compare models.

Appendix I. Detailed results of occupancy models for onset and termination of breeding of Peruvian seabirds.

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# *Chapter III: Site-specific adaptation of seasonal breeding of seabirds in a highly dynamic upwelling ecosystem*
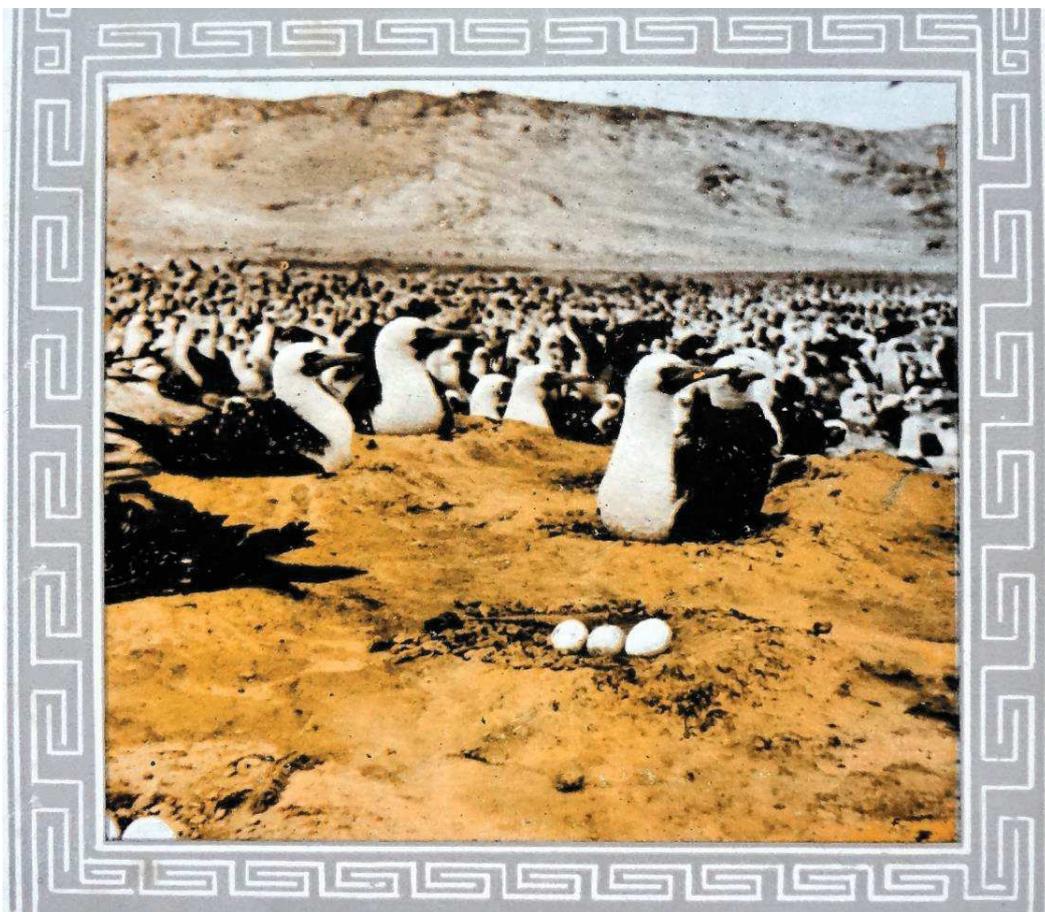
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# *Site-specific adaptation of seasonal breeding of seabirds in a highly dynamic upwelling ecosystem*

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*Abstract*: Adaptation of the timing of breeding to prey abundance and availability is a common strategy in vertebrates to ensure a successful reproduction. Seabirds use proximate factors such as environmental conditions (e.g. latitude, oceanic dynamics) and ultimate factors such as prey availability to adjust their timing. Another factor that may influence the timing of breeding is coloniality and social attraction. These different factors have been studied in the last decades because they are affected by climate change. In this work, we examine the differences in the timing of breeding of three sympatric seabird species (Guanay cormorant, Peruvian booby and Peruvian pelican) in a tropical highly-productive ecosystem (Northern Humboldt Current System). Timing of breeding was evaluated by multiseason occupancy models of the monthly presence/absence of breeders in 30 nesting sites from 2003 to 2014. We classified the site-specific pattern of seasonality with a functional principal component analysis. Finally we related the pattern of breeding seasonality (magnitude and timing) to geographic, local environmental conditions, and social factors. We found differences among nesting sites in the persistence of breeders between seasons and in the timing of breeding. Even though onset of breeding was done in average during late winter and early spring, some nesting sites had onset of breeding earlier, during late autumn and early winter. Earlier breeding were done in larger colonies most of them at lowest latitudes and with high primary production around nesting sites. These results suggest that small scale factors (social attraction, productivity around colonies) rather than large-scale factors (latitude) have more impact on the definition of timing and magnitude of breeding of the three species. Furthermore, we expect that consideration of differences among colonies can also help the management of population, conservancy policies and guano extraction improvement.

*Keywords: Northern Humboldt Current System, Guanay cormorant, Peruvian booby, Peruvian pelican, timing of seasonal breeding, coloniality, latitude, multiseason occupancy model, functional principal component analysis.*

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## 1. Introduction

Breeding at the right time is essential for animals in seasonal climates in order to ensure that the energy demands of reproduction coincide with peak of food availability (Lack 1968; Perrins 1970; Stenseth & Mysterud 2002; Frederiksen *et al.* 2004; Byrd *et al.* 2008). For several decades, phenology (the study of timing of seasonal activities, such as reproduction) has been the subject of an intense research due to its implication in population trends (e.g. Miller-Rushing et al. 2010). Phenology studies are more relevant than ever before, because climate change may generate severe trophic mismatches between supply and demand in food webs (e.g. Cushing 1990; Sydeman & Bograd 2009). In the case of birds, the increased concern about the observed declining trends of several species have called for population modeling approaches (Charmantier & Gienapp 2014) to assess the plasticity of species among the whole range of possible variation of seasonal breeding (Porlier *et al.* 2012; Bourret *et al.* 2015) and also to understand the factors driving differences across a species distribution range (Both *et al.* 2006).

The mechanisms controlling seasonal breeding have been extensively studied in temperate and high latitudes. Latitude was suggested as one of the most important factors shaping the timing of breeding (Baker 1939; Gienapp, Väisänen & Brommer 2010; Gurney *et al.* 2011) because it is representative of several large-scale environmental gradients such as those of photoperiod and temperature. For species with large breeding distributions, it has been proposed that the higher the latitude, the later the breeding (L'Hyver & Millers 1991; Wanless *et al.* 2008). In the same way, the higher the altitude, the later the breeding (Slagsvold 1976). Warmer temperatures were reported to lead to earlier egg laying (Gienapp *et al.* 2010; Jiguet *et al.* 2010). Prey abundance was also proposed as a factor that led birds to breed earlier but also conditioned on latitude, with birds at low latitudes generally exhibiting a greater responsiveness to increase of food (Schoech & Hahn 2008). Other works related the variability of reproduction timing to large-scale changes in environmental conditions such as El Niño events, NAO oscillations and in the last decades, to climate change (Wilson & Arcese 2003; Dunn 2004; Durant *et al.* 2004, 2007).

However, not only large time-space mechanism can control the dynamic of ecosystems. In tropical ecosystems, like the NHCS, it has been shown that mesoscale and sub-mesoscale features (e.g, eddies, fronts) play important role in the ecosystem structuring and functioning (Penven *et al.* 2005; Bertrand *et al.* 2014). Such features may influence the foraging behavior and the displacement of some of the main marine top predators such as seabirds (Hyrenbach *et al.* 2006; Tew Kai *et al.* 2009). Such structures may force seabirds to track down the ecosystem dynamics at finer scales. In that sense, tropical seabirds demonstrate an extraordinary diversity of breeding regimes acquired by the different species and populations to fit with local trophic conditions (Le Corre 2001). In addition, it has been proposed that regulation of breeding, in terms of intensity and onset timing (Bertram *et al.* 2001) should reflect the scale at which seabirds perceive their environment (Frederiksen *et al.* 2004).

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In seabirds, coloniality is also an important aspect that may influence seasonal breeding (e.g. Gochfeld 1983; Oro 2008; Bourret *et al.* 2015). Coloniality is an evolutionary puzzle (Danchin & Wagner 1997) as the trade-off between costs (increased parasites, diseases, competition for food and mates) and benefits (enhanced food finding, reduced predation, habitat and sexual selection) is difficult to evaluate. Yet, social attraction may have evolved as a way of assessing, through a proximate and integrated public information cue, the quality of local environmental conditions (Boulinier & Danchin 1997; Danchin, Boulinier & Massot 1998; Doligez *et al.* 2003). It was shown to be particularly favorable when prey patches are sufficiently large and/or short-lived (Buckley 1997), so that competition for food around the colony (Ashmole 1963), especially in oligotrophic tropical ecosystems, is counterbalanced.

We present here the case of Northern Humboldt current System (NHCS), a low latitude and highly productive upwelling ecosystem with moderate seasonality in its oceanographic conditions yet quite marked seasonality of reproduction for the three most abundant endemic seabird species : the Guanay cormorant (*Phalacrocorax bougainvillii*), the Peruvian booby (*Sula variegata*) and the Peruvian pelican (*Pelecanus thagus*). For the last decade, the three species bred seasonally with an average onset of breeding mainly in austral winter and spring when the availability of prey is lower, and an average ending of reproduction with the fledging of independent juveniles, mainly at the end of summer when availability of prey is maximal (Passuni *et al.*, 2015). We hypothesize that due to the large latitudinal range of this tropical system (6°S-18°S, ≈ 1300 km), one may expect differences in the timing of seasonal breeding and also in the persistence of breeding in nesting sites. Here, our first objective is to describe the variability of breeding seasonality of the three seabird species between the breeding sites in order to provide insights about the ability of seabirds to adapt their timing of breeding to local environmental conditions around the colony. Our second objective is to identify the effects of potential environmental covariates on the site-specific breeding seasonality. The NHCS has a moderate variability at intrannual scale and a high variability at interannual scale (Duffy 1990; Escribano & Hidalgo 2000; Tam *et al.* 2008). High interannual variability makes the environment less predictable in the long term (from year to year) and influences the decision of seabirds of when to breed based on proximate factors related to food availability (Hahn *et al.* 1997). We evaluate the variability of onset of breeding and occupancy of the colony by breeders under the hypothesis that seasonal breeding of seabirds can be influenced by large-scale latitudinal differences, but also by local environmental and geographic effects. We also examine fishery effects as they may limit the local abundance of prey. The NHCS is extremely productive in pelagic forage fish, and the spatial reorganization of the aggregations very rapid (Peraltilla and Bertrand, 2014), what should limit intraspecific competition and Ashmole halo effect around the colonies. Yet, the large-scale fishmeal industrial fishery may be in capacity to create local depletions (Bertrand et al. 2012), what may increase intraspecific competition in seabirds around colonies. Identifying the intraspecific differences in seasonal breeding and the factors leading to such differences between nesting sites help us to (1) understand the plasticity of the breeding of these species (2) understand at which scale the seabirds track the variability of their environment, and (3) to forecast the possible effects of environmental changes on the demography of these species.

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2. **Methodology**

### 2.1. Seabird data and site-specific covariates

Guanay cormorants, Peruvian boobies and Peruvian pelicans occur between 3°S and 38°S of the South American Pacific coast (Nelson 2005; Jeyasingham *et al.* 2013), coinciding with the range of influence of the Humboldt Current System. Most of the breeding sites are located in the NHCS, between 6°S and 14°S (Tovar Serpa *et al.* 1987). Breeding sites consists in arid islands and headlands, all located within the first 20 km from the coast (except for Isla Lobos de Afuera that lies at 60 km from the coast, Table A1).

During the period 2003-2014, 30 historical breeding sites along the Peruvian coast (Figure A1) were monitored on a monthly basis by AGRORURAL (State institution responsible for guano harvesting in seabird colonies). At each breeding site, AGRORURAL had one or two resident wardens in charge of (i) protecting of the breeding sites from human disturbance and predation, and (ii) at the end of each month, realizing a land-based census of the three seabird species. The wardens climbed to the highest point of the site and reported on a standardized map the observed patches of breeders (colonies) and non-breeders (flocks). Seabird individuals were considered as breeders if they were observed incubating eggs, brooding or feeding chicks. Subsequently, wardens converted patch surfaces into abundance using a nest density conversion factor (Passuni *et al* 2015). Since our main interest was the causal relationship between the timing of breeding and environmental conditions, we used information on the monthly presence and absence of seabirds in reproduction to characterize the breeding seasonality.

We used as site-specific covariates, the main parameters that can characterize each breeding site: surface of the breeding site (S, km$^2$), latitude (LAT, °) and nearest distance to the coast (DC, km). The surface of the breeding sites was estimated by AGRORURAL based on maps of the nesting-site that guardians used for monthly land-based census.

### 2.2. Fishery covariates

All three species of seabirds feed mainly on Peruvian anchovy *Engraulis ringens* (Jahncke et al. 2004). Along the Peruvian coast there are ~ 20 major ports where industrial purse seine vessels land anchovy intended for fishmeal and fish oil (Figure A2). The amount of anchovy landed in each port is daily recorded and compiled by the Sea Peruvian Institute (IMARPE). On a spatial point of view, the main fishing grounds and processing plants are localized between latitudes 9°S and 11°S, yet the fishery may redistribute quickly along the entire coast to adapt to drastic changes in anchovy distribution. On a temporal point of view, the fishing seasons overlaps with the seabird breeding period (Bertrand *et al.* 2012). In the north-central stock anchovy area (4°S to 15°S), which hosts the highest biomass of

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anchovy in the NHCS (Arias Schreiber 2012), the main fishing season (November-December) coincides with the average onset of breeding of seabirds. A complementary fishing period during February-April coincides with chick rearing and independence of young. The north-center fisheries activities encompass the location of most of the seabird nesting sites (Figure A2). For the southern stock anchovy fishery (15°S to 18°S), landings are made throughout the year (Diaz *et al.* 2010; Arias Schreiber 2012). Even in such ecosystem, where anchovy is particularly abundant, it was shown that an intensive fishery can locally deplete anchovy stocks and affect seabird foraging (Bertrand *et al.* 2012). That was the case in particular before 2009, when the anchovy fleet was suffering from ~300% overcapacity (Fréon *et al.* 2008), and when a harsh 'race for fish' conducted to fulfill the global quota in less than 50 days. Consequently, we used anchovy landings within a 100km-radius around each breeding site as a proxy of the local fishing pressure. For each breeding site, landings were cumulated for a year and averaged over 2003 – 2014 (LA100, MT). We also included the distance between each breeding site and the nearest port within a 100km-radius (DnP, km).

## 2.3. Seabird covariates

We used as covariates of social attraction the specific abundance for the three species (AbC, AbB and AbP respectively) in each nesting site. The abundance of seabirds was estimated as the average among year from 2003 to 2014 of the annual maximum number of and then categorized into 3 classes of abundance: [0-50[, [50-100 000[ and [100 000-300 000] for cormorants and boobies and [0-2 000[, [2 000-10 000[ and [10 000-50 000] for pelicans. We categorized the size of colony in large classes to avoid the bias of counts (see. Passuni et al. 2015).

## 2.4. Oceanographic conditions

We included four covariates to describe the local oceanographic conditions around the breeding sites: Chlorophyll-a concentrations (Chlo, mg m$^{-3}$), Sea Surface Temperatures (SST, °C), Upwelling Index (UI, m$^3$ s 100 m of coastline) and depth where dissolved oxygen equals 2 ml l$^{-1}$ (Z$_{2ml}$, m).

Chlo and SST were obtained from the MODIS satellite (http://oceancolor.gsfc.nasa.gov/) from July 2002 to December 2012, with a 4×4 km$^2$ spatial resolution and 8-day temporal resolution. UI were obtained from wind speed components produced by QuikSCAT (http://podaac.jpl.nasa.gov/ datasetlist?ids=Platform&values=QuikSCAT) from July 1999 to November 2009 with a 0.5°×0.5° spatial resolution and 8-day temporal resolution. Z$_{2ml}$ were calculated from vertical profiles of dissolved oxygen concentrations acquired from research vessels of the Instituto del Mar del Peru (IMARPE). We used the depth of 2ml l of oxygen because it is associated with the vertical limit of anchovy distribution (Bertrand *et al.* 2010).

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For each covariate and at each nesting site a climatology profile (monthly averages overall years) was computed using data within a 100km-radius around each colony from 2002 to 2012 for Chlo and SST, from 1999 to 2009 for UI, and from 1960 to 2010 for Z2ml. The range of 100km encompassed the maximum-recorded foraging ranges of the three species during breeding: ≈63 km for cormorants (S. Bertrand, unpublished data), ≈90 km for boobies and ≈83 km for pelicans (Zavalaga *et al.* 2011; Bertrand *et al.* 2012).

### 2.5. Occupancy modelling and functional data analysis

The first step consisted in modeling the seasonal breeding of seabirds through multiseason occupancy model (MacKenzie *et al.* 2005). We used presence absence of breeders, in each nesting sites ($j$=1,…, 30), to model the monthly ($t$=1, …, 12) probability of onset ($\gamma_{j,t}$) and termination of breeding ($\varepsilon_{j,t}$) event. A dependent parameter of $\gamma$ and $\varepsilon$ dynamic process was also estimated to represent the duration of seasonal breeding ($\psi_{j,t}$). Probability of onset of breeding events $\left(\gamma_{j,t-1}\right)$ was defined as the probability that a site $j$ unoccupied by breeders in month $t$-1 was occupied by breeders in month $t$. Probability of termination of breeding events $\left(\varepsilon_{j,t-1}\right)$ was defined as the probability that a site $j$ occupied by breeders in month $t$-1 was unoccupied by breeders in month $t$. Occupancy probability of a breeding site ($\psi_{j,t}$) was defined as the probability of presence of breeders. We assumed that probability of detection was equal to 1 given the conspicuousness of colonies, the absence of vegetation and the permanent presence of one or two wardens. Occupancy models were fitted using a Bayesian approach with JAGS (Plummer 2003) through jagsUI (Kellner 2015) in R software (R Development Core Team 3.1.3). We used informatives prior that comes from the mean and standard deviation of onset and extinction calculated in the chapter II and corresponded to the publication Passuni *et al.*, 2016 (TableS2, Chapter IV). We used 4 Markov chains with 100 000 iterations each one, 1000 iterations to adapt and discarded the first 50 000 as burning. We used a measure of model fit based on 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. Finally, we did not use probabilities of termination of breeding ($\varepsilon_i$) because these estimates represented desertion of breeding sites due to both independence of young or abandon of nests due to environmental factors such as shortage of prey which may mask the breeding seasonality we aimed to describe.

The second step consisted in comparing the seasonal breeding ($\gamma_{j,t}$ and $\psi_{j,t}$) between nesting sites. Seasonal variation of $\gamma_{j,t}$ and $\psi_{j,t}$ in nesting sites were represented by a set of curves because it was issued from observations in a range of time ($t$=1,…,12). Therefore, we used functional data analysis (FDA) to explore and classify seasonality curves as a whole (shape, amplitude) between nesting sites. FDA is one of the most powerful and reliable method to explore and analyze curves (Ramsay & Silverman 1997). FDA is still under development yet its applications have been quickly expanding during recent years in ecology (Bjornstad *et al.* 1998; Bouveyron & Jacques 2011; Embling *et al.* 2012;

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Hurley *et al.* 2014; Di Salvo, Ruggieri & Plaia 2015) due to its performance to deal with multivariate time series (Ramsay & Silverman 2005). FDA methods consider that a curve is a function by assuming that the frequency of data observation is fine enough to consider the data as an observation of the continuous family $X = \{X(t); t \in (tmin, tmax)\}$. In our case we are interested in representing the variability of the seasonal breeding curves $\{X_1(t), \dots, X_{30}(t)\}$ into a function space of reduced dimension. Functional principal component analysis (FPCA) is the tool used to search for the dominant modes of variation in seasonality curves. The objective of FPCA, similarly to standard principal component analysis, is to find a small set of orthogonal functions $\{ui, i = 1, \dots, p\}$ whose linear combination $X_j(t) \approx \sum_{k=1}^{p} \beta_{jk} u_k(t)$ allows synthetizing the variability of the original curve set (Bjornstad *et al.* 1998) (see details in Appendix B).

We kept the scores ($\beta_{jk}$) of the first two functional principal components that summarized most of the source of variation within the functional data. Principal component scores are helpful in interpreting the nature of the variation identified by the FPCA, and can be used as variables into a subsequent more conventional multivariate analysis (Ramsay & Silverman 1997). We used the same procedure of FPCA for oceanographic covariates (SST, Chlo, UI and $Z_{2ml}$), and kept the scores of the first two principal components that summarized most of the source of variation within the functional data. We also explored data before FCA by mean and outlier detection. We used exploratory functional data analysis implemented in the library fda.usc of the R software (Febrero-Bande & Oviedo de la Fuente 2012). For calculating the outliers, we used a trimmed mean of 0.5 and 1000 boostraping in the library fda.usc in R (Appendix B).

In the third step, we regressed FPC1 and FPC2 scores of γ and ψ as dependent variables that summarized the spatial pattern of timing of breeding against site-specific covariates (S, DC, LAT), seabird covariates (AbC, AbB, AbP), fisheries covariates (DnP, NP100, LA100), and FPC1 and FPC2 scores of oceanographic seasonal covariates (SSTfpc1, SSTfpc2, Chlofpc1, Chlofpc2, UIfpc1, UIfpc2, $Z_{2ml}$fpc1 and $Z_{2ml}$fpc2) using a random forest regression model. A random forest model was used instead of conventional regression models because of its better performance to detect non-linear interaction effects, its lower sensitivity to small sample size and multicolinearity problems, and because of the large number of covariates (Cutler *et al.* 2007). Although random forest is less sensitive to multicollinear problems we performed a correlation test to identified cases of flagrant correlation.

We used the random forest algorithm implemented in the library randomForest in R.3.2.2 (see details in Appendix C). We build 10 000 trees for each random forest, and at each node split were used one third of the predictor variables. The importance of each variable was assessed by the prediction error on the out-of-bag portion of the data (%IncMSE). The significance of variable importance and correction of bias for continuous variables were calculated by the PIMP procedure which contrasted original prediction to prediction done with the response variable permuted (Altmann *et al.* 2010). We used 1 000 permutation of variable response. We assessed the significance of variables through a *P*-value ≤ 0.05 and corrected the *P*-value at a nominal α level through the two-stage Benjamini- Hochberg procedure for multiple testing (Benjamini, Krieger & Yekutieli 2006). The Benjamini–Hochberg

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procedure is powerful under the assumption of positively dependent test. We used this procedure implemented in the library multtest in R with a nominal $\alpha \leq 0.05$.

## 3. Results

### 3.1. Site specific variables

Even though there were flocks of seabirds at the 30 locations historically monitored, we identified only 25 active nesting sites for cormorants, 27 sites for boobies and 23 sites for pelicans during the study period. The three species shared most of the breeding sites (19) and only four sites had only one breeding species (Figure A1). Most of the active breeding sites were islands and only 7 were headlands (Table A1). Potential surface of nesting sites (S) were in average 112.6 h ± 280.0 h, with headlands (101.0 h ± 39.6 h) larger than islands (49.3 h ± 61.1 h). Most of the nesting sites for the three species were islands localized near to the coast (9.2 ± 12.3 km).

### 3.2. Seabird abundance at breeding sites

In terms of categorical abundance, the largest breeding sites for cormorants and boobies (100 000 – 300 000 breeders) were located between 8°S to 16°S. For pelicans, the largest breeding sites (10 000- 50 000 breeders) were located between 6°S to 10°S (Table A1). In general abundances of the three species were positively yet moderately correlated (Figure A4).

### 3.3. Oceanographic conditions and anchovy fishery covariates

Seasonality of SST and Chlo described a minimum in winter (≈17°C August-October; ≈ 2 mg m$^{-3}$ June to September) and a maximum in spring and summer for Chlo (≈ 6 mg m$^{-3}$ November-April) and summer for SST (≈22°C January to March). By contrast $Z_{2ml}$ and UI had their minimum in summer (<100 December-March; <35 m December-April) and maximum in winter / spring (>150 June-October; ≈40 m July-October) (Figure D2).

This average pattern encloses differences between breeding sites related to the magnitude and timing of the seasonal cycle of the four oceanographic covariates. These differences were well described by the two first functional principal components (FPC >93%). In general, the first FPC of each oceanographic covariate was related to the magnitude of maximum and/or minimum pic, and explained from 66% to 87% of the variability (Table 3.1). The second FPC of each oceanographic covariate explained 6% to 28% of the variability and its interpretation differed between oceanographic variables (Table 3.1, Figures 3.1 and 3.2). $SST_{FPC2}$ described the difference in decrease of SST during autumn and winter and timing of minimal values. For some breeding sites SST decreased steadily during autumn and reached a minimum from July to September, whereas at other sites the decrease occurred during

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autumn but with a slightly increase of SST during June-July and the minimum was only reached in August-September (Figure 3.1). Chlo$_{FPC2}$ had a lower percentage of variance explained and there were only slight differences between breeding sites in the magnitude of minimum concentration during winter (Figure 3.1, Table 3.1). UI $_{FPC2}$ separated groups of sites by their timing of maximal peak, one group of sites with a maximum from May to September and the other group with one peak from August to September (Figure 3.2). Z2ml$_{FPC2}$ separated groups of breeding sites by their timing of shallowest oxycline. Some sites had shallower oxycline from March to July and others from October to February (Figure 3.2).

The largest landings of anchovy were in the port of Chimbote (>1 200 000 T per year) followed by Chicama, Callao, Chancay and Pisco (800 000 – 1 200 000 T.y$^{-1}$) (Appendix A). Most of the ports are located near northern nesting sites.
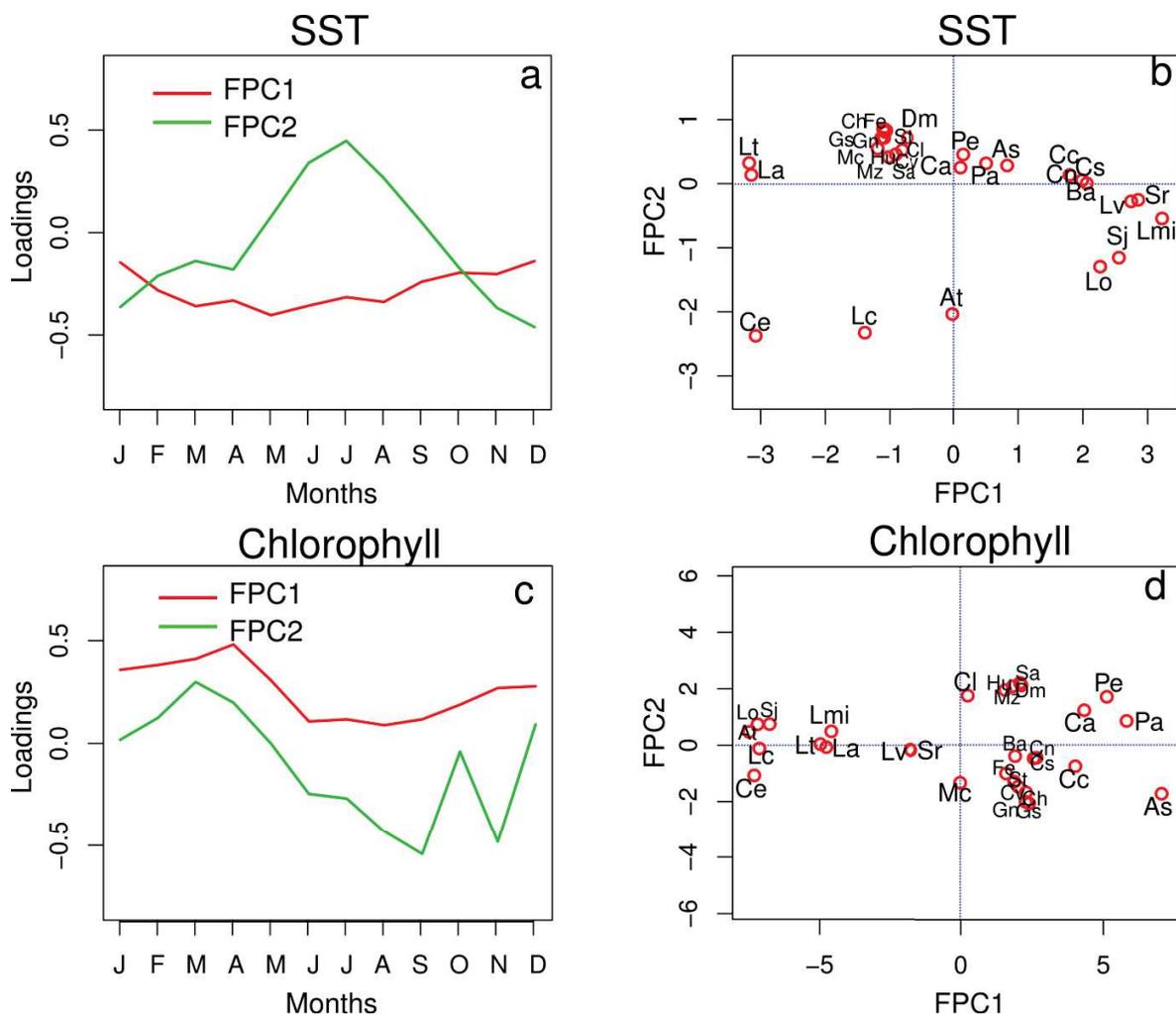


Figure 3.1. Functional Principal components of SST and Chlorophyll. Loadings (a and c) were represented on the left and the bivariate plot of scores of each colony for FPC1 and FPC2 (b and d) were represented on the right. Extended names of the nesting sites are described in Appendix A.
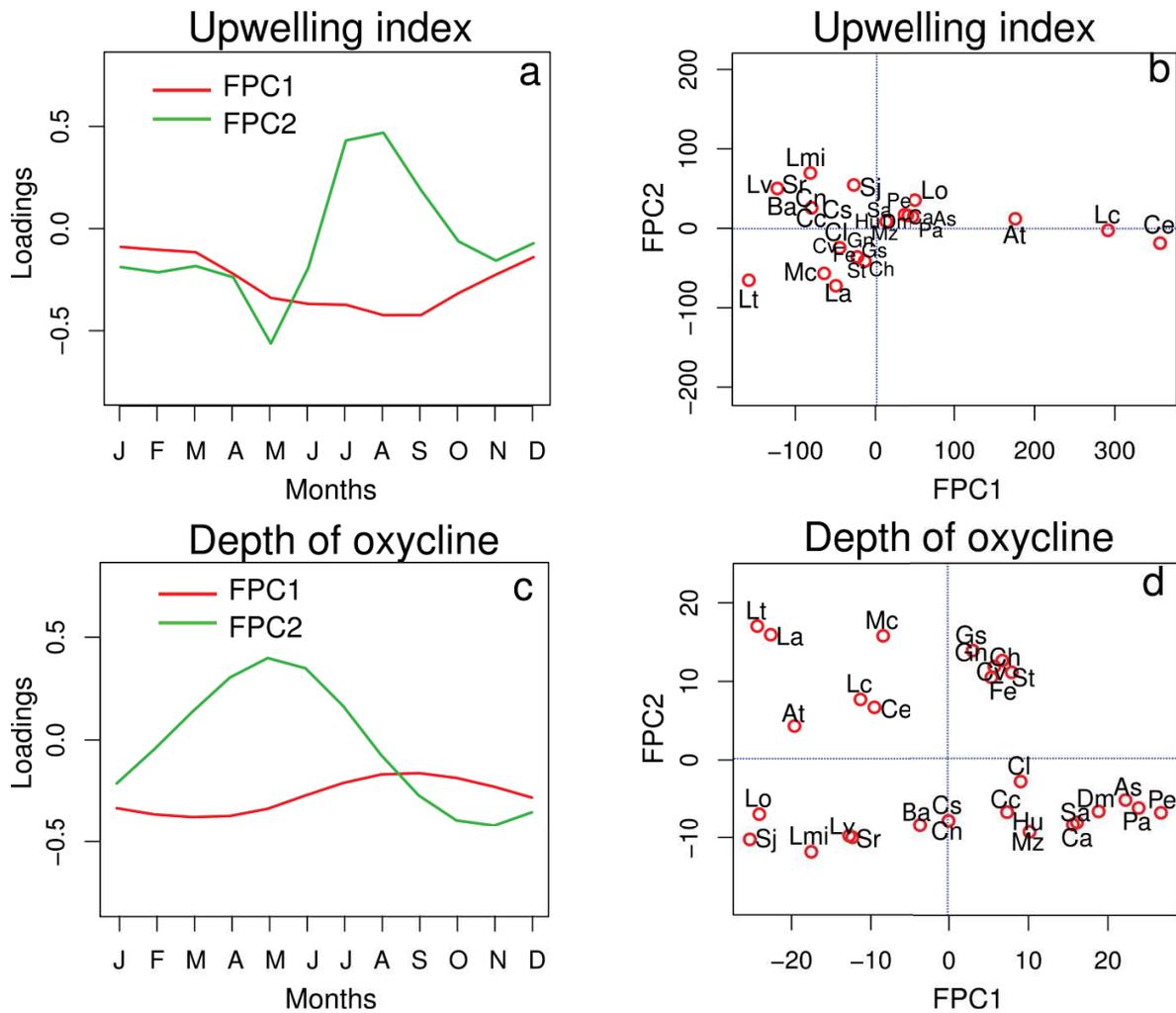
Figure 3.2. Functional Principal components of Upwelling index and Depth of oxycline. Loadings (a and c) were represented on the left and the bivariate plot of scores of each colony for FPC1 and FPC2 (b and d) were represented on the right. Extended names of the nesting sites are described in Appendix A.

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Table 3.1. Results of FPCA for onset and occupancy for each seabird and oceanographic conditions.

| Variables | Parameters | FPCA | %Explained Variance | Interpretation |
|---|---|---|---|---|
| Cormorant | Onset | $C\gamma_{FPC1}$ | 45.37 | Onset in late autumn and winter vs spring and early summer |
| | | $C\gamma_{FP2}$ | 25.67 | Magnitude of the timing of onset in spring/summer |
| | Occupancy | $C\psi_{FPC1}$ | 89.98 | Magnitude in general |
| | | $C\psi_{FP2}$ | 5.40 | Occupancy winter/spring vs spring/summer |
| Booby | Onset | $B\gamma_{FPC1}$ | 46.19 | Magnitude in general |
| | | $B\gamma_{FP2}$ | 20.55 | Onset in late autumn and winter vs late winter and spring |
| | Occupancy | $B\psi_{FPC1}$ | 87.01 | Magnitude in general |
| | | $B\psi_{FP2}$ | 5.87 | Occupancy winter/summer vs spring/summer |
| Pelican | Onset | $P\gamma_{FPC1}$ | 39.29 | Magnitude in general |
| | | $P\gamma_{FP2}$ | 30.52 | Onset with one or two pics in winter and summer vs spring and early summer |
| | Occupancy | $P\psi_{FPC1}$ | 84.47 | Magnitude in general |
| | | $P\psi_{FP2}$ | 6.30 | Occupancy in winter/spring/summer vs spring/summer |
| SST | | $SST_{FPC1}$ | 71.54 | Magnitude of pic maximal (<22°C vs >22°C) and pic minimal (<17°C vs >17°C) |
| | | $SST_{FPC2}$ | 25.34 | Timing of minimal pic August-Septembre vs July-Septembre |
| Chlorophyll | | $Chlo_{FPC1}$ | 87.05 | Magnitude of pic maximal (< 6 mg m$^{-3}$ vs > 6 mg m$^{-3}$) |
| | | $Chlo_{FPC2}$ | 6.66 | Magnitude of pic minimal ≈4 mg m$^{-3}$ vs ≈2 mg m$^{-3}$ |
| Upwelling index | | $UI_{FPC1}$ | 85.94 | Magnitude of maximum (<200 vs >200) |
| | | $UI_{FPC2}$ | 10.12 | Timing of pics maximal |
| Z2ml | | $Z2ml_{FPC1}$ | 66.16 | Magnitude of depth maximal (<45m vs >45m) |
| | | $Z2ml_{FPC2}$ | 28.24 | Timing of shallowest oxycline |

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### 3.4. General pattern of onset and occupancy of breeding

At a first glance, curves of seasonal breeding by nesting sites for the three species were different in magnitude and timing (Figure D1). In general, the functional mean of onset of breeding for the three species was larger than zero from late autumn to spring (May to December for cormorants and boobies and July to January for pelicans, Figure D2). The functional mean of occupancy was lower than zero during autumn ($\psi \approx 0.2$) for cormorants, and autumn and winter ($\psi \approx 0.2$) and for boobies and pelicans. Although several curves differed from the functional mean for the three species in onset and occupancy, only one curve with the highest probabilities of onset of breeding of boobies and occupancy of pelicans was identified as outlier (Figure D2).

### 3.5. Differences of onset and occupancy of breeding between colonies

For the three species the onset and occupancy of breeding were well represented by the two first FPC, which explained almost 70% of the variability for onset (FPC1 $\approx$40%, FPC2 $\approx$30%) and 90% for occupancy (FPC1$\approx$85%, FPC2$\approx$6%). For onset and occupancy, most of the FPC1 for the three species represented the differences in magnitude of probabilities during winter to summer between nesting sites (Table 3.1). The exception was FPC1 of onset of cormorants (C$\gamma_{FPC1}$) that represented differences in timing of onset (Table 3.1). Most of FPC2 represented the difference of timing of onset and occupancy between colonies (Table 3.1).

The C$\gamma_{FPC1}$ separated group of colonies by timing of onset. Onset of breeding in cormorants occurred during late autumn and winter (May-September) or spring / early summer (September-January) (Figure 3.3). Nesting sites where cormorants started breeding early during autumn-winter were characterized by larger abundance of conspecifics, Chlo > 4mg m$^{-3}$ (Chlo$_{FPC2}$), minimum SST during August-September (SST$_{FPC2}$), shallower oxycline Z$_{2mlFPC1}$<45 m) and greater DC (Table 3.2, Figure E1). C$\gamma_{FPC2}$ separated sites with marked onset during spring and summer from sites with a lower or no onset in spring and summer (Figure 3.3, Table 3.1). None of the covariates used explained this specific difference in the timing of onset (Table 3.2).

For occupancy of cormorants, C$\psi_{FPC1}$ separated breeding sites by the magnitude of their occupancy probabilities, independently of the timing (Figure 3.3). Higher magnitudes of occupancy were related to larger abundance of cormorants (AbC), Chlo > 4mg m$^{-3}$, minimum SST during August-September (SST$_{FPC2}$), oxycline < 45m (Z2ml$_{FPC1}$) and higher UI extended during May and September (UI$_{FPC2}$) (Table 3.2 and Figure E2). C$\psi_{FPC2}$ separated sites by timing of occupancy. Cormorants bred at some sites mainly during winter and spring and in other sites mainly during spring and summer (Figure 3.3 and Table 3.1). From the covariates used, only DC described, yet poorly, these differences in timing (Table 3.2).

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Table 3.2. Results of regression models performed with random forest. Regression models were done between timing and magnitude of onset and occupancy of breeders for the three species as dependent variables and site-specific, oceanographic and prey covariates. Variables presented were significant (P-value>0.05, FDR>0.1).

| Parameter | Variability | %VE all var. | Significant important variables | %VE only significant var. |
|---|---|---|---|---|
| $C\gamma_{FPC1}$ | Onset in late autumn and winter vs spring and early summer | 37.66 | AbC, Chlo $_{FPC2}$, DC, SST $_{FPC2}$ | 43.86 |
| $C\gamma_{FP2}$ | Magnitude of the timing of onset in spring/summer | -18.95 | None of the variables used were significant | |
| $C\psi_{FPC1}$ | Magnitude in general | 59.27 | AbC, SST $_{FPC2}$, Chlo $_{FPC2}$, Z2ml $_{FPC1}$ | 58.89 |
| $C\psi_{FP2}$ | Occupancy winter/spring vs spring/summer | 20.38 | DC | 4.34 |
| $B\gamma_{FPC1}$ | Magnitude in general | 25.98 | DC, LA100, Lat, I-H, SST$_{FPC2}$,UI $_{FPC1}$, DNP | 35.56 |
| $B\gamma_{FP2}$ | Onset in late autumn and winter vs late winter and spring | 8.8 | Lat, AbB | 33.15 |
| $B\psi_{FPC1}$ | Magnitude in general | 32.51 | DC, AbB, SST $_{FPC2}$, Lat, UI $_{FPC1}$, I/H, Z2ml $_{FPC2}$ | 44.58 |
| $B\psi_{FP2}$ | Occupancy winter/summer vs spring/summer | 30.92 | DC, LA100, Lat, UI$_{FPC1}$, I/H | 46.5 |
| $P\gamma_{FPC1}$ | Magnitude in general | 67.02 | AbP, SST $_{FPC2}$, Chlo $_{FPC1}$, Lat | 80.79 |
| $P\gamma_{FP2}$ | Onset with one or two pics in winter and summer vs spring and early summer | -4.25 | None of the variables used were significant | |
| $P\psi_{FPC1}$ | Magnitude in general | 76.37 | AbP, SST$_{FPC2}$, Lat, Chlo $_{FPC1}$, Z2ml$_{FPC1}$ | 87.8 |
| $P\psi_{FP2}$ | Occupancy in winter/spring/summer vs spring/summer | 13.01 | Lat, AbP, DC | 16.69 |
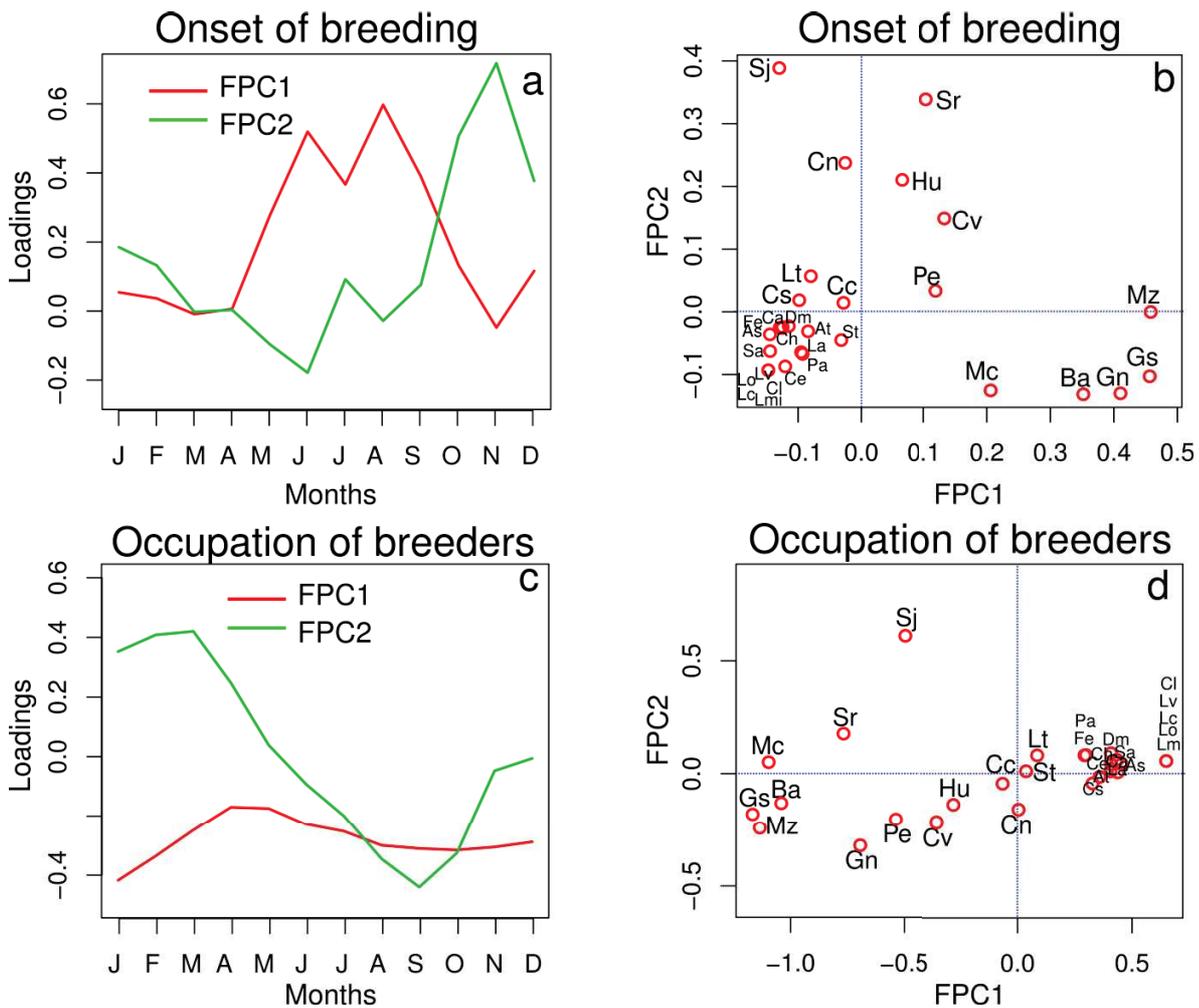
Figure 3.3. Functional Principal components of onset and occupancy of cormorant. Loadings of timing and magnitude of onset of breeding of cormorant were represented on the left (a and c) and the bivariate plot of scores of each colony for FPC1 and FPC2 (b and d) were represented on the right. Extended names of the nesting sites are described in Appendix A.

For breeding onset of boobies, $B\gamma_{FPC1}$ separated sites by their magnitude independently of their timing (Figure 3.4). Higher magnitudes of onset were related to islands (I/H) within 5-20 km off the coast (DC), lower latitudes (<10°S), ports that landed ≈1.5 MT.y$^{-1}$ of anchovy and higher UI (UI$_{FPC1}$) (Table 3.2, Figure E3). $B\gamma_{FPC2}$ separated nesting sites by timing of onset of breeding. At some sites onset of breeding occurred during late autumn and winter (May-September) whereas at others onset occurred during late winter and spring (August-December). Onset during autumn-winter could be explained by larger colonies of boobies (AbB) and higher latitudes (Lat < -9°S) (Table 3.2, Figure E3).

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For occupancy of boobies, Bψ$_{FPC1}$ separated sites by the magnitude of breeding probability independently of its timing (Figure 3.4). Sites with higher occupancy had greater abundance of boobies (AbB), were localized at lower latitudes (Lat>-14°S) and were islands 5 - 20km from the coast (DC). Sites with higher occupancy had minimum SST only during August-September (SST$_{FPC2}$), greater upwelling index in general (UI$_{FPC1}$) and a shallower oxycline during October to February (Z2ml$_{FPC2}$). Bψ$_{FPC2}$ separated sites by the timing of occupancy. Boobies breed at some sites mainly during winter to summer and at other sites during spring and summer. Sites with longest occupancy (winter to summer) were mostly islands localized at lower latitudes (Lat >-14°S) and > 5 km from the coast (DC). Sites with longest occupancy had also a higher upwelling index (UI$_{FPC1}$, Figure E4).
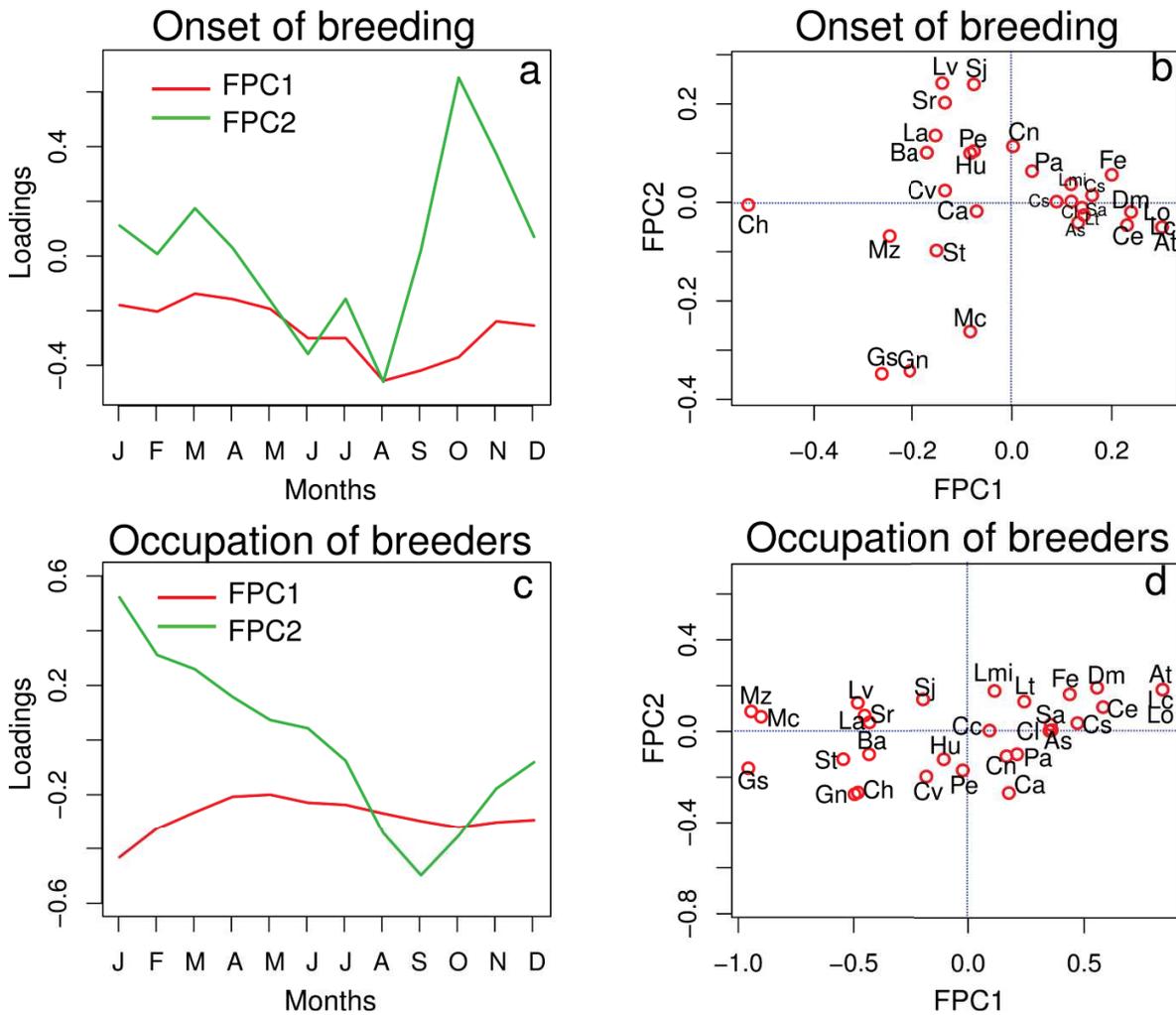


Figure 3.4. Functional Principal components of onset and occupancy of booby. Loadings of timing and magnitude of onset of breeding of pelican were represented on the left (a and c) and the bivariate plot of scores of each colony for FPC1 and FPC2 (b and d) were represented on the right. Extended names of the nesting sites are described in Appendix A.

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For the breeding of pelicans, $P\gamma_{FPC1}$ separated sites by the magnitude of onset independently of its timing (Figure 3.5). Sites with higher magnitudes of onset had greater abundance of pelicans (AbP), had larger surface (S) and were localized at lower latitudes (Lat>-9°S). Sites with higher onset had minimum SST only during August-September ($SST_{FPC2}$) and Chlo > 4mg m$^{-3}$ ($Chlo_{FPC1}$). $P\gamma_{FPC2}$ separated sites by timing of onset of breeding. At some sites, onset of breeding occurred during winter and summer and at other sites during spring and early summer. None of the covariates used explained this difference in the timing of onset (Table 3.2, Figure E4).

 For occupancy of pelicans, $P\psi_{FPC1}$ separated site by the magnitude of probability independently of its timing (Figure 3.5). Sites with higher occupancy had greater abundance of pelicans (AbP) and were localized at lower latitudes (Lat >-10°S). Sites with higher occupancy had minimum SST during August-September ($SST_{FPC2}$), oxycline < 45m ($Z2ml_{FPC1}$) and Chlo > 4mg m$^{-3}$ ($Chlo_{FPC1}$). $P\psi_{FPC2}$ separated sites by the timing of occupancy. Pelicans breed in some sites mainly during winter to summer and in others during spring and summer. Sites with a longer occupancy (winter to summer) had higher abundances of pelicans (AbP) and were localized at lower latitudes (Lat >-14°S) and DC > 5km from the coast (Table 3.2, Figure E5).

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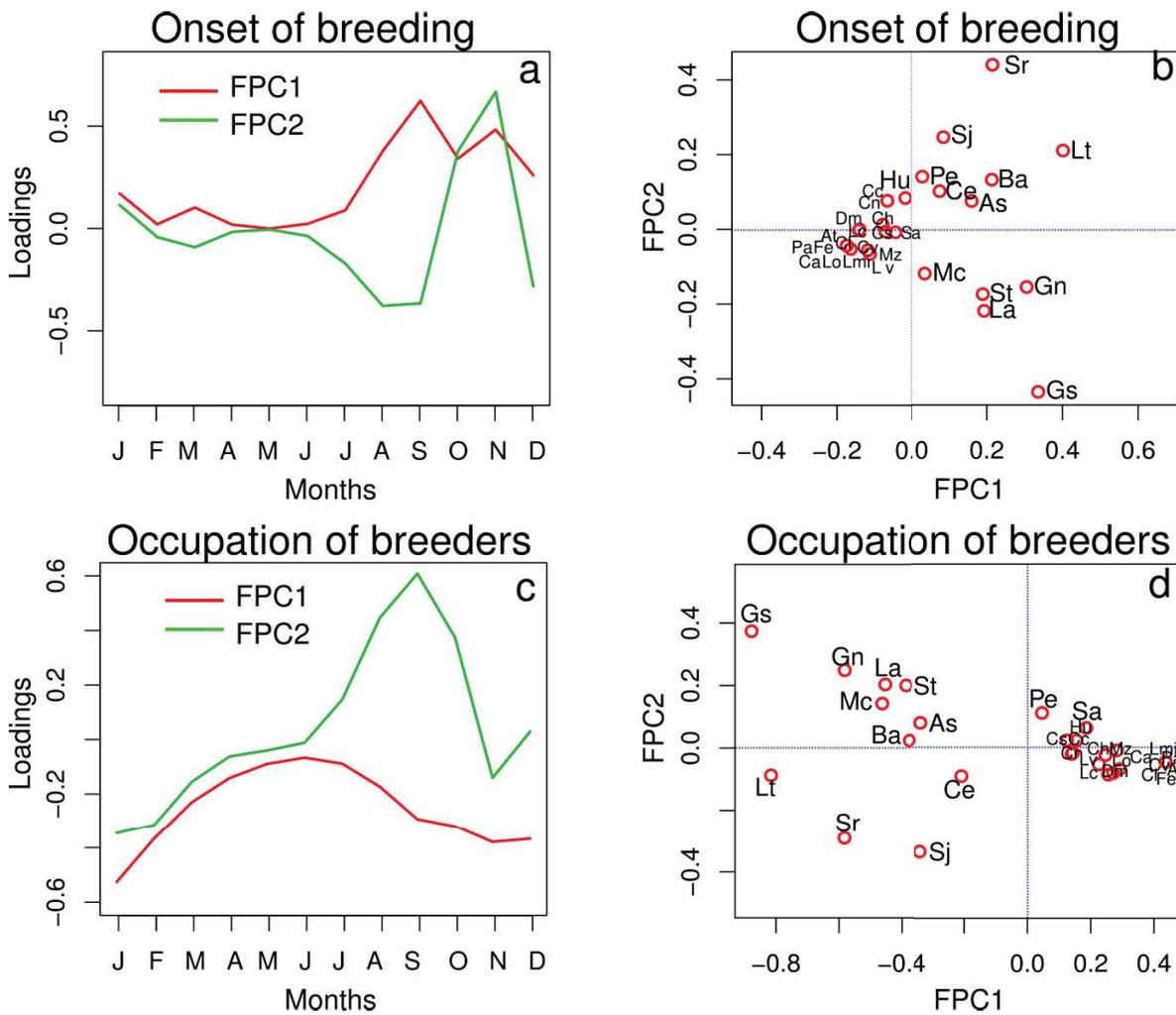


Figure 3.5. Functional Principal components of onset and occupancy of pelican. Loadings of timing and magnitude of onset of breeding of pelican were represented on the left (a and c) and the bivariate plot of scores of each colony for FPC1 and FPC2 (b and d) were represented on the right. Extended names of the nesting sites are described in Appendix A.

## 4. Discussion

### 4.1. Differences in breeding seasonality between sites

In average, Guanay cormorants, Peruvian boobies and Peruvian pelicans initiated breeding in austral winter and spring when prey availability was low and continued breeding until summer when the independence of the young coincided with the highest availability of prey (Passuni *et al.* 2016). However, our results revealed differences between breeding sites in the magnitude and timing of the breeding events. By investigating seasonal breeding at the scale of breeding sites we found that the

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highest differences between nesting sites were associated to the magnitude of onset and occupancy of breeding, which explained most of the variability between sites. Variability in the magnitude of onset and occupancy of breeders between sites can be interpreted as variability in the persistence of breeding birds from year to year.

The second main source of variation between sites was the timing of onset of breeding. Our results showed that the timing of breeding clearly differed between sites. Depending on breeding sites, cormorants, boobies and pelicans can begin breeding early, in late autumn and winter (May to September), or later during spring and early summer (September to January). An early onset of breeding is often associated in seabirds to larger clutch sizes and more surviving offspring (Lack 1968). In case of seabirds living in the NHCS, early onset of breeding can have positive effects in the survival of young and their posterior recruitment. We suggest that if abundance of prey is in average high around breeding sites, parents may fulfill the energy requirement to begin reproduction and brood chicks in autumn-winter when average food availability is still the lowest – yet non limitative - in the year. The independence of young can then be done during spring when anchovy availability is still not the maximal yet anchovy body condition is the best. Juveniles continue to improve their skills of foraging prey when anchovy availability increase in summer then first year young can migrate or explore other nesting sites in better conditions during autumn (Jordan & Cabrera 1960). For juveniles, the increase of food availability balance their inexperience to forage (Haug *et al.* 2015) increasing their probability of survival.

The higher flexibility of cormorants in their timing of breeding compared to the other two species may be explained by their greater diving ability allowing them to forage in a higher range of the water column (max. 74m, Zavalaga and Paredes 1999), lowering the energetic constraints of egg formation and chick brooding.

The variability in timing of onset and occupancy of breeding may be interpreted from two perspectives: i) the high plasticity of seabirds to adapt breeding seasonality to the local environmental conditions, ii) an adaptation to local conditions in evolutionary terms.

We propose that here, differences in timing of breeding is more conceivable as a higher plasticity than an evolutionary adaptation of the seabirds. First, because timing of seasonal breeding is frequently considered as a phenotypic plastic trait that allow birds more rapid changes regarding environmental changes (Charmantier & Gienapp 2014). Phenotypic plasticity moreover has been demonstrated as a crucial feature for other species facing the high multi-scale variability of the NHCS (Bertrand *et al.* 2004; Gutiérrez *et al.* 2008). Second because an evolutional adaptation would mean that seasonal breeding is a heritable trait from differentiated populations among nesting sites. However, there is no evidence of genetic differentiation between populations but of a high gene flow (Taylor *et al.* 2011; Jeyasingham *et al.* 2013).

### 4.2. Factors affecting seasonal breeding between sites

In the NHCS, we found that the magnitude and timing of breeding depended mainly on conspecific abundance, dynamic oceanographic factors and geographic covariates. Also for boobies magnitude and timing of breeding depended on anchovy abundance (reflected through fishery landings) around breeding sites (Figure 3.6).

| | Timing | | Magnitude | |
|---|---|---|---|---|
| | **Early** | **Later** | **Higher** | **Lower** |
| **Cormorant** | Onset(late Autum-Winter) Occupancy(Winter-Summer) | Onset(Spring-early Summer) Occupancy(Spring-Summer) | Occupancy | Occupancy |
| | ↑AbC, ↓Chlo in winter, ↑DC, ↑SST in july | ↓AbC, ↑Chlo in winter, ↓DC, ↓SST in july | ↑AbC, ↑SST in july, ↓Chlo in winter, shallower $Z_{2ml}$ | ↓AbC, ↓SST in july, ↑Chlo in winter, deeper $Z_{2ml}$ |
| | Guanape Sur, Mazorca | San Juan, Santa Rosa | Guanape Sur, Ballestas | Don Martin, Asia |
| **Booby** | Onset(late Autum-Winter) Occupancy(Winter-Summer) | Onset(late winter-Spring) Occupancy(Spring-Summer) | Onset Occupancy | Onset Occupancy |
| | ↑AbB, Nord, ↑DC, ↑LA100, ↑UI, Islands | ↓AbB, Sud, ↓DC, ↓LA100, ↓UI, Headlands | ↑DC, ↑AbB, Nord, ↑UI, Islands, ↑LA100, ↑SST in july, ↑DNP ↓Z2ml in summer and autumn | ↓DC, ↓AbB, Sud, ↓UI, Headlands, ↓LA100, ↓SST in july, ↓DNP ↓Z2ml in spring and summer |
| | Guanape Sur, Guanape Norte | San Juan, La Vieja | Chao, Guanape Sur | Ferrol, Don Martin |
| **Pelican** | Onset(Winter-Summer) Occupancy(Winter-Summer) | Onset(Spring-early Summer) Occupancy(Spring-Summer) | Onset Occupancy | Onset Occupancy |
| | Nord, ↑AbP, ↑DC (occupancy) | Sud, ↓AbP, ↓DC (occupancy) | ↑AbP, ↑SST in july, Nord, ↑Chlo, shallower Z2ml | ↓AbP, ↓SST in july, Sud, ↓Chlo, deeper Z2ml |
| | Guanape Sur, Lobos de Afuera | Santa Rosa, San Juan | Guanape Sur, Lobos de Tierra | Pescadores, Santa |

Figure 3.6. Schematic representation of the variability of seasonal breeding and covariates that explained that variation.

First it is interesting to note that large-scale covariates, such as latitude, were not the most important factors determining the timing and persistence of seasonal breeding for cormorant and pelican in the NHCS while it had been evidenced for related species as Brown pelicans (*Pelecanus occidentalis*) and Double-crested cormorants (*Phalacrocorax auritus*) in the California Current System, CCS (Schreiber 1980; Boekelheide *et al.* 1990). For those species from the CCS, individuals nesting in colonies at high latitudes exhibited restricted and later breeding season while individuals nesting at low latitudes had early and extended breeding seasons. Even if latitude is not the most important factor in the NHCS, it seems to play a role in early breeding at least for boobies and pelicans. Another geographic aspect to consider is the distance to the coast and the effect island versus headland. Disturbance can be the cause

for the preference of the three species to breed more frequently and earlier in coastal islands that in the islands > 10km from the coast.

Another surprising effect was the positive relationship between conspecific abundance and magnitude and timing of breeding. We expected a negative effect of density dependence due to competition for prey (Birt *et al.* 1987) and nesting space (Duffy 1983a). However seabirds, and especially cormorants, breed early and most of the years in nesting sites densely populated. The positive effect of density-dependence can be related to a high social attraction effect by conspecific that may constitute in this highly dynamic ecosystem an efficient integrated cue on the quality of the local environment. For cormorant, high densities are also advantageous as they rely strongly on collective strategies to localize prey (Weimerskirch *et al.* 2010)

In the NHCS, the zone between 6°S - 10°S, where most breeding sites are localized, is considered as quite homogenous in its oceanographic conditions, dominated by the surface equatorward Peru Coastal Current (PCC), which is associated with the coastal upwelling of cold and rich nutrient waters (Penven *et al.* 2005; Graco *et al.* 2007). However, we found that at small scale, there are variations in oceanographic conditions around nesting sites. They can be associated to smaller scales process such as at mesoscale and sub-mesoscale (100m to 100 km) features that are known to structure and modulate strongly the ecosystem dynamics (Bertrand *et al.* 2014). Those processes help to concentrate primary production and preys which attract predators (Bertrand *et al.* 2014). In our case, the influence of local environmental conditions on the magnitude and timing of breeding was evidenced for the three species. Breeding sites with higher occupancy had generally higher primary production, shallower oxycline (especially in summer and autumn) and SST minima only in late winter. For most of the breeding sites these conditions were also associated to an early seasonal breeding, particularly a high primary production. Therefore, this strongly suggests that the timing of seasonal breeding and the frequency of occupancy of breeding sites are highly dependent on the local environmental conditions surrounding the nesting sites, which shape prey availability.

Another surprising effect was the positive relation between landings of anchovy and the timing and magnitude of seasonal breeding for boobies. Higher landings of anchovy were related to early breeding and higher magnitude of breeding. We expected a negative effect of the fisheries in timing of breeding and magnitude of boobies because fisheries remove large amounts of anchovy that in fact are not anymore available to seabirds. We can interpret this positive effect of fisheries from several points of view. First, main colonies of boobies coincide with ports with most important landing of anchovy and positive effect can be only a spatial correlation. Second, large landings reflect also the high abundance of anchovy and boobies may be less impacted by fisheries than the other two species because they can forage individually and do not need a high concentration of fish to prey efficiently as it is the case for cormorants. Third, boobies may cope with fishery competition by modulating other parameters of breeding such as growth rate of chicks and clutch size as observed in similar species (Duffy & Ricklefs 1981; Clifford & Anderson 2001).

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To sum up, for the three species we identified breeding sites which were frequently occupied by breeders and where breeding started early. Most of these sites were localized between 6 °S and 10 °S. However the influence of latitude was not the most important explanatory factor. These sites were often characterized by a high upwelling activity, a high primary production and probably a high abundance of anchovy, but under a high fishery pressure. After these results of variability between nesting sites the next step may be known if these differences had consequence also in the fitness of adults or in the reproduction success.

### 4.3. Implications for the human activities in the ecosystem

These differences in the timing and persistence of breeding between sites constitute useful information in several aspects. For the management of guano harvesting, information of timing of breeding detailed by nesting sites is crucial to forecast activities of extraction. Activities of guano extraction are planned with a year of anticipation because extraction activities ask for the presence in the nesting sites of a large number of workers (50-300 workers) for periods ranging from 1 to 5 months and must be accomplished when seabirds are not in reproduction ("Ley Reserva Islas y Puntas guaneras" 2001). The new detailed seasonal breeding by nesting sites allows a better planning of guano extraction regarding the breeding of seabirds and also a management of tourism activities that respect seasonal breeding by nesting sites to reduce anthropogenic impact on breeding seabirds. Detailed information of timing of seasonal breeders and important factors of variability help also to plan research about the intra-population variability and the sensitivity of seabird population to rapid environmental change such as global warming (Sexton *et al.* 2009).

### 6. Summary of appendix

Appendix A Geographic, environmental, seabird abundance and anchovy fisheries covariates.

Apppendix B. Functional analysis.

Appendix C Random forest.

Appendix D: Exploration of seasonal curves: Mean and outliers.

Appendix E. Importance of covariates evaluated with Random Forest

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# *Chapter IV: Long-term changes in the breeding seasonality of Peruvian seabirds in relation with environmental variability*

# *Long-term changes in the breeding seasonality of Peruvian seabirds in relation with environmental variability*

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**Summary**

1) The Northern Humboldt Current System (NHCS) off the Peruvian coast is a very productive low latitude upwelling ecosystem, yet, with a moderate seasonality, and submitted to a strong climatic variability from intra-seasonal to interdecadal scales. The system hosts three seabird species in large abundances: Guanay cormorant (*Phalacrocorax bougainvillii*), Peruvian booby (*Sula variegata*) and Peruvian pelican (*Pelecanus thagus*). The size of those avian populations varied greatly over the last century in relation with the large fluctuations of their main prey, the Peruvian anchovy (*Engraulis ringens;* large abundances from 1950 to 1970, collapse in 1970-1990 and recovery from 2000s) caused by regime shifts in oceanographic conditions and the development of an industrial fishery in the late 1950's.

2) The goal here is to examine if the seasonality of the seabird reproduction was affected by the regime shifts that triggered the three recent and contrasted decadal periods (1950-1970, 1970-1990 and 2000s).

3) Using dynamic multiseason occupancy models, we estimate the timing and magnitude of onset and occupancy of breeding. Furthermore, we relate the timing and magnitude of breeding seasons to seasonal ecosystem variability in terms of oceanographic conditions, biomass, and availability of anchovy and fishing pressure.

4) We found that cormorants adjusted the timing of onset of their breeding between spring and winter according to regime shift. Pelicans and cormorants modulated the magnitude of their breeding attempts according to regimes. Meanwhile boobies retain the same timing and magnitude of breeding attempt.

5) The fact that cormorants may tune the timing of the onset may be related to their good diving capacities that allow them to exploit a larger vertical range of the water column compared to the other two species. Fixed onset and magnitudes of breeding in boobies may be related to their specific foraging strategy and/or to changes of prey items when anchovy stock was low. Consequently, when facing regime shifts, seabirds competing for the same prey exhibited differences in its breeding seasonality, cormorants showed the highest plasticity whereas boobies showed the lowest plasticity.


**Key words: timing of breeding, oxygen minimum zone, population dynamics, anchovy fisheries, regime shift.**

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# 1. Introduction

Birds have evolved to breed seasonally as an adaptation to match breeding with optimal foraging conditions in the environment where they live. Therefore, timing of breeding is one of the most important factors influencing reproductive performance of parents, optimizing survival of young (Lack 1968; Perrins 1970) and consequently influencing demography and population dynamics (Miller-Rushing *et al.* 2010). In seasonal ecosystems, birds use proximate cues early in the breeding season, such as photoperiod, temperature or rain, to time reproduction (Burger & Piatt 1990; Frederiksen *et al.* 2004; Surman, Nicholson & Santora 2012). The proximate cues used by birds in temperate high latitude ecosystems birds is usually photoperiod and in low latitude ecosystems, supplementary environmental cues (Wingfield *et al.* 1992; Hau 2001).

Climate change is known to affect the breeding seasonality of animals including birds (Visser *et al.* 1998; Stenseth & Mysterud 2002), and most studies focused on the effects of gradual changes in mean temperatures and/or precipitation regimes on breeding seasonality (Crick *et al.* 1997; Bertram *et al.* 2001). However, the consequences of extreme or unexpected changes in environmental conditions, such as extreme climatic events or regime shifts, remain poorly known (Durant et al. 2004). When such abrupt changes occur, the ability of birds to adapt to new conditions for breeding depends on their use of reliable and multiple proximate cues, directly related to the causes of changes in prey availability (Durant *et al.* 2004; Visser 2008; Anderson *et al.* 2013). In this study, we investigate the consequences of regime shifts on the breeding seasonality and potential environmental cues used for timing breeding. The three species are the Guanay cormorant (*Phalacrocorax bougainvilli*), the Peruvian booby (*Sula variegata*) and the Peruvian pelican (*Pelecanus thagus*). They are sympatric in the Northern Humboldt Current System (NHCS) where they nest in large numbers (Duffy 1983a) and compete to feed mainly on Peruvian anchovy (*Engraulis ringens*). In the NHCS, small pelagic fish, mainly anchovy, and during some periods sardine (*Sardinops sagax*), are the dominant forage fish in the NHCS (Salvatteci *et al.* 2014).

The NHCS is an extremely productive upwelling ecosystem with an intense oxygen minimum zone (OMZ) (Chavez *et al.* 2008). Despite its low latitude, it exhibits a moderate seasonality of environmental conditions (Echevin *et al.* 2008). Seasonality was also found in the reproduction of the three seabirds species in the recent period (from 2000) and optimal conditions in terms of oceanographic conditions and availability of prey occur when young become independent (Passuni *et al.* 2016). During the last fifty years, two climatic regime shifts have been reported in the Pacific ocean, separating three interdecadal regimes: 1946-1976, 1977-mid 1990's and after 2000 (Mantua *et al.* 1997; DeYoung *et al.* 2004). These regime shifts heavily affected the NHCS impacting the productivity and oxygen conditions (Bertrand *et al.* 2011).

Fisheries are other of one major driving force of regime shift in marine ecosystems (Jiao 2009). The rise of the Peruvian industrial anchovy fishery during the 1960s resulted into less availability of forage fish for seabirds even though anchovy was more abundant than ever before. Seabird populations decreased from 20 million of individuals during the development of the fishery industry (1952-1964) (Jordan 1963) to ~3 millions of individuals (Tovar Serpa *et al.* 1987) once it was fully developed and the anchovy collapsed in the early 1970's (Tsukayama & Palomares 1987; Chavez *et al.* 2003). After 1990, the total seabird population fluctuated around ~2 to 3 million of individuals (AGRORURAL, *com.pers.*) despite the recovery of the anchovy stock (Gutiérrez *et al.* 2007).

Here, we use a long term dataset of presence/absence of breeding cormorants, boobies and pelicans covering three periods (1952-1968, 1977-1990 and 2003-2014) coinciding with regime shifts in the Pacific in

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general and the NHCS in particular (Mantua *et al.* 1997; Bertrand *et al.* 2011), to address three main questions: (1) Are there any changes in the timing and magnitude of breeding attempts of seabirds after regimen shifts?, (2) Do the three species differ in their response to environmental changes?, and (3) Do the relationships between the onset of breeding and the fluctuations in environmental variables differ between periods?

## 2. Material and methods

### 2.1. Study area and seabird data

The study focuses on Isla Pescadores (11º 46' 22.8"S, 77º 15' 36"W, Fig. 1) located in the central region of Peru and 7 km off the mainland. Isla Pescadores has a surface of 16.45 hectares, and a maximal altitude of 50 m. The island is arid and uninhabited except by one or two wardens in charge of the protection and monitoring of seabirds. Isla Pescadores, like other islands hosting nesting colonies of seabirds in the coast of Peru, is monitored as part of a public program to record monthly abundance of breeding and non-breeding individuals of cormorants, boobies and pelicans since 1952 (see Passuni et al. 2015 for further details). However, historical monthly information for other islands was lost and the only long-term data available consists in a non-continuous time series for Isla Pescadores from 1952 to 2014. Data were available during three periods with almost continuous data (less than a year of missing data, Table S1): 1952-1968, 1977-1990 and 2003-2014.

The data series for 1952-1968 were monthly presence/absence of breeders for each species. Individuals were considered as breeders if they were observed incubating eggs, brooding or feeding chicks. The data series for 1977-1990 were monthly percentages of breeders by species. The most recent data series of 2003-2014 were monthly abundance estimates of breeders by species. Consequently, for the last two periods we converted abundance and percentage data to presence/absence data in order to obtain similar information for the three periods.

### 2.2. Oceanographic data

We used monthly oceanographic data to build climatologies (monthly averages over years) coinciding with the three periods defined above. Oceanographic covariates were sea surface temperatures (SST, in °C), surface chlorophyll-a concentrations (Chlo, in mg m$^{-3}$) and oxycline depths ($Z_{2ml\,l^{-1}}$, in m). These covariates were linked to the timing of onset of breeding of the three species over the most recent period (Passuni *et al.* 2016). Chlo and SST reflected the annual variations of productivity in the ecosystem. $Z_{2ml\,l^{-1}}$ is a proxy of the upper limit of the OMZ (Bertrand *et al.* 2010), defined as the depth where dissolved oxygen equals 2 ml l$^{-1}$. This parameter is a good indicator of the vertical accessibility of the forage fish to seabirds. All the oceanographic covariates were acquired from research vessels belonging to the Consejo de Investigaciones Hidrobiologicas (CIHB, 1952-1959), the Instituto de Investigacion de los Recursos Marinos (IREMAR, 1960-1963), the Instituto del Mar del Peru (IMARPE, 1964 until now) and the World Ocean Database 2013 (https://www.nodc.noaa.gov/OC5/SELECT/dbsearch/dbsearch.html) of the National Oceanographic Data Center. Over the years, the monitoring of the oceanographic conditions of the Peruvian coast consisted in regular

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measures along parallel cross-shore transects of ~100 nm long and ~15 nm intertransects and between 3°30'-18°20'°S (Swartzman *et al.* 2008). However, we used data only between 8°-15°S and from 0 km to 100 km off the coast to build climatologies. We selected this area because oceanographic conditions are homogeneous (e.g. $Z_{2ml\,l^{-1}}$, Bertrand et al 2011) and it encompasses the main nesting sites of the three species as well as their maximum-recorded foraging ranges during breeding: ≈63 km for cormorants (S. Bertrand, unpublished data), ≈90 km for boobies and ≈83 km for pelicans (Zavalaga *et al.* 2011; Bertrand *et al.* 2012). Data for this area were available for the three periods (1952-1968, 1977-1990 and 2003-2014) for SST and $Z_{2\,ml\,l^{-1}}$ but only for the two most recent periods for Chlo (detailed structure of data can be found in Appendix S2). Moreover, we filtered months by El Niño and La Niña events in order to keep only interdecadal signals and remove strongly influencing interannual events (Fig. S3). Differences of median between periods for oceanographic variables were tested with Kruskal-Wallis tests and a posteriori compared by pairs of periods by Wilcoxon test.

## 2.3. Anchovy data: availability and catches

We used two kinds of variables to represent availability and biomass of anchovy estimated from a stock assessment model and acoustic data. Acoustic data was our most direct data to represent availability of prey but it was not available at a monthly scale thereby we used only for interpretation (see details of data collection in Appendix S3). Biomass was calculated, at a monthly scale, from a stock assessment model that combined data on the length of individuals collected from landings, acoustic surveys and gonadosomatic index of anchovy (Oliveros-Ramos & Peña 2011).

Anchovy is exploited by a large and intensive fishery that could influence the availability of prey for seabirds. Thus, we also used as covariates monthly landings of anchovy divided by the global yearly quota to build climatologies of the fishing pressure for the periods 1952-1968, 1977-1990 and 2000-2014. Differences of median between periods for anchovy data variables were tested with Kruskal-Wallis test and a posteriori compared by pairs of periods by Wilcoxon test.

## 2.4. Modeling seabird seasonal breeding and its relation with oceanographic and prey covariates

We used the monthly presence and absence of breeders for the three study periods (1952-1968, 1977-1990, and 2003-2014) to model the occurrence of breeders as a dynamic process of onset (colonization) and termination (local extinction) of breeding events. We used multiseason occupancy models within a Bayesian context, which are dynamic models that allow making inference about the occurrence of events at a collection of sites and about how changes in occurrence are driven by colonization and local extinction (MacKenzie et al. 2005). In our case, we had only one site but multiple years and months. Therefore we adapted the model so that the parameters varied between $i$ years and $t$ months. We defined the occurrence of breeders at month 1 ($z_{i,1}$) for year $i$ as a Bernoulli trial process. The occurrence of breeders ($z_{i,1}$) is a Bernoulli random variable governed by the probability of occupancy of breeders ($\psi_{i,1}$).

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$$z_{i,1} \sim Bernoulli\ (\psi_{i,1})$$

$$z_{i,1} \begin{cases} 0 \text{ if there are no breeders at time } t = 1 \\ 1 \text{ if there are breeders at time } t = 1 \end{cases}$$

In all later months $t = 2, \dots, 12$ of year $i$ the occurrence of breeders $z_{i,t}$ in year $i$ for a month $t$ is a Bernoulli process with an occupancy parameter $(\psi_{i,t})$ that depends on two parameters, termination $(\varepsilon_{i,t-1})$ and onset $(\gamma_{i,t-1})$ of breeding according to the relationship:

$$z_{i,t}|z_{i,t-1} \sim Bernoulli\ (z_{i,t-1} * (1 - \varepsilon_{i,t-1}) + (1 - z_{i,t-1}) * \gamma_{i,t-1})$$

Therefore, three parameters were estimated: probability of onset ($\gamma$), probability of termination ($\varepsilon$) of breeding events and occupancy of breeders ($\psi$) derivated from onset and termination.

Probability of onset of breeding events $(\gamma_{i,t-1})$ was defined as the probability that in a year $i$ the site was unoccupied by breeders in month $t$-1 (i.e., $z_{i,t-1} = 0$) and was occupied by breeders in month $t$. Probability of termination of breeding events $(\varepsilon_{i,t-1})$ was defined as the probability that in a year $i$ the site was occupied by breeders in month $t$-1 (i.e., $z_{i,t-1} = 1$) and was unoccupied by breeders in month $t$. Occupancy probability of a breeding site $(\psi_{i,t})$ was defined as the probability of presence of breeders. Occupancy models were developed to produce unbiased estimates of occurrence when the probability of detecting species is lower than 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.

Occupancy models were fitted using a Bayesian approach with JAGS (Plummer 2003) through jagsUI in R software (R Development Core Team 3.1.3). 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 1000000 iterations each one, 1000 iterations to adapt and discarded the first 500000 as burning. We used a measure of model fit based on 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 choice of use of uninformative or informative priors. We used informative priors after a comparison of posteriors calculated using informative and non-informative priors (Figs S5, S6 and S7). We also tested the identifiability of parameters $\gamma, \psi$ and $\varepsilon$ using the percentage of overlap between uniform prior and posterior distribution ($\tau$), overlaps higher than 35% meant weak identifiability (Gimenez, Morgan & Brooks 2009). We found a lower identifiability of $\varepsilon$ thereafter we only considered the parameters onset of breeding ($\gamma$) and occupancy of breeders ($\psi$) for interpretation (Table S4).

After modeling $\gamma$ and $\psi$ for each species in the three periods we tested whether these probabilities were different between periods with a Kruskal-Wallis and a post hoc test of Dunn with paired periods. We also tested relation between periods with a Pearson correlation coefficient test between paired samples and the asymptotic confidence interval was given based on Fisher's Z transform. Kruskal-Wallis and correlation tests were performed in R software (R Development Core Team 3.1.3). Finally, we modeled the influence of the monthly varying oceanographic and prey covariates only on the onset $(\gamma_{i,t-1})$ of breeding events using a logistic regression. We did not modelled occupancy as a function of covariates because this parameter is directly derived

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from onset and termination and consequently correlated. For the logistic regression we assumed a Bernoulli distribution for the observations $z_{i,t} \sim Bernoulli(\gamma_{i,t-1})$. The functional linear relationship between the *logit* transformed parameter $\theta_{i,t-1} = \gamma_{i,t-1}$ and the covariate $x_i$ was $\text{logit}\ (\theta_{i,t-1}) = \beta_0 + \beta_1 x_{i,t}$, where $\beta_0$ and $\beta_1$ were respectively intercept and slope parameters to be estimated. All values are indicated ± sd unless otherwise indicated.

# 3. Results

## 3.1. Changes in seasonality of oceanographic conditions

The oceanographic conditions presented a moderate to strong seasonality during the three study periods (Fig. 4.1). Although seasonal variations existed for the three periods, months of maxima and minima changed between periods for Chlo (Fig. 4.1) and seasonality was reversed for $Z_{2ml\,l^{-1}}$ (Fig. 4.1).

For Chlo, there were two peaks in the year, in austral spring and autumn, of similar intensity (Chlo>5 mg m$^{-3}$). The spring peak was in September during 1977-1990 and in November during 2003-2014. The autumn peak was in March-April for 1977-1990 and in April for 2003-2014 (Fig. 4.1). Lowest values of Chlo (Chlo <2 mg m$^{-3}$) occurred in austral winter for both periods, June for 1977-1990 and July for 2000-2013. The averages of Chlo and standard deviation were similar for the two periods (3.17±3.39 mg m$^{-3}$ for 1977-1990 and 3.21±3.48 mg m$^{-3}$ for 2003-2014, W = 59, *P*-value = 0.48).

$Z_{2ml\,l^{-1}}$ was the oceanographic parameter that exhibited the strongest decadal changes in seasonal variability between the three periods (Fig. 4.1). Seasonal patterns for 1977-1990 were reverse in comparison to those observed in 1952-1968. During 1977-1990 the oxycline was deeper (>40 m) during austral summer and autumn (February-June). Such deep oxycline conditions were observed in austral winter (July-September) during 1952-1968 and only in June during 2003-2014.

Also, the averages of $Z_{2ml\,l^{-1}}$ of the three periods were significantly different ($X^2$ = 7.96, *P*-value = 0.02). The $Z_{2ml\,l^{-1}}$ was deeper during 1977-1990 (41.3±10.8 m) than during the other two periods (29. 9±9.5 m for 1952-1968 and 31.9±7.0 m for 2003-2014) and this difference was significant for comparisons between 1977-1990/2003-2014 (*W* = 114, *P*-value = 0.01) and 1952-1968/1977-1990 (*W* = 32, *P*-value = 0.02).

For SST, higher values were registered during austral summer and lowest values during austral winter for the three studied periods (Fig. 4.1). The averages of SST for the three periods were similar (18.18±2.19°C for 1952-1968, 18.33±2.22°C for 1977-1990 and 17.88±2.44 for 2003-2014, *W*=1.01, *P*-value=0.60).

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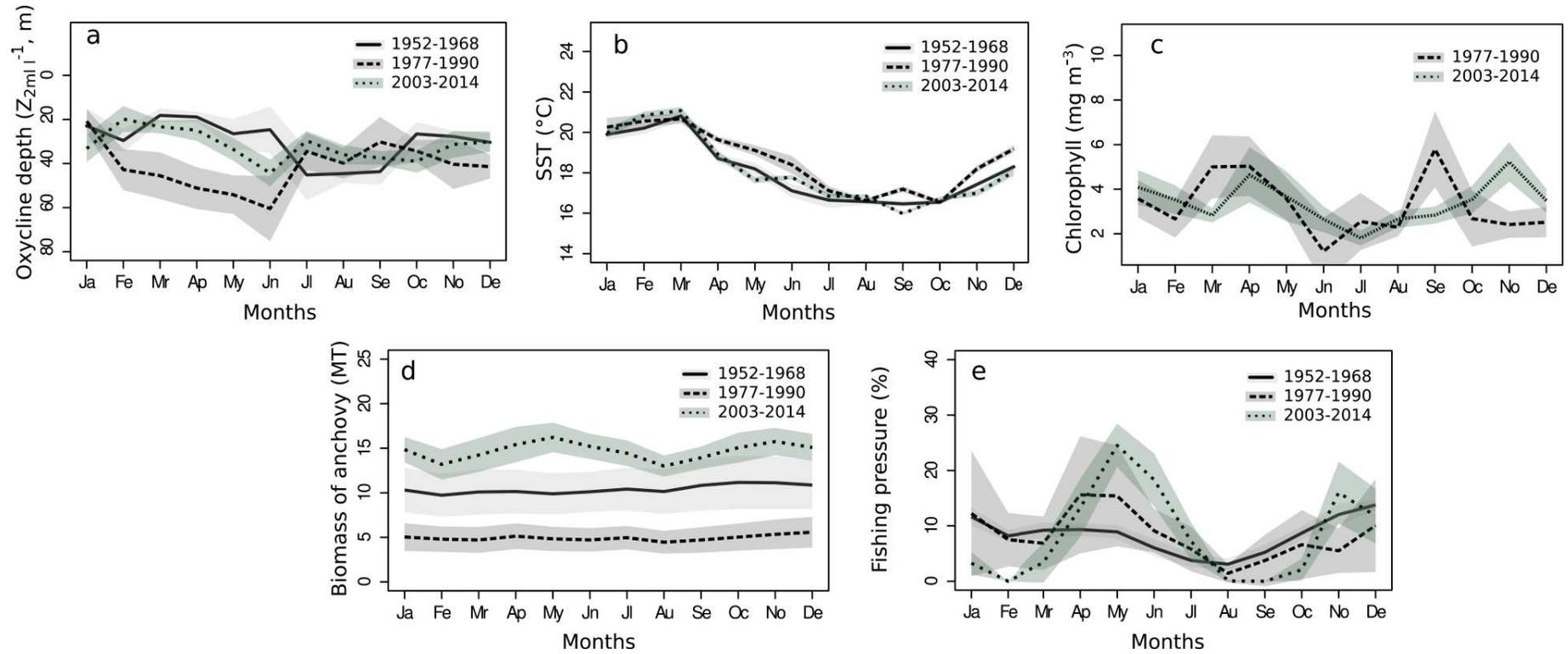


Figure. 4.1. Seasonality of oxycline depth (a), sea surface temperature (b), chlorophyll (c), biomass of anchovy (d) and monthly fishing pressure (e) in the Peruvian coast during the periods of 1952-1968 (solid lines), 1977-1990 (dashed lines) and 2000-2014 (dotted lines). Shaded areas represented the 95% and 5% confidence levels of sample mean.

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## 3.2. Changes in anchovy availability and catches

Biomass estimated from the stock assessment model did not show seasonality but significant differences in average values between periods ($X^2$=31.13, $P$-value=0.00, Fig. 4.1). Biomass was higher during 1952-1968 (10.40±4.92 MT) and 2003-2014 (14.4±2.20 MT) compared to 1977-1990 (4.76±2.49 MT). There were also significant differences in biomass between the three periods when comparing by pairs of periods ($P <= 0.001$).

These differences in anchovy biomass between periods were consistent with acoustic data, regional abundance ($s_A$), local abundance ($s_A$+) and spatial occupation index (ISO) of anchovy were higher during 2003-2014 ($\overline{s_A}$ = 2.74±0.92, $\overline{s_A}$+=5.48±0.82 and ISO = 49.60±12.51) than 1977-1990 ($\overline{s_A}$=1.80±1.34, $\overline{s_A}$+=4.10±0.66 and ISO=41.13±26.76) and the differences were significant for $s_A$ ($W = 103$, $P = 0.02$) and $s_A$+ ($W = 32$, $P$-value = 0.00) but not for ISO ($W$=153, $P = 0.38$).

During the period 1977-1990 anchovy schools were in average slightly deeper and thicker (school depth=14.63±2.58, school height=4.85±1.77) than during the period 2003-2014 (school depth=12.63±3.84, school height=2.75±3.20). These differences were not significant for depth (W=120, $P$-value=0.16) but for height (W=136, $P$-value=0.00).

Fishing pressure (percentage of monthly landings of anchovy from global quota) varied in time according to the abundance of anchovy and the development of the fishing industry (Fig. 4.1). The fishery initiated and developed during 1952-1968, and was poorly regulated: fishing pressure was spread along the year (3.74±3.61MT per year in average over the period) reflecting mainly the fleet and fishmeal factory capacities. During 1977-1990, the fishery got fully developed but anchovy was less abundant and some regulations were implemented, so the landings yielded 1.23±1.17MT per year in average and were mainly realized in autumn (Fig. 1). During 2003-2014, anchovy was more abundant and the fishing was restricted to autumn and spring (Fig. 1) producing landings of 5.31±1.91MT per year in average.

## 3.3. Changes in the seasonality of breeding seabirds

In general, the three study species presented a clear breeding seasonality with an onset during austral spring and occupancy of nesting sites by breeders almost all the year except austral autumn (Figs 4.2 and 4.3). Furthermore, depending on the species, the magnitude and timing of the monthly probability of onset of breeding, as well as occupancy, varied between the three study periods (Figs 4.2 and 4.3).

Cormorants presented two main peaks of onset of breeding, one in austral winter and another in austral spring (Fig. 4.2). Depending on the decadal period, one of the peaks predominated over the other in terms of length or magnitude. During the period 1952-1968, the spring peak (November), was predominant over secondary peaks in winter (July) and autumn (May) while during 1977-1990 and 2003-2014 the winter peak (June-July) was slightly predominant over the spring peak (October) (Fig. 4.2). Occupancy of breeders spread over all the year except austral autumn (Fig. 4.3). Furthermore probabilities of onset and occupancy were much lower during 1977-1990 than during the other two periods (Table S5, Dunn tests for 1977-1990/2003-2014 and

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1952-1968/1977-1990, $P < 0.05$). Probabilities of onset of breeding were significant correlated among the periods 1977-1990 and 2003-2014 (Table S5).

Boobies presented no major difference in timing and magnitude of onset between periods. Onset of breeding mainly occurred in spring, between September and November (Fig. 4.2). Also the seasonality of onset of breeding during the three periods was strongly correlated (Table S5). Site occupancy by breeders mainly occurred over spring and summer during 1952-1968 and 1977-1990 and over austral spring during 2003-2014 (Fig. 4.3). Average probabilities of occupancy were significant different among periods with higher probabilities during 1977-1990 and lower probabilities during 2003-2014 (Table S5, Dunn test for 1977-1990/2003-2014, $P =$ 0.01). The probabilities of occupancy of breeders were correlated for the periods of 1952-1968 and 1977-1990 (Table S5).

As for boobies, onset of breeding for pelicans was similar in timing for the three periods. Onset of breeding was restricted to spring, with a peak in October-November (Fig. 4.2). The occupancy of breeders for the three study periods was constant in timing and mainly occurred over austral spring and summer (Fig. 4.3). The magnitudes of onset and occupancy probabilities were low during 1977-1990 and high during 2003-2014 (Fig. 4.2, Table S5, Dunn test for 1977-1990/2003-2014, $P = 0.01$). The probabilities of onset of breeding were significantly correlated for the three periods and probabilities of occupancy were correlated for the periods 1952-1968 and 1977-1990 (Table S5).

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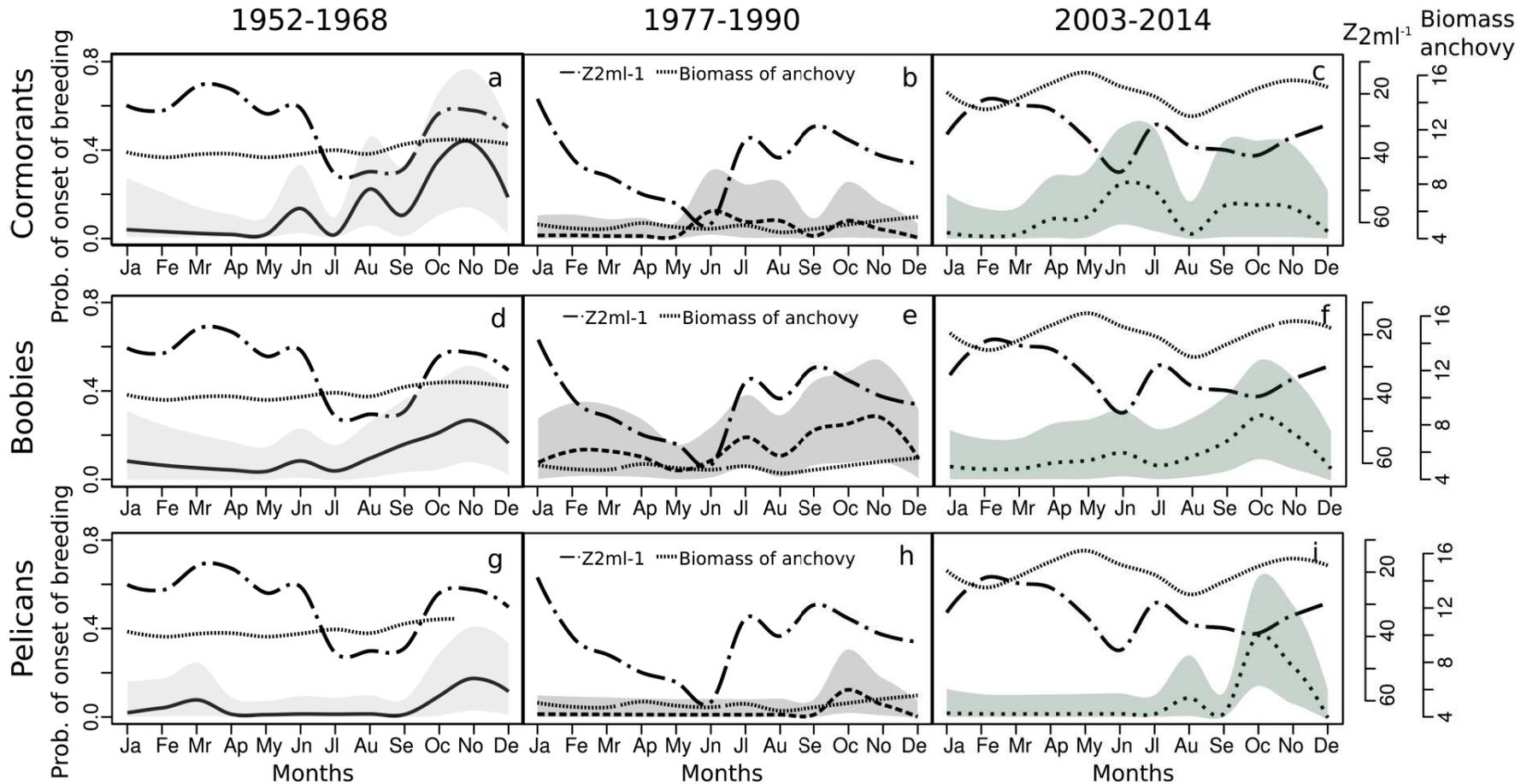


Figure 4.2. Monthly average estimates of probability of onset of breeding during the periods of 1952-1968 (solid lines), 1977-1990 (dashed lines) and 2003-2014 (dotted lines) for cormorants (a, b and c), boobies (d, e and f) and pelicans (g, h and i). Seasonalities of oxycline depth (dashed lines with dots) and biomass of anchovy (dotted thin lines) are also represented for the three periods and its respective axes are at the right of plots. Shaded areas represented the95% and 5% of the posterior distribution of monthly probability of onset of breeding. Breeding onset probability, oxycline depth and biomass of anchovy were smoothed with a loess model with 0.45 of span.

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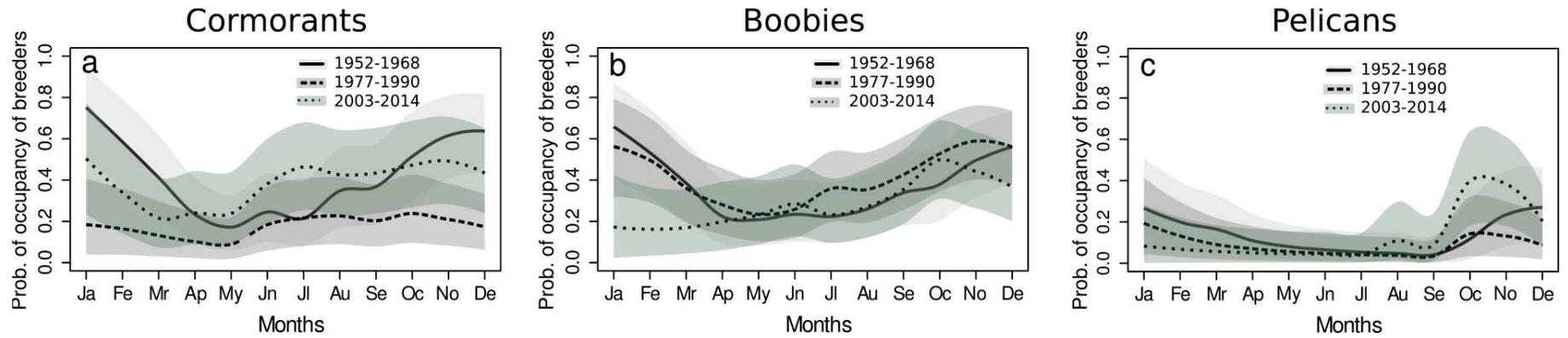


Figure 4.3. Monthly average estimates of probability of occupancy of breeders for cormorants (a), boobies (b) and pelicans (c) during 1952-1968 (solid lines), 1977-1990 (dashed lines) and 2003-2014 (dotted lines). Shaded areas represented the 95% and 5% of the posterior distribution of monthly probability of onset of breeding. Breeding onset probability lines were smoothed with a loess model with 0.45 of span.

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### 3.4. Effects of environmental conditions on breeding seasonality

SST was negatively related to the onset of breeding for the three species and the three periods (Table 4.1). The average slope of the relationship between SST and onset of breeding was $-1.79 \pm 0.80$ (95% CI: -2.31 to -1.27).

Relationships between the depth of the oxycline ($Z_{2ml\,l^{-1}}$) and the onset of breeding were not consistent over time (Table 1). No significant relationship was found for the 1952-1968 period. For the period 1977-1990, $Z_{2ml\,l^{-1}}$ was negatively related with the probability of onset of breeding only for boobies and no significant relationship was observed for cormorants or pelicans (Table 1). In contrast, for the period 2003-2014, $Z_{2ml\,l^{-1}}$ was positively related with the probability of onset of breeding for the three species. The average slope of the relationship between $Z_{2ml\,l^{-1}}$ and onset of breeding during 2003-2014 was $2.62 \pm 0.56$ (95% CI: 2.00 to 3.25). Finally, there was no significant relationship between seasonal breeding and chlorophyll except a negative relationship for cormorants during 1977-1990 (Table 4.1).

There were positive relationships between biomass of anchovy and onset of breeding of boobies and cormorants (and to lesser extent pelicans) for the period 1952-1968 but not for the other 2 periods (Table 4.2).

Fishing pressure was positively related to the onset of breeding and occupancy of boobies and pelicans (and to lesser extent cormorants) during 1952-1968. However, there was some evidence for negative relationships between fishing pressure and onset of breeding for boobies during 1977-1990 and for pelicans during 2003-2014.

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Table 4.1. Models of onset ($\gamma$) of breeding related to the depth of oxycline ($Z_{2ml\,l^{-1}}$), SST and Chlo. Mean ($\mu$) and standard deviation (sd) of intercept ($\beta_0$) and slope ($\beta_1$). The parameter f represents the proportion of posterior with the same sign as the mean. We consider as significant f > 97.5 and the mean and f are indicated in bold.

| | | | Onset of breeding | | | |
|---|---|---|---|---|---|---|
| | Specie | Periodes | $\beta_0$ ($\mu\pm$sd) | f | $\beta_1$($\mu\pm$sd) | f |
| $Z_{2ml\,l^{-1}}$ | Cormorant | 1952-1968 | **-1.67±0.29** | **1.00** | 0.18±0.71 | 0.60 |
| | | 1977-1990 | **-3.62±0.65** | **1.00** | 0.62±1.00 | 0.73 |
| | | 2003-2014 | **-1.86±0.36** | **1.00** | **2.06±1.16** | **0.97** |
| | Booby | 1952-1968 | **-2.02±0.31** | **1.00** | 0. 17±0.77 | 0.59 |
| | | 1977-1990 | **-1.03±0.33** | **1.00** | **-1.44±0.67** | **0.99** |
| | | 2003-2014 | **-2.27±0.37** | **1.00** | **3.17±1.34** | **1.00** |
| | Pelican | 1952-1968 | **-3.30±0.50** | **1.00** | -1.24±1.16 | 0.86 |
| | | 1977-1990 | **-4.20±0.74** | **1.00** | -1.57±1.49 | 0.86 |
| | | 2003-2014 | **-2.87±0.44** | **1.00** | **2.64±1.52** | **0.97** |
| SST | Cormorant | 1952-1968 | **-2.31±0.48** | **1.00** | **-1.82±0.84** | **0.99** |
| | | 1977-1990 | **-3.52±0.55** | **1.00** | **-1.76±1.00** | **0.97** |
| | | 2003-2014 | **-2.14±0.43** | **1.00** | **-1.51±0.76** | **0.99** |
| | Booby | 1952-1968 | **-2.78±0.55** | **1.00** | **-2.05±0.94** | **1.00** |
| | | 1977-1990 | **-1.55±0.28** | **1.00** | **-0.98±0.54** | **0.97** |
| | | 2003-2014 | **-2.89±0.57** | **1.00** | **-2.39±0.94** | **1.00** |
| | Pelican | 1952-1968 | **-3.10±0.42** | **1.00** | -0.29±0.71 | 0.64 |
| | | 1977-1990 | **-5.14±1.00** | **1.00** | **-2.96±1.67** | **0.98** |
| | | 2003-2014 | **-3.59±0.70** | **1.00** | **-2.36±1.09** | **1.00** |
| Chlo | Cormorant | 1977-1990 | **-3.76±0.60** | **1.00** | **-3.07±1.44** | **1.00** |
| | | 2003-2014 | **-1.81±0.34** | **1.00** | -1.07±1.22 | 0.81 |

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| | Booby | 1977-1990 | **-1.53±0.28** | **1.00** | 0.11±0.63 | 0.58 |
|---|---|---|---|---|---|---|
| | | 2003-2014 | -0.84±0.51 | 0.95 | 0.95±1.23 | 0.78 |
| | Pelican | 1977-1990 | -1.34±0.87 | 0.95 | 2.47±2.34 | 0.86 |
| | | 2003-2014 | **-4.53±0.73** | **1.00** | -1.10±1.63 | 0.75 |

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Table 4.2. Models of onset (γ) of breeding related to the anchovy biomass and fishing pressure. Mean (μ) and standard deviation (sd) of intercept ($\beta_0$) and slope ($\beta_1$). The parameter f represents the proportion of posterior with the same sign as the mean. We consider significant as f > 97.5 and the mean and f are indicated in bold.

| | | | Onset of breeding | | | |
|---|---|---|---|---|---|---|
| | Specie | Periodes | $\beta_0$ (μ±sd) | f | $\beta_1$(μ±sd) | f |
| Anchovy biomass | Cormorant | 1952-1968 | **-2.34±0.44-** | **1.00** | **5.29±2.53** | **0.98** |
| | | 1977-1990 | -2.61±2.14 | 0.89 | 0.72±2.21 | 0.63 |
| | | 2003-2014 | 1.93±1.42 | 0.92 | 0.11±1.58 | 0.53 |
| | Booby | 1952-1968 | **-2.80±0.47** | **1.00** | **5.80±2.56** | **0.99** |
| | | 1977-1990 | -1.01±2.04 | 0.69 | 0.50±2.08 | 0.59 |
| | | 2003-2014 | -1.70±1.31 | 0.91 | -0.56±1.53 | 0.65 |
| | Pelican | 1952-1968 | **-3.49±0.55** | **1.00** | 3.53±2.72 | 0.90 |
| | | 1977-1990 | -2.55±2.20 | 0.88 | -1.99±2.28 | 0.81 |
| | | 2003-2014 | -2.18±1.45 | 0.94 | -0.72±1.71 | 0.67 |
| Fishing pressure | Cormorant | 1952-1968 | **-1.60±0.30** | **1.00** | 1.14±0.94 | 0.90 |
| | | 1977-1990 | **-3.46±0.50** | **1.00** | -1.23±1.08 | 0.88 |
| | | 2003-2014 | **1.94±0.37** | **1.00** | 0.38±0.40 | 0.83 |
| | Booby | 1952-1968 | **-2.02±0.31** | **1.00** | **1.83±1.01** | **0.97** |
| | | 1977-1990 | **-1.65±0.30** | **1.00** | **-1.50±0.68** | **0.99** |
| | | 2003-2014 | **-2.22±0.35** | **1.00** | -0.30±0.47 | 0.74 |
| | Pelican | 1952-1968 | **-3.46±0.53** | **1.00** | **3.43±1.38** | **1.00** |
| | | 1977-1990 | **-4.57±0.74** | **1.00** | -0.82±1.44 | 0.41 |
| | | 2003-2014 | **-3.07±0.52** | **1.00** | -0.98±0.69 | 0.94 |

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## 4. Discussion

This study showed that over three time periods covering the last 60 years and two regime shifts, the breeding of sympatric seabird species of the NHCS was seasonal. Yet the timing and magnitude of the probability of onset of breeding events varied among periods and species. The probability of onset of breeding was consistently negatively related to sea surface temperature for all species, suggesting that seabirds may use this oceanographic variable as a proximate cue to initiate breeding. In addition, before the development of the fishing industry the probability of onset of breeding increased with prey biomass, but this relationship disappeared after the fishery was fully developed.

### 4.1. Environmental variability of the NHCS at the decadal scale: changes in seasonality of oceanographic conditions and biological components

Regime shifts involve rapid onset, physically forced, bottom up perturbation that initiate decadal or longer systematic food-web and ecological changes (Steele 1998). In the NHCS, decadal regime shifts strongly affect the oxycline depth, secondary and tertiary production (Ayón *et al.* 2011; Bertrand *et al.* 2011). Oxycline depth presented decadal patterns with a shallow oxycline in the 1960s, a deepening during the 1970s, a maximum depth during the 1980s and shallow oxycline conditions during the 1990s-2000s (Bertrand *et al.* 2011). In addition, our results revealed that the period 1970-1990 had a reversal of the oxycline seasonal dynamics compared with 1952-1968 and (to a lower extend) 2003-2014. During the periods 1952-1968 and 2003-2014, the oxycline was deeper in winter and shallower in summer, while the reverse was observed during the period 1977-1990.

SST and Chlorophyll did not exhibit such changes in their seasonal dynamics among periods. SST values were higher in summer and lower in winter and Chlorophyll values were higher in spring and autumn and lower in winter.

Changes in oceanographic conditions had important consequences on other biological components of the NHCS ecosystem. Although there was no difference in the values of Chlorophyll concentration between the last two periods, differences were observed in secondary and tertiary production (Ayón *et al.* 2011; Bertrand *et al.* 2011). During shallower oxycline periods most life was concentrated in a shallow layer, boosting up the energetic transfer from phytoplankton to zooplankton and fish, in particular anchovy (Bertrand et al. 2011). In contrast, during periods when oxycline was deeper this energetic transfer was less efficient (Bertrand et al. 2011).

Decadal differences in anchovy biomass were remarkable with higher global biomass during 2003-2014 and 1952-1968 than during 1977-1990. Yet, the observed higher anchovy biomass during 2003-2014 compared with 1952-1968 could not be reliable. Indeed, the 1960s was the decade presenting the highest anchovy biomass (Tsukayama & Palomares 1987), and the relatively lower biomass estimated during the 1950s could be due to a drawback in the stock assessment models since the anchovy fishery was still not fully developed at that time. Therefore, an underestimation of anchovy biomass in the 1950s could be at the origin of the lower biomass observed for the period 1952-1968 when compared with 2003-2014. No seasonality could be evidenced for the biomass of anchovy. Unfortunately the lack of monthly biomass data impeded to test for seasonality using local

and regional abundance proxies. However, even if anchovy biomass was similar throughout the year, seasonal modulation in oxycline depth affected probably the actual availability of anchovy for seabirds.

## 4.2. Effects of regime shifts on breeding seasonality of seabirds

Similar to other biological components of the NHCS, seabirds experienced large changes due to regime shifts. Until now, only changes in abundance were well documented (Jahncke 1998). Yet, our results suggest that seabird species also modified their seasonal breeding patterns. The three species responded differently to the decadal environmental changes, perhaps reflecting differences in life history traits, foraging strategies and plasticity. Peaks of onsets of breeding for the three species always occurred in spring (September-November) for all periods and were systematically related to SST, whereas relationships were less consistent with other oceanographic factors. This suggests that sea surface temperature may be one of the proximate cues used by seabirds to time onset of breeding when sea surface temperature is lower (Passuni *et al.* 2016).

A notable exception were cormorants which changed onset of breeding from spring during 1952-1968 to winter during 1977-1990 and 2003-2014. Cormorants may thus use alternative cues, such as the availability of prey, to fine-tune reproduction. Such changes in timing of breeding of cormorants may be possible because, of the three seabird species studied, they have the best diving capacities reaching at least 35 m (Weimerskirch *et al.* 2012). This foraging behavior may allow cormorants to catch prey and breed during winter when anchovy schools are relatively deep but concentrated closer to the coast (Bertrand *et al.* 2005, 2008), and also during 1977-1990 when anchovies were probably more available in winter and spring due to the inversion of the oxycline depth seasonality. Therefore, cormorants can ensure energetic needs for rearing chicks during less productive and deep oxycline periods (1977-1990), and may maximize the survival of fledglings during high productive and shallow oxycline periods (1952-1968 and 2003-2014) by breeding at an optimal time (Passuni *et al.* 2016). Thus, we suggest that the greater variation in the timing of breeding for cormorants may reflect a higher phenotypic plasticity, the latter being currently recognized as responsible for the majority of adaptive phenotypic changes in response to environmental change (Visser *et al.* 2004; Reed *et al.* 2009; Reed, Harris & Wanless 2015).

However, the change in the timing of breeding of cormorants which occurred following the 1970 regime shift also coincided with a change in the fishing pressure. Before the full development of the anchovy industrial fishery, the probability of onset of breeding of the three seabird species increased with anchovy biomass, suggesting that breeding seasons matched the season with high prey biomass. However, this relationship disappeared following the full development of the fishery and the 1970 regime shift. This suggests that changes in the fishing pressure and/or changes in the seasonal patterns of anchovy abundance may have affected breeding seasonality in seabirds. Although the respective effects of the regime shift and fishery cannot be easily separated, we point out the necessity of establishing an adequate management to prevent dramatic changes on seabird reproduction when abundance of anchovies decreases. In other ecosystems, fisheries alone had a profound impact on the timing and success of breeding in seabirds (Scott *et al.* 2006; Votier *et al.* 2009). In the NHCS, poorly regulated fisheries were considered as an aggravating factor of the crash of anchovy stocks during the 1970s and of the decrease of seabird populations (Crawford & Jahncke 1999).

An obvious change in breeding due to regime shifts was the decrease in the magnitude of the probability of onset of breeding (and occupancy) in cormorants and pelicans during 1977-1990. We strongly suspect this

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decrease was mainly caused by the low abundance and low aggregation at the regional level of their main prey (anchovy) during some years of the 1977-1990 period, preventing individuals to reach a sufficient body condition to initiate breeding. 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 1983c; Zavalaga *et al.* 2011), but less likely for cormorants since their diving capacities surpassed the deepening of oxycline that limits anchovy habitat during less productive and low oxygen periods (Weimerskirch *et al.* 2012). Alternatively, cormorants forage in groups and appear to use social information to optimally exploit anchovy schools (Murphy 1936; Duffy 1983c; Weimerskirch *et al.* 2010). This reliance on communal foraging may be a handicap when prey abundance is low. Additionally, the shifts in the 1970s and 1980s in dominance in numbers from cormorants to boobies (Tovar & Guillen 1987; Guillen 1990) may have contributed to lower reproduction of the former species that uses rafts and huge columns that connect food patches and colonies (Weimerskirch *et al.* 2010).

By contrast to cormorants, boobies maintained similar probabilities of breeding during all periods. This could indicate that boobies shifted on alternative preys when anchovy abundance was low but there is limited evidence to assert this hypothesis. While it is true that boobies can replace a percentage of anchovy in their diet by other items, this is not higher than 30% and similar than observed prey replacements for cormorants and pelicans (Tovar & Guillen 1988; Jahncke & Goya 1998). Alternatively boobies, contrary to cormorants, leave colonies solitarily to search for prey by using network foraging and rely mainly on personal information based on memory to forage (Weimerskirch *et al.* 2010), which may facilitate locating prey schools at low abundance. Furthermore, boobies may also rely more on marine mammals such as southern sea lions (*Otaria flavescens*) to forage than cormorant or pelicans do (Duffy 1983c).

The interspecific differences in magnitude of probabilities of onset of breeding during different regimes in the ecosystem can also result from differences in species-specific life history traits (Table S6). Life history theory predicts that the three seabirds are long lived species that must favor the amount of resources invested for parental survival and future reproduction at the expense of those invested in current offspring production (Drent & Daan 1980). If clutch and brood sizes are similar for the three species (maximum of 3 eggs), there are differences in the duration of the chick rearing and post-fledging periods (Nelson 2005). Boobies have notably longer chick rearing and post-fledging periods than cormorants and pelicans (Nelson 2005). Also, although there are no specific measures of growth rates for the three species, at the family level boobies have lower chick growth rates than cormorants and pelicans (Ricklefs 1973; Duffy & Ricklefs 1981). Thus, during favorable conditions (1952-168 and 2003-2014), the three species can rely on the NHCS highly productive ecosystem to initiate breeding and breed successfully. However, during food shortage (1977-1990), the chick rearing period can be more energetically demanding for cormorants and pelicans with high chick growth rates. As a consequence, these two species may defer or skip breeding. By contrast, the lower chick growth rates and longer chick rearing and post-fledging periods for boobies may diminish the immediate energetic constraints for the parents which may maintain breeding activities. Longer time of chick rearing can be seen as an adaptation to the likelihood of food shortage (Schreiber 1994).

## 5. Conclusion

Summarizing, the three seabird species showed moderate to large changes in their breeding seasonality facing different regimes in the NHCS. Changes appeared species-specific and may be explained by the different ways species exploit food resources and by differences in life history traits. Cormorants showed the highest

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plasticity in the timing and magnitude of breeding depending on the level of prey abundance. Cormorants may time breeding in order to secure the rearing of chicks when prey is scarce (less productive and shallow oxycline periods), while they time breeding in order to maximize prey accessibility to fledglings when prey is abundant (high productive, deeper oxycline periods). Consequently, the Guanay cormorant can be seen as a highly plastic species, but also sensitive to regime shifts in the NHCS. Peruvian booby showed less plasticity in breeding seasonality. The timing and magnitude of breeding varied little, which may be linked to lower immediate energetic demands during the chick rearing period due to lower chick growth rates, and/or a specific foraging strategy, thereby allowing individuals to breed when prey availability was low. Peruvian pelican had also a relatively fixed timing of breeding, but the probability to breed appeared to be affected by changes in environmental conditions as for cormorants. Consequently, when facing regime shifts, cormorants showed the highest plasticity (changes in both the timing and probability of breeding) whereas boobies showed the lowest plasticity (abandon of nest only when conditions were extreme).

**Acknowledgments**

## 6. Summary of appendix

Appendix 1. Seabird data

Appendix2. Oceanographic data

Appendix 3. Acoustic data

Appendix 4. Estimation of hyperparameters

Appendix 5.Tests of prior sensitivities and identifiability of parameters

Appendix 6. Kruskal-Wallis and correlation test of onset and occupancy of breeders among the three periods.

Appendix 7. Seabirds life history traits

# *Chapter V Conclusions and Perspectives*



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Understanding the fluctuation of seabird population trajectories is of particular importance in the NHCS since seabirds are at the same time an economical resource through the production of guano (which regained importance since the renewal of organic farming), a possible competitor for the anchovy fishery, and charismatic species valued by the touristic industry and conservation NGOs. Most of the difficulty for establishing retrospective scenarios of the populations, and then to forecast possible future evolutions, comes from the natural multi-scale variability of the NHCS, reinforced by the regional declinations of climate change. Long-term and concomitant time series on seabird, oceanographic conditions and prey are required in order to disentangle the multiples scales and sources of seabird population variability (Lewison *et al.* 2012).

The longest and spatio-temporally best resolved time series available for the three seabird species in the NHCS were the land-based censuses performed by AGRORURAL guardians on the main nesting sites. Unfortunately, most of these data collected monthly at several nesting sites were lost, since the data were primarily collected for guano production purposes and not for scientific activities. Through the support of the TOPINEME project (Top predators as indicators of exploited marine ecosystem dynamics, collaborative project between IRD and IMARPE and AGRORURAL) data that was still available in paper format was rescued, digitalized, compiled and validated for the last decade (2003-2014) for all nesting sites and since 1952-2014 for one nesting site (Isla Pescadores). These consolidated data, on top of sustaining the analysis of this thesis, have been used for providing management advices to decision makers (e.g. Zavalaga 2015).

The observed fluctuations of seabird population are considered as part of population dynamic of seabirds that is a consequence of environmental conditions over the variability and abundance of prey (Figure 5.1, Weimerskirch 2001). In the case of NHCS, fisheries also play an important role in population of seabird as an important competitor for anchovy.

The relation of prey variability and population dynamic of seabirds can be approached from two points of views: i) adult survival and ii) fecundity (Figure 6.1, Weimerskirch 2001). For the three seabirds in NHCS, adult survival has been reported after changes in environmental conditions (e.g. Jordan 1964; Tovar Serpa 1974; Tovar Serpa & Fuentes Tapia 1980) although less has been researched about fecundity. Fecundity is an important aspect that may contribute significantly to population growth rate. Fecundity may be considered as the resultant of several sub-processes such as breeding frequency, growth of offspring and breeding success. Within that perspective, characterizing the breeding seasonality of seabirds from the NHCS has been the core of this thesis objective. Chapter I provided key background elements on the NHCS and multiseason occupancy models, which have been a central methodology in this work. Multiseason occupancy models, which work with a metapopulation approach and take into account the time effect by a Markovian approach (MacKenzie *et al.* 2005), were adapted to our purpose and data availability to describe the seasonal breeding of seabirds through occupancy, onset and termination probabilities. Adapting those models to monthly data of presence/absence of breeders was a novel approach for describing breeding seasonality. Another improvement of those models

consisted in solving the models through Bayesian approach when data are sparse. Finally, we adapted functional data analysis (Ramsay & Silverman 1997) as a second step (after Multiseason occupancy models) to compare patterns of seasonal breeding among nesting sites. Comparison of seasonal breeding between nesting sites were challenging because it included spatial and temporal patterns. Functional analysis and especially functional principal component analysis was performant in classified the seasonality of nesting sites as curves taking into account at the same time temporal and spatial patterns. Functional data analysis is a very powerful method to measure and compare curves that includes most of methods used in statistic for vectorized data. However several of its functions are still in development as regressions of function. Therefore we used as complement a regression tree to regress classification of curves with environmental conditions.
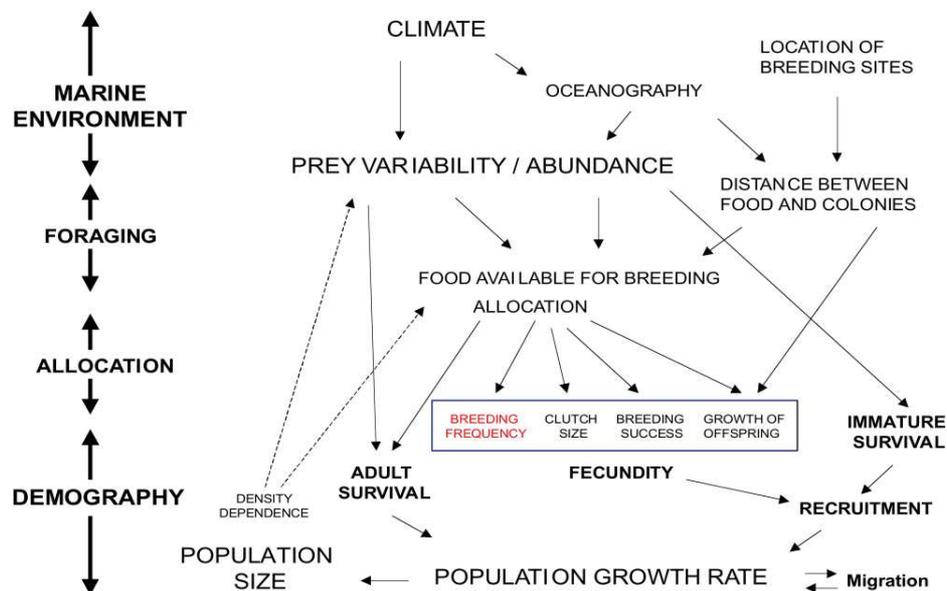


Figure 5.1. Schematic representation of the relationships between seabird demographic traits and the marine environment. The breeding frequency is highlighted in red font because is the central topic of these thesis. Source, Weimerskirch 2001.

Chapter II, proposed a general characterization of the breeding seasonality of the three study seabirds species during 2003-2014 in the main nesting sites of the Peruvian coast (6°S – 18°S). We addressed three questions: i) Do the three seabirds species have a marked seasonality in their breeding? ii) Are there differences between species considering that they feed on the same prey? iii) Which are the environmental factors influencing the most the timing and magnitude of the breeding seasons. We found that the three seabird species had a seasonal breeding related to the seasonal conditions of primary production and prey availability. Breeding mainly started during the winter and spring when primary and secondary productions are lowest and when anchovy is less available and in poor physiological condition. Conversely, the abundance and availability of anchovy improve during chick rearing and peaks around the time of fledging. We discussed

these strategies of timing based on current hypothesis of egg laying constraint and optimal breeding. Relating breeding seasonality of the three species to environmental conditions suggested that breeding timing is generally adjusted so that fledging may occur under optimal environmental conditions, rather than being constrained by nutritional requirements before egg-laying.

Comparing the breeding seasonality of the three species from the NHCS with other seabirds in Eastern Boundary Upwelling System, we found that the case of Peruvian seabirds is unique and may be related to the exceptional, non-limiting abundances of forage fish in this ecosystem. The hypothesis of adaptation of breeding cycle to offspring independence during optimal conditions opposed to egg laying constraint is supported by large clutch size, lack of siblicide, contrasting with related species of Sulidae (Friesen & Anderson 1997) and a possible high reproduction success during particularly abundant food conditions (Galarza Ninaya 1968). Yet, further studies are needed about the control of seabird reproductive physiology and energetics to understand the mechanism of adaptation to breed in the NHCS and also measure the energy allocation of seabirds to survival and breeding.

Some physiological and energetic traits influencing the decision of breeding are easily measurable in breeding and non-breeding seabirds. One of the first approaches is monitored physiological traits of adults through body condition. Body condition can be measured by scaling body mass with structural measured (e.g. wing length, culmen length) (Chastel *et al.* 1995) or by finer methods based on plasma lipid measurement for instance (Jacobs *et al.* 2012). Hormone dosages in blood samples may provide direct information on physiological body conditions. Hormones to analyze are luteinizing hormone (LH), estradiol, and testosterone. These hormones are high during the onset of breeding and can indicate the development of gonads and also control the amplitude of breeding cycle (Schreiber & Burger 2002; Chastel *et al.* 2005). Another interesting hormone is the corticosterone (CORT) which increases in many seabirds in response to nutritional stress (Goutte *et al.* 2014; Will *et al.* 2015). The methodology to measure hormones is relative easy and required blood sample or feathers and a rapid centrifugation after which samples can be stored for a month (Chastel *et al.* 2005). Hormone assays can be the critical phase due to the cost and the lack of Peruvian teams working in hormonal dosage outside the medical area. These direct measures of seabird physiological states could be related to prey availability (already measured by IMARPE), clutch size and foraging success. Physiological studies can be done first at short time scale, during a breeding cycle to explore the mechanism of the breeding control and then used as an indicator of nutritional stress and predictor of breeding decision.

Chapter III, evaluated the variability of seasonal breeding between the main nesting sites. Seasonal breeding of each nesting site was evaluated through multi-seasonal occupancy models and subsequently differences between curves of seasonality were evaluated with functional data analysis (FDA) methods. We found differences in seasonal breeding between sites in terms of time of onset of breeding and magnitude of occupancy. A higher probability of occupancy was associated in order of importance to large colony size, higher primary production and shallower

oxycline and geographic covariates (lower latitude, higher distance to the coast and effect island). The timing of breeding depended also of the nesting site, in some nesting sites seabirds timed onset of breeding early in the autumn-winter, others during winter-spring. Early breeding onset was associated in order of importance to large colony size (more evident in cormorants), geographic covariates (lower latitude, higher distance to the coast and effect island) and high primary production. These results suggested that coloniality and social attraction can play an important role on the adjustment of breeding in the three species of seabirds to environmental conditions. Furthermore, the fact that coloniality and local oceanographic conditions had an important role structuring the dynamics of breeding seasonality is an evidence that seabirds can actively adapt its fecundity traits to much more small than a basin scale.

Further studies are required to investigate these hypotheses. A first procedure would rely on an intensive acoustic sampling of the surroundings of the seabird colonies with a dedicated survey design, in order to quantify precisely the effect of prey abundance, its degree of patchiness and vertical distribution on the installation of seabird breeding colonies. More difficult it is to prove that there is a social stimulation because it would require experimental studies to isolate social stimulation from prey conditions around the nesting sites. Living in large colonies can increase foraging and breeding success since colonies play the role of information center about the localization of prey and avoidance of predator (Brunton 1999; Weimerskirch *et al.* 2010). This fact supports the positive effect of large colonies in higher probabilities and early breeding. The remaining questions are about the optimal size of nesting site to function as information center and increase fitness of individuals (Pulliam & Caraco 1984; Brown 1988) and the stability of colony size and its causes (Jovani & Grimm 2008; Jovani, Mavor & Oro 2008; Jovani *et al.* 2012, 2015; Brown, Brown & Roche 2013). The last point can be easily revised with the data available by multistate mark recapture model (Barbraud *et al.* 2003). In multistate mark recapture model, colonies are seen as individuals, and their probability of occupancy and transit between classes of size are determined with a Markovian approach. Some critical points of this approach can be related to the short time series of data (only 12 years) to obtain robust results and the criteria used to create colony size classes since there is a high variability in size between colonies and there is a bias in counts.

Leaving aside the mechanistic explanation of colony dynamics, the differences between nesting sites is very useful information for the management of guano extraction and tourism. Main nesting colonies of the three seabirds species considered here are part of a National reserve of Guano Island and Headlands. National reserves in Peru are areas of protection and sustainably management of natural resources. SERNANP is the institution responsible for authorizing guano extraction by Agrorural, which in is the institution of guano production. Guano collection is an activity that demands the presence in the colonies of a large number of workers (50-300 workers) for periods ranging from 1 to 5 months (PROABONOS 2010). Activities of guano extraction are proposed with a year of anticipation and SERNANP authorizes guano extraction as long as seabirds did not begin reproduction ("Ley Reserva Islas y Puntas guaneras" 2001). The new

detailed seasonal breeding by nesting sites allows a better planning of guano extraction regarding the breeding of seabirds. These results also help for designing better monitoring programs of population seabirds. For example, the difference of seasonal breeding between nesting sites must be considered when evaluating fecundity parameters such as timing of reproduction, breeding success, growth rates of chicks and clutch size.

Chapter IV addressed the variability of breeding seasonality at decadal time scale. In the last fifty years, the NHCS had two major regime shifts that triggered three contrasted decadal periods (1950-1970, 1970-1990 and 2000s) regarding oceanographic conditions and biological components as the abundance of anchovy and seabirds. The objective of this chapter was to explore if the seasonality of the seabird reproduction was affected by these changes in oceanographic conditions and prey availability, and by the increasing anchovy fishery pressure. Using a dynamic multiseason occupancy models, we estimated the timing and magnitude of onset and occupancy of breeding for a nesting site during the three different periods. Furthermore, we related the timing and magnitude of breeding seasons to seasonal ecosystem variability in terms of oceanographic conditions, biomass, and availability of anchovy and fishing pressure. We found that the degree of change in seasonal breeding between periods varied differently for the three species. Cormorants adjusted the timing of onset of their breeding between spring and winter. Pelicans and cormorants modulated the magnitude of their breeding attempts according to decadal periods. Meanwhile, boobies kept the same timing and magnitude of breeding attempts.

In case of cormorants we can consider a higher plasticity to tune the timing of the onset related to their good diving capacities that allow them to exploit a larger vertical range of the water column compared to the other two species. However, its skipping of breeding some years can also indicate a high sensitivity to lower abundance of anchovy, may be due to its strategy consisting in foraging in groups and using social information to locate prey. Consequently, cormorants need a large number of individuals to locate prey, however during low abundance of anchovy, fewer individuals may be reproducing and its number is not enough to use its information of prey location because patch of anchovy can be more quickly consumed and less predictable. In case of boobies, it can be consider a lower plasticity of seasonal breeding because its maintenance of magnitude and timing of seasonal breeding when lower abundances of anchovy. In particular to explain the booby maintenance of breeding magnitude during lowest anchovy abundances, there were presented three hypotheses: i) booby is not affected by low abundance of anchovy because they can rely in other preys; ii) booby is not affected by low abundance of anchovy because they can forage individually which make that breeding is still done but not in large numbers; and iii) boobies can adjust other fecundity traits as clutch size, growth rate of chicks or eventually abandon nest if prey abundance are insufficient to continue breeding. However there were no data or bibliography to test these hypotheses.

To sum up, we suggested that there is a gradient of seasonal breeding plasticity between the three species of seabirds with cormorants showed the highest plasticity whereas boobies showed the

lowest plasticity. Difference in plasticity between species must be considered when modeling and forecasting the population dynamic of the three seabirds facing sever changes as climate change. Although, further scientific studies would be needed to elucidating the hypothesis made about the possible causes and consequences of seasonal breeding plasticity.

First, there is scarce information about diet composition and fecundity traits. Diet compositions of Peruvian seabirds have been evaluated from pellets for cormorant and regurgitates from boobies and there is no studies for pelicans. If change of prey item during low abundance of anchovy has been reported for booby and cormorant most studies presented average diet compositions (Jahncke *et al.* 1997b; Garcia-Godos & Goya 2000). New studies are needed, possibly at the individual scale, in order to evaluate changes in diet according to age, breeding stage or body condition and the consequence of changes in diet (Sorensen *et al.* 2009; Kowalczyk *et al.* 2015). One cost-effective proposal would be to use the same methodology of pellets and regurgitate collection, yet to identify the samples in such a way that one individual may be traced down (Malacalza, Poretti & Bertellotti 1994). Stable isotopes could provide and alternative and complementary option. Depending on the tissue collected (feather, blood, regurgitates, muscle) diet composition could be inferred at several time scales (Sorensen *et al.* 2009; Kowalczyk *et al.* 2015).

Second, to test plasticity of other fecundity traits in seabirds (as clutch size, growth rate of chicks, reproductive success and productivity) to different regimes of anchovy abundance it can be describe the bases of that plasticity in average conditions. Less is known growth rate of chicks and reproductive success in boobies (Galarza Ninaya 1968) and nothing is known for the other two species except for some approximation of other species from the same genus (Ricklefs 1968). We proposed select at least two different breeding sites in timing and magnitude of breeding (following the results of the previous chapter), and evaluate the number of eggs, hatching success, growth rate of chicks and reproductive success. First evaluated the intraspecific variation of these parameters and then compared between species for an average breeding season. These measures can be coupled with diet composition (pellets and regurgitation collection and isotope analysis) to investigate its effect on fecundity traits. . One critical point in this methodology is the handling of chicks, especially in the case of pelicans that are very sensitive to disturbance. This first approach can be useful to compare between breeding seasons with different environmental conditions.

In summary, the results obtained evidenced a marked seasonal breeding in the three study seabirds. In general they lay eggs in winter-spring and end reproduction with independence of the juveniles during summer. This timing of breeding corresponded with optimal environmental conditions during independence of juveniles. However, breeding can start two-three months earlier and, most probably may occur all year round in large colonies of cormorants. Thus, seabirds may adapt their breeding seasonality to some extent due to spatial effects. The three

seabirds also adapt their timing and magnitude of reproduction to different regime shifts in the ecosystem. The extent of timing and magnitude adaptation depends on the species being cormorant the most sensitive to changes and boobies and pelicans the less sensitive to changes. The difference adjust of the three seabirds in breeding seasonality to cope with temporal and spatial variability suggested that we need to consider species specific approaches to model the population dynamic to cope with environmental fluctuation.

I strongly suggest implementing a project that target understanding the population dynamic than continue to guess through poor data how could be the population of seabirds the next year or the next El Niño event.

Finally, some propositions may be made for improving the modeling of seabird population dynamic in the NHCS. First, nest densities should be frequently estimated in each nesting site so that the bias affecting the conversion from surfaces to seabird numbers would be reduced. Also, standardized maps in each nesting site would ease the guardian work. Agrorural needs also to be supported in the effort of field data collection, notably to store, secure and make them available to the public. State-space models based in counts can be improved by incorporating density-dependent effect (Lande, Engen & Saether 2003; Dennis *et al.* 2006) and observation bias (Dail & Madsen 2011). Furthermore, modeling population dynamic only from counts cannot explain demographic causes of changes because models are only based on growth rate of population. If the aim is to obtain trends in population, estimating survival probability would be more interesting. Models that can estimate survival are more mechanistic as Jolly-Seber, Cormack Jolly-Seber and multistate models (Kéry & Schaub 2012). More mechanistic models are built from capture-recapture over time (Figure 5.2) or marks recover. The flexibility of these models and the richness of the information of capture-recapture method allow incorporating spatial-time effects and individual effects for example age effect.
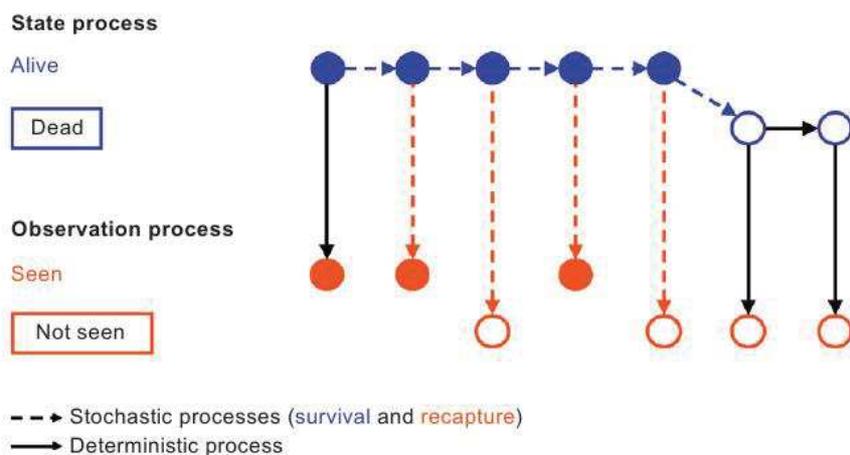


Figure 5.2. Example of the state and observation process of a marked individual over time for the Cormack Jolly Seber model. The sequence of true states in this individual is z = [1, 1, 1, 1 ,1, 0, 0],and the observed capture-history is y = [1, 1, 0, 1, 0, 0, 0].Source Kéry & Schaub 2012.

An integral view is the combination of the counts and capture-recapture data through more powerful Integrated Population Models (IPM). IPM gets deeper insight into population dynamic and better estimates of demographic quantities. In the Figure 5.3 (Kéry & Schaub 2012) we can see the links between Count Data, Capture-recapture data and also reproductive success or productivity data (*f*) which come from number of nestling counted in the year (*J*) and number of surveyed broods (*R*).
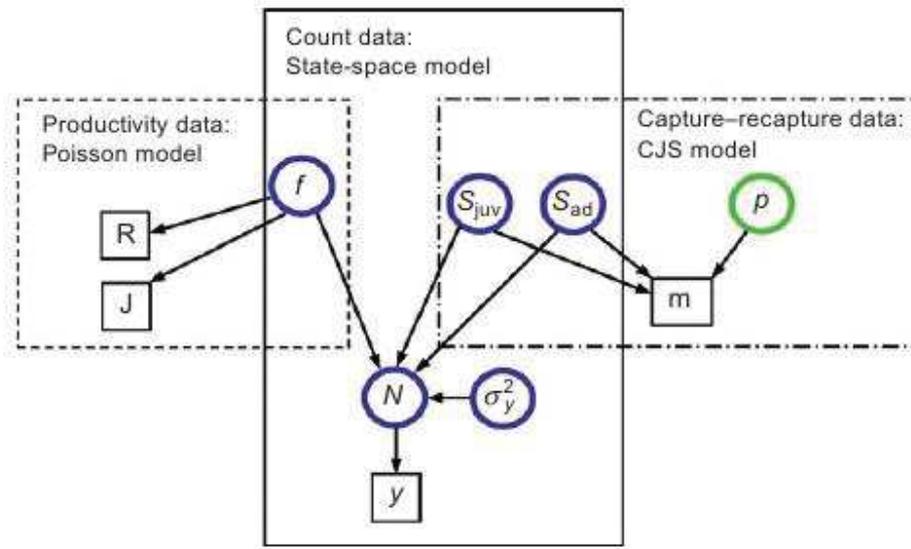


Figure 5.3. Graphical representation of an integrated population model (IPM) within a Bayesian approach. Small squares represent the data, circles the parameters (blue: target parameters, green: nuisance parameters), large squares the individual submodels, and arrows the flux of information. Circles appearing in two submodels indicate that they are informed from two data sources. IPM model represent three data types: i) count data where *y* is the observed data, *N* is the true abundance and $\sigma^2 y$ is the observational error; ii) productivity data where *J* is the number of nestling recorded and *R* is the annual number of surveyed broods; and iii) capture-recapture data where m is the number of released individuals never captured, $S_{juv}$ and $S_{ad}$ are survival of juveniles and adults respectively and *p* is the observational error. Source Kéry & Schaub 2012.

These ultimate hierarchical models could be the best option to understand the population dynamic of the seabirds in the NHCS. However, to fit these kind of models is requested a time series of at least 5-10 years (Kéry & Schaub 2012). The IPM offers an unbiased estimation of demographic variables and can solve several questions about the demography of seabirds as the resilience and eventual sensitivity to climate change. We hope that this approach can interested some of the institution involved in the management and conservation of seabirds in NHCS. Since profits in information get from this approach are higher than the implementation cost.

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# ANNEXE 1

Supplemental material of Chapter 2

APPENDIX A. Summary of the first report on the breeding phenology of guano-producing seabirds and food availability in the NHCS Peruvian ecosystem (adapted from (Vogt 1942).

APPENDIX B. Approximate duration of the main breeding stages of Peruvian seabirds.

APPENDIX C. A detailed description of seabird land-based census methodology.

APPENDIX D.A detailed description of the size of colonies of Peruvian seabirds.

APPENDIX E. Detailed description of oceanographic data used to build monthly climatologies and later synthesized by principal component analysis (PCA).

APPENDIX F. Detailed description of acoustic data used to build monthly climatologies of abundance and horizontal distribution of anchovy

APPENDIX G. Detailed description of data used to build monthly climatologies of physiological conditions of anchovy.

APPENDIX H. Equations of the logit link for occupancy model with covariates and ANODEV test used to compare models.

Appendix I. Detailed results of occupancy models for onset and termination of breeding of Peruvian seabirds.

APPENDIX A. Summary of the first report on the breeding phenology of guano-producing seabirds and food availability in the NHCS Peruvian ecosystem (adapted from (Vogt 1942).

One of the first studies on the phenology of guano-producing seabirds in the NHCS was made by Vogt (1942) from a compilation of monthly reports by island wardens from 1916 to 1941. This included almost 25 years of observations with the exception of 1925 (lost report). Each report consigned monthly data on the percentage of seabirds incubating eggs and the local abundance of anchovy close to the nesting site. Incubating seabirds were reported when the presence of eggs was observed. Anchovy abundance was inferred from seabirds observed feeding close to the nesting site. In total 667 reports for cormorants, 473 for boobies and 138 for pelicans were analyzed from six nesting places: Lobos de Tierra, Guanape, Macabi, Chincha Norte, Ballestas and Santa Rosa. Reports on anchovy abundance were approximate and irregular in time, but the data were consistent for the presence of eggs (Vogt 1942). A peak laying period was observed for all three species from September to January with a maximum reached in November (Fig. A1).
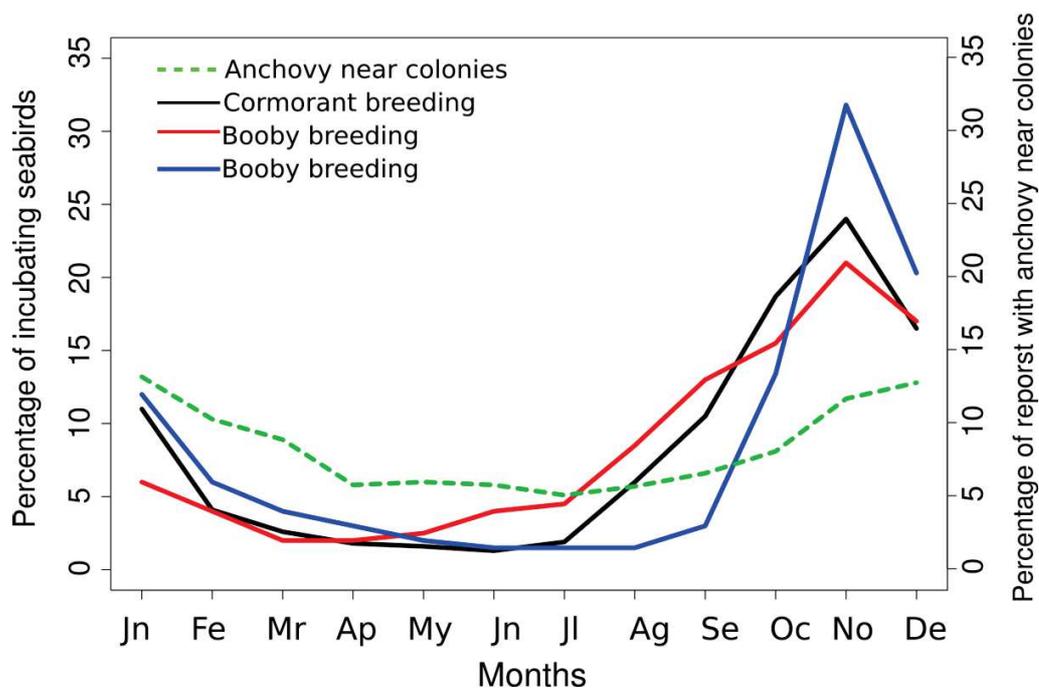


FIG A1. Monthly percentage of seabirds observed incubating eggs for pelicans (blue line), boobies (red line), and cormorants (black line). Monthly percentage of anchovy abundance near the nesting place is also shown (dashed green line). Redrawn from Vogt (1942).

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APPENDIX B. Approximate duration of the main breeding stages of Peruvian seabirds.

Table B1. Approximate duration of the main breeding stages (in days) from pre-laying attendance to the independence of fledglings for cormorants, boobies and pelicans. Information is based on Schreiber (2002), Nelson (2005), Tovar Serpa and Cabrera Quiroz (2005). Pre-laying attendance includes forming a couple and building a nest, post-fledging includes rearing of young by adults after fledging.

|  | Cormorant | Booby | Pelican |
|---|---|---|---|
| Pre-laying attendance | 28 | 28 | 14 |
| Incubation | 28 | 42 | 37 |
| Rearing | 56 | 98 | 80 |
| Post-fledging | 30 | 35 | 30 |
| Total | 142 | 203 | 161 |

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APPENDIX C. A detailed description of seabird land-based census methodology.

The three studied seabird species are considered to produce guano that is commercially exploited as fertilized in the NHCS. Guano has been exploited since the end of the 18th century by Peru. Nowadays AGRORURAL is the state institution in charge of harvesting and trading guano. AGRORURAL also ensures the conservation and protection of seabirds in 31 breeding sites (islands or headlands). These 31 sites are considered to host the densest seabird populations of the Peruvian coast. At each breeding site, AGRORURAL permanently maintains the presence of two wardens in charge of protecting and monitoring seabird colonies. Monitoring consists in monthly land-based censuses, generally performed from the most elevated point of the site, at sunrise at the end of a given month. Wardens plot the observed patches of cormorants, boobies and pelicans on a standardized map of the site (see below). Information on age (adult, young, chick, egg) and reproductive status (reproductive and non-reproductive individuals) are recorded for each observed patch of birds (Fig. C1). The relative surface of each patch is estimated with a sheet of graph paper. The number of seabirds within each patch is then inferred by multiplying those surfaces by a species-specific conversion factor of individuals per m² (Fig. C1). These conversion coefficients were estimated empirically and have not changed since 2003 (AGRORURAL personal communication). Seabirds nesting on cliffs are counted individually. Land-based censuses were conceived in the 1960's (Jordan & Fuentes 1966; Duffy 1994) with the aim of estimating the annual population of seabirds to extrapolate the amount of guano produced. Detailed information by island and by month was lost over the years because only yearly mean data were frequently used and published (Jordan & Fuentes 1966; Jahncke 1998). Detailed monthly colony data is only available since 2003.
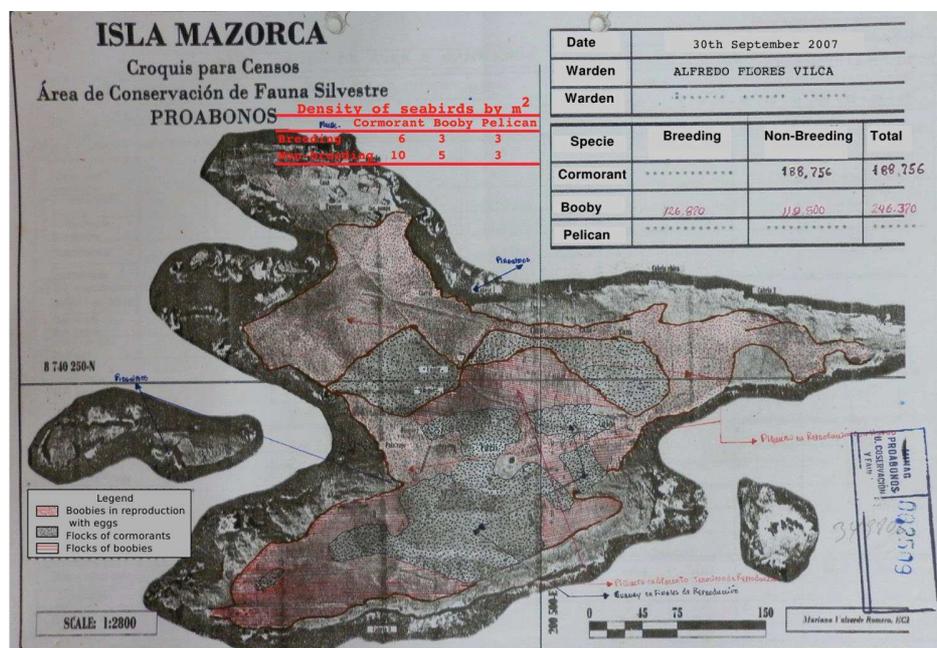


FIG. C1. Example of an original field data sheet of the seabird census for Mazorca Island on September 2007. Information about occupied patches by species, age and reproductive status were recorded. Surface occupancy was converted to abundances by multiplying surface occupancy by a species-specific conversion factor of density by m². Some labels were translated for better understanding.

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APPENDIX D.A detailed description of the size of colonies of Peruvian seabirds.

We define a seabird colony as a group of breeding individuals at a breeding site, while we consider as a flock birds which are gregarious but not breeding (Coulson 2002). Breeding colonies are formed for a few months in the year (Table D2), birds grouping into non-breeding flocks during the rest of the year.

Colony size for the three seabird species, and especially Guanay cormorants and Peruvian boobies, was very large (Nelson 2005). Monthly censuses showed a high variation with a strong right skew in colony size distribution. This skew was largely influenced by the absence of breeders during some months (percentage of data indicating absence of colonies: 78% for cormorants, 65% for boobies and 83% for pelicans). However, the right skew in colony size remained, even when removing the absence of breeders from the data. Highly right-skewed distributions are typical seabird colony size (Jovani *et al.* 2008). A better representation may therefore be obtained with a log10-transformation of abundance data (Fig. D1).

Most of the time, colony size was tens of thousands of breeders for cormorants and boobies, and thousands of breeders for pelicans (Fig. D1). Minimal values of colony size are indicated in Table D1. These small colonies of tens of individuals only represented 1.76% of the abundance data for cormorants, 4.61% for boobies and 5.92% for pelicans. Such small proportions made it possible to work with presence/absence data, as we were confident that in the vast majority of cases presence reports corresponded to large colony sizes.

TABLE D1. Minimum, mean and maximum colonies size (number of individuals) for the Guanay cormorant, the Peruvian booby and the Peruvian pelican.

| Species | Minimum | Mean | Maximum |
|---|---|---|---|
| Cormorant | 18 | 68542 | 875000 |
| Booby | 10 | 34376 | 601520 |
| Pelican | 18 | 9070 | 150000 |

TABLE D2. Percentage of nesting sites occupied in every month, averaged over all years for the Guanay cormorant, the Peruvian booby and the Peruvian pelican.

| Months | Cormorant | Booby | Pelican |
|---|---|---|---|
| January | 19.35 | 35.81 | 21.61 |
| February | 15.16 | 20.97 | 15.48 |
| March | 10.32 | 15.16 | 9.03 |
| April | 5.81 | 12.58 | 4.19 |
| May | 6.77 | 12.90 | 1.29 |
| June | 10.00 | 11.94 | 1.94 |
| July | 13.87 | 13.87 | 3.87 |
| August | 19.35 | 20.97 | 8.39 |
| September | 21.29 | 37.42 | 17.10 |
| October | 26.77 | 53.87 | 23.23 |
| November | 27.74 | 50.00 | 27.10 |
| December | 27.10 | 46.77 | 25.81 |
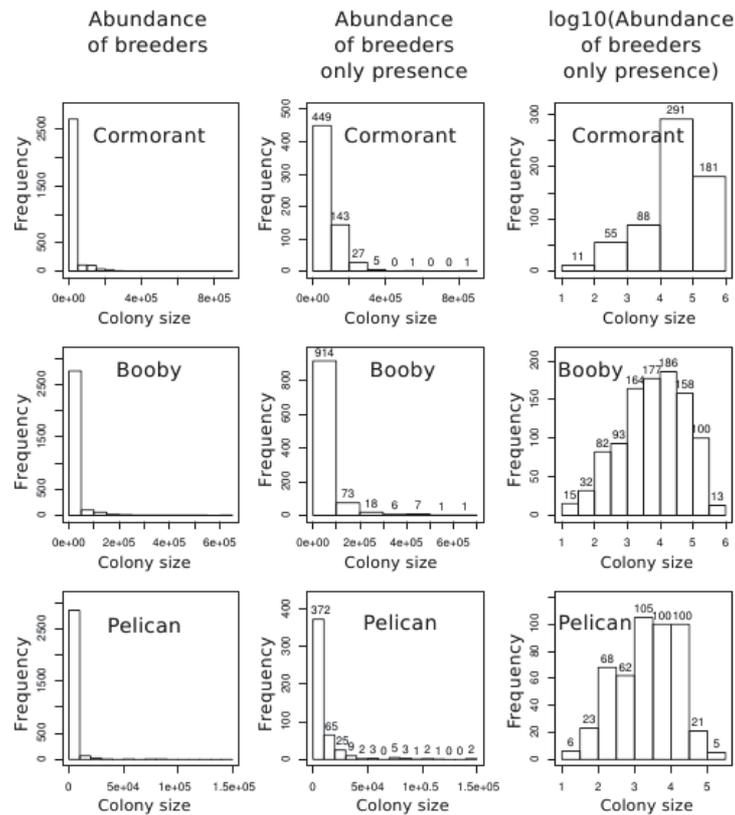
FIG. D1. Colony size frequency distribution for the three species of cormorants, boobies and pelicans. Histograms correspond to the raw abundance data (left column), the abundance data without breeder absences (central column), the abundance data without breeder absences once log10-transformed (right column).

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Nelson, B. 2005. Pelicans, Cormorants and their relatives Pelecanidae, Sulidae, Phalacrocoracidae, Anhingidae, Fregatidae, Phaethontidae. Pages 1–661 Bird Families of the World. Oxford University Press, Oxford.

APPENDIX E. Detailed description of oceanographic data used to build monthly climatologies and later synthesized by principal component analysis (PCA).

Satellite remotely sensed chlorophyll-a concentrations (Chlo, mg m$^{-3}$) and sea surface temperatures (SST, °C) were obtained from the MODIS satellite (http://oceancolor.gsfc.nasa.gov/) from July 2002 to December 2012, with a 4×4 km$^2$ spatial resolution and 8-day temporal resolution. The upwelling index was calculated from wind speed components obtained from QuikSCAT (http://podaac.jpl.nasa.gov/datasetlist?ids=Platform&values=QuikSCAT) using the equation: $UI = \dfrac{\tau}{\rho f} 100$ where $\tau$ is the projection of the wind stress on the axis parallel to the coast, $\rho$=1025 kg.m$^{-3}$ is the seawater density and $f$ the Coriolis parameter. UI is expressed in units of cubic meters per second per 100 meters of coastline.

The wind speed components were obtained from July 1999 to November 2009 with a 0.5°×0.5° spatial resolution and 8-day temporal resolution. Dissolved oxygen concentration in the surface layer (DO, ml l$^{-1}$) and the oxycline depth ($Z_{2ml\,l^{-1}}$, m) were obtained from regional climatology profiles at a 0.1°×0.1° spatial resolution produced from *in situ* observations collected by Instituto del Mar del Perú (IMARPE) from the 1960's to 2010. The oxycline depth was defined as the depth of the 2ml l$^{-1}$ isopleth (Bertrand *et al.* 2011). Chlo, SST, UI, DO and $Z_{2ml\,l^{-1}}$ values were spatially averaged over a 100 km-radius area surrounding each breeding colony, and temporally averaged to produce monthly climatology profiles (Fig. E1).

Monthly climatology profiles of oceanographic covariates described above were synthesized using the first axis of a principal component analysis (PCA) to use instead of the original variables, thereby limiting the number of covariates in the analyses and control for variable interdependence.
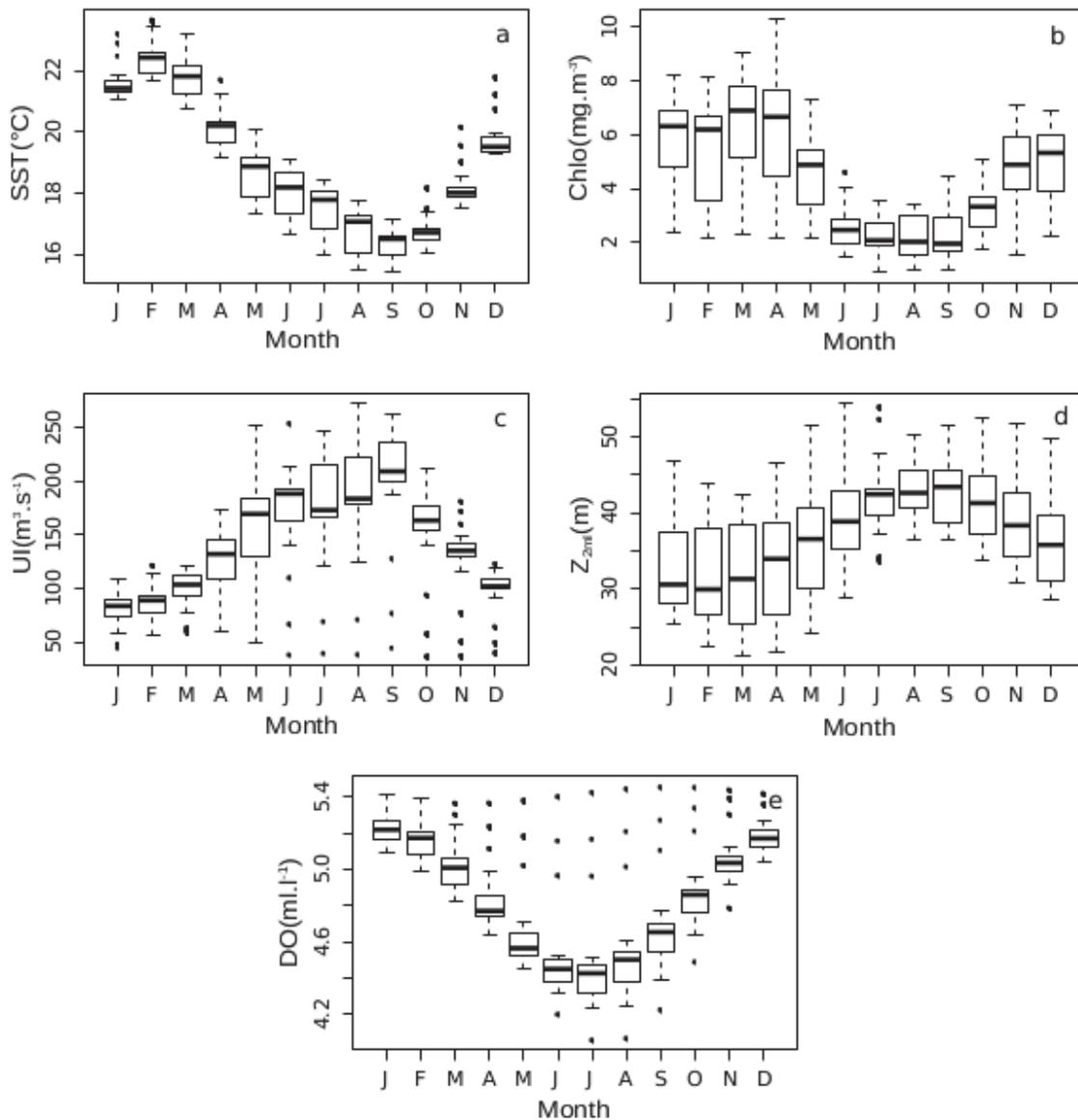
FIG.. E1. Monthly climatology profiles of (a) sea-surface temperature (SST), (b) chlorophyll (Chlo), (c) upwelling index (UI), (d) oxycline depth ($Z_{2ml\,l^{-1}}$) and (e) dissolved oxygen concentration (DO) at the surface. The boxplots were constructed from the site-specific climatology profiles built over an area covering a radius of 100 km around each breeding site. Periods encompassed 1999-2009 for SST, Chlo and UI and 1960-2010 for DO and $Z_{2ml\,l^{-1}}$.
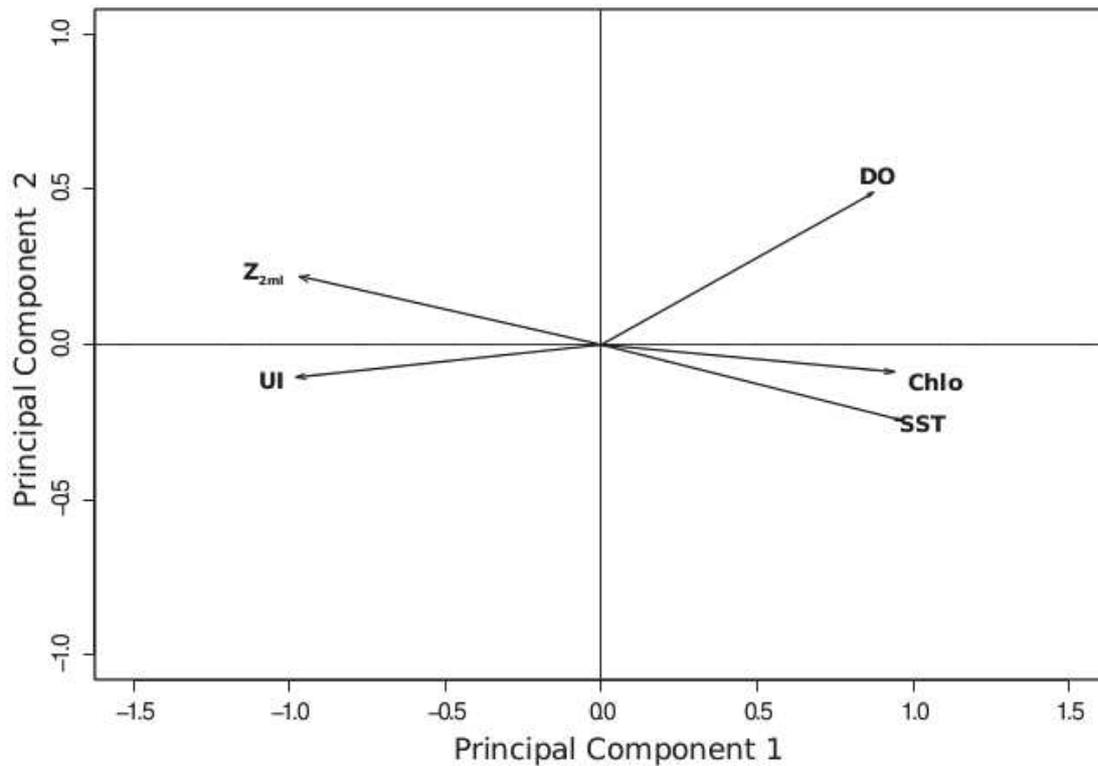
FIG. E2. Results from a principal component analysis of oceanographic covariates. The x-axis represents the first principal component (89.1% of the variance) and the y-axis represents the second principal component (7.3% variance).

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APPENDIX F. Detailed description of acoustic data used to build monthly climatologies of abundance and horizontal distribution of anchovy

Acoustic data were acquired by routine acoustic surveys performed along the Peruvian coast (3°S-18°S) by the Instituto del Mar del Perú (IMARPE). Acoustic surveys have been performed by IMARPE to measure anchovy biomass of since 1983. These surveys were done 2-3 times per year and lasted between 1-3 months. In general, the survey design consisted in parallel cross-shore transects of ~100 nm long and ~15 nm inter-transects (Fig. F1). Surveys were undertaken with scientific vessels, most commonly the RV "Humboldt" (76 m long), the RV "Olaya" (41 m long), and the RV "SNP-2" (36 m long). Vessels were equipped with hull mounted 38 and 120 kHz Simrad split beam scientific echosounders (EK, EKS, EK400, EY500, EK500, and EK60). Further details on the acoustic methodology are provided by Gutiérrez et al. (2007) and Simmonds et al. (2009). For the purpose of our study, we used the 1999-2011 surveys in order to compare them with the onset and termination of seabird breeding events. This period was chosen to match seabird data and besides, the 2000's are considered as a "full anchovy era" markedly different from the 1990's (Gutiérrez *et al.* 2007). We also subsampled the area between latitudes 6°S and 14°S and between the coast and 40 km offshore to cover the observable range of anchovy distribution and reduce bias in anchovy abundance due to latitudinal and longitudinal extents of surveys. Climatologies were built for each index using 38 acoustic surveys from 1999 to 2011(Table F1, Fig. F2).
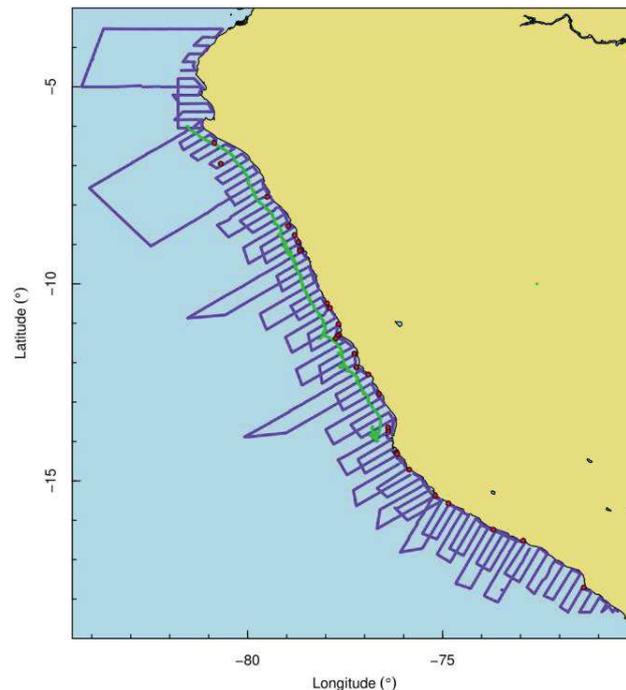


FIG. F1. An example of a systematic parallel cross-shore transects used on a Peruvian acoustic anchovy survey from November to December of 2006 involving one vessel research. Red points indicate seabird nesting sites and the green line indicates the first 40 km offshore limit used to calculate montly climatologies of abundance and horizontal distribution of anchovy.

TABLE F1. List of cruises which data have been used to compute monthly climatologies of abundance and horizontal distribution of anchovy.

| Name | Latitude start | Latitude end | Date start | Date end | Months designated in climatology |
|---|---|---|---|---|---|
| Cr9902-03 | -3.75 | -18.34 | 14/02/1999 | 28/03/1999 | February-March |
| Cr9906-06 | -4.98 | -14.42 | 14/06/1999 | 24/06/1999 | June |
| Cr9908-09 | -3.493 | -13.9138 | 28/08/1999 | 17/09/1999 | September |
| Cr9911-12 | -6.01 | -15.3032 | 25/11/1999 | 14/12/1999 | December |
| Cr0001-02 | -3.55 | -18.34 | 20/01/2000 | 26/02/2000 | February |
| Cr0006-07 | -4.99 | -16.12 | 10/06/2000 | 07/07/2000 | June |
| Cr0008-09 | -5.88 | -13.96 | 28/08/2000 | 23/09/2000 | September |
| Cr0010-11 | -4.567 | -18.3355 | 11/10/2000 | 13/11/2000 | October |
| Cr0102-04 | -3.54 | -18.33 | 03/03/2001 | 10/04/2001 | March |
| Cr0107-08 | -3.4615 | -18.3314 | 05/07/2001 | 06/08/2001 | July |
| Cr0108-09 | -5.8357 | -14.2933 | 30/08/2001 | 28/09/2001 | September |
| Cr0110-11 | -3.417 | -18.333 | 07/10/2001 | 10/11/2001 | October |
| Cr0202-03 | -3.4955 | -18.3496 | 21/02/2002 | 28/03/2002 | March |
| Cr0208-08 | -3.6567 | -14.8369 | 10/08/2002 | 31/08/2002 | August |
| Cr0210-11 | -4.25 | -18.40 | 01/10/2002 | 13/11/2002 | October-November |
| Cr0302-03 | -3.4914 | -18.3257 | 28/02/2003 | 31/03/2003 | March |
| Cr0308-09 | -3.6104 | -14.3488 | 16/08/2003 | 15/09/2003 | August-September |
| Cr0310-11 | -3.64 | -18.30 | 27/10/2003 | 08/12/2003 | November |
| Cr0402-03 | -3.65 | -18.29 | 09/02/2004 | 22/03/2004 | February |
| Cr040809 | -4.96 | -15.38 | 07/08/2004 | 03/09/2004 | August |
| Cr0411-12 | -4.99 | -14.75 | 30/11/2004 | 17/12/2004 | December |
| Cr050204 | -2.39 | -18.33 | 23/02/2005 | 31/03/2005 | March |
| Cr0508-09 | -4.606 | -16.28 | 16/08/2005 | 22/09/2005 | August-September |
| Cr0511-12 | -4.98 | -13.69 | 28/11/2005 | 23/12/2005 | December |

| Cr0602-04 | -3.48 | -17.504 | 25/02/2006 | 12/04/2006 | March |
|-----------|-------|---------|------------|------------|-------|
| Cr0608-09 | -4.25 | -14.38 | 11/08/2006 | 04/09/2006 | August |
| Cr0611-12 | -3.523 | -18.34 | 11/11/2006 | 21/12/2006 | December |
| Cr0702-04 | -3.53 | -18.36 | 25/02/2007 | 05/04/2007 | March |
| Cr0708-09 | -4.06 | -18.32 | 11/08/2007 | 19/09/2007 | August-September |
| Cr080204 | -3.55 | -18.26 | 29/02/2008 | 08/04/2008 | March |
| Cr0811-12 | -4.98 | -17.99 | 23/11/2008 | 22/12/2008 | November-December |
| Cr090204 | -3.48 | -18.34 | 28/02/2009 | 13/04/2009 | March |
| Cr0912-12 | -8.23 | -16.40 | 08/12/2009 | 29/12/2009 | December |
| Cr100102 | -4.98 | -14.56 | 26/01/2010 | 15/02/2010 | February |
| Cr1008-09 | -4.50 | -15.02 | 17/08/2010 | 17/09/2010 | August-September |
| Cr1011-12 | -3.63 | -16.24 | 13/11/2010 | 21/12/2010 | November-December |
| Cr1102-04 | -3.41 | -18.30 | 26/02/2011 | 15/04/2011 | March |
| Cr1111-12 | -3.58 | -18.32 | 01/11/2011 | 15/12/2011 | November |
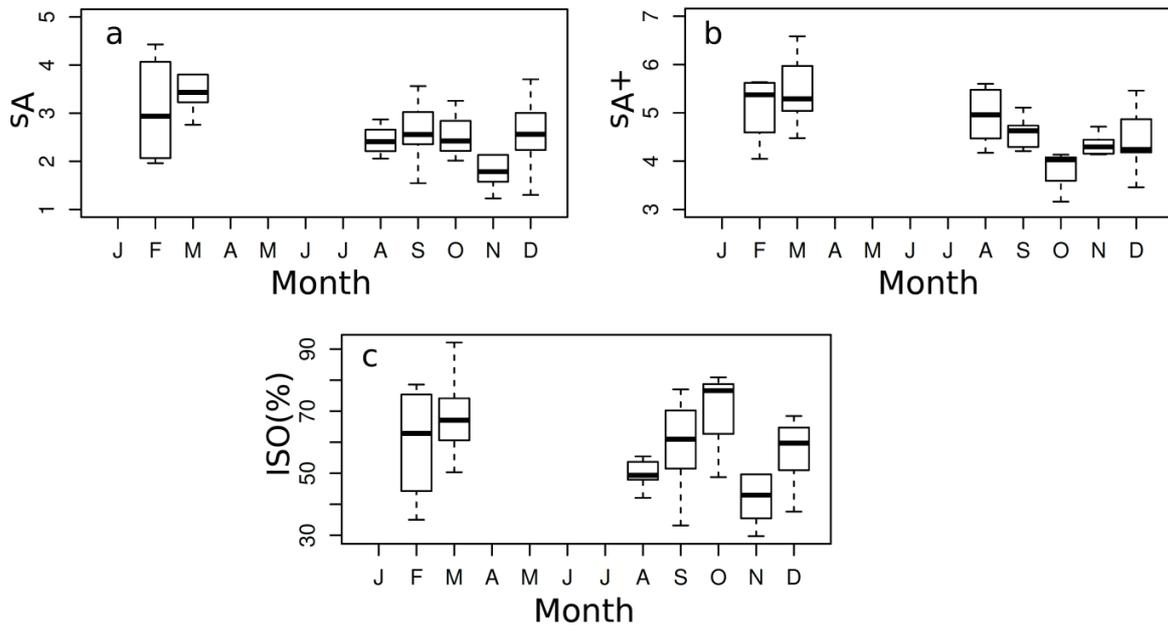
F_IG_. F2. Monthly variations of anchovy abundance (a) $s_A$, (b) $s_A+$ and (c) index of space occupation (ISO). The boxplots were constructed from the monthly variations of the metrics between 6° and 14°S over the period 1999-2011.

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Gutiérrez, M., G. Swartzman, A. Bertrand, and S. Bertrand. 2007. Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983-2003. Fisheries Oceanography 16:155–168.

Simmonds, J., M. Gutierrez, A. Chipollini, F. Gerlotto, M. Woillez, and A. Bertrand. 2009. Optimizing the design of acoustic surveys of Peruvian anchoveta. ICES Journal of Marine Science 66:1341–1348.

APPENDIX G. Detailed description of data used to build monthly climatologies of physiological conditions of anchovy.

Data collection was performed onboard fishing vessels or at fishmeal factories in the main ports of the Peruvian coast. For each catch, a sample of ≈2 kg of adult anchovy (≈ 12-20 cm) was collected. For each anchovy several measurements were taken *in situ*: anchovy total length (TL), total mass (TW) and gonadal mass (GW). The Gonado-somatic index (GSI) and the Body condition factor (BCF) were determined using these measurements (Buitron et al. 2011). GSI and BCF time series were obtained for two regions of the Peruvian coast i) the North-central stock (06°- 14° S) and ii) the South stock (16°-19°S). For the purpose of our study, we built a climatology for the North-central stock data from 2002 to 2012, since most seabird colonies were located within this area (Fig. G1).

Indices were calculated as follows:

The Body Condition Factor (BCF, in g.cm$^{-3}$) was defined as:

$$BCF = \left( \frac{TW - GW}{TL^{3}} \right) \times 100$$

where TW is the anchovy's total mass, GW its gonadal mass and TL its total body length.

The Gonado-somatic Index (GSI) was defined as:

$$GSI = \left( \frac{GW}{TW} \right) \times 100$$
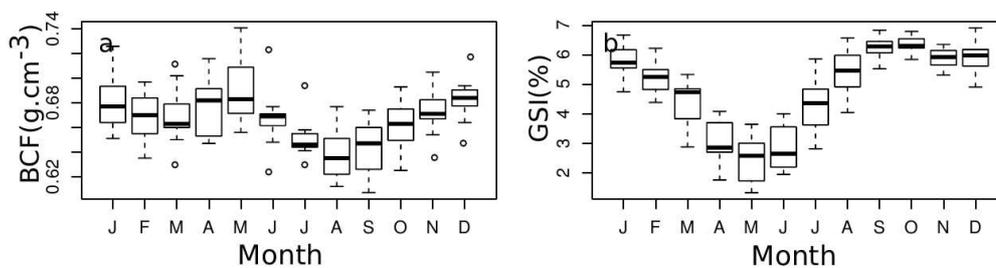


FIG. G1. Monthly variations of anchovy physiological condition metrics (a) body condition factor, BCF; and (b) Gonado-somatic index: GSI. Boxplots were constructed from monthly variations of the metrics between the 6° to 14°S over the 2000-2012 period.

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APPENDIX H. Equations of the logit link for occupancy model with covariates and ANODEV test used to compare models.

The linear model on the logit scale was defined as follows:

$$\log \left( \frac{y}{(1 - y)} \right) = \alpha + X\beta$$

where $y$ is the response variable (i.e. $\varepsilon$ or $\gamma$), $\alpha$ is the intercept, $X$ is a row vector containing the covariate values (geographic covariates, oceanographic and prey availability distribution, and physiological condition covariates), and $\beta$ is a slope parameter. When $\beta > 0$, the covariate has a positive effect on $y$. We used the logit function as it ensures response values to be comprised between 0 and 1 (MacKenzie *et al.* 2003).

ANODEV (Skalski, Hoffman & Smith 1993) is a method used to compare deviance explained by a covariate against deviance explained by the time-dependent model and the constant model.

The ANODEV ($F_{cst/cov/t}$) was defined as:

$$F_{cst \, / \, cov/ \, t} = \frac{\dfrac{Dev \, (F_{cst}) - Dev \, (F_{cov})}{J - 1}}{\dfrac{Dev \, (F_{cov}) - Dev \, (F_{t})}{n - J}}$$

where $Dev(F_{cst})$ is the deviance of the constant model, $Dev(F_{cov})$ is the deviance of the model with covariates, $Dev(F_{t})$ is the deviance of the time-dependent model, $n$ is the number of parameters for model $F_t$, and $J$ is the number of parameters for model $F_{cov}$. For the *F-test* tabular values, $J$-1 and $n$-$J$ are the degrees of freedom. The corresponding *F*-statistic tests the null hypothesis that the covariate has no effect on probabilities of breeding onset and termination. To quantify the proportion of time variation in probabilities of breeding onset and termination that was explained by a covariate, we used the following formula for $R^2$ (Grosbois *et al.* 2008):

$$R^2 = \frac{Dev \, (F_{cst}) - Dev \, (F_{cov})}{Dev \, (F_{cst}) - Dev \, (F_{t})}$$

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Grosbois, V., O. Gimenez, J. M. Gaillard, R. Pradel, C. Barbraud, J. Clobert, A. P. Møller, and H. Weimerskirch. 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews of the Cambridge Philosophical Society 83:357–399.

MacKenzie, D., J. Nichols, J. Hines, M. Knutson, and A. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Skalski, J. R., A. Hoffman, and S. G. Smith. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. Pages 9–28 in J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhauser Verlag, Basel, Switzerland.

Passuni, Giannina

Appendix I. Detailed results of occupancy models for onset and termination of breeding of Peruvian seabirds.

TABLE I1. Testing for Markovian processes in probabilities of breeding onset (γ) and breeding termination (ε) in cormorants, boobies and pelicans. The AIC (Akaike Information Criterion), ΔAIC (difference in Akaike Information Criterion), w (Akaike weight) and np (number of parameters of the model) are given.

| Biological hypothesis | Model | np | Cormorant | | | Booby | | | Pelican | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | AIC | ΔAIC | w | AIC | ΔAIC | w | AIC | ΔAIC | w |
| Markovian onset and termination | [γ,ε] | 4 | 1620.7 | 0 | 1 | 2336.6 | 0 | 1 | 1615.7 | 0 | 1 |
| Non-Markovian onset and termination | [γ=ε] | 3 | 3080.9 | 1460 | 0 | 3845.7 | 1509.1 | 0 | 2675.8 | 1060.1 | 0 |

TABLE I2. Modelling time variation of probabilities of breeding onset (γ) and termination (ε) in cormorants, boobies and pelicans. AIC (Akaike Information Criteria), ΔAIC (difference in Akaike Information Criteria), w (Akaike weight) and np (number of parameters of the model).

| Biological hypothesis | Model | np | Cormorant | | | Booby | | | Pelican | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | AIC | ΔAIC | w | AIC | ΔAIC | w | AIC | ΔAIC | w |
| Monthly onset and termination | [γ(m) ε(m)] | 26 | 1532.6 | 0.0 | 1 | 2105.0 | 0.0 | 1 | 1447.5 | 0.0 | 1 |
| Monthly onset | [γ(m) ε(.)] | 15 | 1574.8 | 42.2 | 0 | 2215.1 | 110.1 | 0 | 1514.5 | 67.0 | 0 |
| Monthly termination | [γ(.) ε(m)] | 15 | 1576.0 | 43.4 | 0 | 2247.3 | 142.3 | 0 | 1543.2 | 95.7 | 0 |
| Full time onset and termination | [γ(i) ε(i)] | 240 | 1687.1 | 154.5 | 0 | 2245.1 | 140.1 | 0 | 1663.8 | 216.3 | 0 |
| Full time onset | [γ(i) ε(.)] | 122 | 1681.3 | 148.7 | 0 | 2290.7 | 185.7 | 0 | 1627.5 | 180.0 | 0 |
| Full time termination | [γ(.) ε(i)] | 122 | 1632.0 | 99.4 | 0 | 2313.4 | 208.4 | 0 | 1645.3 | 197.8 | 0 |
| Constant onset and termination | [γ(.) ε(.)] | 4 | 1620.7 | 88.1 | 0 | 2336.6 | 231.6 | 0 | 1615.7 | 168.2 | 0 |

FIG. I1. Estimates of monthly probabilities of breeding onset (green solid line) and breeding termination (orange solid line) for (a) cormorants, (b) boobies and (c) pelicans in the Northern Humboldt Current System over 10 years. Shaded areas correspond to 95% confidence intervals.

TABLE I3. Modelling the effects of geographical covariates on the probabilities of breeding onset ($\gamma$) and breeding termination ($\varepsilon$) for cormorants, boobies and pelicans. AIC (Akaike Information Criteria), $\Delta$AIC (difference in Akaike Information Criteria), w (Akaike weight) and np (number of parameters of the model).

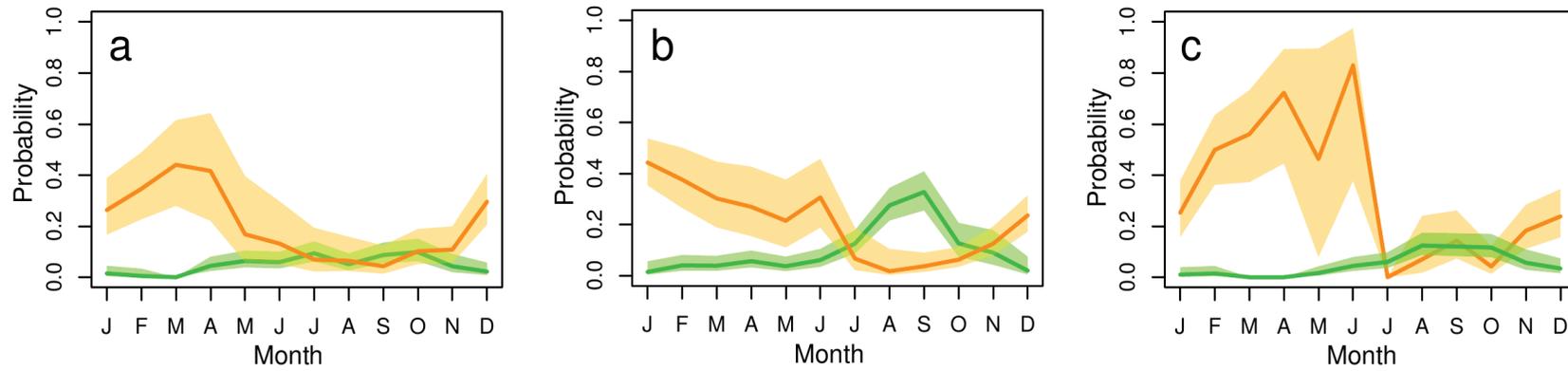| Biological hypothesis | Model | | Cormorant | | | Booby | | | Pelican | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | np | AIC | $\Delta$AIC | w | AIC | $\Delta$AIC | w | AIC | $\Delta$AIC | w |
| Effect of island/headland on onset | [$\gamma$(m+I/H) $\varepsilon$(m)] | 27 | 1499.1 | 0.0 | 0.72 | 1968.4 | 0.0 | 0.50 | 1425.4 | 20.1 | 0.00 |
| Effect of island/headland on onset and termination | [$\gamma$(m+I/H) $\varepsilon$(m+I/H)] | 28 | 1501.0 | 1.9 | 0.28 | 1968.4 | 0.0 | 0.50 | 1426.4 | 21.1 | 0.00 |
| Effect of island/headland on termination | [$\gamma$(m) $\varepsilon$(m+I/H)] | 27 | 1533.6 | 34.5 | 0.00 | 2100.5 | 132.1 | 0.00 | 1449.2 | 43.9 | 0.00 |
| Effect of distance to coast on onset | [$\gamma$(m+DC) $\varepsilon$(m)] | 27 | 1534.0 | 34.9 | 0.00 | 2077.5 | 109.1 | 0.00 | 1405.3 | 0.0 | 1.00 |
| Effect of distance to coast on onset and termination | [$\gamma$(m+DC) $\varepsilon$(m+DC)] | 28 | 1534.5 | 35.4 | 0.00 | 2078.2 | 109.8 | 0.00 | 1427.6 | 22.3 | 0.00 |
| Effect of distance to coast on termination | [$\gamma$(m) $\varepsilon$(m+DC)] | 27 | 1535.9 | 36.8 | 0.00 | 2105.3 | 136.9 | 0.00 | 1449.1 | 21.5 | 0.00 |
| Effect of latitude on onset | [$\gamma$(m+LAT) $\varepsilon$(m)] | 27 | 1527.3 | 28.2 | 0.00 | 2041.1 | 72.7 | 0.00 | 1428.5 | 23.2 | 0.00 |
| Effect of latitude on onset and termination | [$\gamma$(m+LAT) $\varepsilon$(m+LAT)] | 28 | 1526.6 | 27.5 | 0.00 | 2038.9 | 70.5 | 0.00 | 1428.4 | 23.1 | 0.00 |
| Effect of latitude on termination | [$\gamma$(m) $\varepsilon$(m+LAT)] | 27 | 1531.2 | 32.1 | 0.00 | 2100.8 | 132.4 | 0.00 | 1446.8 | 41.5 | 0.00 |
| Monthly onset and termination | [$\gamma$(m) $\varepsilon$(m)] | 26 | 1532.6 | 33.5 | 0.00 | 2105.0 | 136.6 | 0.00 | 1447.5 | 42.2 | 0.00 |

TABLE I4. Testing for the effects of oceanographic covariates on the probabilities of breeding onset ($\gamma$) and breeding termination ($\varepsilon$) for cormorants, boobies and pelicans using ANODEV. Oceanographic covariates are synthesized by the first component (PC1) of a principal component analysis (see Appendix M). Dev is the deviance of the model, the $F$ statistic of ANODEV (noted $F_{cst/cov/t}$) and its associated value ($P$) test the effect of the oceanographic covariate on monthly onset and termination probabilities, while $R^2$ provides a measure of the magnitude effect. I/H is the geographical effect that, for pelicans, changes to DC. The slope ($\beta$) ± SE indicates the shape of the relationship between $\gamma$ or $\varepsilon$ and PC1 taken with a one to three-month lag.

| Models | Cormorant | | | | | | Booby | | | | | | Pelican | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dev | $F_{cst/cov/t}$ | P | $R^2$ | $\beta$ | SE | Dev | $F_{cst/cov/t}$ | P | $R^2$ | $\beta$ | SE | Dev | $F_{cst/cov/t}$ | P | $R^2$ | $\beta$ | SE |
| [$\gamma$(m+I/H) $\varepsilon$(m)] | 1445.1 | | | | | | 1914.4 | | | | | | 1351.3 | | | | | |
| [$\gamma$(I/H) $\varepsilon$(m)] | 1489.0 | | | | | | 2103.0 | | | | | | 1426.2 | | | | | |
| [$\gamma$(I/H+PC1) $\varepsilon$(m)] | 1459.1 | 21.38 | **0.00** | 0.68 | -0.27 | 0.05 | 1979.7 | 18.89 | **0.00** | 0.65 | -0.46 | 0.05 | 1382.1 | 14.33 | **0.00** | 0.59 | -0.36 | 0.06 |
| [$\gamma$(I/H+PC1-1) $\varepsilon$(m)] | 1466.3 | 10.67 | **0.01** | 0.52 | -0.23 | 0.05 | 1956.7 | 34.58 | **0.00** | 0.78 | -0.48 | 0.05 | 1355.6 | 160.82 | **0.00** | 0.94 | -0.51 | 0.07 |
| [$\gamma$(I/H+PC1-2) $\varepsilon$(m)] | 1483.4 | 1.44 | 0.26 | 0.13 | -0.11 | 0.04 | 1979.8 | 18.85 | **0.00** | 0.65 | -0.45 | 0.04 | 1374.6 | 22.06 | **0.00** | 0.69 | -0.41 | 0.06 |
| [$\gamma$(I/H+PC1-3) $\varepsilon$(m)] | 1488.9 | 0.01 | 0.94 | 0.00 | 0.01 | 0.04 | 2058.2 | 3.12 | 0.10 | 0.24 | -0.27 | 0.04 | 1411.4 | 2.45 | 0.15 | 0.20 | -0.18 | 0.04 |
| [$\gamma$(m+I/H) $\varepsilon$(m)] | 1445.1 | | | | | | 1914.4 | | | | | | 1351.3 | | | | | |
| [$\gamma$(m+I/H) $\varepsilon$(.)] | 1509.0 | | | | | | 2048.1 | | | | | | 1432.8 | | | | | |
| [$\gamma$(m+I/H) $\varepsilon$(PC1)] | 1457.4 | 41.81 | **0.00** | 0.81 | 0.37 | 0.05 | 1945.9 | 32.49 | **0.00** | 0.76 | 0.4 | 0.05 | 1402.0 | 6.07 | **0.03** | 0.38 | 0.30 | 0.05 |
| [$\gamma$(m+I/H) $\varepsilon$(PC1-1)] | 1454.5 | 58.16 | **0.00** | 0.85 | 0.38 | 0.05 | 1946.9 | 31.15 | **0.00** | 0.76 | 0.41 | 0.04 | 1375.0 | 24.26 | **0.00** | 0.71 | 0.39 | 0.06 |
| [$\gamma$(m+I/H) $\varepsilon$(PC1-2)] | 1476.7 | 10.22 | **0.01** | 0.51 | 0.29 | 0.05 | 1986.9 | 8.44 | **0.02** | 0.46 | 0.39 | 0.04 | 1370.2 | 33.04 | **0.00** | 0.77 | 0.43 | 0.05 |
| [$\gamma$(m+I/H) $\varepsilon$(PC1-3)] | 1504.9 | 0.68 | 0.43 | 0.01 | 0.10 | 0.05 | 2036.0 | 0.99 | 0.34 | 0.09 | 0.13 | 0.03 | 1382.1 | 16.5 | **0.00** | 0.62 | 0.45 | 0.06 |

TABLE I5 . Testing for the effects of global ($s_A$) and local ($s_A+$) anchovy abundance and distribution (ISO) on the probabilities of breeding onset and breeding termination for cormorants, boobies and pelicans using ANODEV. Dev is the deviance of the model, the $F$ statistic of ANODEV (noted $F_{cst/cov/t}$) and its associated value ($P$) test the effect of prey abundance and distribution on monthly onset and termination probabilities, while $R^2$ provides a measure of the magnitude effect. I/H is the geographical effect that, for pelicans, pelican changes to DC. The slope ($\beta$) $\pm$ SE indicates the shape of the relationship between $\gamma$ or $\varepsilon$ and anchovy abundance and distribution.

| Models | Cormorant | | | | | | Booby | | | | | | Pelican | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dev | $F_{cst/cov/t}$ | $P$ | $R^2$ | $\beta$ | SE | Dev | $F_{cst/cov/t}$ | $P$ | $R^2$ | $\beta$ | SE | Dev | $F_{cst/cov/t}$ | $P$ | $R^2$ | $\beta$ | SE |
| [$\gamma$(m+I/H) $\varepsilon$(m)] | 1445.1 | | | | | | 1914.4 | | | | | | 1351.3 | | | | | |
| [$\gamma$( I/H) $\varepsilon$(m)] | 1489.0 | | | | | | 2103.0 | | | | | | 1426.2 | | | | | |
| [$\gamma$( I/H+$s_A$) $\varepsilon$(m)] | 1470.6 | 7.21 | **0.02** | 0.42 | -0.65 | 0.16 | 1981.5 | 18.11 | **0.00** | 0.64 | -2.57 | 0.10 | 1389.5 | 9.61 | **0.01** | 0.49 | -0.90 | 0.16 |
| [$\gamma$( I/H+$s_A$+) $\varepsilon$(m)] | 1479.7 | 2.69 | 0.13 | 0.21 | -0.40 | 0.13 | 1988.2 | 15.50 | **0.00** | 0.61 | -1.15 | 0.11 | 1386.1 | 11.52 | **0.01** | 0.54 | -0.75 | 0.11 |
| [$\gamma$(ISO) $\varepsilon$(m)] | 1480.4 | 2.44 | 0.15 | 0.20 | -0.40 | 0.13 | 2099.0 | 0.22 | 0.65 | 0.02 | -0.22 | 0.11 | 1423.8 | 0.33 | 0.58 | 0.03 | -0.19 | 0.12 |
| [$\gamma$( m+I/H) $\varepsilon$(m)] | 1445.1 | | | | | | 1914.4 | | | | | | 1351.3 | | | | | |
| [$\gamma$( m+I/H) $\varepsilon$(.)] | 1509.0 | | | | | | 2048.1 | | | | | | 1432.8 | | | | | |
| [$\gamma$( m+I/H) $\varepsilon$($s_A$)] | 1490.3 | 4.13 | 0.07 | 0.29 | 0.55 | 0.12 | 1974.1 | 12.33 | **0.01** | 0.55 | 0.83 | 0.10 | 1430.2 | 0.33 | 0.58 | 0.03 | 0.22 | 0.12 |
| [$\gamma$( m+I/H) $\varepsilon$($s_A$+)] | 1487.3 | 5.40 | **0.04** | 0.34 | 0.66 | 0.14 | 1959.5 | 19.91 | **0.00** | 0.67 | 1.11 | 0.12 | 1425.9 | 0.92 | 0.36 | 0.08 | 0.40 | 0.14 |
| [$\gamma$( m+I/H) $\varepsilon$(ISO)] | 1504.5 | 0.76 | 0.40 | 0.07 | 0.30 | 0.14 | 2020.1 | 2.64 | 0.14 | 0.21 | 0.58 | 0.11 | 1432.6 | 0.02 | 0.89 | 0.00 | 0.07 | 0.14 |

TABLE I6. Testing for the effects of anchovy physiological condition (BCF and GSI) on the probabilities of breeding onset and termination by cormorants, boobies and pelicans using ANODEV. Dev is the deviance of the model, the $F$ statistic of ANODEV (noted $F_{cst/cov/t}$) and its associated value ($P$) test the effect of anchovy condition on monthly onset and termination probabilities, while $R^2$ provides a measure of the magnitude effect. I/H is the geographical effect that, for pelicans, changes to DC. The slope ($\beta$) ± SE indicates the shape of the relationship between γ or ε and anchovy physiological condition, taken with a one to three-month lag.

| Models | Cormorant | | | | | | Booby | | | | | | Pelican | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dev | $F_{cst/cov/t}$ | P | $R^2$ | $\beta$ | SE | Dev | $F_{cst/cov/t}$ | P | $R^2$ | $\beta$ | SE | Dev | $F_{cst/cov/t}$ | P | $R^2$ | $\beta$ | SE |
| [γ(m+I/H) ε(m)] | 1445.1 | | | | | | 1914.4 | | | | | | 1351.3 | | | | | |
| [γ(I/H) ε(m)] | 1489.0 | | | | | | 2103.0 | | | | | | 1426.2 | | | | | |
| [γ(I/H+BCF) ε(m)] | 1479.7 | 2.69 | 0.13 | 0.21 | -0.45 | 0.15 | 1951.8 | 40.43 | **0.00** | 0.80 | -1.60 | 0.14 | 1377.2 | 18.92 | **0.00** | 0.65 | -1.04 | 0.16 |
| [γ(I/H+BCF-1) ε(m)] | 1475.9 | 4.25 | 0.07 | 0.30 | -0.54 | 0.15 | 1951.5 | 40.84 | **0.00** | 0.80 | -1.68 | 0.14 | 1367.8 | 35.39 | **0.00** | 0.78 | -1.09 | 0.14 |
| [γ(I/H+BCF-2) ε(m)] | 1485.9 | 0.76 | 0.40 | 0.07 | -0.28 | 0.16 | 2060.6 | 2.90 | 0.12 | 0.22 | -0.94 | 0.14 | 1414.2 | 1.91 | 0.20 | 0.16 | -0.70 | 0.15 |
| [γ(I/H+BCF-3) ε(m)] | 1488.9 | 0.02 | 0.89 | 0.00 | 0.05 | 0.17 | 2094.7 | 0.46 | 0.51 | 0.04 | 0.48 | 0.17 | 1423.8 | 0.33 | 0.58 | 0.03 | 0.27 | 0.17 |
| [γ(I/H+GSI) ε(m)] | 1489.0 | 0.00 | 0.99 | 0.00 | -0.01 | 0.01 | 2042.5 | 4.72 | 0.05 | 0.32 | 0.73 | 0.10 | 1404.4 | 4.11 | 0.07 | 0.29 | 0.53 | 0.12 |
| [γ(I/H+GSI-1) ε(m)] | 1485.0 | 1.00 | 0.34 | 0.09 | -0.19 | 0.01 | 2101.7 | 0.07 | 0.80 | 0.01 | -0.02 | 0.10 | 1423.5 | 0.37 | 0.55 | 0.04 | 0.16 | 0.10 |
| [γ(I/H+GSI-2) ε(m)] | 1476.6 | 3.94 | 0.08 | 0.28 | -0.36 | 0.10 | 2060.5 | 2.91 | 0.12 | 0.23 | -0.55 | 0.09 | 1419.7 | 0.95 | 0.35 | 0.09 | -0.25 | 0.10 |
| [γ(I/H+GSI-3) ε(m)] | 1468.9 | 8.45 | **0.02** | 0.46 | -0.46 | 0.10 | 1957.3 | 33.96 | **0.00** | 0.77 | -1.02 | 0.09 | 1381.4 | 14.88 | **0.00** | 0.60 | -0.70 | 0.11 |
| [γ(m+I/H) ε(m)] | 1445.1 | | | | | | 1914.4 | | | | | | 1351.3 | | | | | |
| [γ(m+I/H) ε(.)] | 1509.0 | | | | | | 2048.1 | | | | | | 1432.8 | | | | | |
| [γ(m+I/H) ε(BCF)] | 1478.5 | 9.13 | **0.01** | 0.48 | 1.06 | 0.21 | 1976.3 | 11.60 | **0.01** | 0.54 | 1.37 | 0.18 | 1421.0 | 1.69 | 0.22 | 0.14 | 0.72 | 0.22 |
| [γ(m+I/H) ε(BCF-1)] | 1481.2 | 7.70 | **0.02** | 0.44 | 0.92 | 0.18 | 1937.1 | 48.90 | **0.00** | 0.83 | 1.54 | 0.17 | 1393.4 | 9.36 | **0.01** | 0.48 | 1.17 | 0.20 |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| [γ(m+I/H) ε(BCF-2)] | 1496.1 | 2.53 | | 0.14 | 0.20 | 0.59 | 0.17 | 1996.6 | 6.27 | | **0.03** | 0.39 | 0.96 | 0.14 | 1384.8 | 14.33 | **0.00** | 0.59 | 1.29 | 0.19 |
| [γ(m+I/H) ε(BCF-3)] | 1508.9 | 0.02 | | 0.89 | 0.00 | 0.04 | 0.16 | 2047.6 | 0.04 | | 0.85 | 0.00 | -1.44 | 0.08 | 1416.9 | 2.42 | | 0.15 | 0.20 | 0.67 | 0.17 |
| [γ(m+I/H) ε(GSI)] | 1504.6 | 0.74 | | 0.41 | 0.07 | -0.27 | 0.05 | 2034.7 | 1.11 | | 0.32 | 0.10 | -0.36 | 0.10 | 1377.3 | 21.35 | **0.00** | 0.68 | -1.39 | 0.21 |
| [γ(m+I/H) ε(GSI-1)] | 1507.1 | 0.30 | | 0.60 | 0.03 | 0.19 | 0.13 | 2048.1 | 0.01 | | 0.92 | 0.00 | -0.02 | 0.10 | 1415.2 | 6.21 | **0.03** | 0.22 | -0.85 | 0.20 |
| [γ(m+I/H) ε(GSI-2)] | 1486.0 | 5.62 | **0.04** | 0.36 | 0.63 | 0.14 | 2024.9 | 2.10 | | 0.18 | 0.17 | 0.53 | 0.12 | 1431.2 | 0.20 | | 0.66 | 0.02 | 0.21 | 0.17 |
| [γ(m+I/H) ε(GSI-3)] | 1461.7 | 28.49 | **0.00** | 0.74 | 0.88 | 0.14 | 1952.9 | 24.73 | **0.00** | 0.71 | 1.08 | 0.13 | 1411.4 | 3.56 | | 0.09 | 0.26 | 0.63 | 0.15 |

# ANNEXE 2

Supplemental material of Chapter 3

Appendix A Geographic, environmental, seabird abundance and anchovy fisheries covariates

Apppendix B. Functional analysis

Appendix C Random forest

Appendix D: Exploration of seasonal curves: Mean and outliers

Appendix E. Importance of covariates evaluated with Random Forest

Appendix A Geographic, environmental, seabird abundance and anchovy fisheries covariates

Table A1. Main nesting colonies of cormorants, its geographic characteristics and average size total and for each species.

| Names | Code | Type | Latitude | Longitude | Surface (h) | Distance to the coast (km) | Cormorant | Booby | Pelican | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| Lobos de Tierra | Lt | I | -6.43 | -76.63 | 1426.25 | 16.61 | 17367 | 19309 | 41487 | 68413 |
| Lobos de Afuera | La | I | -6.95 | -73.70 | 235.81 | 60.63 | 50 | 40675 | 25183 | 64096 |
| Macabi | Mc | I | -7.79 | -76.40 | 7.78 | 8.85 | 152233 | 162903 | 36022 | 315969 |
| Guanape Norte | Gn | I | -8.53 | -77.21 | 34.87 | 9.90 | 87373 | 298419 | 17006 | 376675 |
| Guanape Sur | Gs | I | -8.57 | -78.80 | 26.17 | 13.08 | 209871 | 166911 | 18994 | 358300 |
| Chao | Ch | I | -8.76 | -76.40 | 15.33 | 3.61 | 214 | 7178 | 22 | 7390 |
| Corcovado | Cv | I | -8.94 | -76.39 | 3.75 | 5.53 | 1347 | 9484 | 0 | 10418 |
| Ferrol | Fe | I | -9.14 | -76.40 | 156 | 2.20 | 7625 | 6177 | 0 | 13470 |
| Santa | St | I | -9.16 | -71.38 | 142.42 | 5.49 | 19418 | 10390 | 15284 | 42165 |
| Colorado | Cl | H | -10.49 | -77.96 | 17.53 | 0.00 | 0 | 282 | 0 | 282 |
| D. Martin | Dm | I | -11.02 | -77.67 | 16.5 | 1.03 | 2958 | 142 | 66 | 3068 |
| Salinas | Sl | H | -11.29 | -78.62 | 91 | 0.00 | 14 | 22 | 21 | 56 |
| Huampanu | Hu | I | -11.33 | -78.96 | 2.25 | 6.75 | 11781 | 13132 | 118 | 23401 |
| Mazorca | Mz | I | -11.39 | -78.97 | 11.63 | 13.45 | 84095 | 109613 | 3 | 186540 |
| Pescadores | Pe | I | -11.77 | -77.71 | 16.45 | 6.71 | 161490 | 37689 | 1970 | 198982 |
| Cavinzas | Ca | I | -12.12 | -72.93 | 6.33 | 6.26 | 42 | 624 | 17 | 663 |
| Pachacamac | Pa | I | -12.30 | -77.89 | 23.6 | 2.48 | 523 | 238 | 1700 | 2395 |
| Asia | As | I | -12.79 | -76.20 | 70.86 | 2.66 | 49 | 408 | 6344 | 6613 |
| Chincha N. | Cn | I | -13.63 | -80.69 | 64.45 | 19.20 | 15958 | 182713 | 339 | 192737 |
| Chincha C. | Cc | I | -13.64 | -80.86 | 63.63 | 17.85 | 50934 | 108764 | 1037 | 152259 |
| Chincha S. | Cs | I | -13.65 | -74.85 | 27.38 | 17.01 | 6750 | 75277 | 857 | 81106 |
| Ballestas | Ba | I | -13.73 | -75.85 | 32.37 | 8.31 | 115384 | 43013 | 3690 | 145243 |
| La Vieja | Lv | I | -14.28 | -79.50 | 60.86 | 7.52 | 0 | 6600 | 31 | 6600 |

| Sta. Rosa | Sr | I | -14.32 | -77.74 | 27.7 | 2.21 | 167391 | 26308 | 12740 | 201270 |
|-----------|-----|---|--------|--------|------|------|--------|-------|-------|--------|
| Lomitas | Lmi | H | -14.72 | -76.90 | 6.9 | 0.00 | 0 | 17 | 0 | 17 |
| S. Juan | Sj | H | -15.37 | -77.26 | 54 | 0.00 | 132954 | 2417 | 6832 | 139881 |
| Lomas | Lo | H | -15.57 | -77.65 | 6 | 0.00 | 0 | 0 | 8 | 8 |
| Atico | At | H | -16.24 | -75.19 | 110 | 0.00 | 200 | 0 | 0 | 200 |
| La Chira | Lc | H | -16.52 | -78.66 | 16 | 0.00 | 0 | 0 | 28 | 28 |
| Coles | Ce | H | -17.71 | -76.16 | 149 | 0.00 | 11091 | 5773 | 2655 | 19518 |
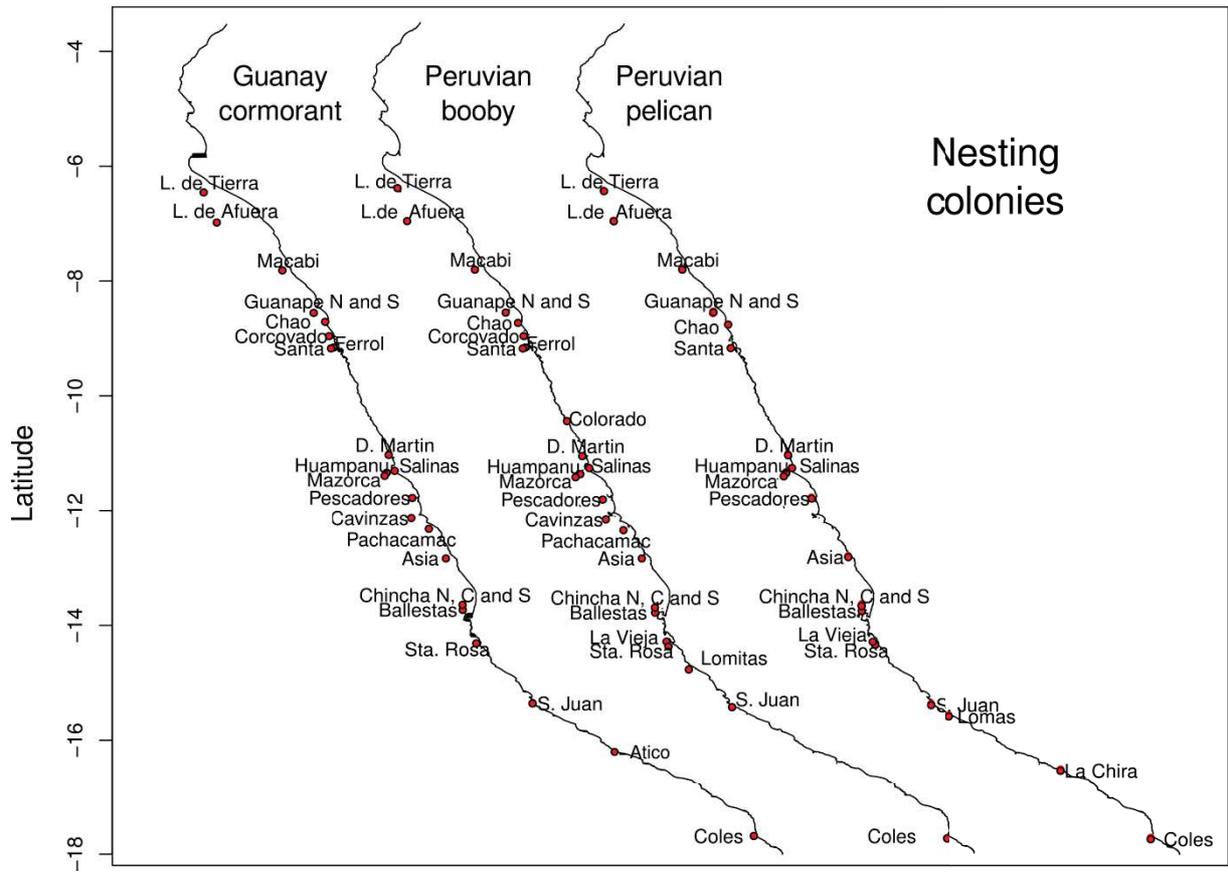
Figure A1. Schematic map of the localization of the main colonies of Guanay cormorant, Peruvian booby and Peruvian pelican.
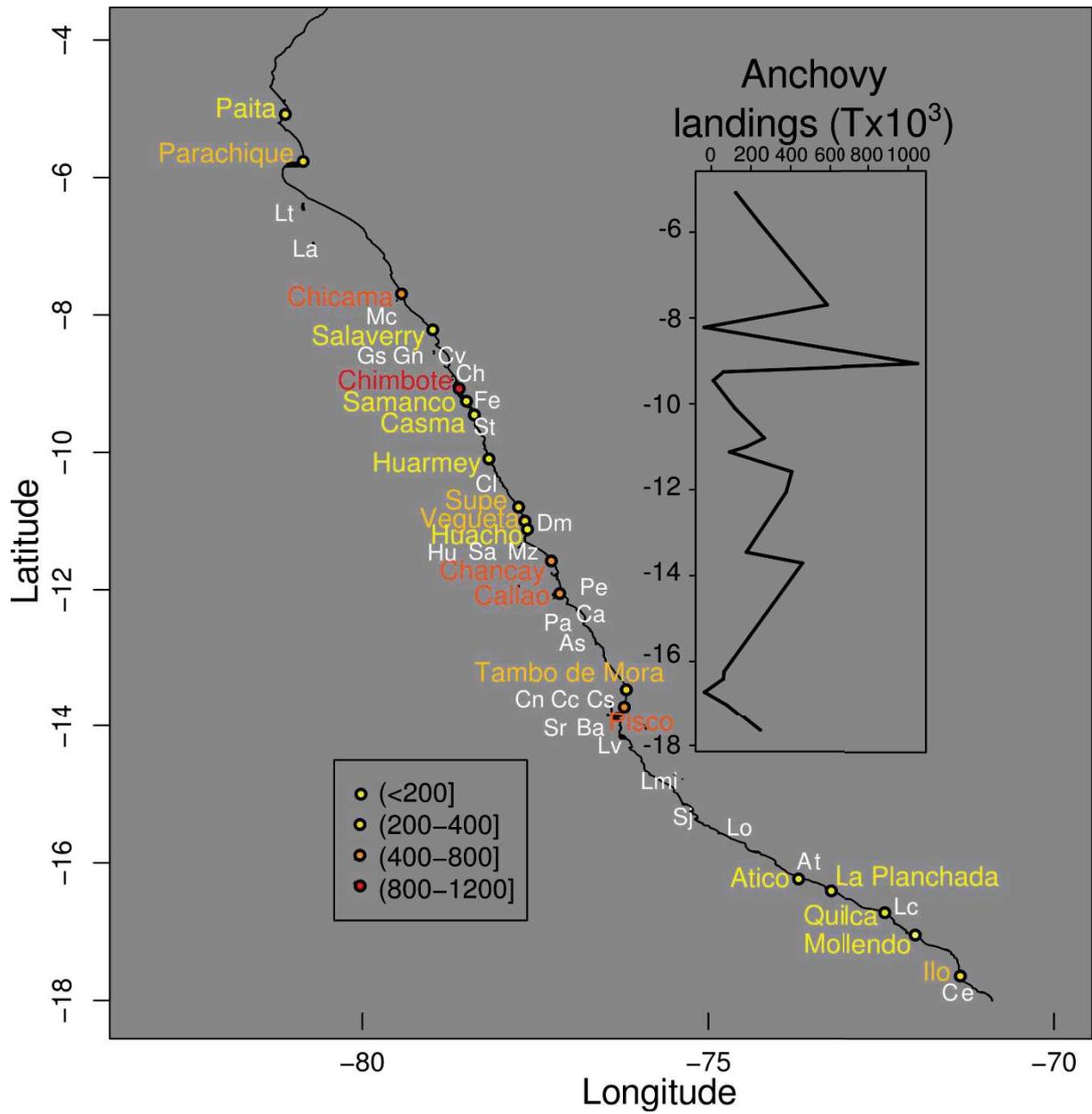
Figure A2. Main ports of landings of anchovy, in gray letters nesting colonies near the ports.
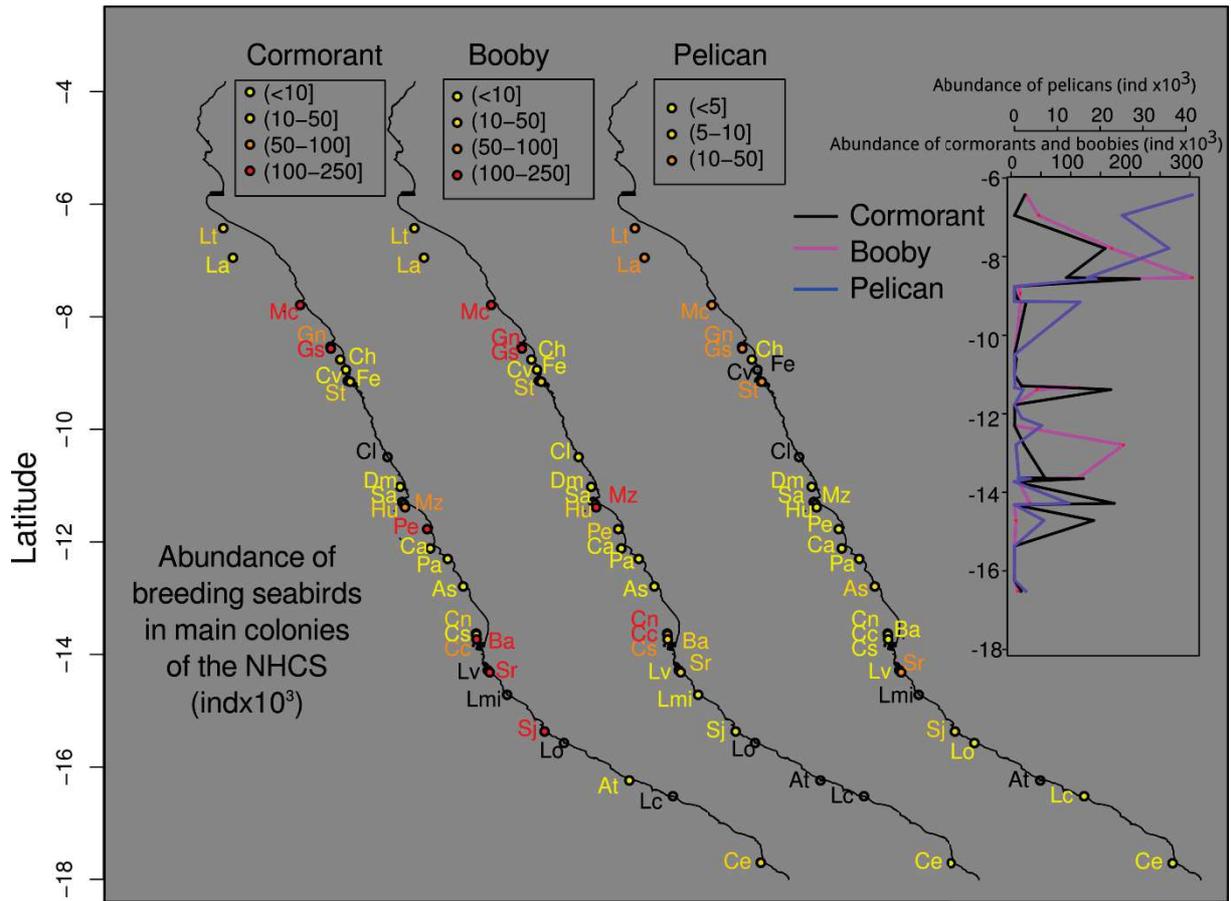
Figure A3. Map of localization of nesting colonies for the three seabirds. Colony size is represented by colors. Largest colonies are represented in red (100 000 – 250 000 for cormorant and booby and 10 000 – 50 000 for pelican) and smallest colonies in yellow (<10 000 for cormorant and booby and <5 000 for pelican). In the left panel longitude is suppressed and latitudinal effect on colony size is showed for the thee species.
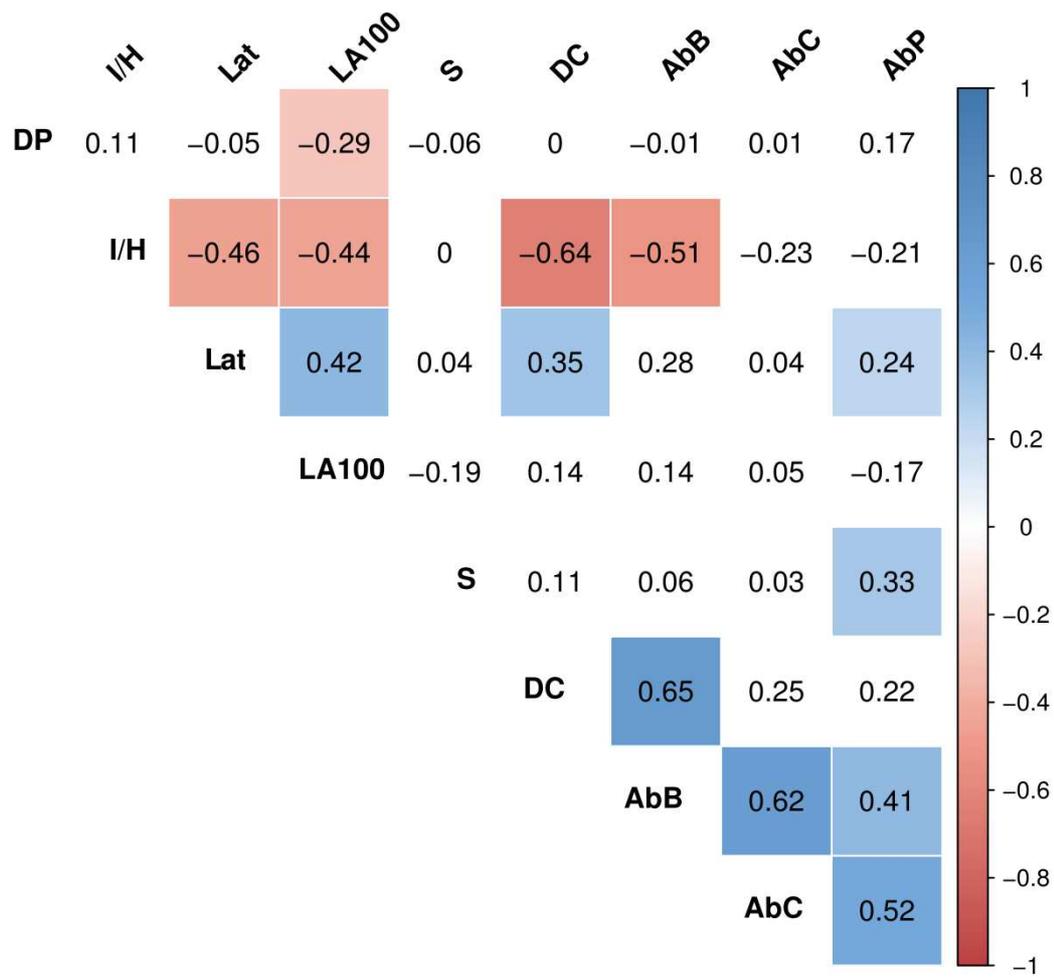
Figure A4. Correlation matrix of Site-specific, abundance of seabirds and fisheries variables.

Apppendix B. Functional analysis

In functional analysis, a curve $X(t)$ is a random variable taking values in a functional space $\mathcal{E}$ at $t$ discretization points. In our case we have for each parameter a data set of $i$ curves $Xi = \{X_1(t), ..., X_n(t)\}$ where $i = 1, ..., n$. The functional space $\mathcal{E}$ where the dataset of curves is represented is assumed to be a normed or seminormed metric space. Some of the methods implemented for functional data analyses are parametric and is it compulsory that $\mathcal{E}$ is in a Hilbert space. Therefore, the curves must be represented in a space of $\mathcal{L}_2$ functions (the Hilbert space of all square integrable functions over a certain interval) through basis (Ramsay and Silverman 2002). A basis (Fourier, β-spline) is a set of known functions $\{\phi_k\}_{k \in \mathbb{N}}$ that approximate the curve by a large number of $k_n$ of these functions.

$$X(t) = \sum_{k=1}^{k_n} c_k \phi_k(t)$$

Other most recent methods used a grid of discretization points $\{t_1, ..., t_m\}$ in an equispaced or non-equispaced way. These methods are non-parametric and have a drawback that every analysis (distance, norm, etc.) is a numerical approximation and the design and density of the grid could affect the accuracy of calculations (Ferrero-Bande and Oviedo de la Fuente 2012). For these methods the smoothing of functional data is given by the smoothing matrix $S = (s_{ij})$. Non parametric methods implemented are Kernel, k-nearest neighbour (Wasserman 2006) and local linear regression estimator (Ferraty and Vieu 2006).

There is not a universal rule about the amount of smoothing in parametric and non-parametric methods; it depends on the interpretation of the phenomenon and the objective of the analysis (Ferrero-Bande and Oviedo de la Fuente 2012). In our case of study the curves to analyzed ($\gamma$, $\varepsilon$ and $\psi$) are already a representation of the average seasonality for each nesting colonies. Thereby we consider that is not interesting done a smoothing of curves, which are already in $\mathcal{L}_2$ space, because it cans distortion the pattern that is described with the occupancy model.

Exploration of functional data

Exploration of functional data can be done by functional mean, functional variance and functional depth.

a) Functional mean

$$\bar{X}(t) = N^{-1} \sum_{i=1}^{N} X_i(t)$$

b) Functional variance

$$Var\big(X(t)\big) = (N-1)^{-1} \sum_{i=1}^{N} (X_i(t) - \bar{X}(t))^2$$

Functional principal components analysis

PCA may be defined as the search for an eigenfunction $\xi$ that reveals the most important type of variation in the data $X_i(t)$. The algorithm used to perform PCA first search for the function $\xi_1(t)$ of norm 1 (i.e. $\int \xi_1^2(t)dt = 1$) such that $N^{-1}\sum_i f_{i1}^2$ is maximized with $f_{i1} = \int \xi_1(t)X_i^c(t)dt$, where $X_i^c$ is the functional residual after removed the mean $X_i^c = X_i(t) - \bar{X}(t)$. Mean is removed because is a known source of variation. Therefore as in multivariate PCA a non-increasing sequences of eigenvalues can be constructed stepwise by requiring new eigenfunctions, then for the $m$th step $(m > 1)$, the $\xi_m(t)$ is computed with orthogonality constraint: $\int \xi_m(t)\xi_k(t)dt = 0$ for $k < m$. Finally the functional data can be predicted from the eigenfunction and eigenvalues as $\widehat{X_i}(t) = \sum_{k=1}^{M} f_{ik}\hat{\xi}_k(t)$, where $f_{ik} = \int \xi_k(t)X_i^c(t)$. Coefficients vectors $c_{ik}$ known as scores can be helpful in interpreting the nature of variation. Scores are defined as following: $c_{ik} = \int \xi_k(t) \, X_i^c$. Therefore in PCA, the covariance matrix is split into scale part (eigenvalues) and direction part (eigenvectors). One of the outputs is loadings which are the covariances/correlations between the original variables and the unit-scaled components.

Appendix C Random forest

Random forest is a classification method that operate by constructing a large number of random tree classifiers $\{h(x, \Theta_k), k = 1, ....\}$ where the $\{\Theta_k\}$ are independent identically distributed random vectors and each tree cast a unit vote for the most popular class at input $x$ (Breiman 2001).

For build each tree $\{\Theta_k\}$, 63.2% of the original data is random sampled with replacement, it constitute the training data, said "*in bag*". An unpruned tree is growing by selected at each node the best split among a random sample (*m*) of all the predictor variables. By default for regression random forest, *m* is the total number of all predictors divided by 3 and the minimum node size is 5.The value of *m* is held constant for all the threes in forest. The random sample over the covariates *m* was built to alleviate the multicollinearity problem.

There are two ways to find variable importance in random forest. The first way is using the Gini-splitting index. The importance measure attributed to a variable *j* is the improvement done by this variable at a split of a tree $\{\Theta_k\}$. Then this important measure is accumulated over all trees in the forest separately for each variable. All variables have a chance to get included in the importance list because random forest take at each split a random sample of variables (*m*) (Hastie, Tibshirani & Friedman 2009). The second way of measuring importance variable is done through measuring the prediction strength of each predictor from data not used in training trees. The data not used in training trees is called "*out of bag*" (*OOB*) and is 36.8% of the data. After a tree $\{\Theta_k\}$, is grown the prediction is compared with *OOB* sample by mean square error (MSE) and the accuracy is recorded. Then the values of a predictor variable *j* are random permuted in the *OOB* sample and accuracy is recorded using the same model with the permuted variable *j* to predict the *OOB* response. Permuting the values of *j* should have a negative influence on prediction and is expected a decrease in accuracy of predictions. The decrease in accuracy is averaged over all trees and normalized by the standard deviation of the differences. Decrease in accuracy is expressed as a percentage of maximum increase in mean square error (IncMSE%) in the implementation of randomForest in R. For regression models the second way is the most used (Figure C1).

Another parameter to control in random forest is the number of trees. Typically, a few hundred to several thousand trees are used, depending on the size and nature of the training set. An optimal number of trees B can be found using cross-validation, or by observing the OOB error. The training and test error tend to level off after some number of trees has been fit.

Random forest is a robust method that needs almost no a priori hypothesis. Random forest is a classification method that allowed at the same time build accurate models and provides predictor variable importance measure (Breiman 2001). Random forest also is a performant methods that could detect even non-linear interaction effects, it is also less sensitive to small sample size, large number of covariates, and multicollinearity (Cutler *et al.* 2007). The multicollinearity problem is alleviated in random forest by random selection of a subset of variables to try at each node. We used the functionality of random forest for ranked the importance of environmental, site and densodependence covariates on the variability of seasonal breeding. We also demonstrated the partial effects of covariates on the variability of seasonal breeding through partial dependence plots of the most important covariates
However a bias in measure of variable importance was detected, continuous variables or categorical variables with a large number of categories are preferred (Strobl *et al.* 2007; Altmann *et al.* 2010). We corrected this bias using a permutation importance algorithm to correct random forest (PIMP-RF) (Altmann *et al.* 2010) and a.

The method PIMP-RF has the following steps: first training a classical random forest model on the training data and recuperate the vector of variable importance. Then perform $s$ random forest where the variable response is permuted and recuperated the vector of variable importance at each times. The importance variable of permuted response is considered as the null importances. After recuperate the variable importance through all permutation $s$, it is fitted a probability distribution to the population of null importance. Given the fitted distribution, $P$-values are calculated as $P=b/s$ where $b$ is the number of permutations where the variable $j$ exceeds the importance given without permutation of response variable and $s$ is the total number of permutations (Altmann *et al.* 2010). $P$-values can be adjusted by false discovery rate under positive dependence asumption (Benjamini–Hochberg–Yekutieli) procedure (Benjamini *et al.* 2006). Thereafter, a new random forest model is trained with only significant predictor variables ($P \leq 0.05$).
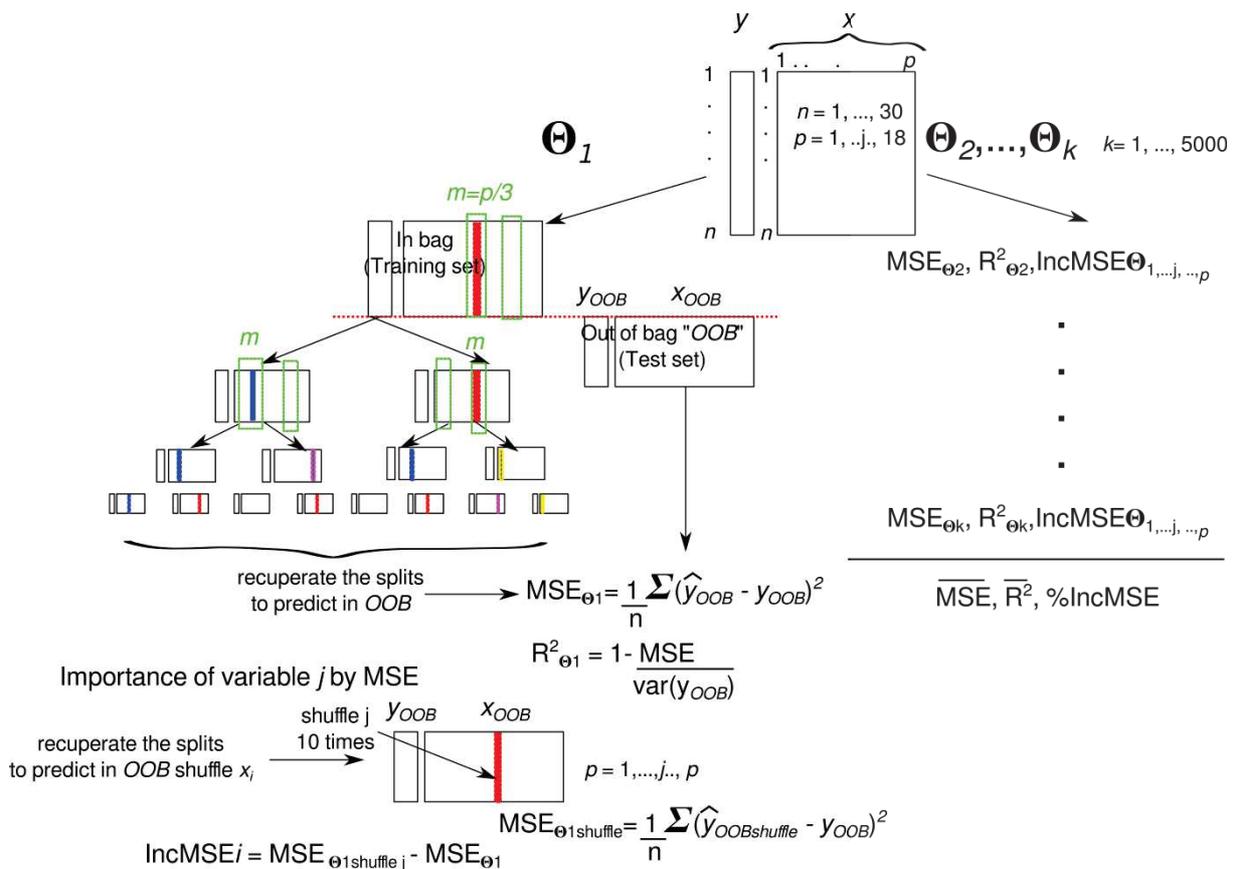


Figure C1. Schema of procedure in Random forest.
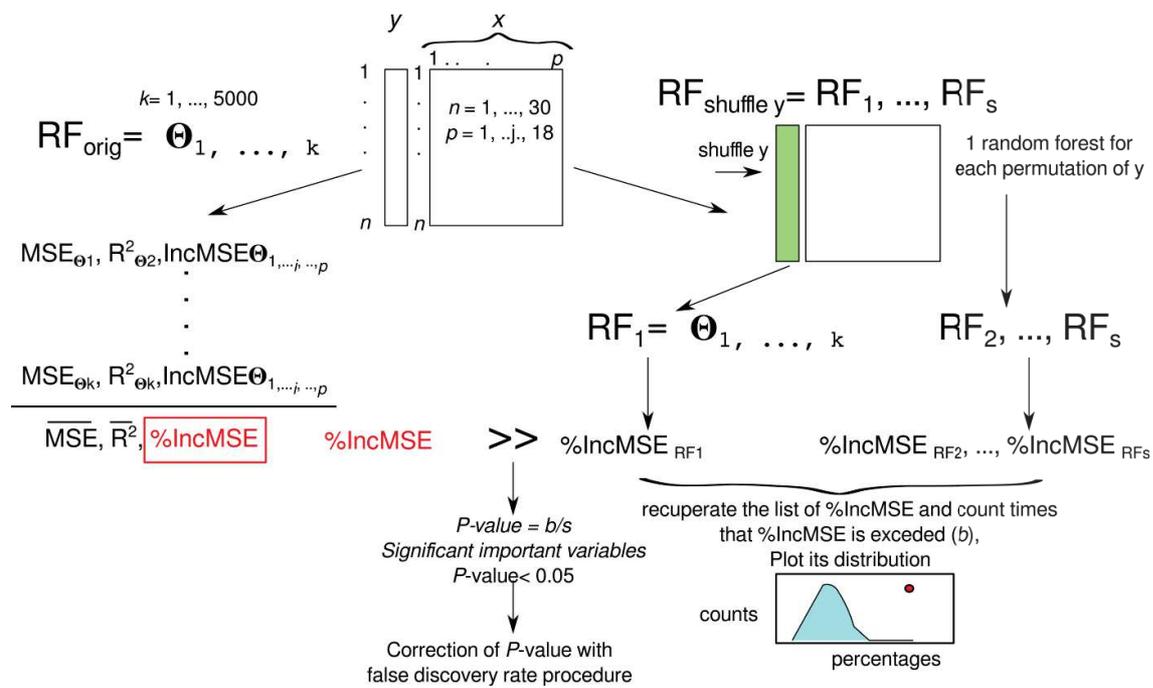
Figure C2.Schema of PIMP procedure for correct categorical variable bias importance and select only significant important variables.

Appendix D: Exploration of seasonal curves: Mean and outliers
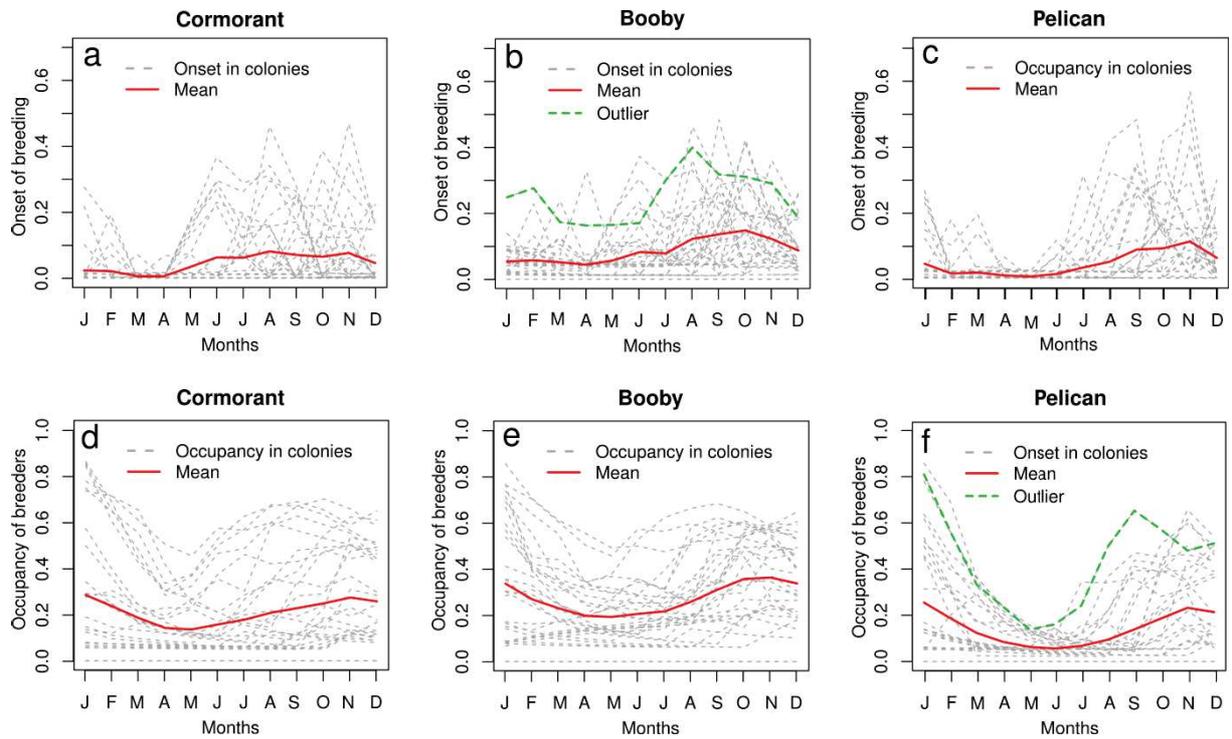


Figure D1. Mean (red line) and outliers (green lines) of onset and occupancy for cormorant, booby and pelican.
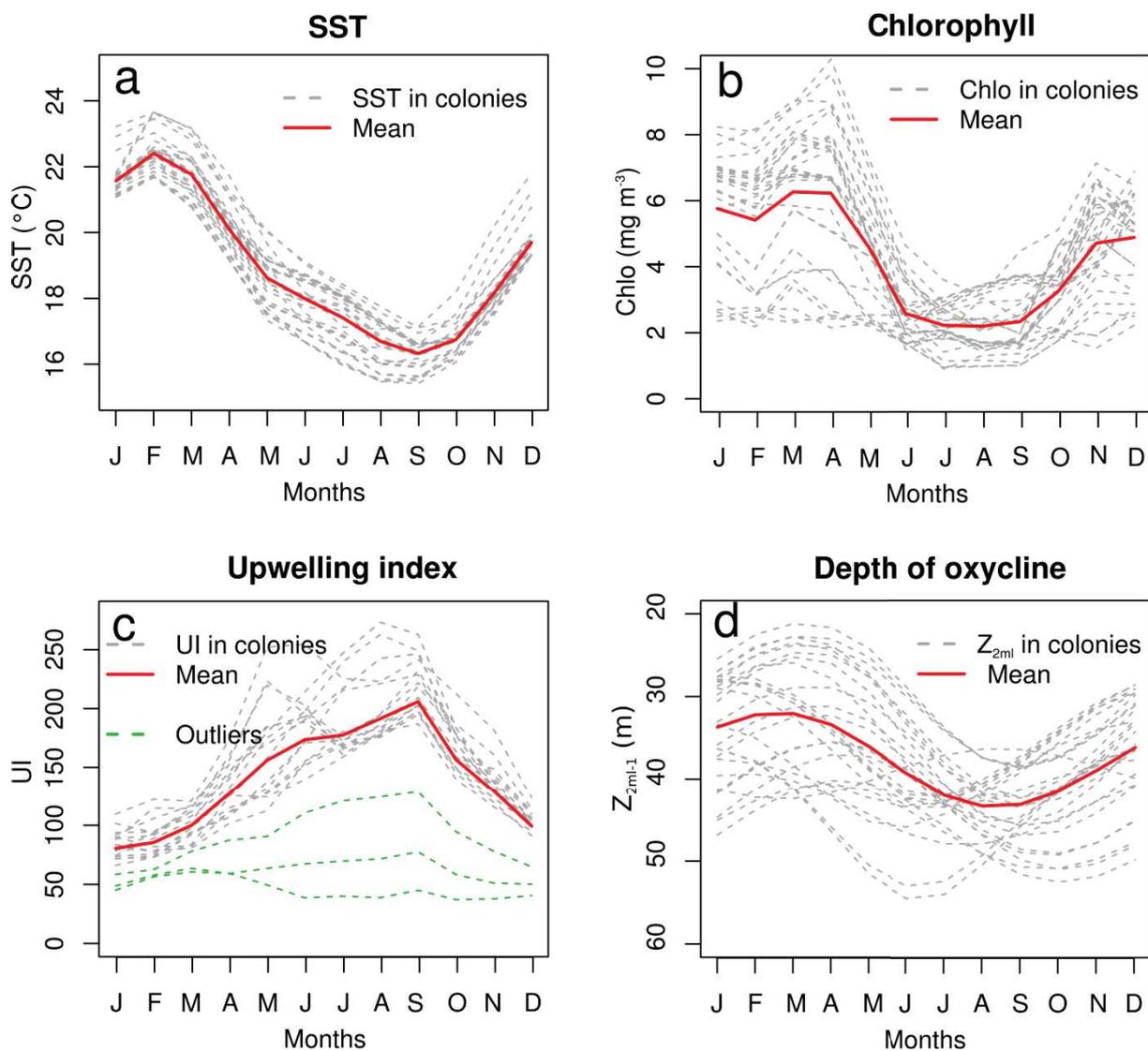
Figure D2. Mean (red lines) and outliers (green lines) of oceanographic conditions.

Appendix E. Importance of covariates evaluated with Random Forest



Figure E1. The right plot sorts the variables by importance to explain the FPC1 of the onset of breeding of cormorant. Variables were geographic (Lat, S, I/H), scores of functional components of oceanographic covariates ($SST_{FPC}$, $Chlo_{FPC}$, $Z2ml_{FPC}$, $UI_{FPC}$), fisheries pressure (LA100, DNP). On the left, there are represented the partial plot of the significant variables.social variables (AbC). The important significant variables fall above the red line (p>0.05).

Figure E2. The right plot sorts the variables by importance to explain the FPC1 and FPC2 of the occupancy of breeders of cormorant. Variables were geographic (Lat, S, I/H), scores of functional components of oceanographic covariates (SST$_{FPC}$, Chlo$_{FPC}$, Z2ml$_{FPC}$, UI$_{FPC}$), fisheries pressure (LA100, DNP). On the left, there are represented the partial plot of the significant variables.social variables (AbC). The important significant variables fall above the red line (p>0.05).
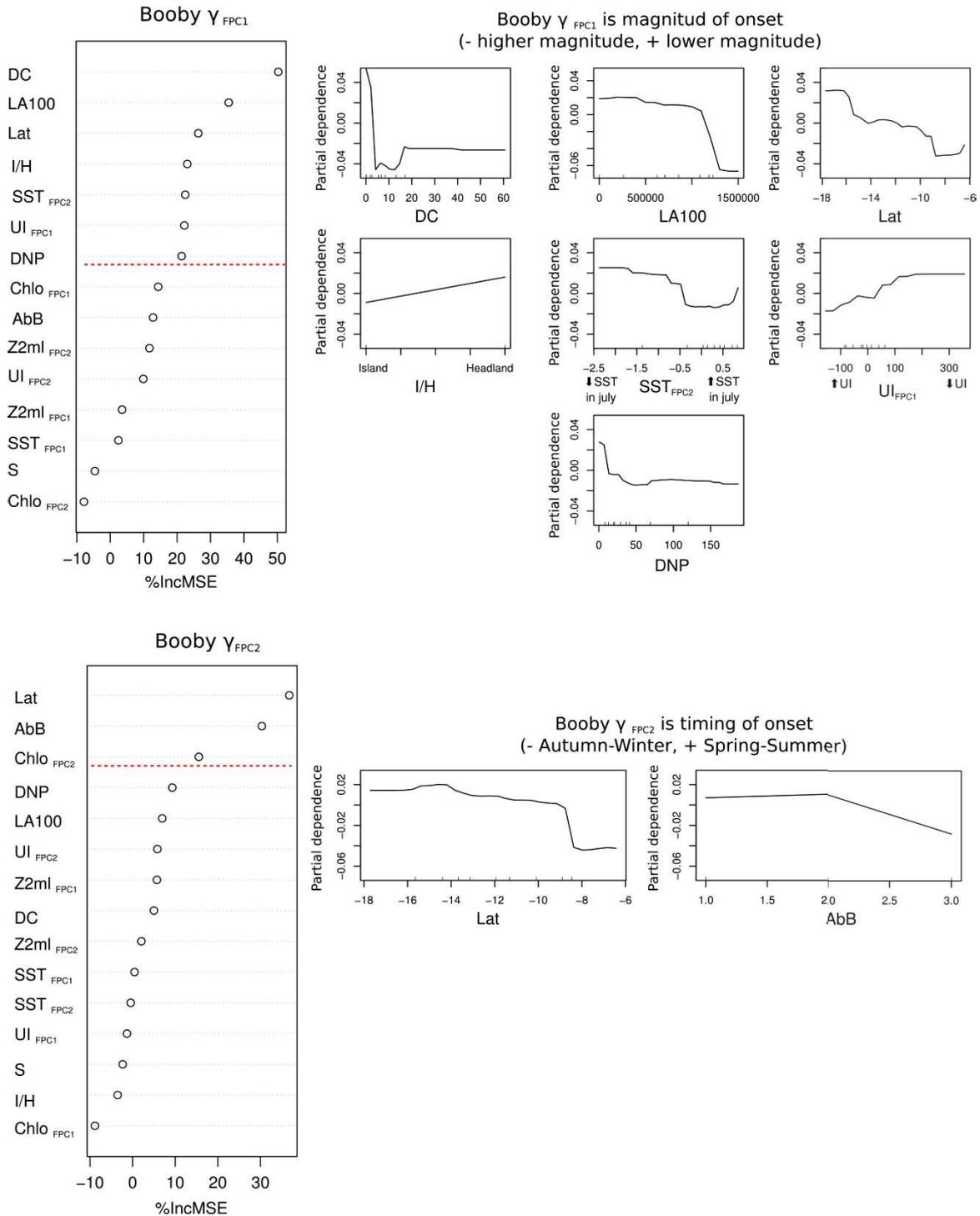
Figure E3. The right plot sorts the variables by importance to explain the FPC1 and FPC2 of the onset of breeding of booby. Variables were geographic (Lat, S, I/H), scores of functional components of oceanographic covariates ($SST_{FPC}$, $Chlo_{FPC}$, $Z2ml_{FPC}$, $UI_{FPC}$), fisheries pressure (LA100, DNP). On the left, there are represented the partial plot of the significant variables.social variables (AbC). The important significant variables fall above the red line ($p>0.05$).
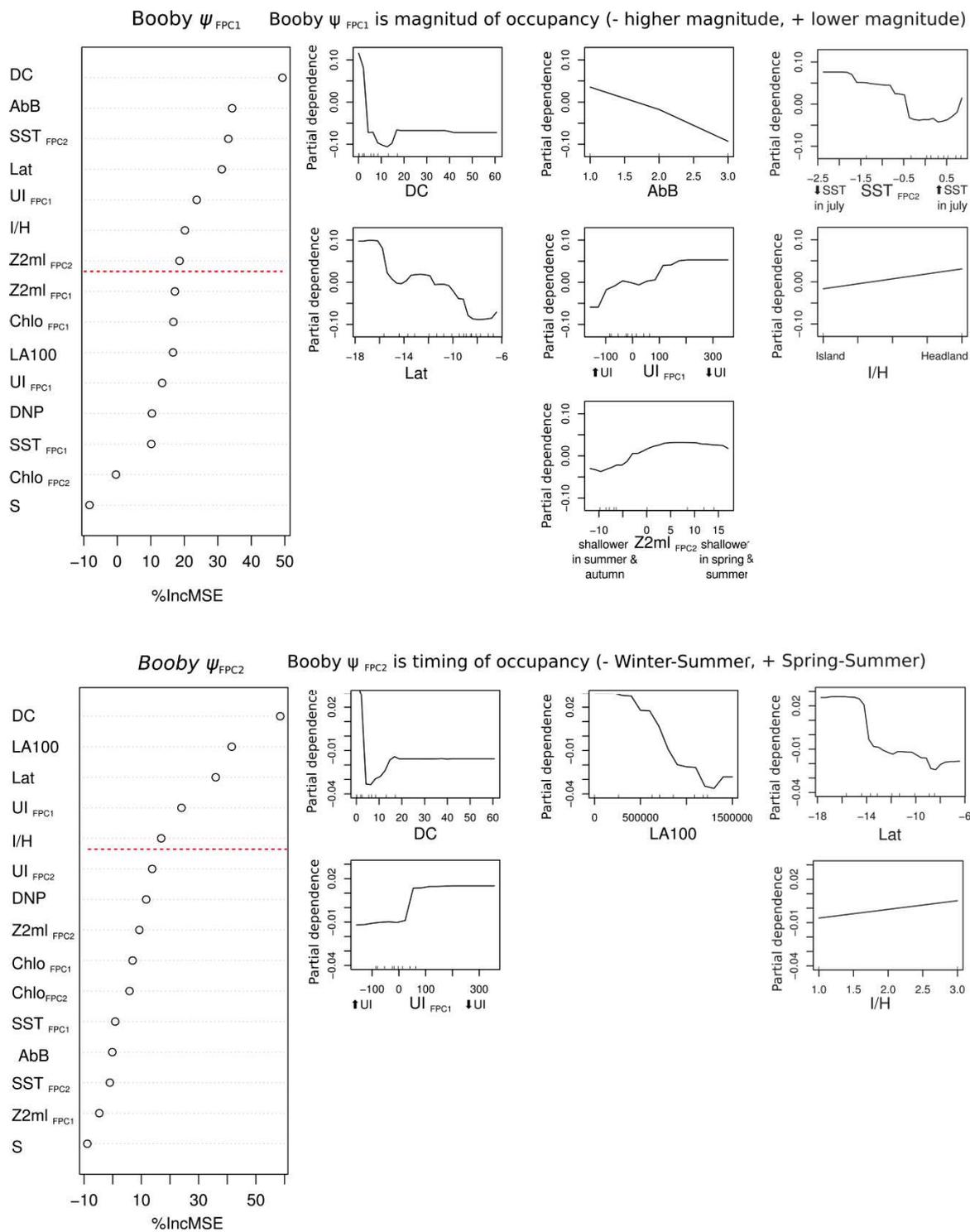
Figure E4. The right plot sorts the variables by importance to explain the FPC1 and FPC2 of the occupancy of breeders of booby. Variables were geographic (Lat, S, I/H), scores of functional components of oceanographic covariates ($SST_{FPC}$, $Chlo_{FPC}$, $Z2ml_{FPC}$, $UI_{FPC}$), fisheries pressure (LA100, DNP). On the left, there are represented the partial plot of the significant variables.social variables (AbC). The important significant variables fall above the red line ($p>0.05$).
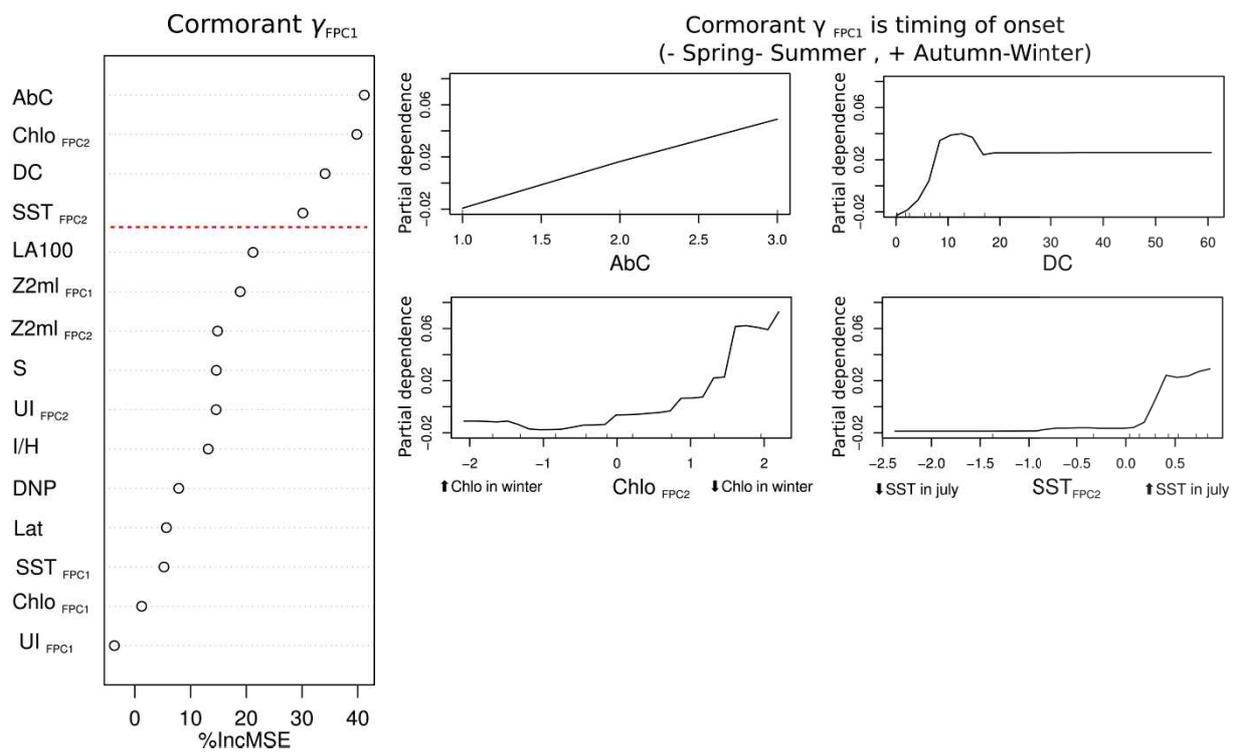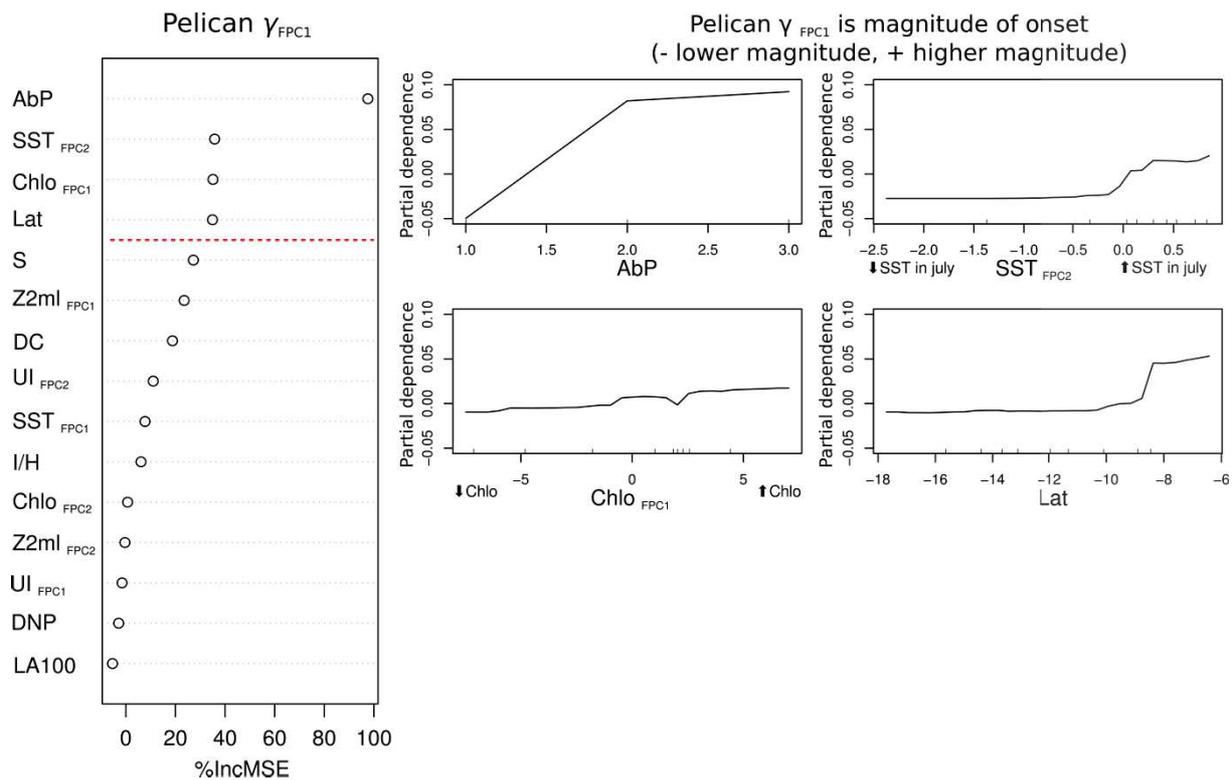
Figure E5. The right plot sorts the variables by importance to explain the FPC1 of the onset of breeding of pelican. Variables were geographic (Lat, S, I/H), scores of functional components of oceanographic covariates (SST_{FPC}, Chlo_{FPC}, Z2ml_{FPC}, UI_{FPC}), fisheries pressure (LA100, DNP). On the left, there are represented the partial plot of the significant variables.social variables (AbC). The important significant variables fall above the red line (p>0.05).
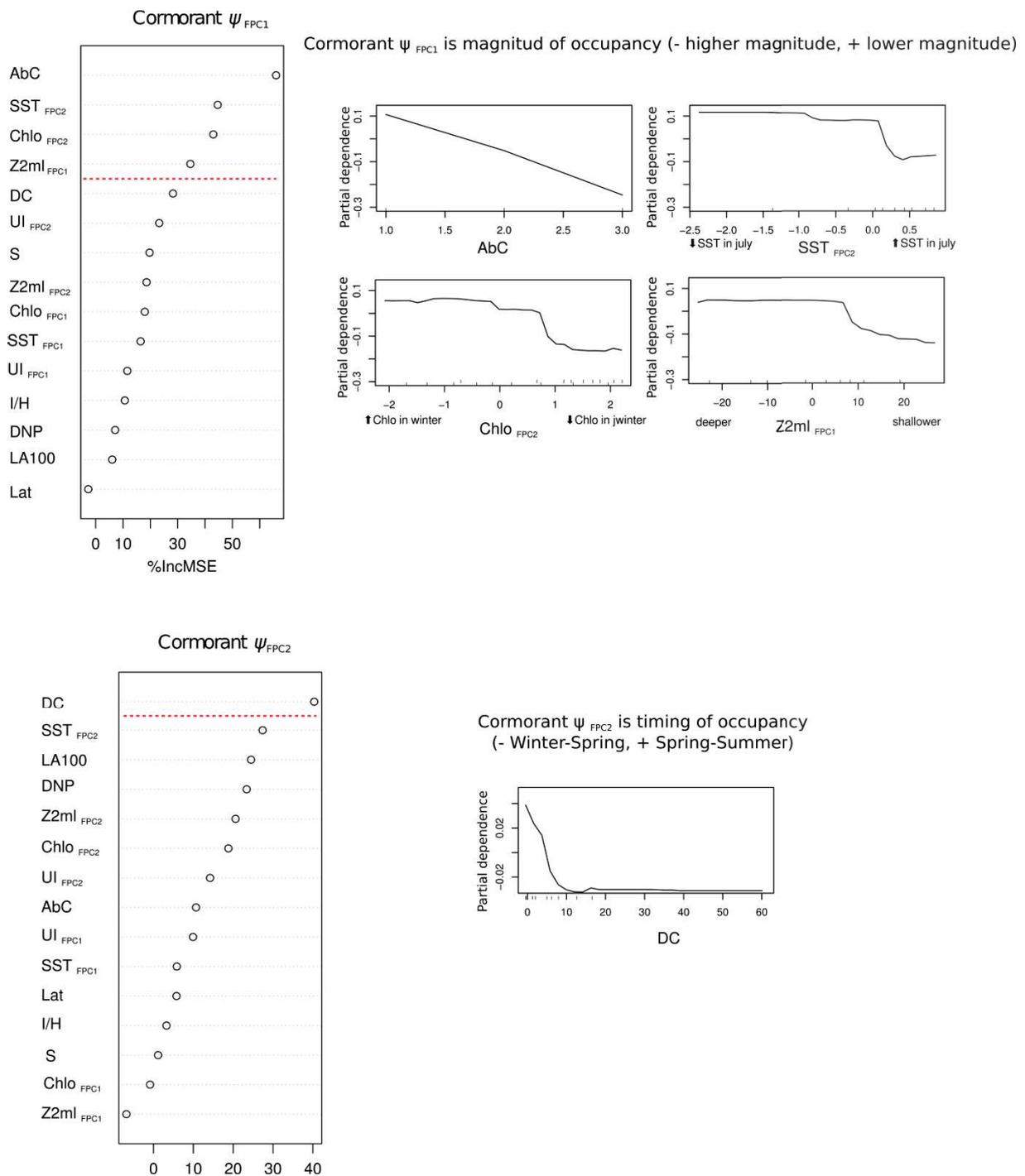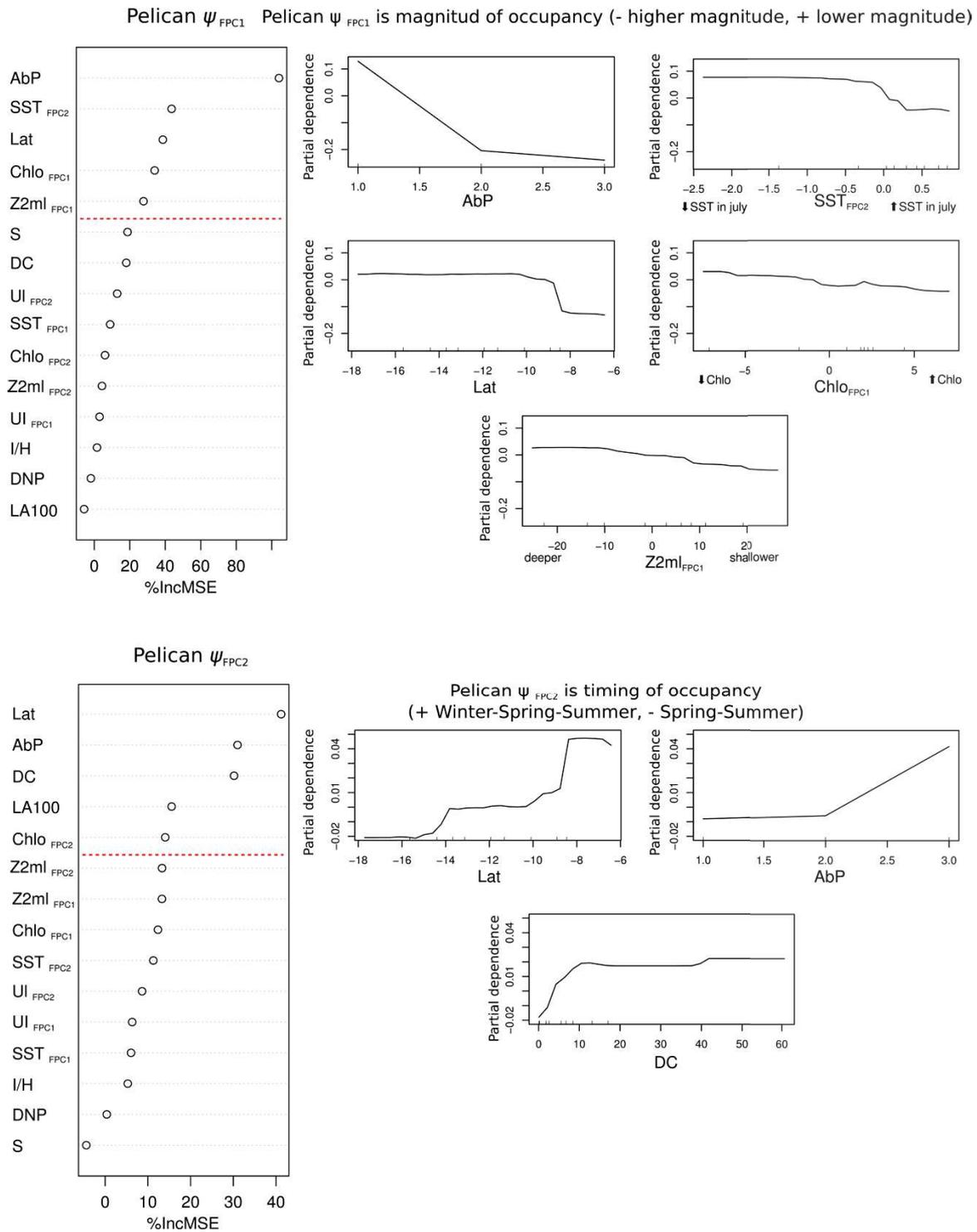
Figure E6. The right plot sorts the variables by importance to explain the FPC1 and FPC2 of the occupancy of breeders of pelican. Variables were geographic (Lat, S, I/H), scores of functional components of oceanographic covariates (SST$_{FPC}$, Chlo$_{FPC}$, Z2ml$_{FPC}$, UI$_{FPC}$), fisheries pressure (LA100, DNP). On the left, there are represented the partial plot of the significant variables.social variables (AbC). The important significant variables fall above the red line (p>0.05).

# ANNEXE 3

Supplemental material of Chapter 4

1. Seabird data

2. Oceanographic data

3. Acoustic data

4. Estimation of hyperparameters

5. Tests of prior sensitivities and identifiability of parameters

6. Kruskal-Wallis and correlation test of onset and occupancy of breeders among the three periods.

7. Seabirds life history traits

1.Seabird data

Table S1. Number of months consigned for each period of data time series. In parenthesis the years were data was missing for each month.

| | Number of data point by period | | |
|---|---|---|---|
| Months | 1952-1968 | 1977-1990 | 2003-2014 |
| January | 12 (1957, 1959, 1964, 1967,1968) | 13 (1977) | 10 (2005, 2009) |
| February | 13 (1957, 1959, 1964, 1967) | 14 | 10 (2005, 2009) |
| March | 14 (1957, 1964, 1967) | 14 | 10 (2005, 2009) |
| April | 14 (1957, 1964, 1967) | 14 | 9 (2005, 2007, 2009) |
| May | 13(1957, 1964, 1966, 1967) | 14 | 9 (2005, 2007, 2009) |
| June | 13 (1957, 1964, 1966, 1967) | 14 | 10 (2005, 2009) |
| July | 13 (1957, 1964, 1966, 1967) | 14 | 11 (2009) |
| August | 12 (1957, 1960, 1964, 1966, 1967) | 14 | 10 (2005, 2009) |
| September | 12 (1957, 1960, 1964, 1966, 1967) | 14 | 11 (2014) |
| October | 11 (1952, 1957, 1960, 1964, 1966, 1967) | 14 | 11 (2014) |
| November | 13 (1957, 1960, 1966, 1967) | 14 | 11 (2014) |
| December | 13 (1957, 1960, 1966, 1967) | 14 | 10 (2004, 2014) |

## 2. Oceanographic data
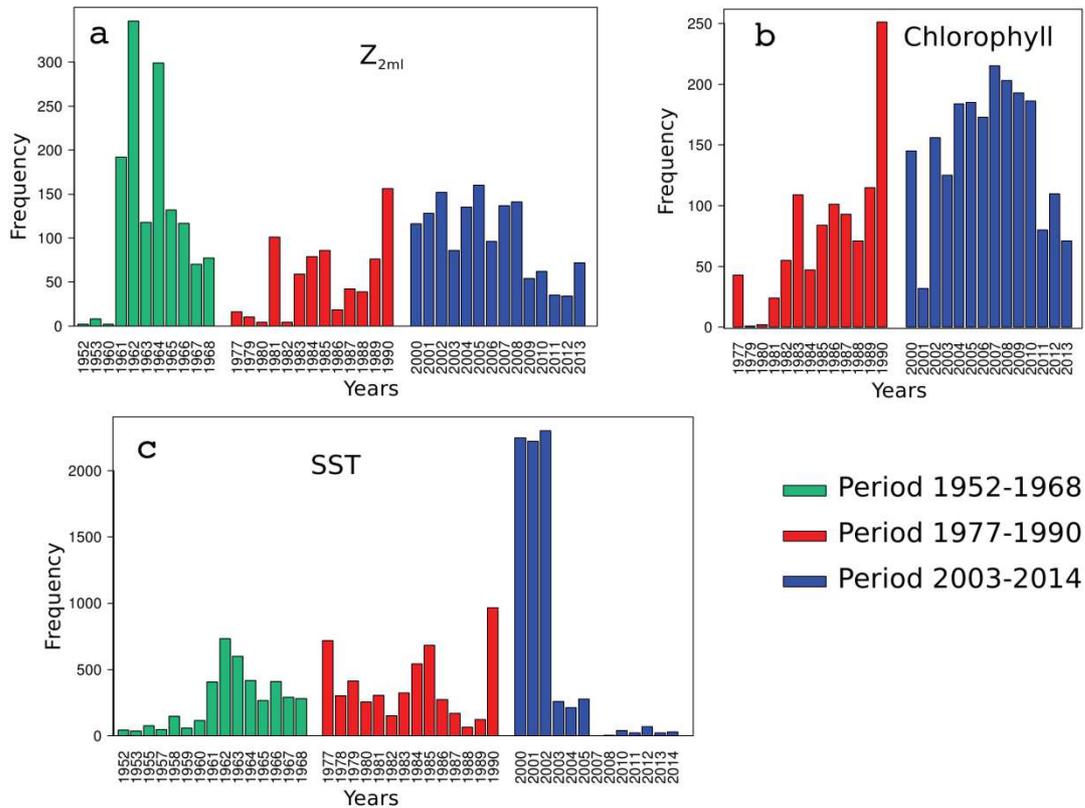


Figure S1. Barplots of data available among the years for a) $Z_{2mll^{-1}}$, b)Chlorophyll and c)SST. Data are classified by periods: green 1952-1968, red 1977-1990 and blue 2000-2012. For the most recent period we use oceanographic data since 2000 because it corresponded to the same regime and allowed us to build a stronger climatology.
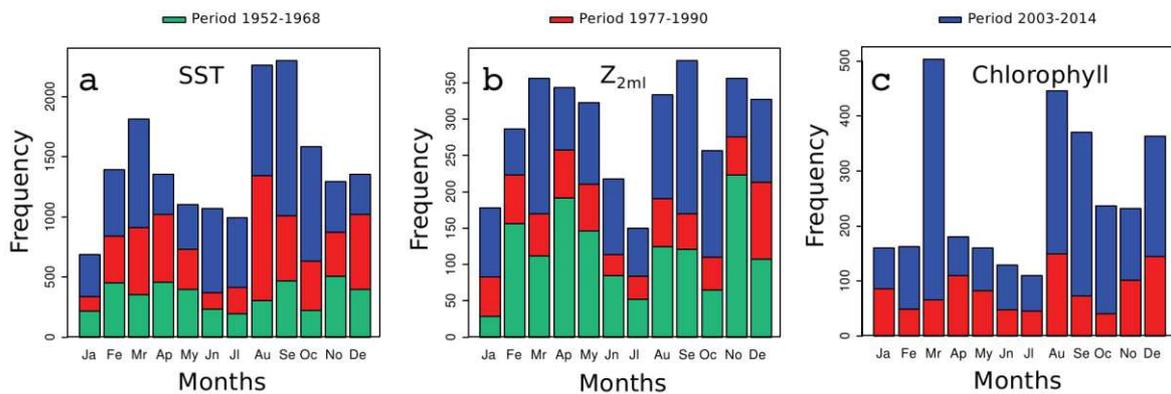


Figure S2. Barplots of data available of a) SST, b) $Z_{2mll^{-1}}$ and c) Chlorophyll for each month during the periods: 1952-1968 (green), 1977-1990 (red) and 2003-2014 (blue).
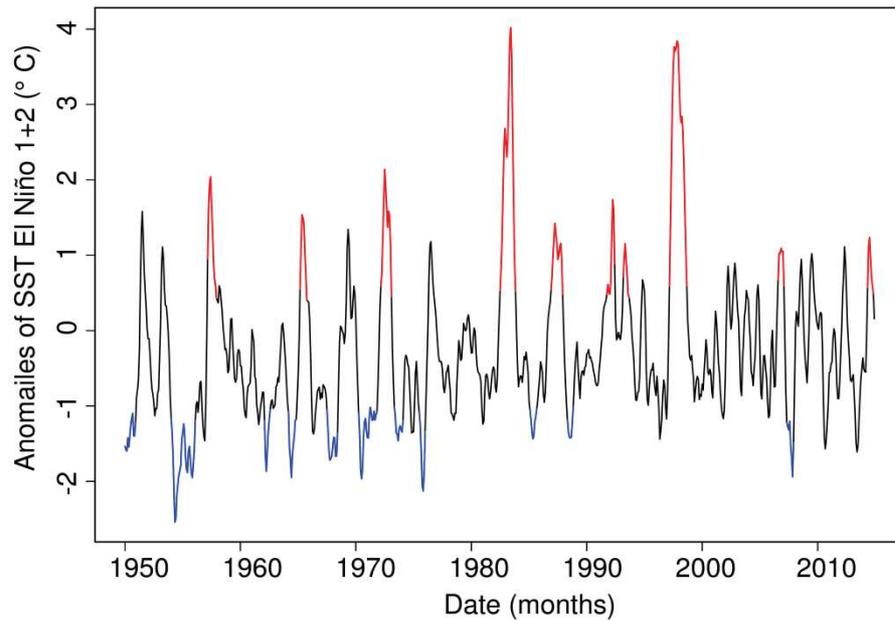
Figure S3. Anomalies of sea surface temperature of the zone El Nino 1+2 since 1950 to 2014. Base climatology to analyze the anomalies was built from 1981-2010 (http://www.cpc.ncep.noaa.gov/data/indices/ersst3b.nino.mth.81-10.ascii). Continuous anomalies for more than 5 months and higher than 0.4°C are identified as El Nino events (Trenberth 1997, red lines) and continuous anomalies for more than 5 months and lower than -1.0°C are identified as La Nina (Trasmonte & Silva 2008, blue lines).

Trasmonte, G. & Silva, Y. (2008) La Nina event: Proposal of definition and classification according to the sea surface temperature anomalies in El Nino 1+2 area. Informe del Instituto del Mar del Peru, 35, 199–207.

Trenberth, K.E. (1997) The Definition of El Nino. Bulletin of the American Meteorological Society, 78, 2771–2777.

## 3. Acoustic data

Acoustic data have been acquired by routine scientific surveys performed along the Peruvian coast by IMARPE to estimate anchovy biomass since 1985.

Surveys were performed two to four times per year and lasted between one and three months. In general, the survey design consisted in parallel cross-shore transects of ~100 nm long and ~15 nm intertransects (Gutiérrez et al. 2007, Simmonds et al. 2009). Surveys were performed by research vessels equipped with hull mounted 38 and 120 kHz Simrad split beam scientific echosounders (EKS, EK500 and/or EK60). The echosounders were calibrated with a standard sphere (Foote et al. 1987). Nautical-area-backscattering coefficients ($s_A$ or NASC) were recorded in each georeferenced elementary distance sampling unit (ESDU = 2 nautical miles during 1985-1993 and 1 nautical miles from 1994-2011) (Simmonds and Maclennan 2005). The volume-backscattering strengths were thresholded at -65 dB. The identification of records of anchovy and other species before 1999 was performed by the results of fishing hauls and the characteristics of the records; after 1999 the identification was performed using Echoview software.

Only acoustic data between 8ºS and 15ºS were retained and as a measure of abundance of anchovy we used 3 distinct metrics: i) the seasonal average of $s_A$ (nautical-area-backscattering coefficient) per ESDU (georeferenced elementary distance sampling unit) representing a regional abundance of anchovy, ii) the seasonal average of $s_A$ per ESDU only when anchovy was present ($s_A+$) representing local density of anchovy and iii) the seasonal spatial occupation index (ISO) computed as the percentage of ESDU with presence of anchovy, that represents the spatial distribution of anchovy. We calculated these metrics for two periods: during 1985-1990 (associated with the 1977-1990 period) and 2000-2011 (associated with the 2003-2014 period). We also calculated by period the average depth and height of schools of anchovy during day and night from acoustic data into the sub sampled area (100 km, 8ºS and 15ºS).

4. Estimation of hyperparameters

We used the largest variances of the probabilities of onset and termination of breeding obtained in Passuni et al. (2015, Figure S4) to estimate α and β parameters of the beta distribution. For example, for onset of breeding we used the variance estimated for boobies since it was the largest estimate of all three species (Table S2).
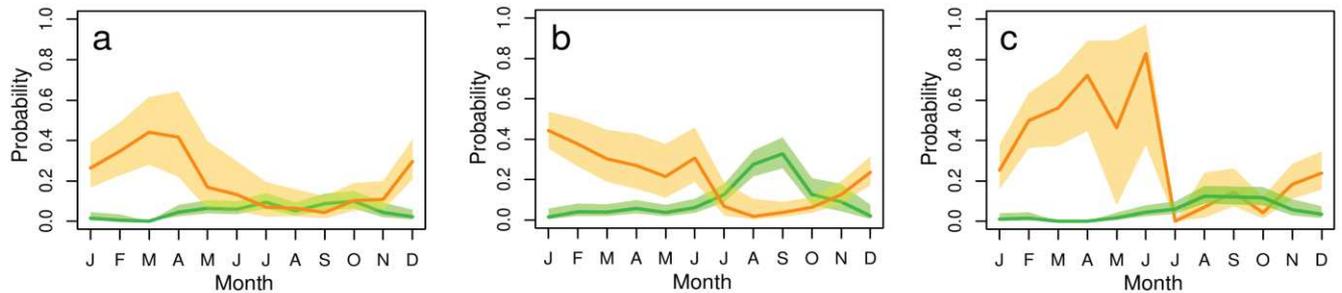


Figure S4. Estimates of monthly probabilities of onset of breeding (green solid line) and termination of breeding (orange solid line) at the breeding sites for (a) cormorants, (b) boobies and (c) pelicans in the Northern Humboldt Current System for the period 2003-2012 from Passuni et al. (2015). Shaded areas correspond to 95% confidence intervals.

Table S2. Mean (μ), variance ($\sigma^2$) and enlarged variance ($\sigma^2$ used) of the onset and termination of breeding for the cormorants, boobies and pelicans from 2003-2012 of 31 breeding sites in the Peruvian coast obtained from Passuni et al. (2015). Enlarged variance (maximum for onset 0.01 and termination 0.02), the hyperparameters α and β of the beta distribution were calculated for the three species. β and α hyperparameters for informative prior distribution were calculated from mean and enlarged variance.

| Species | Onset | | | | | Termination | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | μ | $\sigma^2$ | $\sigma^2$ used | α | β | μ | $\sigma^2$ | $\sigma^2$ used | α | β |
| Cormorants | 0.05 | 0.00 | 0.01 | 0.18 | 3.44 | 0.20 | 0.02 | 0.02 | 1.45 | 5.67 |
| Boobies | 0.10 | 0.01 | 0.01 | 0.82 | 7.27 | 0.20 | 0.02 | 0.02 | 1.46 | 5.68 |
| Pelicans | 0.05 | 0.00 | 0.01 | 0.19 | 3.54 | 0.33 | 0.08 | 0.02 | 3.38 | 6.74 |

5. Tests of prior sensitivities and identifiability of parameters

Informative priors add a priori knowledge about output posteriors. The use of informative priors is advised to increase precision of posterior estimates when sample size is small (Morris et al. 2015). Since our data sample was small (17 years was the longest period) we used three different priors to test sensitivity: uninformative priors as Uniform and Jeffrey's prior, and informative priors. Informative priors (Gelman et al. 2003) came from our previous work on modelling breeding seasonality of seabirds of the NHCS (Passuni et al. 2015, Figure S4). To homogenize the distribution of the three priors and make them comparable, we use conjugate priors. Conjugate priors are used when the posterior distribution $f(\gamma \mid z)$ is in the same family as the prior probability distribution $f(\gamma)$. In our case, probability of onset and termination followed a Bernoulli distribution and its conjugate prior distribution was a beta distribution [Beta $(\alpha, \beta)$]. Conjugate priors for a Uniform prior was Beta $(1, 1)$ and for Jeffrey's prior Beta $(0.5, 0.5)$. In the case of informative priors mean and variance could be expressed in terms of $\alpha$ and $\beta$ such as $\mu = \dfrac{\alpha}{\alpha + \beta}$ and

$$\sigma^2 = \frac{\alpha\beta}{(\alpha + \beta)^2 (\alpha + \beta + 1)}.$$

So we can solve these equations for the parameters $\alpha$ and $\beta$ of the prior distribution in terms of $\mu$ and $\sigma^2$:

$$\alpha = \mu\left(\frac{\mu(1 - \mu)}{\sigma^2} - 1\right) \text{ and } \beta = (1 - \mu)\left(\frac{\mu(1 - \mu)}{\sigma^2} - 1\right).$$ We used the $\mu$ and the largest possible $\sigma^2$ found for each species (Table S2). We compared posteriors calculated using informative and non-informative priors through visual comparison and the deviance information criteria (DIC, Spiegelhalter et al. 2002). DIC is considered as a measure of model complexity and adequacy of posteriors. The model with the smallest DIC was selected as the best and we considered a difference in > 5 units as substantial evidence in favour of the model with the smaller DIC, and a difference in > 10 units as strong evidence (Spiegelhalter et al. 2002).

We obtained similar patterns of occupancy and onset of breeding using either uninformative or informative priors for the three seabird species (Figs S5-S7). Therefore posteriors were not sensitive to the prior used. Nevertheless we preferred using informative priors to estimates posteriors of onset of breeding because they were more coherent with the observed data than estimates obtained using uninformative priors (Table S3). In the case of termination of breeding, there was sensitivity to the use of priors. There were clear differences between posteriors resulting from informative and uninformative priors (Figs S5-S7). Uninformative priors resulted in posterior estimates much larger than those observed for months where zero or only one event of termination was observed. Hence the use of informative priors is advised but also it indicates that there was not enough data to make robust inferences. Sensitivity to prior choice has been complemented with identifiability of parameters.

Table S3. Comparison of deviance information criterion (DIC) between the three priors used to model probabilities of occupancy, onset of breeding and termination of breeding: Uniform, Jeffrey and informative for the three species and the three periods. Comparison between models was only done when the dependent variable did not change, i.e. by rows. The lower DIC with a difference of 5 was selected in bold.

| Periods | Species | Uniform<br>DIC | Jeffrey<br>DIC | Informative<br>DIC |
|---------|---------|---------|---------|-------------|
| 1952-1968 | Cormorants | 158.44 | **148.39** | **147.46** |
| | Boobies | 149.41 | **135.50** | **137.01** |
| | Pelicans | 111.12 | 96.73 | **84.63** |
| 1977-1990 | Cormorants | 116.24 | 100.54 | **86.12** |
| | Boobies | 193.17 | **188.07** | **188.61** |
| | Pelicans | 77.79 | 58.15 | **43.27** |
| 2003-2014 | Cormorants | 138.46 | **126.77** | **128.14** |
| | Boobies | 114.77 | **102.61** | 108.58 |
| | Pelicans | 86.73 | 73.16 | **63.09** |

Figure S5. Output of a-c) onset, d-f) termination, and g-i) occupancy of breeding for Guanay cormorants for the periods 1952-1968, 1977-1990 and 2003-2014 with different hyperparameters: Uniform (red boxes), Jeffrey (green boxes) and Informative (blue boxes).

Figure S6. Output of a-c) onset, d-f) termination, and g-i) occupancy of breeding for Peruvian boobies for the periods 1952-1968, 1977-1990 and 2003-2014 with different hyperparameters: Uniform (red boxes), Jeffrey (green boxes) and Informative (blue boxes).
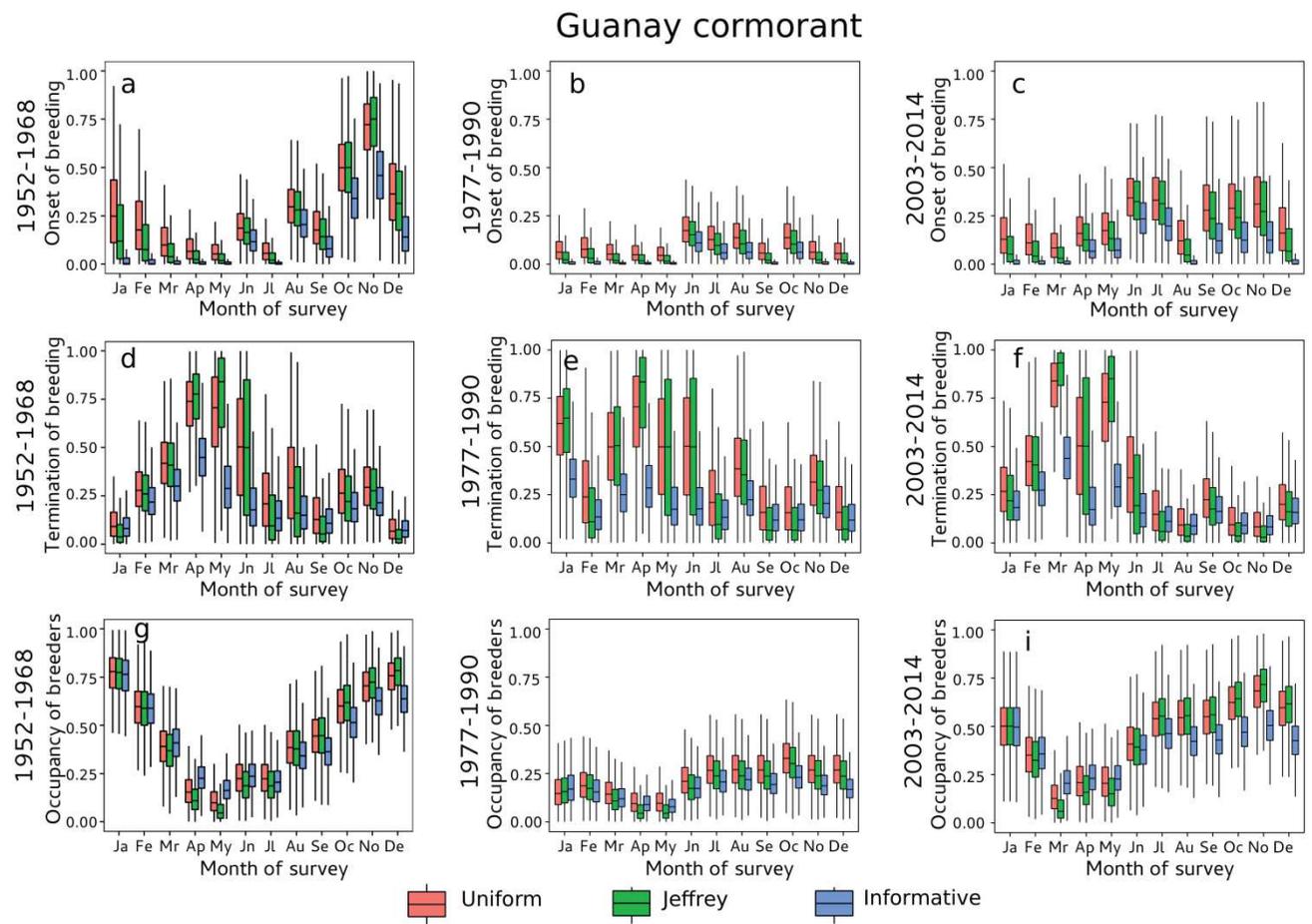
Figure S7. Output of a-c) onset, d-f) termination, and g-i) occupancy of breeding for Peruvian pelicans for the periods 1952-1968, 1977-1990 and 2003-2014 with different hyperparameters: Uniform (red boxes), Jeffrey (green boxes) and Informative (blue boxes).
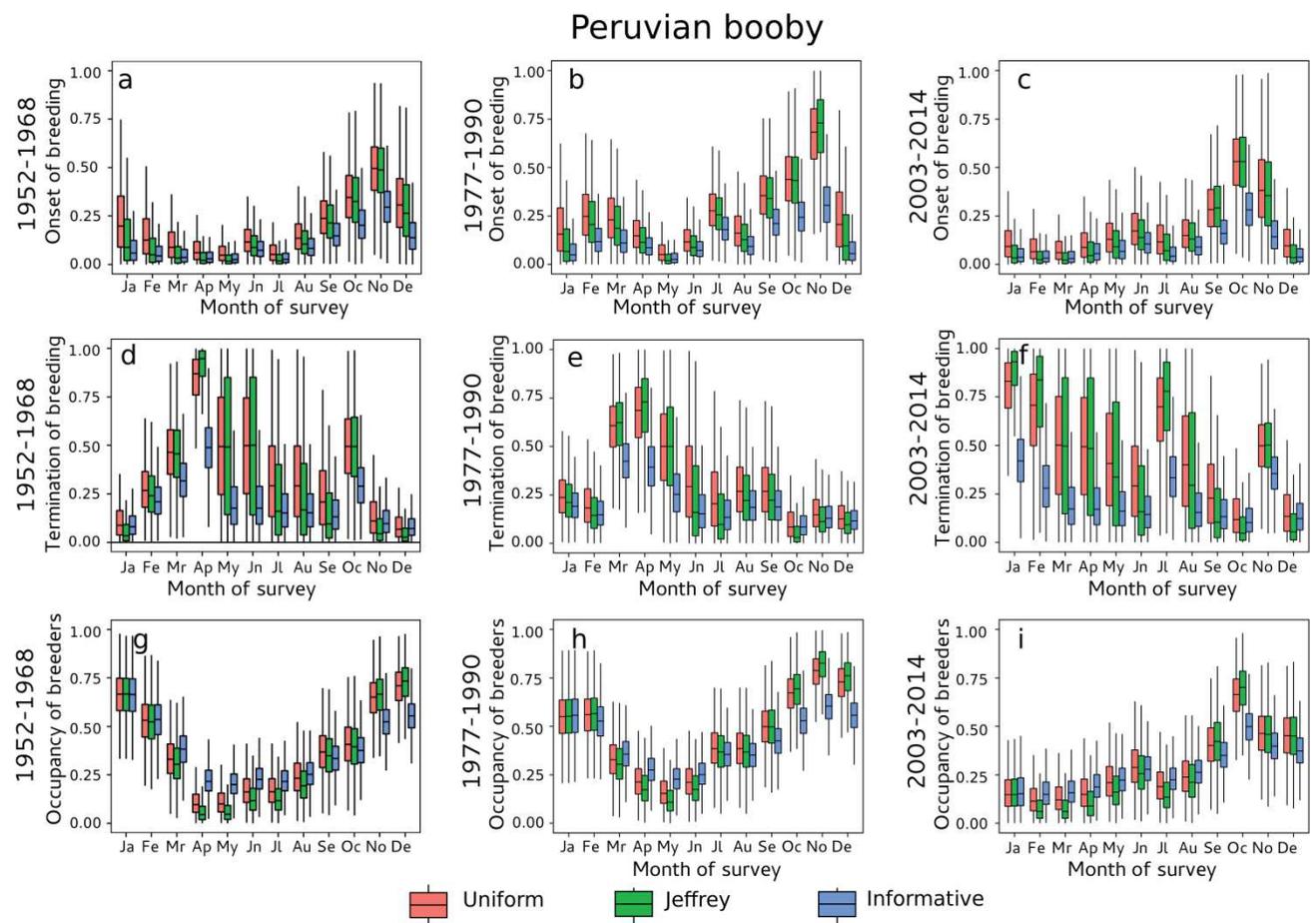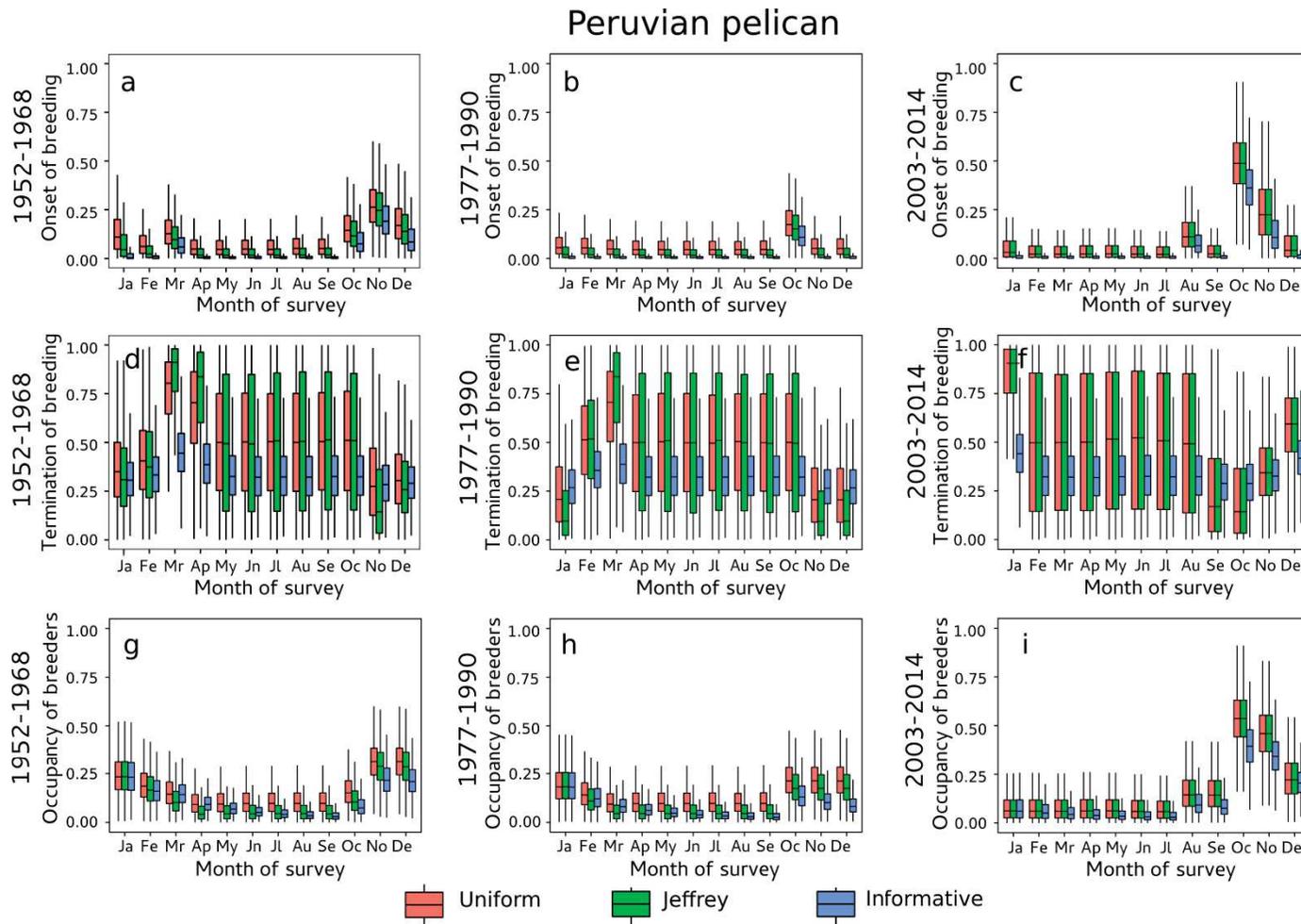
We performed an identifiability test because sample size was limited for the three periods and since the posterior probability mode could be located at one of the extremes of the domain of the parameter space (for example $\gamma_{i,t-1} = 0$ or $\gamma_{i,t-1} = 1$). We tested the identifiability of the parameters $\gamma$ and $\varepsilon$ using the percentage of overlap between uniform prior and posterior distribution ($\tau$), overlaps higher than 35% meant weak identifiability (Gimenez et al. 2009).

Overall, probabilities of onset of breeding were from well to weakly identifiable (mean percentage of overlap between uniform prior and posterior distribution for the three species and the three periods using uniform priors: $\tau'_{\gamma_i} = 39.6 \pm 11.7$), but probabilities of termination of breeding were not identifiable ($\tau'_{\varepsilon_i} = 69 \pm 15.8$). Occupation of breeders, derived from onset and termination, were weakly identified ($\tau'_{\psi_i} = 42.16 \pm 6.21$, Table S4). The low identifiability of termination of breeding could be associated to the fact that events of termination were widespread in time including normal terminations (end of the breeding season) and abandon of nest (almost every month) and therefore the signal was blurred. Consequently, we only considered the parameters onset of breeding ($\gamma$) and occupancy of breeders ($\psi$) for interpretation.

Table S4. Identifiability of onset ($\tau_\gamma$), termination ($\tau_\varepsilon$) and occupancy ($\tau_\psi$) of breeders for the three seabirds during the three periods analyzed. Values indicated with * were not considered as not identifiable because >70% of overlap between the prior and posterior distribution. 70% were the average of overlap for the probabilities of termination of breeding.

| | Cormorants | | | Boobies | | | Pelicans | | |
|---|---|---|---|---|---|---|---|---|---|
| Parameter | 1952 - 1968 | 1977- 1990 | 2003- 2014 | 1952- 1968 | 1977- 1990 | 2003- 2014 | 1952- 1968 | 1977- 1990 | 2003- 2014 |
| $\tau_{\gamma_1}$ | 68.88 | 28.71 | 47.22 | 60.83 | 52.92 | 35.88 | 40.28 | 26.19 | 33.39 |
| $\tau_{\gamma_2}$ | 55.73 | 29.83 | 41.69 | 46.18 | 56.93 | 31.44 | 29.11 | 26.25 | 28.01 |
| $\tau_{\gamma_3}$ | 39.42 | 24.74 | 36.17 | 36.74 | 57.05 | 29.14 | 36.01 | 24.12 | 28.32 |
| $\tau_{\gamma_4}$ | 30.23 | 23.26 | 42.14 | 28.05 | 41.56 | 34.31 | 23.74 | 23.44 | 28.87 |
| $\tau_{\gamma_5}$ | 24.31 | 23.35 | 46.34 | 23.77 | 25.22 | 40.30 | 25.38 | 23.44 | 29.11 |
| $\tau_{\gamma_6}$ | 41.40 | 40.62 | 54.03 | 35.27 | 34.47 | 45.38 | 24.73 | 23.82 | 28.24 |
| $\tau_{\gamma_7}$ | 27.34 | 35.42 | 61.31 | 24.46 | 49.01 | 39.01 | 24.00 | 22.75 | 27.05 |
| $\tau_{\gamma_8}$ | 49.75 | 38.19 | 44.12 | 39.77 | 43.98 | 41.61 | 24.68 | 22.99 | 39.57 |
| $\tau_{\gamma_9}$ | 47.13 | 26.77 | 60.61 | 48.20 | 56.36 | 52.62 | 25.31 | 22.03 | 29.37 |
| $\tau_{\gamma_{10}}$ | 64.32* | 39.17 | 62.15 | 58.78 | 60.96 | 64.32 | 39.15 | 40.82 | 57.65 |
| $\tau_{\gamma_{11}}$ | 62.84 | 29.11 | 65.88 | 61.62 | 64.40 | 72.82* | 49.18 | 25.95 | 59.00 |
| $\tau_{\gamma_{12}}$ | 69.15 | 26.85 | 54.00 | 64.10 | 60.67 | 39.83 | 44.59 | 25.72 | 41.66 |
| $\tau_{\varepsilon_1}$ | 35.04 | 71.68* | 59.18 | 34.99 | 48.93 | 54.80 | 71.29* | 59.41 | 62.79 |
| $\tau_{\varepsilon_2}$ | 52.29 | 67.29 | 66.98 | 52.23 | 47.36 | 76.40* | 73.75* | 80.65* | 93.65* |
| $\tau_{\varepsilon_3}$ | 57.87 | 79.30* | 52.31 | 61.53 | 57.03 | 93.00* | 60.14 | 73.54* | 94.19* |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| $\tau_{\varepsilon_4}$ | 60.56 | 74.10* | 94.04* | 46.20 | 64.79 | 93.05* | 76.35* | 93.88* | 91.91* |
| $\tau_{\varepsilon_5}$ | 75.74* | 92.57* | 74.34* | 93.29* | 80.73* | 89.61* | 92.96* | 93.36* | 93.07* |
| $\tau_{\varepsilon_6}$ | 93.04* | 92.55* | 78.57* | 92.50* | 75.75* | 73.58* | 93.10* | 93.47* | 94.08* |
| $\tau_{\varepsilon_7}$ | 60.49 | 61.75 | 48.61 | 75.58* | 60.91 | 70.93* | 92.58* | 92.32* | 91.21* |
| $\tau_{\varepsilon_8}$ | 74.40* | 74.18* | 37.02 | 75.45* | 59.90 | 86.37* | 91.79* | 93.32* | 92.91* |
| $\tau_{\varepsilon_9}$ | 46.63 | 53.16 | 53.43 | 60.93 | 61.18 | 64.90 | 93.18* | 93.30* | 76.20* |
| $\tau_{\varepsilon_{10}}$ | 60.92 | 54.64 | 39.51 | 72.47* | 34.85 | 43.65 | 93.20* | 93.46* | 71.80* |
| $\tau_{\varepsilon_{11}}$ | 55.47 | 65.41 | 35.09 | 43.24 | 42.71 | 60.35 | 72.45* | 61.78 | 62.58 |
| $\tau_{\varepsilon_{12}}$ | 29.91 | 51.79 | 49.24 | 30.69 | 36.07 | 49.78 | 66.14 | 61.05 | 66.82 |
| $\tau_{\psi_1}$ | 45.37 | 38.43 | 56.58 | 49.33 | 51.83 | 42.24 | 47.60 | 40.80 | 29.81 |
| $\tau_{\psi_2}$ | 49.44 | 38.60 | 51.51 | 50.64 | 49.29 | 35.95 | 42.67 | 34.95 | 34.16 |
| $\tau_{\psi_3}$ | 48.28 | 34.58 | 35.97 | 46.21 | 44.71 | 36.96 | 36.04 | 29.85 | 34.23 |
| $\tau_{\psi_4}$ | 37.46 | 28.61 | 44.75 | 30.33 | 41.58 | 40.14 | 29.44 | 30.21 | 35.75 |
| $\tau_{\psi_5}$ | 31.48 | 29.78 | 45.76 | 31.06 | 36.62 | 44.11 | 31.03 | 29.97 | 35.79 |
| $\tau_{\psi_6}$ | 42.66 | 41.06 | 51.06 | 38.47 | 40.50 | 49.77 | 31.76 | 30.39 | 35.70 |
| $\tau_{\psi_7}$ | 43.68 | 43.79 | 52.37 | 38.75 | 47.64 | 41.01 | 31.35 | 30.99 | 34.55 |
| $\tau_{\psi_8}$ | 49.02 | 43.88 | 52.71 | 44.49 | 47.52 | 46.54 | 31.74 | 30.95 | 43.08 |
| $\tau_{\psi_9}$ | 50.33 | 44.10 | 51.34 | 48.55 | 48.43 | 50.64 | 32.90 | 30.43 | 42.52 |
| $\tau_{\psi_{10}}$ | 51.24 | 45.92 | 49.78 | 50.24 | 44.50 | 49.45 | 41.82 | 41.20 | 53.42 |
| $\tau_{\psi_{11}}$ | 45.80 | 43.81 | 49.31 | 48.36 | 41.69 | 52.31 | 46.79 | 42.06 | 53.15 |
| $\tau_{\psi_{12}}$ | 42.78 | 43.27 | 52.61 | 44.90 | 43.88 | 53.77 | 47.86 | 41.34 | 47.97 |

6. Kruskal-Wallis and correlation test of onset and occupancy of breeders among the three periods.

Table S5.. Mean and standard deviation of onset ($\gamma$) and occupancy ($\psi$) probabilities, Kruskal-Wallis tests and correlation tests for the three periods and the three species. Dunn post-hoc tests were performed when Kruskal-Wallis tests were significant. Significant differences between periods ($P < 0.05$) are highlighted in bold (mean and standard deviation). For correlation tests with a Pearson coefficient ($Z$) significant results are in bold ($P < 0.05$).

| Species | Parameters | Mean and standard deviation | | | Kruskal-Wallis | Correlation test | | |
|---|---|---|---|---|---|---|---|---|
| | | 1952-1968 | 1977-1990 | 2003-2014 | All groups | 1952-1968 / 1977-1990 | 1952-1968 / 2003-2014 | 1977-1990 / 2003-2014 |
| | | | | | $X^2$ (P) | Z (P) | Z (P) | Z (P) |
| Cormorants | Onset | 0.13±0.15 | **0.04±0.04** | 0.10±0.08 | 8.45(**0.01**) | 0.20 (0.53) | 0.45 (0.14) | 0.60 (**0.04**) |
| | Occupancy | 0.43±0.20 | **0.18±0.05** | 0.39±0.10 | 18.45 (**0.00**) | 0.32 (0.31) | 0.54 (0.07) | 0.86 (**0.00**) |
| Boobies | Onset | 0.11±0.08 | 0.14±0.08 | 0.11±0.07 | 2.40 (0.30) | 0.68 (**0.02**) | 0.89 (**0.00**) | 0.67 (**0.02**) |
| | Occupancy | 0.38±0.16 | 0.42±0.13 | **0.23±0.11** | 6.85 (**0.03**) | 0.89 (**0.00**) | 0.06 (0.85) | 0.41 (0.19) |
| Pelicans | Onset | 0.05±0.06 | 0.03±0.02 | **0.10±006** | 10.17 (**0.01**) | 0.80 (**0.00**) | 0.85 (**0.00**) | 0.93 (**0.00**) |
| | Occupancy | 0.14±0.09 | 0.09±0.05 | 0.13±0.12 | 1.68 (0.43) | 0.78 (**0.00**) | 0.39 (0.21) | 0.40 (0.20) |

7. Seabirds life history traits

Table S6. Life history traits of cormorants, boobies and pelicans. [1, 2] and [3] are approximate measures corresponding to family members or similar species. Information is based on Nelson 2005, Duffy and Ricklefs 1981, Nelson 1977.

| History life traits | Cormorants | Boobies | Pelicans |
|---|---|---|---|
| Egg as percentage of female weight [1] | 2-3% | 5% | 3% |
| Duration of incubation (days) | 28 | 42 | 37 |
| Rearing of chicks | 56 | 98 | 80 |
| Post-fledging feeding | 30 | 35 | 30 |
| Maximum brood size [2] | 4 | 3 | 3 |
| Growth rate of chicks[3] | 0.08 - 1.33 | 0.040 - 0.99 | 0.07 |

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